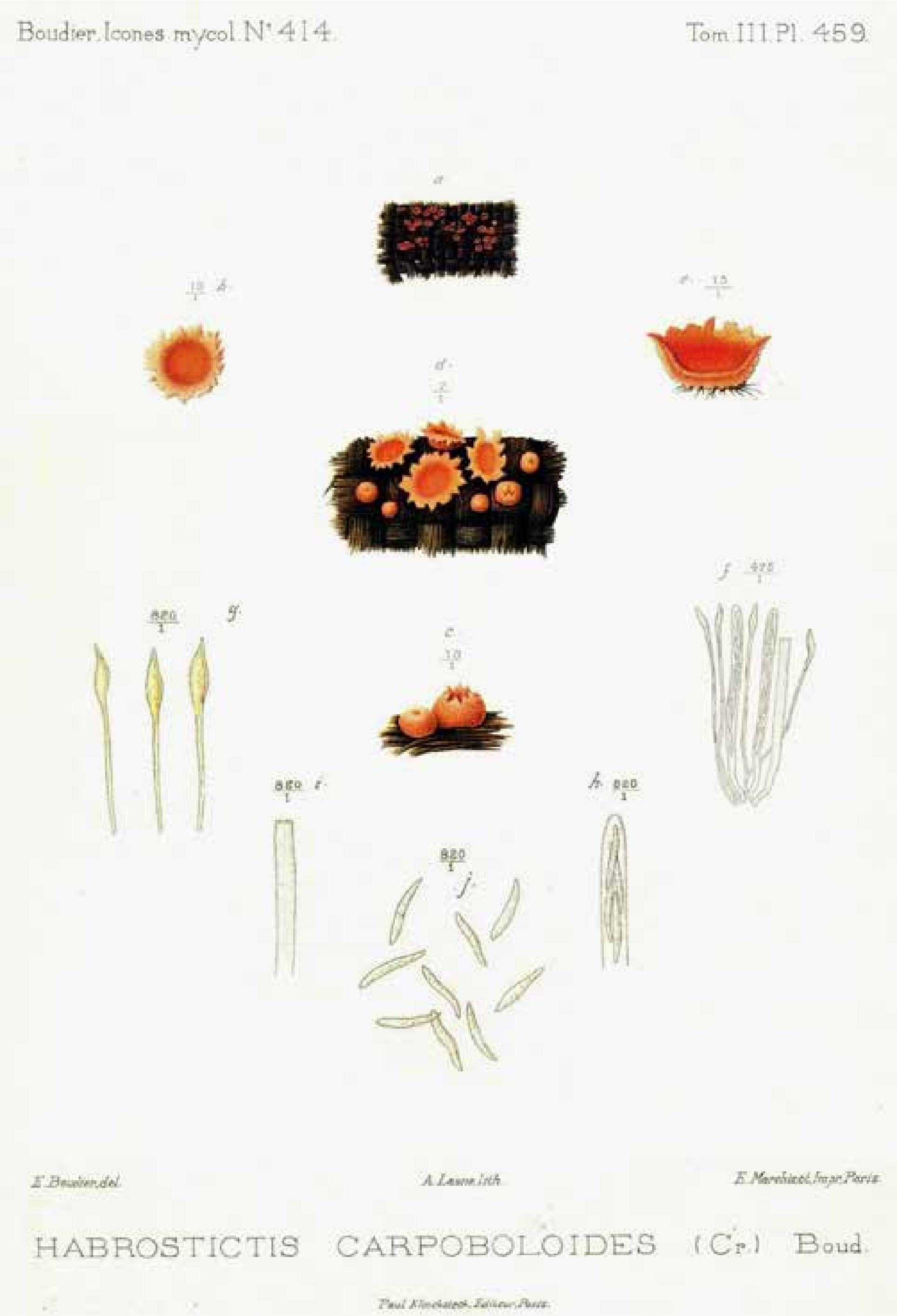
Hans-Otto Baral, Evi Weber & Guy Marson

MONOGRAPH OF ORBILIOMYCETES (ASCOMYCOTA) BASED ON VITAL TAXONOMY

Part I

MONOGRAPH OF ORBILIOMYCETES (ASCOMYCOTA) BASED ON VITAL TAXONOMY



Orbilia carpoboloides (= *Habrostictis rubra*), drawn by the famous French mycologist Émile Boudier (Icones fungorum 1904–10, pl. 459). Boudier was among the first to practice vital taxonomy. Nevertheless, his illustrations of orbiliaceous fungi are an exception: all microscopic elements on this plate originate from dead cells, including the ascospores which would contain a prominent spore body in the living state.

‘The sense of science lies in scepticism and not in preservation of achieved knowledge. The present work is thus hopefully soon obsolete.’
(Prof. Klaus Grawe, psychotherapy researcher, Bern, Switzerland).

‘The world would be a better place if more people were working on the inventory of its biota. How could they be encouraged to do so?’
(L.R. Landrum 2001. What has happened to descriptive systematics? What would make a thrive? Systematic Botany 26: 438–442 [440])

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Cover photo:
View from mountain west of Col Lebraut to the south showing Mt. La Viste (left) and Mt. Colombis (right), la Vallée de la Durance behind and la Montagne de la Scie in background (centre) in Southern French Alps, Provence-Alpes-Côte d’Azur, dépt. Hautes-Alpes, France. Orotemperate to orosubmediterranean humid mixed conifer forests, in which *Lilapila oculispora*, *L. oculisporella*, *Amphosoma resinicola*, and *A. atroolivaceum* on resinous wounds of coniferous trees and various *Orbilia* spp. occur. 15.VIII.2009, phot. G. Marson.

Back cover:
Lilapila oculispora, *Amphosoma atroolivacea*, *Hyalorbilia japonica*, *H. fusispora*, *Orbilia patellarioides*
Orbilia arizonensis, *O. macrocarpa*, *O. multiaustraliensis*, *O. multicurvula*, *O.* cf. *angustoaristata*

Book spine:
Orbilia spermoides

Front cover:
O. fimbriata, *O. helicoobliqua*, *O. aradi*, *O. denticulata*, *O. euphorbiae*, *O. phragmotricha*
O. aurantiorubra, *O. xanthoguttulata*, *O. crenatomarginata*, *O. carminorosea*, *O. pilifera*, *O. gemma*

MONOGRAPH OF ORBILIOMYCETES (ASCOMYCOTA) BASED ON VITAL TAXONOMY

— Part I —

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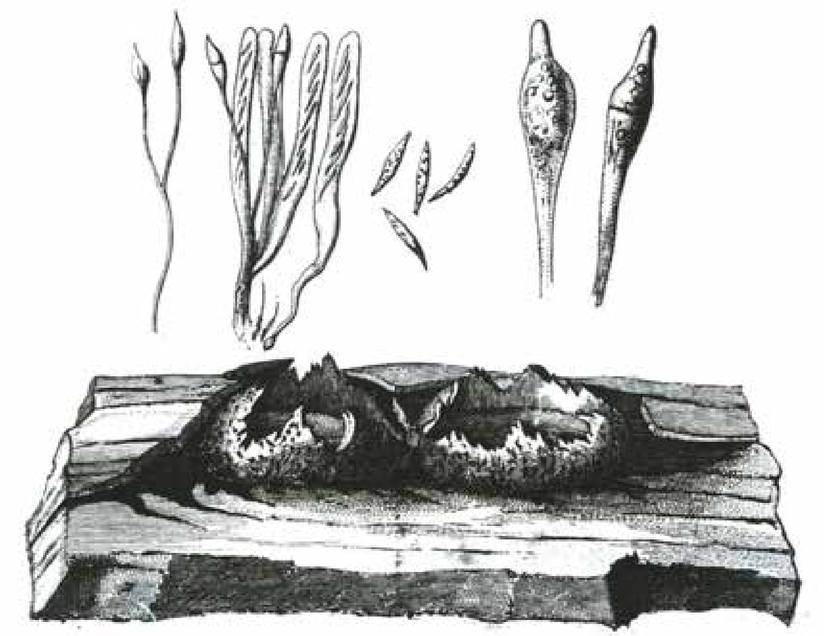

Orbilia carpoboloides (holotype of *Orbilia lasia*, on bark of *Ulmus*) drawn by M.J. Berkeley (from Berkeley & Broome 1873: pl. VIII fig. 10). Asci, ascospores and paraphyses are illustrated in the dead state, therefore the spores do not show the characteristic spore body.

National Museum of Natural History Luxembourg (2020)

About the authors

Evi Weber made her thesis on polyploidy of discomycetes under Andreas Bresinsky at the University of Regensburg and later worked at the University of Tübingen on the *Lecythophora-Coniochaeta* complex during a project on storm-damaged forests. In the course of the present monograph she was employed at the National Natural History Museum in Luxembourg for a four years study on anamorphs of *Orbiliomycetes*. Since 2014 she is managing editor of the journal Mycological Progress.

Hans-Otto Baral got interested in fungi through the 'Pilzverein Stuttgart', a mycological association in which also his father was a member. At the University of Tübingen under Franz Oberwinkler he made his diploma on the *Sarcoscypha* species complex. Later he concentrated on inoperculate discomycetes and, after presenting together with German Krieglsteiner a survey of the species known in Germany, published on various genera, including a taxonomic clarification around *Hymenoscyphus fraxineus*, the cause of the ash dieback disease. In 2016 he covered the non-lichenized discomycetes in a survey ('syllabus') of the families of ascomycetes. Various projects were done in collaboration with institutional and amateur colleagues world-wide.

Guy Marson was educated as a metalworker and worked until his retirement as an engine driver for the Luxembourg railroad company CFL. Because of his interest in fungi since 1968 he became 1983 a foundation member of the mycological working group (GRM) of the 'Société des naturalistes luxembourgeois' (SNL). One year later he was accepted as scientific collaborator of the National Museum of Natural History of Luxembourg. His interest for fungi soon concentrated on ascomycetes and particularly those growing on xeric dead plant parts. His technical skill resulted in many self-made equipments around microscopy and photography. At the museum he obtained numerous cultures and since 2011 he concentrated on molecular research.

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The complete monograph, including all supplementary data listed above, is available under the following link:
https://www.mnhn.lu/pub/mono_orb
Scans of all drawings with original annotations and entire set of macro- and microphotographs can be found under the following link:
https://www.in-vivo-veritas.de

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ABSTRACT

The present work is the result of an over 30 years extensive study of discomycetes recognized in the family *Orbiliaceae*, which was previously considered as a comparatively small group within the *Helotiales* but later raised to the level of a class. Our study resulted in the recognition of worldwide ~ 470 species with a known teleomorph, 331 of which being validly described here as new to science. We also propose 38 new combinations and 2 nomina nova, and designate 33 epitypes, 39 lectotypes, 3 neotypes, and 4 reference specimens, including some misplaced species now referred to other classes. The *Orbiliomycetes* are circumscribed here with 1 order *Orbiliales*, 1 family *Orbiliaceae*, 7 accepted teleomorph-typified genera [*Amphosoma* gen. nov. (4 spp.), *Bryorbilia* gen. nov. (1 sp.), *Liladisca* gen. nov. (1 sp.), *Lilapila* gen. nov. (3 spp.), *Pseudorbilia* (1 sp.), *Hyalorbilia* (37 spp.), *Orbilia* (~ 415 spp.)], and 3 anamorph-typified genera [*Lecophagus* (7 spp.), *Mycoceros* (1 sp.), *Retiarius* (4 spp.)], the latter two without known teleomorph. The large genus *Orbilia* is divided into 3 subgenera, 8 sections, and 30 series. Apart from the accepted ~ 470 species, about 90 further teleomorph-based species are treated without a valid name (aff. or nom. prov.). As a consequence of the taxonomic relevance of four main types of plasmatic organelles, the present study was predominantly based on vital taxonomy, a comparative morphological method focused on the living state of fungal cells by using recently collected specimens whenever possible.

Most of the previously known species turned out to be hygrobiotic (desiccation-sensitive), growing in humid regions on damp substrate on the ground. For vital taxonomy studies these species required examination within a few days during which their viability can be maintained in a moist chamber. Their often very small hymenial elements are difficult to study under the light microscope, which explains why these fungi have often insufficiently been investigated in the past. The vast majority of new species are described from subhumid to arid regions with more or less long-lasting dry seasons, representing an overlooked ecological niche for various groups of desiccation-tolerant fungi. The capacity of these xerobiotic taxa to tolerate complete desiccation of the holomorph for one or several years and their often much larger asci and ascospores providing a higher optical resolution considerably facilitated our vital taxonomic and cultural work.

The most remarkable and relevant discovery in this study of *Orbiliomycetes* was an organelle of vacuolar nature inside the living ascospores, the spore body (SB), as it is currently called. Due to their high refractivity, SBs are usually very easily observed when studying viable spores, whereas in dead spores they get more or less completely invisible. This organelle, which was found to be formed by invagination of the plasmalemma, not from mitochondria as earlier believed, could by now not be observed in any other class of *Ascomycota* and thus permits recognition of a taxon as orbiliaceous. A high diversity in size and shape of the spore bodies was recorded when comparing the many species and infrageneric groups, which provided more important criteria for classification than the high variety of ascospore shapes which often derived from convergent evolution. In the large genus *Orbilia*, but also in *Liladisca*, *Lilapila*, and *Lecophagus*, only one spore body is enclosed in each ascospore, rarely none, whereas more than one spore body is typical of *Amphosoma*, ?*Bryorbilia*, *Hyalorbilia*, and *Pseudorbilia*. Characteristic but transient cytoplasmic bodies (SCBs) in the living cells of paraphyses and ectal excipulum turned out to provide further important species markers.

The present study confirms the consistent absence of amyloidity in any part of the *Orbiliomycetes* holomorph. Further remarkable characteristics of the teleomorph include different types of ascus apices (thin- vs. thick-walled, truncate-shouldered vs. hemispherical) and ascogenous hyphae (croziers vs. simple septa), the latter feature often coupled with sessile vs. stalked/bifurcate ascus bases. Within *Orbiliomycetes*, ascus apical thickenings were exclusively observed in xerobiotic taxa, whereas truncate-shouldered asci occurred with a similar frequency in both ecological groups. A surprizing number of xerobiotic *Orbilia* species show different degrees of polyspory (16–128-spored), which appear in various subgroups and provide valuable species markers of otherwise very similar taxa. A further peculiarity of *Orbiliomycetes* was found in the inverse orientation of a varying number of spores within an ascus: usually the lower, more rarely the upper spores point with their spore body downwards.

Capitate paraphyses and waxy apothecia have been considered as typical of *Orbilia* in ancient treatments, but are attributed little taxonomic value in the present study. Likewise, lanceolate paraphyses, glassy processes, and septate hairs, previously used to define *Habrostictis*, *Hyalinia*, and *Orbiliaster*, are found to be unsuitable generic markers. Instead, the earlier overlooked croziers at the ascus base turned out to be useful at the generic level, characterizing *Lecophagus*, *Liladisca*, *Lilapila*, *Hyalorbilia*, and *Pseudorbilia* (with the restriction that in *Lecophagus* also simple-septate bases occur), whereas stalked and bifurcate simple-septate ascus bases characterize *Amphosoma*, *Bryorbilia*, and *Orbilia*. Ascus apices, excipular textures, and anchoring hyphae also support phylogenetic relationships, e.g., thick-walled hemispherical apices characterize *Orbilia* subgenus *Hemiorbilia*, a textura prismatica *Hyalorbilia*, and exceedingly broad anchoring hyphae *Lecophagus*.

For many teleomorph-typified species of *Orbiliomycetes* a connection to an anamorph could be affirmed based on either pure culture and/or sequence data. Possibly all members of the class possess an anamorph, but the connection is uncertain or unknown in a fairly large number of taxa. Orbiliaceous anamorphs are hyphomycetous, rarely synnematal. Conidiophores and conidia are consistently hyaline, and conidiogenesis is holoblastic. The conidia have frequently been found close to the apothecia on the natural substrate, particularly in xerobiotic taxa. They exhibit a high morphological diversity, including multicellular, unbranched or variously branched types. Although branched conidia are known as Ingoldian fungi from water courses and lakes, those of *Orbiliomycetes* are almost exclusively formed on xeric substrate, where they are adapted to transport by stemflow during rainfalls.

Anamorphs of *Orbiliomycetes* have earlier been classified in numerous genera, viz. *Anguillospora*, *Arthrobotrys*, *Brachyphoris*, *Curucispora*, *Dactylella*, *Dactylellina*, *Descalsia*, *Dicranidion*, *Drechslerella*, *Dwayaangam*, *Gamsylella*, *Helicoon*, *Lecophagus*, *Microdochiella*, *Pseudotripoconidium*, *Tridentaria*, *Trinacrium*, and *Vermispora*. Under the new rules of nomenclature that give anamorph names equal priority, most of these generic names fell into synonymy with *Orbilia* s.l. and a few with *Hyalorbilia*, with exception of *Lecophagus*, *Mycoceros*, and *Retiarius*. Teleomorphs of *Lecophagus* are reported here for the first time, and curucispora-, descalsia-, and tridentaria-like anamorphs for the first time as belonging to *Orbiliomycetes*. Many, mainly hygrobiotic species of section *Arthrobotrys* are reported to capture minute invertebrates such as amoebae, nematodes, rotifers, springtails, and tardigrades by means of sophisticated trapping organs, for which reason they can be used as a biocontrol agent against plant parasites, particularly nematodes. Which role the spore body plays in the life cycle of *Orbiliomycetes*, particularly its function in regard to endoparasitism, could not be clarified, but the high diversity in ascospore and spore body shapes hints at some kind of coevolution with unknown parameters, perhaps in animal trapping.

Increasing availability of molecular data questioned current species and higher taxa concepts and revealed cryptic species without evident distinguishing features, or various unexpected synonymies among hyphomycetous, mainly nematode-trapping taxa. Although the here practised classification was largely based on rDNA data (SSU V8–V9, ITS1-5.8S-ITS2, LSU D1–D2), priority was given in critical cases, especially when DNA data were poorly available, to morphological criteria. For instance, the three series within section *Habrostictis* are predominantly morphology-based.

A broad generic concept was applied to the genus *Orbilia*, and paraphyly was accepted as a natural consequence of evolution in genetically heterogeneous groups such as subgenus *Hemiorbilia* and section *Aurantiorubrae*, or when sharp morphological differences do not correlate with DNA data, e.g., in the separation of series *Phanosomates* from series *Lentiformes*.

INTRODUCTION

The first studies of members of the class *Orbiliomycetes* by first author were undertaken between 1974–1977. At that time, this group of inoperculate discomycetes was recognized as a family *Orbiliaceae* of the *Helotiales* and was believed to constitute one of the smallest families within this order (Kimbrough 1970, Spooner 1987). As a result, species numbers in various regional systematic treatments ranged between about five and ten. On the other hand, a large number of more or less dubious taxa have been assigned in the older literature to the genera *Orbilia* Fr. and *Hyalinia* Boud. Therefore, *Orbilia*, which comprised in its earlier circumscription also taxa now recognized in *Hyalorbilia* Baral & G. Marson (2001), was considered by Korf (1973) to be 'a large genus', at least when including also *Hyalinia* in its scope. Critical revisions with detailed illustrations are largely lacking, for which reason Dennis (1978: 187) stated that 'the genus is one of those which most needs monographic study on modern lines'.

The family *Orbiliaceae* received comparatively little attention, probably because asci and ascospores in most of the hitherto known species are very small, being regarded as close to the resolution limit of the light microscope. The reported differences in spore characters are, therefore, often vague and inexact, and resulted in much confusion about the proper application of names. As an example of the small microscopic features, Nannfeldt (1936: 199) stated that the cells of *Orbilia*, particularly the spores, were usually 'extremely difficult to see [..] in herbarium specimens'. Also Dennis (1978: 187) wrote: 'The essential characters, apart from colour, are largely those of the ascospores, which are small and often hard to see'. In his treatise on the Macaronesian *Orbiliaceae*, Korf (1992) similarly argued that 'species identification is exceptionally difficult and requires good oil-immersion optics and staining with Cotton blue in lactophenol for many species' in order 'to see what is not to be seen'.

Such experiences appear surprising when comparing Boudier's (1904–10 [1906, 1908–9]: pl. 459–467) detailed drawings of nine, mostly small-spored taxa of *Orbiliaceae* made with a microscope with a presumably less advanced technical standard than we have today. Contrary to the prevailing custom, Boudier exclusively examined fresh specimens in water as mounting medium, which enables to study living cells (vital taxonomy, Baral 1992). This method resulted in distinctly larger cell sizes due to internal turgor and cell wall elasticity, stronger optical contrast and transparency on account of the high water content of the cytoplasm, and visibility of cytoplasmic organelles that become irreversibly destroyed in dead cells.

For instance, spores inside asci are very clearly visible when the asci are intact, but often hardly discernible in dead material, sometimes despite the application of cytoplasmic stains. As a consequence, polyspory of asci has repeatedly been overlooked in herbarium material. Free spores are often rare, and those inside asci cannot easily be seen in the dead state, which prompted authors to consider mature collections to be immature. This difficulty with herbarium material explains the frequent use of stains in combination with clearing agents to make spores inside asci better visible. The spores of *Orbilia* exhibit an extraordinarily broad diversity in both shape and size, hence without the spores a collection definitely remains unidentified.

The idea to do this monograph was born between 1988–1989, stimulated by the discovery of the peculiar spore body, a taxonomically highly important and biologically interesting cytoplasmic inclusion inside the living ascospores. This spore body shows a strong contrast under the light microscope, but is very sensitive to lethal media or storage in the herbarium for a shorter or longer period of time. Because of the strong preference of previous taxonomic researchers to study herbarium specimens, spore bodies are largely absent from their descriptions.

In 1989 we knew only twelve central European species of *Orbiliaceae* and could not imagine that these twelve species finally turned out to represent just 2.5% of the diversity recognized in the present work within the family. In the following 20–30 years the number of taxa increased enormously whenever collecting trips were undertaken and the numerous collections taxonomically documented and compared. Once their prevalence for xeric habitats was detected, a strongly neglected niche of any kind of air-exposed, more or less decayed substrate that periodically falls dry, and their widespread occurrence in areas with longer periods of drought, our collecting efforts concentrated on xeric vegetation, particularly of the Mediterranean region, later also western North America and Australia. Despite the vast number of species recognized during each expedition, most collections could be studied in the living state, since these fungi remain viable for about 1–3 years in the herbarium. The detection of these often very small fungi is more or less a matter of accident, therefore, we are convinced that numerous further species await discovery worldwide.

Comparatively few collections from tropical humid regions were available during our study, which explains the distinctly lower species diversity compared to desertic and temperate humid regions and suggests that many more species would occur in the tropical belt. In fact, subtropical humid evergreen forests in southeastern Asia turned out to house a rather diverse species composition and provided many novelties, thanks to the activities of various Chinese scientists. Due to their collecting focus on hygric substrate in these mountain forests, most of the species from China known at present are hygrobionts. They were sent in the dry state as they would otherwise have been ruined during shipment. Therefore, many of these records were studied in the dead state, though sometimes living ascospores were still present, whereby vital characters from the fresh apothecia were often available on photos provided by these Chinese workers.

One of our focuses was to explore the morphological variation of each species. Following the suggestions of Huhtinen (1990a, b) we tried to clarify by drawings and/or photographs of ideally each collection how sharply the taxa are delimited from each other. Single gatherings, which were not sufficiently deviant to be recognized as a separate species, were mentioned and illustrated under the closest taxon. During the past 2.5 decades an increasing interest arose among the mycological community to collect and document samples of *Orbiliomycetes*. We have included these records in our work whenever photographs sent by the collectors allowed recognition of the species, as they increased our taxonomical and ecological knowledge of many species. During sampling and scanning collections we came across a lot of other groups of non-lichenized ascomycetes which co-occurred with members of *Orbiliomycetes* and also frequently appeared to represent new or little explored species. As a consequence, we also often documented these fungi in order to show the transient vital characters.

A large number of type specimens have been reexamined in the present study, because the protologues often did not permit recognition at the species level, and illustrated revisions were lacking for most of them. It was our experience that a detailed knowledge of the relevant characters of a group, including those of the living fungus, is required prior to performing type studies. For instance, although spore bodies are usually invisible in herbarium material, they can sometimes be discerned as very faint 'empty' regions in the spore apices in appropriate mounting media, but only when one's attention is focused on them.

The vast diversity of conidial shapes being connected to members of *Orbiliomycetes*, together with the variance of spore body morphology, caused serious problems in identification of herbarium material, particularly of type specimens, since both serve as key characters of many taxa. Based on this experience, we regard monographic work on living specimens, carried out over a reasonable period of years, as the most important prerequisite for achieving sound taxa concepts and functional identification keys. We prefer comprehensive monographic work on closely related species in a single publication over numerous small papers or large ones on diversely related taxa and groups. If we had published our observations every year, a lot of subsequent corrections to previous papers would have resulted, including a final outline of the whole group.

Another challenge arose when molecular data were included in our study. Ribosomal DNA sequences offered a new perspective on species concepts. The obtained results permitted clarification of controversial opinions on species aggregates, such as *O. vinosa*/*O. subvinosa* or *O. leucostigma*/*O. xanthostigma*, and suggested also the existence of morphologically cryptic species, e. g., in the unsettled *O. auricolor* aggregate, or in *O. tremulae*/*Dicranidion inaequale*. Sequence data also resulted in various infrageneric rearrangements within *Orbilia*, but we hesitated when morphological data did not support the new placement. Last not least, the family had to be raised to the rank of a class, *Orbiliomycetes*, based on morphological and molecular data (Eriksson et al. 2003). It forms a unique monophyletic group of ascocarp-forming *Ascomycota* that occupies a rather basal position within the *Pezizomycotina*.

Since sequences were only available for a small minority of collections of a given taxon, identification was mainly based on morphology, which fairly often caused problems in the correct identification of similar taxa, for instance in *O. luteorubella*/*O. rosea*, *O. eucalypti*/*O. tremulae*, or *O. brochopaga*/*O. orientalis*/*O. yunnanensis*. Specimens older than ~10–20 years usually cannot at present be treated by molecular methods regarding their rDNA, therefore, many type specimens remained unidentified at the molecular level, and epitypes or reference specimens had to be proposed for them.

Although molecular data experience an inflationary increase in databases, many of them originate from environmental samples without knowledge of the fertile structures or the natural substrate. These data obviously neglect important ecological niches by focusing on continuously moist environments such as soil, water, damp wood, or living tissue, though including also air isolates. For this reason, the vast diversity of xerobiotic ascomycetes and other fungi is largely absent in these data.

Because of the time-consuming technique of molecular research, we have laid our main focus on the attractive features of light-optical microscopy, which include (1) comparatively low costs, (2) rapid results, (3) ease of use, and (4) clarity of morphological, particularly vital characters. According to Korf (1994: 16), the increasing application of modern techniques like transmission (TEM) and scanning electron microscopy (SEM), molecular analysis of DNA, numerical taxonomy, chemistry, and genetic mating systems has 'decreased rather than increased the production of monographs'. The paucity of monographs in the past decades is seen as a reason for the hypothesis that '95 or 96 % of the fungi we haven't yet catalogued'.

In summary, the outstanding feature of the present study lies in the large number of new species. This has four main sources: (1) collecting on xeric substrate, particularly in regions with long-lasting periods of drought; (2) the consistently applied method of vital taxonomy, resulting in an increased array of microscopic characteristics for the delimitation of taxa; (3) cultural characteristics, mainly regarding conidial morphology; (4) molecular data, which resulted in splitting of taxa without clear morphological differences.

MATERIALS AND METHODS

Fungal material

More than 7200 records of *Orbiliomycetes* teleomorphs are treated in the present study. In the case of mixed collections, this number includes all orbiliaceous species detected within each sample. Circa 4500 of these 7100 records have been studied by the first author. Almost 3400 of these 4500 records were examined in the living state, the apothecia being either viable regarding all their elements or only for some of them, particularly the ascospores. A majority of the remaining nearly 2700 records came to our attention only through microscopic drawings or macro- and/or microphotographs made by various collaborators and earlier authors. All these records are mentioned under 'Specimens examined', and all those from which we have not seen specimens or microscopical images are marked by 'non vid.'.

3125 teleomorphic records included in this study originate from our personal collecting efforts, while the remaining ca. 4100 were made by other contemporary or historical collectors. Many of these samples have been sent to us in the living state, at least in regard to the ascospores. Herbarium specimens without any living elements were mainly studied regarding type material, but included also various non-type collections, particularly from Asia and Middle America. Five public herbaria (LUX, M, MPU, TAAM, TNS) were thoroughly investigated for orbiliaceous specimens, and some others (CUP, FH, PDD, TU) only regarding selected material. For further consulted official herbaria see p. 15. 90 % of all records were made after 1989, hence the present monograph is mainly based on the study of contemporary collections.

Roughly 2700 of the studied samples were preserved in the first author's herbarium or sent to an official herbarium in case of types of new species. Many samples were not kept since they were either in bad shape or too sparse, or they belonged to frequently recorded species. Collections of the third author which lack a H.B. number were frequently not preserved. More or less comprehensive data (microscopic drawings, macro- and microphotographs, rarely only descriptions) exist for most of the collections reported here. Microscopic drawings were made on ca. 2300 samples, and macro- and/or microphotographs on ca. 3400 samples, including those made by other collectors. Nearly

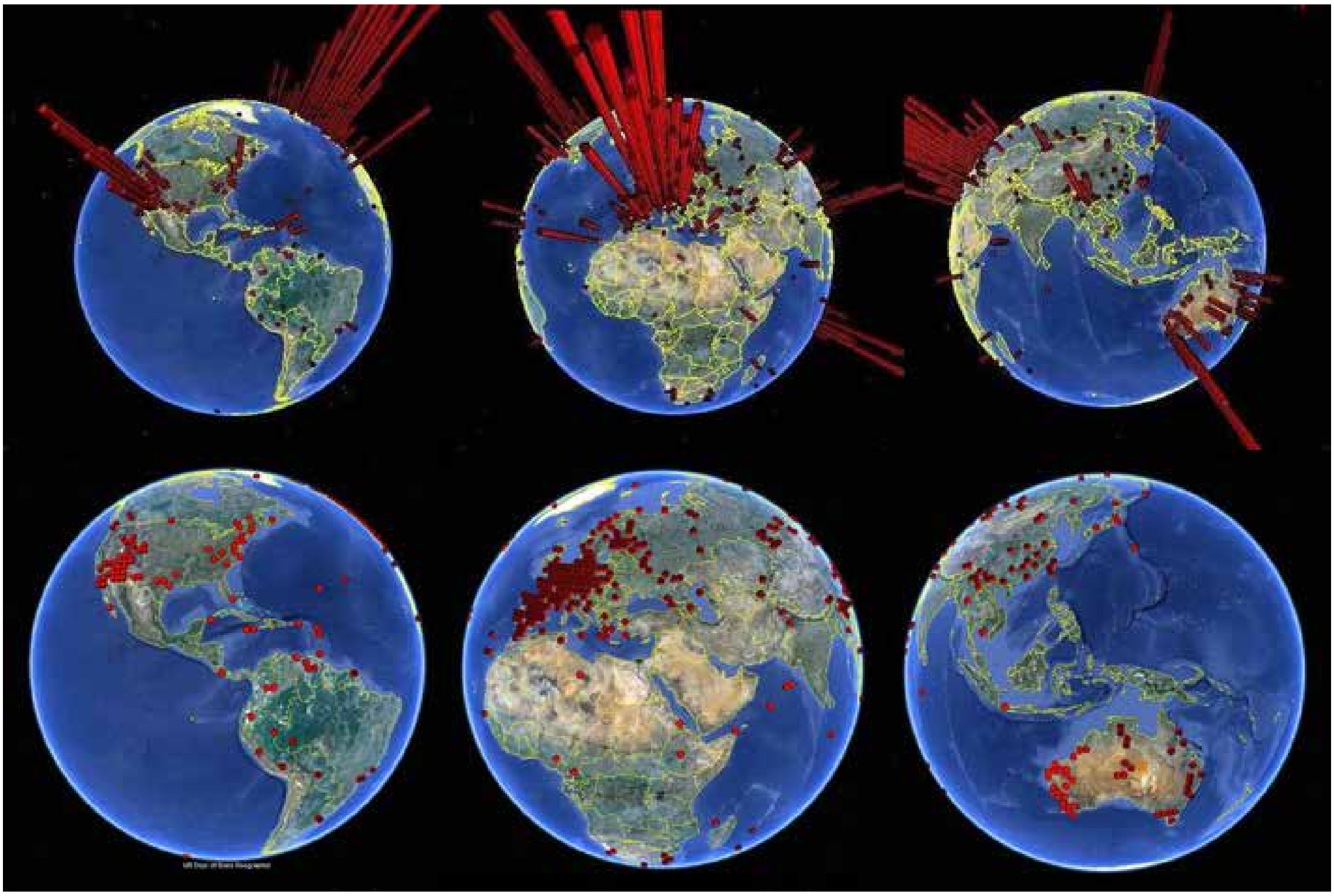


Figure 1: Geographical origin of collections of *Orbiliomycetes* investigated in this monograph (created in 2013 with Google Earth using R2G2: https://recology.info/2012/10/r2g2-package/, later collections not included). In the upper row the height of the polygon indicates the abundance of the collections, whereas the lower row gives a clearer idea of the dispersion of the collection sites. See also Fig. 127.

all drawings by the first author and some by G. Marson and N. Matočec are reproduced in this monograph.

A considerable part of the teleomorph collections treated in this monograph emanates from different, humid to semihumid parts of Europe (~5300 records). An also rather high number of records has a Northern American origin (over 600, particularly from the semiarid southwest) or comes from different, often semiarid parts of Australia (over 450). Records from mainly humid regions of Africa (51), Middle and South America (127), and New Zealand (52) are scanty because we had little opportunity to obtain collections from there. Almost 230 samples came from predominantly semihumid to semiarid sites in Macaronesia (mainly Tenerife), and 80 from mainly humid sites in Middle America (mainly Antilles). Records from Asia (over 370) predominantly derive from China (over 200, many of them from Yunnan Province), but comparatively few from Mongolia, Japan, eastern Russia, Turkey, and the Caucasus region, see also Figs 1 & 127 and Appendix 2.

As to the different ombrotypes, about 8% of all collected populations were from semi- to hyperarid regions, 16% from semi- to subhumid regions (mediterranean and savannah-like climates), and 76% from humid (including winter-dry) climates. The comparatively low proportion of samples from arid regions stands in contrast to the observed high species diversity in this ombrotype (see Tab. 33). Regarding the different thermotypes, 14.5% of the collected populations came from montane-boreal-subarctic (including hemiboreal and orosubmediterranean), 57% from cold- to warm-temperate (including mild-maritime), 7% from submediterranean, 18.5% from subtropical (including mediterranean), and 3% from tropical regions (2% from a tropical humid climate). About 88% of the collections were made on woody substrates, 8% on more or less herbaceous substrates (including leaves of trees), > 4% on fungi (basidiomycetes, pyrenomycetes, discomycetes), 0.2% on animal dung, and 0.07% on bryophytes.

The types of our new taxa were mainly deposited in M, with the exception of those from Australia (MEL, BRI), Japan (TNS), China (YMFT), Russia and Caucasus (TAAM), Puerto Rico (FH), and some from Spain (AH). Because of the frequent intermingled growth and the impossibility to recognize most species macroscopically, a complete separation of the different populations on a given piece of substrate was often difficult or impossible. Therefore, many of our herbarium specimens probably contain different taxa in a single envelope.

Pure cultures gained between 2000–2004 were deposited in BBA (77 strains) and most of them also in CBS (73 strains). They comprise a total of 78 living cultures of 73 species (76 isolates from ascospores and two from conidia). Various further isolates were obtained during the past decades, but most of them were not conserved.

Equipment and documentation techniques

Microscopes. Most drawings were made free-hand by the first author using a Zeiss Standard 14 microscope with 100×/1.25 oil immersion phase contrast achromatic objective and 15× Euromex wide field oculars. Some drawings of conidia were made with a Standard 20 by E. Weber. Drawings by G.

Marson were made with a modified Olympus CH–2 microscope with a Zeiss 100/1.25 oil immersion plan-achromatic objective, Zeiss Kpl W 16×/16 wide field oculars, often with the aid of an Olympus drawing tube (tubus factor 1.25×, equipped with an Euromex 20× ocular used as projective). Most observations were carried out under bright field, i.e. with open or only very slightly closed aperture, whereas photographs were taken at an up to ~⅓ closed aperture. Phase contrast was very rarely applied since it proved quite useless for the observation of taxonomically important intracellular microstructures: in most cases these structures have enough refractivity within the living cytoplasm in order to be easily seen. They often occur in small or narrow cells, or in sections of tissues consisting of several cell layers, conditions being inappropriate for the application of phase contrast. The same applies to differential (Nomarski) interference contrast (DIC) which severely obscures the apical attachment of spore bodies (some photographs taken with this technique at Chinese and Russian laboratories are reproduced in this monograph). Microscopic study was done using oil immersion at 1500× (H.B., E.W.) or 2000× (G.M.) regarding drawings and direct observations. Illumination of the microscopes was either with a high-power LED (Luxeon 3W, H.B., G.M.) or a halogen bulb (H.B., E.W.). For macroscopy, different dissecting microscopes were used: Euromex (10–40×), LOMO MBS–10, Leitz (10–40×).

Drawings. Drawings of asci and paraphyses were generally made at a standard scale of 3000×, ascospores and ascus apices at 4000×, excipular elements at 1500×, 2000×, or 3000×, and conidia at 2000×, exceptionally 3000× or 1000× (see p. 20–21, About illustrations). Drawing free-hand at a uniform scale was done by measuring length and width of the element and transferring the calculated values to the drawing sheet (e.g., an ascospore of 10 × 2 µm is on the drawing sheet 40 × 8 mm). On the printed figures the drawn or photographed ascospores and ascus apices are consistently reproduced at a magnification of 2000×, asci and paraphyses at 1500×, and conidia at 1000×. In order to obtain this standard magnification, the drawings had to be reduced in most cases to 50% of their original size.

Drawings were finished directly onto the original sheet using graphite pencil leads of medium hardness ('HB') and varying thickness (mainly 0.5 mm, sometimes 0.3 or 0.7 mm), in some cases also with a felt-tip pen. When using graphite for the final drawing, a solid base plate was placed below the original drawing which was cleaned step by step with a soft eraser pencil. This method saves much of the original appearance and aesthetic appeal of a drawing, whereas drawing onto a tracing paper over the original sketch, or using a computer program usually results in a more schematic appearance (see Barber & Keane 2007, fig. 1).

The thickness of the drawn line more or less indicates the thickness of the cell wall. Walls thicker than ~0.3 µm are shown as two parallel lines. More than two lines are drawn in the case of a thick, layered wall, e.g., in ascus apical thickenings. The outer boundary of the detached cytoplasm in dead cells is shown as a further line, and the granular cytoplasm is graphically indicated. In the case of cytoplasmic inclusions of living cells (LBs, SBs, SCBs, vacuoles, VBs, nuclei), the thickness of the line indicates the strength of refractivity of the organelle.

Most of the final drawings were scanned at 300 dpi and the elements arranged with Corel Photopaint 10 on plates of 5650 × 4250 pixel (= 48 × 36 cm), resulting in a 600 dpi resolution on the 24 × 18 cm large print space. Older drawings were conventionally photocopied and cut, and the arrangements later scanned and cleaned with Corel Photopaint.

Photographs. Most macro- and microphotographs were made with digital cameras, only a few dating back before ~2003 were made with traditional film cameras. Microphotographs were taken with a Nikon Coolpix 4500 adapted free-hand to a Kpl 10×/20 Zeiss wide field ocular and 10×, 40×, and 100× Zeiss achromatic objectives (H.B.), or with a Canon S70 firmly adapted to a Leitz Periplan 10×/18 mm ocular and plan-achromatic objectives (G.M., older photos were made with a Nikon Coolpix 995). Coolpix 4500 photos were taken at minimum zoom (7.85 mm focal length) in order to avoid ring artifacts (Baral 2004), Canon photos at different zoom positions (mainly 13.15 mm). Contrast was only rarely improved by oblique illumination. Photographs of conidia were rarely taken under dark field illumination.

Most macrophotos were made indoors with Coolpix 4500 on a solid mono- or tripod, usually in combination with several self-adapted macro lenses (Russian Horizon lens 10×, Zeiss wide field oculars 10×, 20×, and 25×) usually at maximum zoom of the camera (32 mm). Apothecia were illuminated by a self-made ring of 4 miniature LEDs, enabling a shutter speed of ~1/15–1/60 sec at an aperture of 7.5–10. The sensitivity was generally retained at 100 ISO in order to avoid optical noise. Some photos of yellowish apothecia were in addition illuminated with a Luxeon-LED (3 W) in order to obtain a characteristic yellow fluorescence which is not seen under halogen or normal LED light.

Photographs were enhanced in contrast and/or adjusted in colour if necessary. Mostly they were made at constant magnification using a fixed zoom position. Microphotos were calibrated using a Zeiss calibration slide; their resolution with Coolpix 4500 at minimum zoom under oil immersion was ~0.1 µm per pixel. Microphotos were enlarged with Corel Photopaint 10 by 230% for ascospores, 173% for asci, and 115% for conidia, so that their magnification on the 2825 × 2125 pixel large plates coincide with that of the drawings.

Methods of collecting

Desiccation-sensitive species were harvested from pieces of substrate close to the forest floor, mainly in shady woods or near water. They were carefully transported in water-tight boxes in order to preserve the vital characters of the apothecia. Fresh apothecia were kept viable and in good condition for a few days or sometimes 1–2 weeks. For this purpose, specimens were stored in these boxes in the refrigerator at ~6–10 °C.

Desiccation-tolerant species were harvested on air-exposed substrate at a height of usually 0.5–2.5 m above the ground. They were for the most part collected in the dry state, and were rehydrated prior to examination using a sprayer. Rarely, desiccation-tolerant species were collected in the hydrated state shortly after rainfalls, or on hydrated substrate recently fallen to the ground. In some cases, substrate at about 3–6 m above the ground was gathered by using a long branch, a rope with a heavy object at one end, or a wire saw attached to a rope. A few collections are from up to 25 m ground level, harvested either during a crane project in the vicinity of the university of Leipzig (Germany), or through the window of buildings, also from trees recently fallen by a storm or when felled by forestry workers.

Whenever possible, the approximate height of the substrate above the ground level was noted for each collection.

Because of the difficulty of detecting apothecia in the field, collecting of desiccation-sensitive species was often done by gathering ample, favourably looking dry substrate in plastic or paper bags. The substrate was usually scanned for apothecia with a handlens (8–15 ×) in the field, but a majority of apothecia and particularly species were generally later detected under the dissecting microscope, often only after rehydration. Branches were cut into ~10–30 cm long pieces in the field in order to be more easily transported and handled. Frequently, a single collection comprised 10–20 or more such pieces from different branches of one or several neighbouring trees from the same species. Bright LED-illumination proved helpful in better detecting dry or hydrated *Orbilia* apothecia due to their more bluish spectrum and a resulting higher contrast between apothecium and substrate. Scattered groups of small apothecia were often tagged using water-insoluble paint markers (Edding Matt Paint Pen) in order to facilitate their redetection, using different colours for *Orbiliomycetes* and other ascomycetes.

The scope of observed branch thickness was noted for each lignicolous species. Thereby, the term 'twig' was usually applied below a thickness of 5–6 mm, the term 'branch' for ~5–100 mm, and the term 'trunk' or 'log' above 100 mm, irrespective of whether it was a young or old branch or a trunk. Besides the rate of decay, we carefully distinguished between bark and wood as support of the apothecia, and also noted the presence of algae and black yeasts causing greying of the substrate. Other fungi (including lichens) and bryophytes growing in more or less close association were noted for each species whenever their identity at some taxonomic level could be assessed. High attention has thereby been paid to discomycetes, whereas pyrenomycetes, mitosporic fungi, lichens, and basidiomycetes were more occasionally identified. Usually we have not distinguished between organisms occurring on the same piece of branch or on other branches, when they were of the same host plant, in a similar state of decay, and collected at the same site and day.

Conidia on the natural substrate. In many collections we have observed conidia on the natural substrate in close association with the apothecia, either lying detached on the substrate surface, or on conidiophores growing out of the apothecia or the surrounding substrate. Conidia occurring on the substrate surface were gathered by placing a drop of water close to the apothecia, and repeatedly transferring the liquid by a glass rod with an inflated globose end or by tweezers to a microscope slide. If the substrate is strongly absorptive for water, several drops were placed on the same spot before transferring liquid to the slide.

In many cases the conidia coincided with those obtained in pure culture, either from the same or another sample of the same species. Often, however, different conidial types belonging to different species were harvested on a given spot. Therefore, records of anamorphs from the natural substrate can often only tentatively be assigned to the associated teleomorph of *Orbilia*. In those species in which we obtained conidia only from the natural substrate, we referred to the anamorph as 'presumed', even if the conidia were repeatedly encountered in different samples of the same species.

Host identification. Host plants were identified whenever living or dead leaves, flowers or fruits were present. Identification was facilitated if the inhabited branches, herbaceous stems, or leaves were still-attached to the plant. Photos were often taken of the inhabited substrate in situ, the host plant, and the vegetation at the collection site, and hosts were sometimes identified from such photos. In the case of substrate being detached from the plant, or attached to entirely dead host plants without characteristic organs, determination of the genus was frequently done on the basis of wood (xylotomy) or herbaceous stem microanatomy. Microscopic cross, radial, and tangential sections of wood were compared with keys (Hassler & Hirschmann 1985; Höster 1969, 1970; Schweingruber 1990, Schweingruber online: http://www.wsl.ch/dendro/xylemdb), and with a personal reference collection of permanent slides and photos. Macrophotographs of transversely broken or cut wood taken with the above-mentioned Horizon macrolens mounted on Coolpix 4500 were made from a large number of substrates, which permitted identification of many genera and revealed various misdetermined hosts.

Plant nomenclature and systematics followed the modern classification, for which mainly Wikipedia and the International Plant Names Index (www.ipni.org) or the Kew plant list (http://www.theplantlist.org) were used. Regarding angiosperms the host list (Appendix 1) is sorted according to Angiosperm Phylogeny Group IV (see https://en.wikipedia.org/wiki/APG_IV_system).

Geographic and climatic data

For georeferencing collection sites, longitude-latitude coordinates (WGS84) were often gained by collectors, either by a GPS device or in Google Earth©, from which also the altitude was taken. Distances between collection sites and towns or villages were taken from the approximate city centre using the distance tool in Google Earth. Distribution maps were generated by exporting the geographical data from the personal database (DBASE IV) to Microsoft© Excel and conversion with the online program http://www.earthpoint.us/ExcelToKml.aspx to a kml file which can be opened in Google Earth. Phenological data are summarized in tables only for those species with more than ca. 25 collections.

Different online maps for bioclimatic zones (thermo- and ombrotypes), biogeographic regions (ecoregions), geology, and vegetation groups were used to analyse the ecological preferences of a species. These were mainly the following:

World: http://portal.onegeology.org/OnegeologyGlobal/.

North America: climate zones, moisture index: http://www.bonap.org/Climate%20Maps/ClimateMaps.html; ecoregions: https://en.wikipedia.org/wiki/United_States_physiographic_region; plant associations: Bennett et al. (2004), Vankat et al. (2013), Forest Cover Types (nationalatlas.gov).

Europe: thermoclimatic belts: http://www.globalbioclimatics.org; geology: http://infoterre.brgm.fr/geoservices-ogc (France), https://map.geo.admin.ch (Switzerland), https://apl.geology.sk (Slovakia) and others, maps of Germany, Luxembourg etc.

Australia: plant associations: http://www.environment.gov.au/resource/major-vegetation-groups-australia; ecoregions: http://www.environment.gov.au/parks/nrs/science/bioregion-framework/ibra/index.html.

Macaronesia: plant associations: http://www.tenerife.es/planes/PTEOActIndustrial/adjuntos/PINF_105.pdf; climatic zones: Del-Arco et al. (2006); geology: https://visor.grafcan.es/visorweb/.

The climate of collection sites (thermo- and ombrotype) was also looked up in Wikipedia in cases when towns were in close vicinity, for which climate charts were available. For thermotypes the terms supratemperate and meso-/thermo-/infratemperate are used in Europe and Azores as equivalents to cold- and warm-temperate in other continents. For ombrotypes the term semihumid instead of 'dry' was used within Europe and Macaronesia for pluviseasonal climates with distinctly less precipitation and humidity during summer, and the term subhumid instead of 'dry' was used for a boreal sagebrush desert scrub in Pinedale in the Wyoming Basin adjacent to the Wind River Range of Middle Rocky Mountains, showing a little more rain in summer than in winter. Because of the low resolution of most online maps, the altitude of collection sites was used to determine their most probable bioclimatic zone. For Europe we mainly used the map of thermoclimatic belts, but a few data of this map were modified: the region of Bretagne in western France was classified by us as mesotemperate, not mesosubmediterranean, following its classification as temperate oceanic on the map of bioclimates, Dalmatian lowlands as thermo- instead of mesomediterranean (N. Matočec pers. comm.), and the northern Caspian lowlands as warm-continental instead of supramediterranean, following the climate charts of Volgograd and Astrakhan. Some small hills and mountains are not included in this map: for instance, Fruška Gora in northern Serbia lies in a suprasubmediterranean lowland of 75 m altitude, but its forests at 250–540 m are classified by us as supratemperate.

Definition of continents (see Fig. 127). The term 'Northern America' is used here to comprise USA, Canada, and Greenland and 'Middle America' to include Mexico to Panama and the Carribean islands (by excluding Trinidad and Tobago though currently referred to the Lesser Antilles). Both regions represent the continent of North America. The South American continent includes all mainland countries south of Panama (including Trinidad and Tobago). Africa includes the islands around Madagascar, whereas Macaronesia shows closer affinities to Europe. Asia includes Turkey to the southwest and the Indonesian islands to the southeast. Australasia is considered to comprise Australia, Tasmania, and New Zealand, and Melanesia to include New Guinea, Solomon Islands and others. Europe is adopted as extending eastwards to the Ural mountain range and Ural river, and southeastwards to the Caucasus and Bosporus, by excluding most of Georgia, Azerbaijan, and Turkey. For practical reasons, the Ural and Caucasus mountains are treated in chorological respect as entities. Central Europe is roughly circumscribed by including Luxembourg and the Pannonio-Carpatian regions, and by excluding subatlantic, hemiboreal (Baltic), continental, and submediterranean regions.

Methods of examination

General. Within each collection, usually a few apothecia were examined, except for very scanty specimens. In rich collections consisting of many pieces of substrate, often up to 10–20 apothecia were examined. Due to the frequent occurrence of mixed populations, different apothecia from each piece of substrate were tested in order to explore the species composition. For instance, about 2–5 more or less remote apothecia were examined from each piece of a xeric branch which has been cut in the field into ca. 10–20 cm long pieces. In the species descriptions, a number in curled parentheses {} indicates the number of collections from which the given data were gained. This number is often lower than the total number of collections studied because of the impossibility to check every collection for the whole set of characters.

Macroscopic examination. In the descriptions, macroscopic data on the hydrated apothecia observed under the dissecting microscope refer either to the fresh (= moist) or the rewetted (= rehydrated) mature apothecia. Shape and colour of dry apothecia are reported separately. Dry apothecia were rewetted either by spraying with tap water, sometimes also by submersing the substrate in tap water for a few seconds, or by placing a water drop on a single apothecium (in order to avoid water stress to the whole population in case that living elements might still be present). Before taking macrophotographs, excess surface water must be allowed to disappear. Depending on the hydrophily or absorptivity of the substrate surface, this usually takes ~1–2 or rarely up to 10 min. In addition to the hydrated state, photos were sometimes also made in the dry state, especially in desiccation-tolerant taxa. Due to the frequent fading of apothecial colour in specimens older than about 5–10 years, the original colour is indicated whenever it was stated by the author, while altered pigmentation is sometimes mentioned separate from the original colour.

Date of examination, **desiccation tolerance**. Fresh collections of desiccation-sensitive species were studied within a few days after they were collected (about one week as a maximum when sent by mail). A few collections from Northern America and China were received by air-mail in the fresh living state without damage. Desiccation-tolerant species were likewise studied within a few days if they were collected close to a working room with available microscopes. Those collected on dry xeric substrate in continents other than Europe were posted in the dry state and studied within a period of some weeks or months, or often ~1–3 years later. After more than 3 years have passed, living elements were only exceptionally found.

Desiccation tolerance was evaluated at random for most of the species seen in the living state. In the descriptions, only the maximum period of time is mentioned after which a given element was found to be still viable when stored at room temperature in the herbarium. This period starts with the moment of collection, but it neglects the fact that the apothecia were dormant the field for an unknown period of time, depending on the weather conditions at that time. The desiccation tolerance given in the descriptions thus refers either to the moment when the fresh specimens were dried in the laboratory, or when the dry specimens were collected.

In rare cases, immature populations were kept under damp conditions in watertight boxes or plastic bags for some weeks (with periodical intervals of dryness in the case of desiccation-tolerant species) in order to obtain mature asci and spores. Fully turgescent asci with tight spore packing, and even active spore discharge could then sometimes be observed, but frequently the maturation process was not initialized.

Sections versus squash mounts. Apothecia were studied in squash mounts or in median sections made free-hand under the dissecting microscope (20 ×) using razor blades. Whenever possible, the study of sections was preferred since they allow to view the marginal region of the ectal excipulum and also the asci and paraphyses in situ, e. g., how much the paraphyses protrude beyond the asci. Sections were executed more or less exactly across the centre of the apothecium (median), in order to permit correct interpretation of tissues in the lower part of the apothecium. Apothecia were usually sectioned in the hydrated state, while in the dry state some species are too brittle, especially *Hyalorbilia*, and others too small. Free-hand sectioning requires firmly attached apothecia and a tough substrate. Sections gained from hydrated apothecia have a thickness of ~20–50 µm, whereas dry apothecia allow to obtain a thickness below ~20 µm. Depending on the diameter of the asci or excipular cells, sections require a minimum thickness in order to study undamaged living tissue. Thanks to the transparency of the living cells, sections of 40–50 µm thickness still allow to see the cells including their contents, even if they are covered by others. For microphotography, however, better results are obtained with thinner sections. In the case of very minute apothecia, the excipular anatomy was sometimes studied by viewing on the cut surface of an apothecium being divided into halves.

To follow a paraphysis or ascus from top to base in situ is often only possible in sections of apothecia in which most of their elements are viable. Studying sections of living apothecia in water mounts thus makes any separation of the elements, or any staining procedure generally superfluous. In dead material, on the contrary, the subhymenial region is usually highly intransparent, and separation of the elements by pressure frequently results in breakage of the asci at the level of their stalks. In order to obtain at least some complete, unbroken asci, enough amounts of water or KOH and a medium strong pressure is required. Alternatively, sections in KOH are treated with iodine in order to stain the ascoplasm (see p. 10).

In addition to sections, entire (dead or living) apothecia, or marginal fragments of apothecia, were examined in top view. This allows to study the marginal cortical cells (Fig. 77: d, f), and also to focus on the hymenial exudate.

Study of living material. All parts of the fungus (anamorph and teleomorph) were examined and illustrated in the living state whenever living cells were available (vital taxonomy, Baral 1992). Living specimens were always studied and measured in tap water mounts. Thereby only gentle pressure on the cover slip was applied in the case of squash mounts, and no pressure in the case of sections, at least during the first minutes of observation. Living fungal cells are highly sensitive to pressure. Any too strong deformation causes irreversible damage to the plasmalemma. When pressing on the slide, thick elements are affected at first, therefore, asci usually die already at a slight pressure and paraphyses and spores when pressing more strongly.

Concerning apothecia of *Hyalorbilia* with generally abundant gel between the hymenial elements, much care and skill is necessary in order to save vitality in a microscopic preparation. Due to this gel, any pressure on the cover slip must be avoided, otherwise asci and paraphyses rapidly die. Very sharp razor blades are necessary to minimize the shearing forces on the hydrated cells in order to avoid destruction of their plasmalemma. When viewing vertically on the surface of the hymenium of an entire apothecium mounted in ample water under the cover slip, the living state of the asci and their spores, and of the paraphyses with their pale chlorinaceous VBs can easily be recognized in optical cross section under oil immersion (Fig. 75: a).

Due to their often rather high refractivity and sharp outline, organelles such as LBs, SBs, SCBs, and VBs are very clearly visible inside living cells, even though being often fairly small. The requirements for their observation are: (1) oil immersion at a magnification of min. 1000×, (2) normal bright field optics, (3) water as mounting medium, and above all (4) living elements. No phase or interference contrast is necessary, even for microphotography (Figs 83–90). On the contrary, such enhancement of contrast obscures, e. g., the exact shape of SBs, particularly their fine attachment. Best contrast and resolution is gained from elements lying close to the cover glass. Due to a slightly higher specific weight of free spores compared to water, spores of seemingly all fungi soon settle on the slide. Therefore, they can usually only be photographed in this situation.

Basic dyes were used for staining the contents of living cells (vital staining), and for staining cell wall layers and extracellular structures. Different dyes were tested [Cresyl blue (CRB), Toluidine blue (TB), Cotton blue = Methyl blue (CB_a), Neutral red (NR)]. For the study of living cells the solution must be aqueous (in tap or distilled water), since current ingredients of these dyes are lethal to the cells. Both CRB and TB have a strong metachromatic property, i. e., they change their colour depending on the pH of the stained microstructure (in Baral 1992: 364 it was erroneously stated that TB does not change its colour in acids towards turquoise, in contrast to CRB, although both dyes turn turquoise when accumulated in VBs).

Staining of living cells was done to determine the type of cell organelle. Basic dyes selectively stain refractive vacuoles (VBs in paraphyses, SBs in ascospores) in a greenish- to violet-blue, and therefore, allow differentiation against LBs and SCBs which remain either unstained in these agents or turn pale rose-red (LBs). Basic dyes were also sometimes used for testing vitality of single cells, and for improving visibility of nuclei and nucleoli, for which also IKI was sometimes applied as a vital stain.

Basic dyes were frequently applied to test the metachromatic staining properties of cell wall layers, external gels, and exudates. Basic dyes were found to stain ascus apical thickenings blue-violet, and external gel lilac. They show a high affinity to exudate, which stains turquoise-blue and thus allows to differentiate glassy processes which remain unstained.

Staining was carried out by adding a drop of the dye to the edge of the cover slip of a water mount. Thereby, the cover slip is slightly liftet so that enough dye comes in contact with all of the cells, then excess liquid is removed. Since staining of cell inclusions usually takes a few minutes until the dye enters both plasmalemma and tonoplast, the process was sometimes accelerated by making the solution very weakly alkaline (by adding a drop of ~0.1 % KOH or NH_4OH to the mount = CRB_A, Baral 1992: 341, Le Gal 1947: 78).

Because CRB and also IKI are slightly toxic, these agents permit vital studies only for some minutes. Clémençon (1972: 52) found aqueous CRB to become useless after some months by flocculation of the pigment, therefore, he added high amounts of concentrated glycerol and alcohol 96 % in order to stabilize the solution. However, although the metachromatic reaction of exudate and gel is not diminished by these high-concentrated ingredients in Clémençon's CRB solution, they destroy the vacuoles and other organelles and shrink the cells. We found aqueous CRB to work well even after many years, despite its flocculation, although it seems advisable to filter the solution once in a while.

Study of dead herbarium material. Quite a large number of figures in this monograph show dead elements. This mainly concerns type specimens of previously described taxa, sometimes also recent records being examined too late. These figures demonstrate the alterations in cell shape and especially the loss of cell contents. Herbarium material was first studied in tap water. If no living elements were found, the dead spores were first examined in water in order to see if the spore bodies are still perceptible as a transparent or (rarely) refractive region. Next, a small drop of KOH (~5%) was added at the edge of the cover slip to the water mount in order to swell the elements and clear the dead cytoplasm. Mostly, a small drop of CR was soon added to the KOH-mount for creating a better contrast of the cell walls, particularly concerning septa of paraphyses and ascogenous hyphae. In such KOH+CR mounts the walls of the spores inside the asci become better visible, and sometimes even the spore body region is faintly perceptible. CR_{SDS} was mainly used to stain ascus apical thickenings. It was either added to a water mount, or (in herbarium material) to a KOH mount. Staining of the swollen endotunica takes some minutes and needs quite a high concentration of the reagent (presence of KOH is not necessary). Best results are obtained when placing the fungus directly in a drop of CR_{SDS}.

If the spores are still not clearly visible within the asci, IKI (rarely MLZ) was added to a KOH+CR (or KOH) mount. By staining the glycogen in the surrounding ascoplasm, the spores of many taxa become more distinctly visible (Figs 10: d–e, 91: a). A method to make the transparent region of the SBs more clearly visible was sometimes applied, especially in order to see spore orientation within the asci: the apothecial fragment was placed in a drop of cytoplasmic stain (CRB, CB_L, or phloxine) for some minutes, then a drop of KOH and a coverslip was added, and the excess liquid removed. Thereby the sporoplasm stains violet or blue whereas the SBs may become perceptible in some taxa as unstained areas. Alternatively, the cytoplasmic stain can be added to the KOH-mount. This method worked quite well in species with comparatively large SBs, but in others, especially those with small globose SBs, it completely failed.

On the drawing plates and in the legends to the photo plates the applied mountants are indicated for each element, except for the frequent case of living cells mounted in water. Since media like KOH, MLZ, or CB_L are immediately toxic to fungal cells (with the exception of brown and thick-walled spores which do not occur in *Orbiliomycetes*), only aqueous mountants (H_2O, IKI, CRB) are headed by the cross (†) in order to indicate the dead state.

Ascus apex. As an exception throughout the monograph, the ascus apex is almost always figured in the dead state because the truncate shouldered apex are only apparent in the dead state, and the apical wall thickening and much more pronounced, due to the loss of ascus turgor. This is in concordance with the practice in other groups of ascomycetes, e. g., the *Helotiales* or *Lecanorales* which often have an amyloid apical apparatus that exhibits its ultrastructure much clearer in the dead (particularly immature) state where the apical thickening is inflated ~2–4-fold in thickness (imbibition effect, Baral 1992: 351). Entire mature asci, however, are figured in the living state whenever such asci were available.

Evaporation. When examining sections of apothecia of *Orbilia* in water mounts, the constant evaporation of water causes a mechanical pressure on the hymenium evoked by the adhesive power between water and glass. This results in a tighter packing of asci and paraphyses, especially when studying living specimens, which strongly diminishes transparency and disables to see branching and anastomoses, or the base of these hymenial elements. Moreover, evaporation may cause flattening of large cells (asci, conidia). Adding water solves this problem instantly. Enough liquid also prevents hymenia in median section from becoming more convex than they are in the natural state, or branched 3-dimensional conidia from getting 2-dimensional. On the other hand, too much water leads to diminished contrast and resolution if the examined structures reside at some distance from the cover slip.

Iodine reagents, **amyloidity and dextrinoidity**. Almost every species of *Orbiliomycetes* was at least once tested with IKI, either directly or, especially in dead material, when KOH-pretreated. KOH (~5%) was applied for ~0.2–1 min, usually at room temperature, rarely by briefly heating the slide. IKI was usually directly applied to the KOH-mount (thereby a part of the IKI gets discoloured): often it gives a dextrinoid reaction to the ascoplasm (rarely to the sporoplasm) due to glycogen, whereas an amyloid reaction (rarely a dextrinoid reaction) to the cell walls was never observed. Sometimes MLZ was used instead of IKI, particularly when testing ascus apical thickenings for dextrinoidity.

Croziers versus simple septa. Croziers and simple-septate ascus bases are best recognized in asci still adhering to the ascogenous hyphae. It is, therefore, recommended to observe the ascus bases preferably in sections in the context of the tissue. In *Hyalorbilia* there is usually no other way to clearly see the ascus base because the asci are firmly conglutinated with the paraphyses and, therefore, impossible to separate. It is further recommended to study specimens in a not too mature stage of development, in order to see the ascogenous hyphae during ascus formation. One of the reasons for the frequent neglect of ascus base characters is that they are difficult to observe in dead herbarium material. Dead specimens require application of CR (Congo red) to a KOH-mount and careful observation of the not too strongly squashed elements, in order to avoid breakage of the ascus stalks. In living material the character is often very easily and immediately seen. Ascus bases are also easily misinterpreted as variable because the visibility of croziers as well as furcate or T-/L-shaped bases depends on the viewing direction (see also Huhtinen 1990a: 66).

Polyspory. Spore numbers in asci were mainly evaluated by counting, predominantly from living material. Dead herbarium specimens were treated by KOH and stained in IKI/MLZ, CR, or CB/CRB. In cases when spore counting was too difficult, a calculation method was used based on the estimated volume of the spore cluster divided by the mean spore volume. This method was only applied to living asci in which the spores are tightly arranged in a cluster at moderate but not full turgescence. In order to determine its volume, the spore cluster was regarded as a cylinder [formula: mean length × mean width^2 × 0.785], its length and width being averaged in order to compensate for the rounded outline of the cluster. The spores were considered as a cuboid [mean length × mean width^2] in order to compensate for the space between the spores. Drawings of asci with spore numbers above 16 usually do not show all spores because the spores lie in several layers one upon the other. Also photographs show only those spores which are in focus.

Microscopic measurements

General considerations. Measurements of asci, ascospores, spore bodies, paraphyses, excipular cells, conidia etc. were taken directly at the microscope, and only sometimes they were evaluated from photos. The latter method may be subjected to some errors, e. g., diminished values are obtained due to eccentric focusing of an element. The length or vertical extension of an element is always given before its width, even if the width is greater than the length (e. g., in short apothecial stipes, marginal teeth, lens-shaped spore bodies, staurosporous conidia, or glassy processes). Excipular cell size is mostly gained in median section, except when 'in surface view' is stated. Their hyphal origin is often not recognizable, therefore, a definition of length and width is problematic here.

A minimum of about 5–15 asci (or ascospores) was usually measured in each collection. Length and width of individual elements were only noted for spores figured on the drawing sheet. Single () and double (()) parenthesis indicate the rarity of extreme values. Values were approximately determined when merging data from all included collections. Statistical methods were not applied, instead, the strict separation between living and dead cells was practised, which usually provides distinctly different ranges.

The stated ascus length consistently refers to the total length of the ascus cell, i. e., from the ascus apex down to the lowermost end of the ascus stalk, including all of its (non-septate) branches. The complete ascus base in *Orbilia* is easily overlooked because (1) the flexuous ascus stalk is often very long and thin, and then difficult to follow among the densely intermingled hyphae when the ascus is still in situ, (2) the asci very easily break at the thinnest part of the stalk above the branching point, when the hymenial elements are squashed by pressure in order to get separated. In order to obtain compatible values, such broken asci must be disregarded for length measurements. Complete separation including their base is generally only successful in some of the asci of a preparation. After gentle pressure on the cover slip, even turgescent asci may sometimes be found detached and floating in the medium. Literature reports sometimes do not encompass the total ascus length as here defined, and those authors being aware of this specified their measurements by a remark (e. g., Velenovský 1934: *sine pedicello* = excluding the stalk).

Whenever available, we recommend to observe and measure asci in the living state in situ, because their stalks are then much easier to follow to the very base due to the transparency of the living cytoplasm and a larger width of the stalk. In the case of dead asci, application of IKI (or MLZ, added to a KOH mount) often yields very clear results by staining the ascoplasm in a bright red-brown. The ascus stalks and their branches thereby strongly contrast with the unstained surrounding paraphyses and ascogenous hyphae, and that without separating the elements (Figs 91b–c, 92a). The effect is due to glycogen which is present in high quantity usually only in ± mature asci.

The measured cell width always refers to the widest point of an element. This is of special impact in biradial symmetrical asci which are in the dead state apically truncate and provided with two shoulders: in our values of ascus width we included these shoulders as seen in front view, but we also included those asci seen in profile view which appear distinctly narrower and rounded at the apex. Another complication is caused by the fact that asci with a truncate apex are not perfectly round in cross section below these shoulders, apparently irrespective of the living and dead state. Because in living asci front and profile view are not clearly recognizable, these deviations in width between the two views can hardly be separately evaluated. Drawings in the dead state of biradial symmetrical ascus apices at 4000 × always refer to the front view (the rare case when we figure apices in profile view is specified on the plates). Similarly, marginal cortical cells in *Hyalorbilia* are in external view often wider than in median sections (in top view on the hymenium the marginal cells often look broadly ellipsoid). In such cases we preferred to note two separate values instead of merging in one.

For a practical reason, curved elements like spores, spore bodies, or flexuous ascus bases were always measured ***in situ***. These in-situ values refer to the straight distance between the two ends of the element, or in very strongly curved spores the distance between the most protruding parts of the spore. In the case of distinctly curved spores and spore bodies, the actual length along the two- or three-dimensional curvature was estimated and indicated separately. The actual length has an undoubtedly higher taxonomic significance, but its evaluation is difficult, and for helicoid or irregularly bent elements it requires inclusion of the third dimension.

In branched (staurosporous) conidia there is some controversy concerning terminology, measurements, and number of septa of the extremities. We preferred to measure the stipe length, but some authors, e. g., Ando & Tubaki (1984c), Matsushima (1987, 2005), and Tzean & Chen (1989), measured the length of the 'axis' or 'main axis' by including the entire central cell, which is obvious from their measurements (see Fig. 104). Likewise, we use the term arm, whereas some authors prefer the equivalent term branch. A few authors considered two adjacent extremities as a single element regarding length and number of septa, e. g., Matsushima (1980) in *Trinacrium* with two horizontally projecting arms, Matsushima (1981) and Ando & Tubaki (1984a) in *Curucispora* with two arms forming a 'V', and Matsushima (1981) in *Curucispora* with the apical arm and the stipe included in his term 'axis'.

The number of septa in branched conidia given in our descriptions includes for the stipe the uppermost transversal septum, and for the arms the basal septum (see Fig. 104 left). Arm septa were also counted this way by Peek & Solheim (1958), Tzean & Chen (1989a) and others, whereas, e. g., Ando & Tubaki (1984b) and generally Matsushima omitted the basal septum of the arms. We consider the latter method to be problematic because the basal septum of some of the arms may tend to be more or less away from the arm base, also because of cases in which arms are devoid of any septa, even at their base.

Our measurements of conidia first give the total size (total length × total width, because of pressure by the cover slip a certain inexactness in measurements of total size is possible), and then the size of stipe and arms. Stipe length refers to the distance from base up to the point where the branches emerge, arm length to the straight distance between insertion and tip (see Fig. 104, top left).

Living versus dead elements. Due to the shrinking effect (see Huhtinen 1985a, Baral 1992, and p. below [shrinking effect]), measurements of living and dead cells were separately established. Measurements from living cells were taken whenever new collections with at least a few such elements were available. In the descriptions data on living elements are headed by an asterisk (*). Data in the dead state are headed by a cross (†), and were often evaluated in addition, in order to provide compatibility with specimens which were only available in the dead state. For elements which did not markedly differ in size between the living and dead state, both states were usually combined and headed by (*/†).

Huhtinen (1990a) considered also the influence of mounting media on the size of dead cells as important. However, killing of the cells has a distinctly higher influence than the employed media. Therefore, we refrained in our measurements from indicating the employed mountant. The media in which dead cells were measured were KOH, KOH+CR, KOH+IKI, sometimes also H_2O, H_2O+IKI or H_2O+CRB, rarely MLZ or CB_L. These mountants are indicated on our drawing figures or in the legends of the photo plates.

Measurements of living asci and ascospores always refer to the mature stage of development (for the definition of maturity of ascospores see p. 30, Recognition of maturity). In the dead state, estimation of maturity is much complicated, so that submature or overmature stages are easily mistaken as mature. Estimation of maturity of conidia is more difficult. Generally, all conidia which appeared to being detached from their conidiophores without external influence were considered to be mature.

Separation of measurement data between the living and dead state is of special importance in asci. This involves not only a strong shrinkage (Fig. 25: 1a, 2a), but also inflation of the apical wall, and often also increase in length of the pars sporifera. A speciality of the genus *Orbilia* concerns the fact that living mature asci strongly raise the internal turgor shortly before spore discharge and, therefore, noticeably increase in size (Fig. 25: 1a, 1b). Whenever fully turgescent asci were observed in species of this genus, ascus measurements were gained from both the moderate and the fully turgescent state, and are given as two separate values (before and after the arrow →). Because the spore cluster strongly retracts in length at full turgescence, the pars sporifera is likewise given separately for moderate and full turgescence. The length of the pars sporifera was taken as the distance between ascus tip (including ascus wall) and lower end of lowermost spore, provided that the upper spores reside close to the ascus apex (see Fig. 16).

Separation of the living and dead state is also recommended for ascospores, paraphyses and excipular cells, though these usually show less pronounced shrinkage in the *Orbiliomycetes*. In some descriptions, the stated measurements of the dead elements are larger than those in the living state. This may have different reasons. Often such data are based on different collections, that is, the variation of the taxon could not be fully explored in the living state. Flattening of dead cells is another source for this paradox effect.

Living spores inside dead asci. Because free spores are often not present in sufficient quantities in the *Orbiliomycetes*, a significant part of the drawings and measurements in this study originate from spores inside living, sometimes also dead asci. Due to the rather inelastic spore walls in the *Orbiliomycetes*, the size of living spores is about the same irrespective of whether they are measured inside asci of moderate turgescence, inside dead asci, or when ejected. The observed differences are below the general intraspecific variability and will hardly cause taxonomic conflicts. More obvious are differences in size between living and dead spores. In order to avoid too much complication, we have usually not specified the origin of the drawn spores and their measurements. In any case, living spores inside dead asci are usually difficult to measure since the spore wall is completely invisible and only the transparent sporoplasm is striking (Fig. 25: c left, d left). Due to a reduced vitality in some of the specimens studied, the only chance we had in order to draw and measure living spores was to use those inside dead asci.

Dead spores inside dead asci. Great problems arise whenever dead spores, which always have a thin delicate wall in the *Orbiliomycetes*, have to be studied inside dead asci (Figs 10: b–c; 25: c right). When adding cytoplasmic stains (IKI, CB_L, CRB) to a KOH mount, the ascoplasm is usually deeply stained whereas cell walls and sporoplasm remain unstained (Fig. 10: d–e). Such staining often enables to see the shape of the spores, also their orientation in the case of heteropolar spores, and sometimes the LBs. In rare cases, the SBs become perceptible as an unstained region. Problematic in regard to recognizing spore shape or spore numbers are species with filiform spores or with long spore tails. A clearer image of the spores is obtained in CR, because CR stains the spore walls, while asco- and sporoplasm are not stained. Also in this reagent the region of the SBs may become faintly perceptible, whereas LBs are shown with high contrast.

These two methods worked well in a lot of species, though in some cases the spores remained more or less invisible (Fig. 10: b–c). A final method in such a case is to cut the asci. A median section of an apothecium is placed on the slide in a very small drop of water. Under the dissecting microscope the asci are cross-cut by pressing the edge of a razor blade across the hymenium. Free, more or less mature spores escape from the broken asci and are then found in abundance.

The unstained spore wall inside dead asci may easily be considered as a spore sheath (Fig. 10: d–e). However, it seems to originate not only from the spore wall itself but also from some detachment of either the sporo- or the ascoplasm and leads to too small spore measurements if only the sporoplasm is measured. A membrane outside the spores is rarely seen in living asci, and it seems to be the investing membrane that here detaches from the surface of the spore wall. In the dead state, however, this could only be clarified in cases when spores emerged from broken asci. The sheath-like transparent layer has a thickness of ~0.3 µm and thus may provoke an error in spore measurements of ~0.6 µm in both length and width, which is quite significant, especially in the case of narrow spores.

But even living spores may cause problems, when they have a thin basal tail. These tails are usually only well seen in free spores. Sometimes they are visible inside living asci, and rarely inside dead asci, even if the spores are still alive.

Culturing techniques

Isolation. Isolates were taken in most cases from ascospores. Fresh or rehydrated apothecia (often with small pieces of substrate) were put inside the lid of a Petri dish on a drop of vaseline and allowed to shoot their spores on the agar. Illumination with a 40 W light bulb from a distance of ~40 cm was only used in a few cultures by one of us (G.M.). Alternatively, stimulation by vibration and slight heating, e. g., by placing on a running warm harddisk, was found to accelerate spore discharge (P. Perz, pers. comm.). Rarely, apothecia were placed on the agar surface to produce a mycelium or, more frequently, mycelia were observed growing out from apothecia attached inside the lid. Germinating spores were directly observed at a 150 × magnification through the unopened Petri dish. We have not tried to obtain single spore isolates, therefore, the isolated mycelia have always a polysporous origin. When enough spores were on the agar, the apothecia were removed from the lid and mostly checked microscopically for their identity because mixed populations of macroscopically indistinguishable species were often encountered on the same piece of substrate, especially in desiccation-tolerant species.

Agar media and incubation. Spore germination was obtained on CMA:2 (E.W., G.M.), CMA:3, CMA:4, CMA:5, CMA (1 : 1, G.M.), or MEA 2 % (without antibiotics). The plates were kept at room temperature (15–25 °C) under natural light-dark-change. Secondary cultures were incubated under artificial light-dark-change (20/12 °C, each lasting 12 hours, E.W.) or at natural light conditions in Petri dishes (90 mm diam., E.W. & G.M.). Later they were often deposited in the dark at 8 °C (E.W.). The strains were mainly plated on CMA:2, MEA 2 %, or water agar (WA), with the following composition: CMA:2 (half-strength cornmeal agar, Rubner 1996): 8.5 g cornmeal agar (Difco), 12.5 g agar (Merck), 1 l aqua dest.; CMA:3, CMA:4 and CMA:5: 5 g/4 g/3.5 g cornmeal agar (Fluka), 12 g agar (Merck), 1 l aqua dest.; CMA cornmeal agar (Fluka) 17 g, 1 l aqua dest.; MEA 2 % (malt extract agar, Gams et al. 2007): 20 g malt extract (Merck), 15 g agar (Merck), 1 l aqua dest.; WA (water agar): 20 g agar (Merck), 1 l aqua dest.

Water agar with sterilized pieces of rotten wood (*Rosa*, *Salix*), and CMA:2 with sterilized pieces of original substrate of collections were used in order to stimulate formation of conidia or apothecia (E.W.). We also frequently used a method which was often employed in aquatic hyphomycetes for inducing sporulation: submersing in water (see, for example, Ingold 1942, Marvanová & Bärlocher 2001). Thereby, 1–2 large agar blocks with fungal mycelium were placed in sterile, empty Petri dishes and flooded with distilled water; no parafilm was used in this case. Within some days the first conidia could be observed. No near-UV was available during our experiments to induce sporulation. Only in rare cases developed apothecia in our cultures.

Tests with nematodes, rotifers, and pollen

Nematodes were used for inducing the formation of trapping devices in pure culture: either *Acrobeloides maximus* or unidentified nematodes which were isolated from manure, from a contaminated fungal culture, or from a dead xeric trunk of *Ulmus minor* from Spain; in each case some individuals were transferred on agar cultures of ca. 30 species of *Orbilia* and *Hyalorbilia polypori*.

We used individuals of bdelloid rotifers, an unidentified species from dead xeric branches of *Cercocarpus ledifolius* from Navajo Loop Trail, USA, and *Macrotrachela quadricornifera*. The latter was cultivated in deionized water and fed with powdered pellets of goldfish food, according to instructions of M. Caprioli (pers. comm.), who provided us with this species. Some drops of a suspension of this rotifer were given to each of the tested cultures in order to induce trapping organs. Individuals of the unidentified bdelloid rotifer were picked off and given directly to *Orbilia* cultures, and for control also to uninoculated agar plates in order to see whether they might be infected already on their natural substrate.

Fresh pollen grains of *Sambucus nigra* and *Corylus avellana* were added to our cultures in order to observe whether the fungal mycelium invades them. Pollen grains were harvested by wrapping their inflorescences in aluminium foil for a few days. They were placed with a sterilized spatula into sterile distilled water. Some drops of this suspension were given with a sterile pipette directly on the mycelium. The mycelia were cultured on water agar, and inoculated 2 or 4 weeks prior to treating with pollen grains.

Molecular methods

Sequences were gained from pure cultures or dried apothecia. In the latter case, contaminations were frequent, and particularly here sequences were cautiously controlled with the chromatograms. Specimens older than about 5–10 years often failed, and only exceptionally a sequence of a desiccation-sensitive species was successful after 16–20 years. Our methods of rDNA isolation and sequencing at the National Natural History Museum in Luxembourg are explained in Baral et al. (2017a). For the methods used by G. Hagedorn see Hagedorn & Scholler (1999). An incomplete survey of the primers used in the different laboratories involved in this study are listed in Tab. 1. Their location in the rDNA is shown in the example of *Orbilia xanthostigma* (Tab. S1).

Searches for similar sequences were done in GenBank (BLAST, https://www.ncbi.nlm.nih.gov/genbank/) (Benson et al. 2017) and in CBS (http://www.westerdijkinstitute.nl/Collections/BioloMICSSequences.aspx, now under https://wi.knaw.nl/page/Pairwise_alignment). Searches for short motifs of ~15–30 nt length were only possible in GenBank because in CBS a minimum of 100 nt was required. BLAST (blastn) searches were done separately for ITS1-5.8S-ITS2 (by removing adjacent parts of SSU and LSU), LSU D1–D2, SSU V8–V9, or the S1506 intron, but also for other regions of SSU and LSU. Queries for shorter regions such as ITS1, ITS2, 5.8S, D1, D2 were done in some cases.

Molecular phylogenetic analyses. All phylogenetic analyses were done with the freeware program MEGA6 or 7 (Molecular Evolutionary Genetics Analysis) available from http://www.megasoftware.net/, see also Kumar et al. 2016, https://www.megasoftware.net/pdfs/KumarStecher16.pdf), with which also the best nucleotide substitution model was determined. Datasets of sequences were curated and annotated in Microsoft Word. Sequences were aligned using Muscle (integrated in MEGA) or in difficult cases with the online version of MAFFT (https://mafft.cbrc.jp/alignment/server/index.html), generally followed by a manual sorting according to the phylogenetic similarity and a manual adjustment in order to minimize distances between closely related species. Ambiguously aligned sites in the ITS1 and ITS2 region were not excluded from the analysis.

Each rDNA marker region (gene locus) was individually subjected to analysis in order to assess gene congruence, but combined analyses of two or three regions were also often done. The following regions were used: partial SSU (V8–V9: 362 nt, rarely V1–V5: 1057 nt), entire ITS (ITS1-5.8S-ITS2: ~500–550 nt), LSU (D1–D2: ~635 nt, rarely D1–D3: ~830 nt or D1–D6: ~1420 nt). The mentioned regions of the small and large ribosomal subunit are in this work briefly referred to as SSU and LSU, although 'partial SSU' or 'partial LSU' would be more correct as they only represent a small part of the entire SSU (V1–V9) and LSU (D1–D12). The frequent S1506 intron at the 3'-end of SSU was phylogenetically analysed whenever it occurred in more than a few species of the given group, but never in combination with other regions. It was obtained with the primers ITS5, ITS1-F, or SF16a, while being missed with the primer ITS1, which was used in sequences generated early in this study.

Table 1. Primers for the rDNA used in this study by Gregor Hagedorn (GH), Eric Kuhnert (EK), Guy Marson (GM), and Michael Weiß (MW), including some other primers. The approximate gene region obtained by the respective primer is indicated (for the location of regions and primers in rDNA see Fig. 112 and Tab. S1). For primers running in reverse direction ('Rev'), the forward version ('Fwd') is given in the subsequent line to permit localization in single sequences or alignments (in case the forward version is inofficial and unnamed it is given in brackets). Primers can be found, e. g., in the following lists: https://nature.berkeley.edu/brunslab/tour/primers.html, https://sites.duke.edu/vilgalyslab/rdna_primers_for_fungi/, http://lutzonilab.org/nuclear-ribosomal-dna/. Some minor deviations among authors can sometimes be found. Nucleotides deviating between *Orbiliomycetes* and other classes are given in small font. * = personally designed primer, † = according to AFTOL (a variant with GGG instead of GGGG does not fit *Orbiliomycetes* and various other fungi), # = primer includes position of S1506 intron, § = primer includes position of L2449 intron (therefore primers # and § do not work when the strain possesses the intron). Corresponding parts of primers are highlighted in blue; r.c. = reverse complement.

Abbreviation	Direction	Primer	Approximate rDNA region	Reference	Used by
SR1R	Fwd	TACCTGGTTGATtCTGC	SSU V1–V3	Vilgalys & Hester 1990	GM
SR3R*	Fwd	GCCCTATCAACTTTCGATGG	SSU V3–V4	this study	GM
SR1	Rev	ATTACCGCGGCTGCT	SSU V1–V3	Vilgalys unpubl.	
SR7	Rev	GTTCAACTACGAGCTTTTTAA	SSU V1–V3	Vilgalys unpubl.	GM
SR7R	Fwd	TTAAAAAGCTCGTAGTTGAAC	SSU V4–V6	Vilgalys unpubl.	
NS3 (SR1 r.c.)	Fwd Fwd	GCAAGTCTGGTGCCAGCAGCCGCGG (AGCAGCCGCGGTAAT)	SSU V4–V6	White et. al. 1990	
SR5	Rev	GTGCCCTTCCGTCAATT	SSU V3–V5	Vilgalys unpubl.	GM
NS5 (SR5 r.c.)	Fwd Rev	AACTTAAAGGAATTGACGGAAG (AATTGACGGAAGGGCAC)	SSU V6–V8, S943	White et. al. 1990	GH, GM
NS23	Fwd	GACTCAACACGGGGAAACTC†	SSU V6–V9 (S1506)	Gargas & Taylor 1992	MW
SR2	Rev	CGGCCATGCACCACC	SSU V4–V6	Elwood et al. 1985	GM
SR2R*	Fwd	GGTGGTGCATGGCCG	SSU V7–V9, ITS1 (S1506)	this study	GM
NS6	Rev	GCATCACAGACCTGTTATTGCCTC	SSU V5–V7	White et al. 1990	GH
NS7 (= NS6 r.c.)	Fwd	GAGGCAATAACAGGTCTGTGATGC	SSU V8–V9, ITS (S1506)	White et al. 1990	GH
SF16a*	Fwd	TCGCTACTACCGATTGAATG	SSU V9, ITS (S1506)	this study	GM
ITS1-F	Fwd	CTTGGTCATTTAGAGGAAGTAA	ITS (S1506)	Gardes & Bruns 1993	GM, MW, EK
ITS5	Fwd	GGAAGTAAAAGTCGTAACAAGG	ITS (S1506)	White et al. 1990	GH
NS24	Rev Fwd	AAACCTTGTTACGACTTTTA# (TAAAAGTCGTAACAAGGTTT#)	SSU V7–V9 ITS	Gargas & Taylor 1992	MW
ITS1	Fwd	TCCGTAGGTGAACCTGCGG	ITS	White et al. 1990	GH, GM
5.8S	Rev	CGCTGCGTTCTTCATCG	ITS1, SSU V8–9 (S1506)	Vilgalys & Hester 1990	GM
5.8SR (≈ 5.8S r.c.)	Fwd	TCGATGAAGAACGCAGC	ITS2, LSU D1–D2	Vilgalys & Hester 1990	GM
Orb5.8s1F	Fwd	GCAGCGAAACGCGATAGT	(partial overlap with 5.8SR)	Smith & Jaffee 2009	Sm. & Jaffee
Orb5.8s3F	Fwd	GCATGTCTGTTTGAGCGTCAT	(includes GAGCGTC)	Smith & Jaffee 2009	Sm. & Jaffee
LR0R	Fwd	ACCCGCTGAACTTAAGC	LSU D1–D2	Vilgalys unpubl.	MW
ITS4 (ITS4 r.c.)	Rev Fwd	TCCTCCGCTTATTGATATGC (GCATATCAATAAGCGGAGGA)	ITS	White et al. 1990	GH, MW, EK
CTB6	Fwd	GCATATCAATAAGCGGAGG	LSU D1–D2	Garbelotto et al. 1997, White et al. 1990	
NL1	Fwd	GCATATCAATAAGCGGAGGAAAAG	D1–D2	O'Donnell 1993	GH
LR1	Rev Fwd	gGTTGGTTTCTTTTCCT (AGGAAAAGAAACCAACc)	ITS LSU D1–D2	Vilgalys & Hester 1990	GM
LR2	Fwd	ATGAAAAGCACTTTGAAA	LSU D2–D3	Vilgalys lab	
Orb28s2R	Rev Fwd	ACAACCATTAAGCCAGCATCC (GGATGCTGGCTTAATGGTTGT)	(upstream of LR3)	Smith & Jaffee 2009	Sm. & Jaffee
LR3 NL4 (NL4 r.c.)	Rev Rev Fwd	GGTCCGTGTTTCAAGAC GGTCCGTGTTTCAAGACGG (CCGTCTTGAAACACGGACC)	LSU D1–D2	Vilgalys & Hester 1990, O'Donnell 1993	GM/GH, MW
LR3R	Fwd	GTCTTGAAACACGGACC	LSU D3–D6	Vilgalys lab	GM
LR4	Fwd	CCAGAGGAAACTCTGGT	LSU D4–D7	Vilgalys lab	
LR5	Rev Fwd	ATCCTGAGGGAAACTTC (GAAGTTTCCCTCAGGAT)	LSU D1–D4 LSU D4–D7	Vilgalys & Hester 1990	GM
LR5g*	Fwd	GTTTTATGAGGTAAAGCGAATG	LSU D5–D7	this study	GM
LR6	Rev Fwd	CGCCAGTTCTGCTTACC (GGTAAGCAGAACTGGCG)	LSU D3–D5 LSU D6–D7	Vilgalys & Hester 1990	GM
LR17a*	Rev	GCTACTACCACCAAGATCTGC	LSU D3–D6	this study	GM
LR7R LR17b* (= LR17a r.c.)	Fwd Fwd	GCAGATCTTGGTGGTAGTAG CAGATCTTGGTGGTAGTAGCA	LSU D7–D8	Vilgalys & Hester 1990, this study	GM
LR8R	Fwd	AGCAGGTCTCCAAGGTG	LSU D8–D9 (L1921)	Vilgalys lab	GM
LR9	Rev	AGAGCACTGGGCAGAAA	LSU D7-D8	Vilgalys lab	
LR9R*	Fwd	TTTCTGCCCAGTGCTCT	LSU D9–D10	this study	GM
LR9-10a*	Fwd	CTTAAGGTAGCCAAATGCCT	LSU D9–D10	this study	GM
LR9-10b*	Rev Fwd	TTCTTTCCCCGCTGAT (ATCAGCGGGGAAAGAA)	LSU D7–D8 (L1921) D10	this study	GM
LR11	Rev Fwd	GCCAGTTATCCCTGTGGTAA§ (TTACCACAGGGATAACTGGC§)	LSU D9–D10 LSU D11–D12	Vilgalys lab	
LR11-14*	Fwd	TGTCGGCTCTTCCTATCAT	LSU D11–D12	this study	GM
LR20R	Fwd	GTGAGACAGGTTAGTTTTACCCT	LSU D11–D12	Vilgalys lab	GM
LR13*	Rev Fwd	TCAGCAGATCGTAACAACAA (TTGTTGTTACGATCTGCTGA)	LSU D11–D12 IGS1	this study	GM

For most analyses Maximum Likelihood (ML) was used, with the settings 'use all sites, nearest-neighbour-interchange, weak branch swap filter'. Neighbour joining (NJ) analyses were done on datasets with very few deviating nucleotides or in rare cases if important clades in the resulting tree received strong support under NJ but no support under ML, using the settings 'p-distance, uniform rates, pairwise deletion'. Branch support is given as maximum likelihood bootstrap percentages from 500 replicates, except for the large Phyls 5 and 7 with only 100 replicates, and S15 with 1000 replicates. Bootstrap values below 50 % are not shown in the trees. At or above 90 % the support was called strong, between 70 and 90 % medium, and between 50 and 70 % weak.

Numbering of nucleotide positions. Following Kim et al. (2006), nucleotide positions in the ITS1 were evaluated by starting after ATCATTA (3'-end of SSU), those in the 5.8S by starting with AAAACTTT (5'-end of 5.8S, in alignments of closely related species also after ATCATTA), those in the ITS2 by starting after GAGCGTC (3'-end of 5.8S), and those in the LSU by starting with TGACCT (5'-end of LSU). Positions in the frequently sequenced V8–V9 region of SSU were counted by starting with CCTTAGAT, a consistent motif adjacent to the NS7 primer downstream. Alternatively, counting was done across the entire ITS1-5.8S-ITS2 region in some cases.

For evaluating position numbers in alignments of conservative gene regions, gappy positions caused by rare inserts were excluded. Due to the rarity of inserts in the SSU V8–V9 (362 nt, starting after NS7) and 5.8S region (155 nt, including AAAACTTT and GAGCGTC), consistent position numbers across the entire *Orbiliomycetes* could be used for these regions. Also in the LSU inserts or omissions occur only infrequently, and the complete deletion of predominant gaps in an overall alignment resulted in invariable position numbers in the D1–D4 domain for all groups. Accordingly, the LR1 primer occurs at pos. 54–69, LR2 at 367–384, LR3 at 636–652, and LR4 at 832–848 (Tab. 1). In contrast to this numbering system, the position number, after which introns in SSU and LSU are named, follows an alignment with *Escherichia coli* (J01695, Gutell 1993).

Specific nucleotides and motifs. Nucleotide positions in different rDNA regions, which were found to be specific to species or groups of species, have been visually explored in MEGA 6 or 7 from alignments of entire datasets of a given genus or infrageneric group, which was sorted according to phylogenetic relationships.

Distance analyses were done with MEGA7 using the settings p-distances, transitions + transversions, uniform rates, pairwise deletion. Distances were mainly evaluated for the entire ITS region (ITS1-5.8S-ITS2, with exclusion of ATCATTA and TGACCT, see p. 18), sometimes also for one of its subregions. Distances were also evaluated for the partial LSU (D1–D2) and sometimes the partial SSU (V8–V9). Whenever the S1506 intron was present, distances were evaluated for this region by excluding the conserved motifs TCGTAACAAGGT and TTCCGTAGGTGAA of the adjacent SSU.

Because of high interspecific variation with numerous gaps in alignments of the ITS1/ITS2 and S1506 intron, distance analyses of these regions were done pairwise or in groups of about 3–5 species, whereas analyses of conserved regions (SSU, 5.8S, LSU) produce unequivocal alignments rare in gaps and allow to analyse large data sets in one matrix.

Abbreviations, Terminology

__General__: **ad int**. = *ad interim* (in the meantime), **aff**. = *affinis* (akin to, used for deviating collections which probably belong to distinct, undescribed species), **agg**. = species aggregate, collective species, **a.s.l**. = above sea level (altitude), **ca**. = *circa*, **cf**. = *conferatur* (compare, used for deviating though possibly conspecific collections), **comb**. **nov**. = *combinatio nova* (new combination), **d** = day(s), **depos**. = deposited, **diam**. = *diametro* (in diameter), **e.g**. = *exempli gratia* (for example), **emend**. = *emendavit* (amended, rectified), **erron**. = erroneously, **et al**. = *et alia* (and co-workers), **etc**. = *et cetera* (and so forth), **excl**. = excluding, **f**. = *forma* (form), **f./ff**. = *folio* (including the following page/s), **gen**. **nov**. = *genus novum* (new genus), **herb**. = herbarium, **hwy** = highway, **i.e**. = *id est* (that is, in other words), **id**. = *idem* (the same, the aforesaid), **ICN** = International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code, Turland et al. 2018), **in litt**. = *in litteris* (in correspondence), **in sched**. = *in schedula* (on herbarium label), **inc**. **sed**. = *incertae sedis*, **incl**. = including, **indet**. = *indeterminavit* (unidentified), **ined**. = *ineditus* (unpublished), **isol**. = isolated, **IVV** = www.in-vivo-veritas.de (link to drawings and photographs), **lat**. **diagn**. = Latin diagnosis, **l.c**. = *loco citato* (at the place cited), **max**. = maximal, **min**. = minimal, **min** = minute(s), **Mt**. = Mountain (or in French 'Mont'), **myr** = 1 million years, **no**. or **nr**. = number, **nom**. **cons**. = *nomen conservandum* (a name which was illegitimate or lacked priority when published but was later conserved), **nom**. **dub**. = *nomen dubium* (a name of unresolved identity), **nom**. **illegit**. = *nomen illegitimum* (a validly published name which is, nevertheless, in conflict with the Code, mostly a binomial which already exists as a homonym), **nom**. **inval**. = *nomen invalidum* (a name which did not meet the requirements of the Code when published), **nom**. **nov**. = *nomen novum* (a new name published in order to avoid an illegitimate combination, i.e., a homonym), **nom**. **nud**. = *nomen nudum* (a name published without a diagnosis), **nom**. **prov**. = *nomen provisorium* (a provisional name published without the intention to fulfil the rules of the Code), **nom**. **[utique] rej**. = *nomen [utique] rejiciendum* (a [by all means] rejected name in favour of a conserved name), **nom**. **sanct**. = *nomen sanctionatum* (a name having priority through acceptance in a sanctioning work), **OCI** = oil content index, **p.p**. = *pro parte* (for a part of the cited taxa or specimens), **p.p.maj**. = *pro parte majore* (for the greater part), **p.p.min**. = *pro parte minore* (for a smaller part), **phot**. = photographed, **pos**. = position, **Rd** = Road, **Rte**. = Route, **s**. = *sensu* (in the sense of), **s.auct**. = *sensu auctorum* (in the sense of authors), **s.l**. = *sensu lato* (in a broad sense), **s.n**. = *sine nomine* (without name), **s.str**. = *sensu stricto* (in a narrow sense), **sec** = second(s), **sect**. **nov**. = *sectio nova* (new section), **ser**. **nov**. = *series nova* (new series), **soc**. = associated with, **sp**. **nov**. = *species nova* (new species), **stat**. **nov**. = *status novus* (new rank) **subsp**. = *subspecies*, **var**. = *varietas* (variety), **viz**. = *videlicet* (namely), **vs**. = *versus* (against).

__Collection data__: **anam**. **apoth**. = anamorph grown out from ascocarp (at lid of Petri dish or rarely on agar), **anam**. **cult**. = anamorph obtained from ascospore isolate in pure culture, **anam**. **only** = only anamorph present on natural substrate, **anam**. **substr**. = anamorph from natural substrate in association with teleomorph, **apoth**. **cult**. = apothecia obtained in pure culture, **conid**. **isol**. = conidial isolate (pure culture gained from conidia or from substrate/soil), **doc**. **vid**. = *documentum vidimus* (microphotographs or drawings seen, rarely only descriptions, but no specimen studied), **ibid**. = *ibidem* (in the same place), **mol**. **extr**. = molecular (DNA) extract from soil, wood etc. (uncultured, without anamorph or teleomorph), **myc**. **only** = mycelium only, **non vid**. = *non vidimus* (no specimen and no images seen by us), **vid**. = vidit (seen), **#** = GPS number of G.M.'s collection site.

__Symbols__: ***** = living (viable) state, **†** = dead state, **ø** = no specimen preserved, **{}** = values in curled parenthesis refer to the number of collections that were examined, **~** = circa. After the host plant and the associated taxa the curled parenthesis contains the number of records with certain/uncertain identity. The arrow (→) is used between measurement values and indicates changes in development or direction: concerning the ascus size and the length of the pars sporifera it stands between moderate and full turgescence; concerning the apical thickening it stands between immature and mature asci; concerning spore body size it stands between mature and overmature spores, and concerning the thickness of the receptacle or the ectal excipulum it stands between lower and mid flanks or margin (if no arrow is present, the values refer to the first of the two cases).

Type specimens (in descriptions and phylogenetic analyses): **T** = type, **ET** = epitype, **NT** = neotype, **RefSpec** = reference specimen.

Mountants and Reagents: **CB$_a$** = aqueous Cotton blue (Methyl blue), **CB$_L$** = CB in lactic acid or lactophenol, **CR** = Congo red (aqueous), **CR$_{SDS}$** = CR with SDS, **CRB** = (Brilliant) Cresyl blue (aqueous), **CRB$_A$** = CRB slightly alkalinized by ~0.1% KOH or NH_4OH, **H_2O** = (tap) water, **HCl** = hydrochloric acid (~90%), **H_2SO_4** = sulphuric acid (1–60%), **IKI** = Lugol's solution of strong concentration (~1% I_2, 2% KI, in H_2O), **KOH** = potassium hydroxide ~3–5% (rarely 10–20%), **MLZ** = Melzer's Reagent (IKI + chloral hydrate 1:1), **NH_4OH** = ammonium hydroxide, **NR** = Neutral red (aqueous), **SDS** = sodium dodecyl sulfate, **TB** = Toluidine blue (aqueous), **PVA** = polyvinyl acetate. On the plates the sign for living state is generally omitted, and that for the dead state is omitted in lethal media such as CB$_L$, MLZ and KOH (the latter stands also for KOH+CR and KOH+IKI), **Réactif de Bailenger**: 0.05 g Crystal violet, 0.01 g Basic Fuchsin, 20 ccm 95% ethanol, 4 ccm phenol crystals, 100 ml H_2O.

Cytoplasmic inclusions: **LB** = lipid body (oil drop), **MC** = metachromatic body, **N** = nucleus, **SB** = spore body, **SCB** = KOH- and HCl-soluble (sensitive), refractive cytoplasmic body, **VB** = KOH- and HCl-soluble (sensitive), refractive vacuolar body, **WB** = Woronin body.

Iodine reactions: **RR** = red at both a high and low concentration of iodine (hemiamyloid), **RB** = red at a high, blue at a low iodine concentration (hemiamyloid), **BB** = blue at either concentration (euamyloid).

Microscopes: **LM** = light microscope, **TEM** = transmission electron microscope, **SEM** = scanning electron microscope, **DIC** = differential interference contrast.

Agar media: **CMA** cornmeal agar (CMA:2 = with half the concentration of undiluted CMA), **MEA** malt extract agar, **PDA** = potato-dextrose agar, **WA** water agar.

Molecular terms: **BLAST** = Basic Local Alignment Search Tool (**blastn** compares a sequence against a nucleotide database, freely available in GenBank); **gene regions** [see also Tab. 1 for primer names]: **ITS** = internal transcribed spacer region of rDNA (composed of three subregions: ITS1, 5.8S, ITS2), **LSU** (or **28S**) = large subunit of rDNA (including twelve domains: D1–D12), **nt**/bp = nucleotide(s)/basepair(s), **rDNA** = ribosomal DNA, **sq**. = sequence (usually rDNA), **SSU** (or **18S**) = small subunit of rDNA (composed of nine regions V1–V9), **nuSSU** = nuclear SSU, **mtSSU** = mitochondrial SSU; **S1506** = group I intron at position 1506 of SSU, **L1921** = group I intron at position 1921 of LSU (in reference to *Escherichia coli* J01695); protein-coding genes: ***RPB1/2*** = largest subunits B1/B2 of RNA polymerase II, ***TEF1*** = translation elongation factor EF-1α, ***MAD1*** = mitotic checkpoint family protein, ***MCM7*** = mini-chromosome maintenance proteins (DNA replication licensing factor), ***TUBB*** = β-tubulin; **phylogenetic analysis**: **ML** = maximum likelihood, **NJ** = neighbour joining, **JC** = Jukes-Cantor, **T3** = Tamura 3-parameter model, **TN** = Tamura Nei model, **K2** = Kimura 2-parameter model, **GTR** = General Time Reversible, **G** = gamma distributed, **I** = with invariant sites.

Repositories of taxonomic and molecular data: **CBS** (http://www.westerdijkinstitute.nl/Collections/BioloMICSSequences.aspx), **GenBank** (NCBI, https://www.ncbi.nlm.nih.gov/genbank/), **MycoBank** (**MB**, http://www.mycobank.org/), **Index & Species Fungorum** (http://www.indexfungorum.org, http://www.speciesfungorum.org), **NBRC** (http://www.nbrc.nite.go.jp/NBRC2/NBRCDispSearchServlet?lang=en), **UNITE** (**UDB**) (https://unite.ut.ee/, https://plutof.ut.ee/#/clipboard).

Ecological terms: **xeric/hygric** = substrate periodically dry/ permanently moist, **xero-/hygrobiotic** = ascomata or conidiophores/ conidiomata drought-tolerant/-intolerant; **thermotypes** (in Europe): **eumediterranean** zone comprising oro- (Or), supra- (Sm), meso- (Mm), thermo- (Tm), and inframediterranean (Im); **submediterranean** zone comprising orosub- (Osm), suprasub- (Ssm), meso- (Msm), and thermosubmediterranean (Tsm); **temperate** zone comprising cryoro- (Ct), oro- (Ot), supra- (St), meso- (Mt), and thermotemperate (Tt); **hemiboreal** zone (Hb); **boreal** zone comprising cryoro- (Cr), oro- (Ob), supra- (Sb), meso- (Mb) and thermoboreal (Tb); **ombrotypes**: precipitation > evaporation: humid (winter- to somewhat summer-dry); precipitation < evaporation: subhumid (winter-dry or not), semihumid (summer-dry), semiarid, arid.

Acronyms of institutional herbaria (abbreviated according to Index Herbariorum, http://sweetgum.nybg.org/ih/, * = not included in Index Herbariorum): AH (Alcalá de Henares, Spain), ARAN (San Sebastián, Spain), ARSEF (Robert W. Holley Center for Agriculture & Health, USDA ARS, Ithaca, USA), B (Berlin, Germany), BAFC (Buenos Aires, Argentina), BAK (Baku, Azerbaijan), BP (Budapest, Hungary), BPI (Beltsville, USA), BR (Meise, Belgium), BRA (Bratislava, Slovakia), BRI (Brisbane, Australia), BSIP (Honiara, Solomon Islands), C (Copenhagen, Denmark), CAS (California Academy of Sciences, USA), CBCD* (College of Biology and Chemistry, Dali University, China), CMMF (Montréal, Canada), CNF (Croatian Mycological Society, Zagreb, Croatia), CO (Concarneau, France), CUP (Cornell University, Ithaca, USA), CWU (Kharkiv, Ukraine), DAOM (Ottawa, Canada), DMS* (Danish Mycological Society), FFPRI* (Forestry and Forest Research Products Institute, Japan), FG* (Fruška Gora National Park, Vojvodina, Serbia), FH (Farlow Herbarium, Cambridge, USA), FLAS (Gainesville, Florida, USA), FR (Frankfurt, Germany), G (Genève, Switzerland), GENT (Gent, Belgium), GH (Harvard University, Cambridge, USA), GJO (Joanneum, Graz, Austria), GXU* = (University of Nanning, Guangxi, China), GZU (Karl-Franzens-University, Graz, Austria), H (Helsinki, Finland), HBG (Hamburg, Germany), HKU (Hong Kong, China), HMAS (Chinese Academy of Sciences, Beijing, China), HR (Hradec Králové, Czechia), HT* (Kunming, Yunnan, China), IMI (Egham, England), IMS (Chapel Hill, North Carolina, USA), JA-CUSSTA (Junta de Andalucía, La Trufa, Zagrilla, Priego de Córdoba, Spain), JE (Jena, Germany), JOE (Joensuu, Finland), K(M) (Kew, London, England), KMU* (Karamanoğlu Mehmetbey University, Karaman, Turkey), L (Leiden, Netherlands), LE (St. Petersburg, Russia), LPS (Buenos Aires, Argentina), LUX (Luxembourg [J. Feltgen]), LZ (Leipzig, Germany), M (Botanische Staatssammlung München, Germany), MA (Madrid, Spain), MAMU* (Mykologischer Arbeitskreis München Umland), MEL (Melbourne, Australia), MFC* (Matsushima Fungus Collection, Japan), MFLU (Mae Fah Luang University, Thailand), MPU (Montpellier, France), MSTR (Münster, Germany), NMLU (Luzern, Switzerland), NY (New York, USA), O (Oslo, Norway), PAD (Padova, Italy), PC (Paris, France), PDD (Auckland, New Zealand), PH (Philadelphia, USA), PRM (Praha, Czechia), PUL (Purdue University, Indiana, USA), REG (Regensburg, Germany), RO (Roma, Italy), S (Stockholm, Sweden), SBP* (Herbarium of Laboratory for Microorganisms, Dali, China), STU (Stuttgart, Germany), TAAM (Tartu, Estonia), TFC (La Laguna, Tenerife, Spain), TMUE* (Taipei, Taiwan), TNM (Taichung, Taiwan), TNS (Tsukuba, Japan), TRL* (Tsukuba Research Laboratories, Japan, transferred to TNS), TU (Tartu, Estonia), UBC (British Columbia, Vancouver), UME (Umeå, Sweden), UPS (Uppsala, Sweden), W (Naturhistorisches Museum Wien, Austria), WU (University Wien, Austria), YMFT* (Kunming, Yunnan, China).

Culture collections: APCC = Aquatic Phycomycete Culture Collection (Reading, England), AS = Academia Sinica (later changed to CGMCC), ATCC = American Type Culture Collection (Virginia, USA), BBA = Biologischen Bundesanstalt für Land- und Forstwirtschaft (Braunschweig, Germany), BCRC = Bioresource Collection and Research Center (Taiwan), CBS = Centraalbureau foor Schimmelcultures, now: Westerdijk Fungal Biodiversity Institute (Utrecht, Netherlands), CCRC = Culture Collection and Research Center (Hsinchu, Taiwan), CCT = Coleção de Culturas Tropical (Brazil), CGMCC = China General Microbiological Cultural Collection Center (Beijing, China), GA/TF = University of Georgia (Tifton, USA), IFM = Medical Mycology Research Center, Chiba University (Chiba, Japan), IFO = Institute for Fermentation (part of NBRC), IMI = CABI Bioscience UK Centre (U.K., England, Egham), MUCL = Université Catholique de Louvain (Belgium, Louvain-la-Neuve), NBRC = National Institute of Technology and Evaluation (Osaka, Japan), NHL = National Institute of Hygienic Sciences (Tokyo, Japan), NRRL = Northern Regional Research Center (Peoria, USA), SBUG = Biological department, University of Greifswald (Germany), SQU = Sultan Qaboos University (Oman), UCR = University of California, Culture Collection of Nematode-Destroying Fungi (Riverside, USA), USDA-ARS = United States Department of Agriculture, Agricultural Research Service (USA), VKM = All-Russian Collection of Microorganisms, Russian Academy of Sciences (Russia), WAC = Plant Research Division Culture Collection, Western Australian Department of Agriculture, (Australia), YMF = Key Laboratory of Industrial Microbiology and Fermentation Technology of Yunnan (Kunming, China), YNUCC = Yunnan University Culture Collection etc.

Exsiccatae: FFE = Karsten, Fungi Fenn. Exs. (Fungi Fenniae exsiccati), P.A. Karsten (1861–1870); FSE = Fungi Sel. Exs. (Fungi selecti exsiccati), O. Jaap (1903–1923); MFE = Triebel, Microf. exs. (Microfungi exsiccati), D. Triebel (1991–); NAF = Ellis, N. Amer. Fungi (North American Fungi), J.B. Ellis (1878–1885); Rehm Ascomyc. (Ascomyceten), H. Rehm (1870–1914).

Private herbaria or culture isolates (an 'ex' before the private herbarium means that the entire specimen was transferred to another herbarium): A.G. = Andreas Gminder (Jena, Germany), A.Ga. = Alain Gardiennet (Véronnes, France), A.K. = A. Kujawa (Poland), A.Ka. = Attila Koszka (Hungary), A.Ky. = Abdullah Kaya (Karamanoğlu Mehmetbey Univ., Turkey, in KMU), A.P. = Adam Polhorský (Bratislava Univ., Slovakia), A.R. = Annemarthe Rubner (Karlsruhe, Germany), B.C. = Bernard Clesse (Fagnolle, Belgium), B.C.P. = B.C. Paulus (New Zealand), B.Ca. = Brigitte Capoen (Penvénan, France), B.D. = Bernard Declercq (Stekene, Belgium), B.G. = Bernt Grauwinkel (Bremen, Germany), B.H. = Bernd Hanff (Coburg, Germany), B.L. = Bin Liu (Nanning Univ., China), B.P. = Branislav Perić (Podgorica, Montenegro), B.S.I. = Beatrice Senn-Irlet (Birmensdorf Res. Inst., Switzerland), B.W. = Björn Wergen (Hornberg, Germany), C.C. = C.J. Chen (Taiwan), C.L.D. = C.L. Duddington (†, London, UK), C.L.L. = Christian Lechat (Villiers-en-Bois, France), C.R. = Claude Roux (Mirabeau, France), C.Y. = Chris Yeates (Huddersfield, Great Britain), D.H.P. = D.H. Pfister (Harvard Univ., USA, in FH), D.M. = Donát Magyar (Budapest, Hungary), E.B. = Edward Batten (†, Wenhaston, Great Britain, in K), E.C. = Erio Camporesi (Emilia Romagna, Italy), E.R.D. = Enrique Rubio Domínguez (Avilés, Spain), E.S. = Elisabeth Stöckli (Rüschegg, Switzerland), E.S.P. = Eugene S. Popov (St. Petersburg Univ., Russia), F.B. = François Bartholomeeusen (Turnhout, Belgium), F.G.A. = Fernando García Alonso (Alicante, Spain), F.J.B. = Francisco Javier Balda (Pamplona, Spain), F.O. = Franz Oberwinkler (†, Tübingen Univ., Germany), G.B. = George L. Barron (Ontario, Canada), G.F. = Gernot Friebes (Graz, Austria), G.G. = Guy Garcia (Montpellier, France), G.K. = Gerhard Kost (Marburg Univ., Germany), G.M. = Guy Marson (Luxembourg), G.My. = Gilbert Moyne (Besançon, France), G.R. = Gerhard Rambold (Bayreuth Univ., Germany), G.v.R. = Gunther Van Ryckegem (Brussels, Belgium), G.V. = Gerard Verkley (CBS, Utrecht, Netherlands), H.B. = H.O. Baral (Tübingen, Germany), H.E. = Heinz Engel (†, Coburg, Germany), H.H. = Hans Haas (†, Schnait, Germany, in STU), H.Ho. = Håkon Holien (Nord-Trøndelag, Norway), H.S. = Helmuth Schmid (Eching, Germany), H.Y.S. = Hong-yan Su (Dali Univ., China), H.V. = Hermann Voglmayr (Wien Univ., Austria), H.W. = Howard Williams (Carlton-In-Lindrick, Great Britain), I.A. = Iglaz Akata (Ankara Univ., Turkey), I.M. = Irina I. Morozova (Kharkiv Univ., Ukraine), I.W. = Ingo Wagner (Sonneberg, Germany), J.A.C. = Jerry A. Cooper (Lincoln, New Zealand), J.B. = Javier Bometón (Terrassa, Spain), J.C. = Jules Cimon (Québec, Canada), J.C.M. = Jean-Claude Malaval (Rouen, France), J.Ca. = Joseba Castillo (Cambrils, Spain), J.F. = Jacques Fournier (Rimont, France), J.G. = Jörg Gilgen (Burgdorf, Switzerland), J.H.P. = Jens H. Petersen (Tirstrup, Denmark), J.K. = Jan Kohlmeyer (North Carolina Univ., USA), J.L.C. = Jean-Louis Cheype (Passy, France), J.M. = J. Mornand (†, Maillé, France), J.N. = Jan Gert Borgergren Nielsen (Denmark), J.O. = Javier Ormad (Valencia, Spain), J.P.P. = Jean-Paul Priou (La Gacilly, France), J.S. = J. de Sloover (Louvain-la-Neuve, Belgium), J.T.P. = J. Terry Palmer (†, Runcorn, UK), J.W.G. = Jian-Wei Guo (Kunming Univ., China), K.H. = Kaare Homble (Nannestad, Norway), L.B. = Ludwig Beenken (ETH Birmersdorf Res. Inst., Switzerland), L.G. = Lucien Gauthier (Cepoy, France), L.K. = Lothar G. Krieglsteiner (Spraitbach, Germany, in STU), L.Q.F. = Luis Quijada (Univ. La Laguna, Tenerife & Harvard, USA), L.R. = Lucien Rommelaars (Tilburg, Netherlands), M.A.R. = Miguel Ángel Ribes (Madrid, Spain), M.B. = Martin Bemmann (Ziegelhausen, Germany), M.E. = Matthias Eckel (†, Taura, Germany), M.H. = Michel Hairaud (Poivendre de Marigny, France), M.L. = Marc Langlois (Isles-sur-Suippe, France), M.M. = Matthias Mann (Wien, Austria), M.H.M. = MingHe Mo (Kunming Univ., China), M.P. = Marja Pennanen (Joensuu, Finland), M.P.P. = M.P. Peach (Great Britain), M.R. = Matthias Reul (Marktredwitz, Germany), M.W. = Mei Lee Wu (Taipei Univ., Taiwan), M.Wi. = Markus Wilhelm (Zürich, Switzerland), N.A. = Nick Aplin (Crawley, Sussex), N.V. = Nicolas Van Vooren (Lyon, France), O.C. = Oluna Ceska (Victoria, Canada, in UBC), P.B. = P. Blank (†, Schaffhausen, Switzerland), P.D. = Peter Döbbeler (München Herbarium, Germany), P.K. = Peter Karasch (München, Germany), P.P. = Piotr Perz (Kłodzko, Poland), P.R.J. = Peter Johnston (Auckland Univ., New Zealand), P.T. = Peter Thompson (Wolverhampton, Great Britain), P.Y.C. = Pierre Ives Courio (Rédené, France), R.B. = Rafael Blasco (Zaragoza, Spain), R.I. = Ricardo Ibarretxe (Galdakao, Spain), R.K. = Roland Kirschner (Taipei Univ., Taiwan), R.M. = Roman De Marchi (Winterthur, Switzerland), R.P. = René Pacaud (La Roche-sur-Yon, France), R.S. = René Klaus Schumacher (Fürstenwalde, Germany), R.Tü. = Roman Türk (Austria), R.T.L. = Raúl Tena (Teruel, Spain), S.G. = Susana García (Larrasoaña, Spain), S.H. = Stip Helleman (Boxmeer, Netherlands), S.M.D. = Sylvia M. Dixon (†, UK), S.T. = Salvador Tello Mora (Valdepeñas de Jaén, Spain), T.A. = Tülin Askun (Balıkesir Univ., Turkey), T.H.D. = Tove H. Dahl (Arendal, Norway), T.L. = Thomas Læssøe (København Univ., Denmark), T.R. = Torsten Richter (Rehna, Germany), T.R.L. Till Reinhard Lohmeyer (Taching am See, Germany), U.G. = Ueli Graf (Hochdorf, Switzerland), U.L. = Uwe Lindemann (Berlin, Germany), U.R. = Urs Roffler (Switzerland), U.S. = Unto Söderholm (Tampere, Finland), V.H. = Viktorie Halasů (Olomouc, Czechia), V.K. = Volker Kummer (Potsdam Univ., Brandenburg), V.R. = V. Rodriguez (Harvard Univ., USA), W.D. = Wolfgang Dämon (St. Georgen, Austria), W.J. = Walter M. Jaklitsch (Wien, Austria), W.H. = Wolfgang Huth (Naumburg, Germany), W.H.H. = WaiHong Ho (Hong Kong Univ., China), W.M. = Willibald Maurer (Graz, Austria), W.Y.Z. = WenYing Zhuang (Beijing Univ., China), X.J. = XianZhi Jiang (Beijing Univ., China), X.Z.L. = Xing-Zhong Liu (Beijing Univ., China), Y.Z. = Ying Zhang (Kunming Univ., China), Z.F.Y. = ZeFen Yu (Kunming Univ., China).

The employed terminology of cell inclusions follows Baral (1992: 356f.), that of ascus structures Verkley (1992: 5), with the exception that the 'ecto-' and 'endotunica' are preferred over outer and inner layer, and 'dome' is used as an equivalent of 'apical thickening'. We have dispensed with an alphabetical order of the species in order to facilitate comparison of similar taxa, and also the genera, subgenera, sections, and series are sorted according to phylogenetic considerations. In addition to Appendix 3, a hidden hash (#) tag search enables location of the main page of a taxon by adding it ahead of the generic, infrageneric, or specific epithet, for instance, '*#Orbilia*', '*#Hemiorbilia*', or '*#vinosa*'.

Taxa concepts, naming of taxa

Species delimitation. In many of the taxa described as new in the present monograph, but also in some of those described by earlier authors, only a single specimen or a few collections were available for study. As a consequence, little is known about morphological variability and delimitation against closely related taxa. Much future work will be necessary to settle the taxonomic status and ecological range of all these poorly known taxa. Especially when dealing with extra-European collections, problems with the dichotomous key will certainly arise, which indicate that the concerned taxa are either missing in the monograph, or their variation not fully explored.

It is a common experience in morphological taxonomy of fungi that a species can only be defined and delimited on the basis of detailed microscopic data gained from a series of collections. Describing new taxa based on single collections is generally problematic, nevertheless, we decided to do so in a number of cases, because describing such collections in detail without attaching a name to them would perhaps be even more unfavourable for the user. Those collections which deviate from the established taxa only in some minor points are usually only mentioned under that taxon which appears to be most closely related, but they are not included in a description, nor are they proposed as a separate new species.

Problems in species delimitation occurred in almost every group of *Orbiliomycetes*. Considerations on how to define a species depended on our results about the consistency and reliability of both persistent and vital characters. Although the huge number of species recognized here suggests a narrow species concept at first glance, we have actually tended to prefer a wide concept whenever no clear limits were found. Quite a large number of cases could not sharply be resolved due to a remarkable variability in micromorphology among the living populations examined. Nevertheless, we decided to distinguish different taxa whenever the differences were strong enough, even if intermediate populations appear to prohibit such a split. Such problems were particularly encountered in section *Habrostictis*, and in *Hyalorbilia*. Groups of species often appeared to be connected by intermediate populations and suggest interbreeding between them. Especially in *Hyalorbilia* such intermediate populations appeared to occur between almost each of the morphologically similar taxa. Many of these variants observed by us might represent different ecotypes which have evolved under distinct geographical and environmental circumstances and, therefore, need not be separated at the species level. On the other hand, cultural and/or molecular results sometimes supported an even stronger split into different taxa, although distinguishing characteristics of the teleomorph or anamorph could hardly be found.

In some cases the observed variation occurred only between geographically separate collections. We then excluded one of the two groups from the description of the taxon. Such deviations might indicate a separate species, but we decided to describe a separate taxon only if either the deviation was strong enough, or the deviation was constant enough among the collections studied.

Until molecular data became available, we were unable to solve the question as to whether differences in spore numbers need distinction at the species level in every case. One out of many examples is series *Microspermae*, comprising four taxa around *Orbilia euonymi* which differ mainly in four different spore numbers (see p. 57). Their molecular data strongly support their distinction at the species level. But virtually all morphological characteristics of *Orbiliomycetes*, including spore numbers, are subjected to a more or less high extent of variation, and this variation may occur within an apothecium, a population, or between different collections that are considered to belong to a single species. Such variable characteristics comprise also ascus size, thickness of apical thickenings, shape and size of ascospores and SBs, shape and width of paraphysis apices, presence of SCBs, presence and length of glassy processes, rate of gelatinization of excipular cells, etc.

Examples of closely related and, as molecular data were not available for every species, in some cases only tentatively separated *Orbilia* species, which differ more or less in ascospore shape and size, are: *O. ocellata* – *O. lentiformis* – *O. foliicola*, *O. obtusispora* – *O. trapeziformis* – *O. subtrapeziformis* – *O. filiformis*, *O. ovoidea* – *O. subovoidea*, *O. macrotrapeziformis* – *O. pyrenaica* – *O. curvatitrapeziformis* – *O. edulis* – *O. flexisoma* – *O. idahoensis*, *O. myriourosperma* – *O. sedonensis*.

The genus *Hyalorbilia* provides a further impressive example. The following series of taxa are accepted as different species in the present study, but are more or less unsharply delimited from each other (see Pl. 58): *H. citrina* – *H. japonica* – *H. inflatula* – *H. juliae* – *H. berberidis* – *H. arcuata*. Further species are connected to this series: e. g., *H. fomentarii* is only tentatively separated from both *H. juliae* and *H. berberidis*, the series *H. andina* – *H. polypori* – *H. texensis* appears not sharply delimited from *H. inflatula* and *H. juliae*, and another series connected to *H. inflatula* is represented by *H. fagi* – *H. tortuosa* – *H. helicospora* – *H. sibirica*, with a problematic connection between *H. tortuosa* and *H. citrina*.

For various of these taxa we could study many collections and were thus able to explore their variability. When taking only those populations into consideration which possessed the typical morphologies, the specific differences are usually very clear and the existence of distinct species appeared unquestionable. But a few specimens were intermediate, and it has often remained uncertain to which taxon they belong.

Closely related taxa that deviated in just one or two features are sometimes found growing intermingled on the same piece of substrate. Their macroscopical similarity and mixed growth give the impression of a single species that possesses some genetic variability, but the features of each phenotype generally showed little variation. The existence of different though very similar species is supported by the fact that also very different, distantly related *Orbilia* species frequently grow intermingled, and the species composition of mixed populations varies from collection to collection. Therefore, we came to the conclusion that an intimate occurrence of apothecia does not provide any evidence for a close genetic relationship between populations, and a separation into different taxa was usually unavoidable.

Some of the species have earlier been thought to be well characterized, but later proved to represent an assemblage of different taxa that are difficult to distinguish. For example, the cicrumscription of the very frequent *Orbilia vinosa* s.l. turned out to be heterogeneous within Europe. Collections from orotemperate to orosubmediterranean regions now separated as *O. subvinosa* differs from typical *O. vinosa* with trinacrium-like conidia in higher-branched, dwayaangam-like ones, and this distinction is genetically supported, although in the teleomorph they differ only gradually in some minor details. In contrast to this, a similar and likewise very frequent European species with a very similar trinacrium-like anamorph, *O. aprilis*, which was synonymised with *O. vinosa* by Svrček (1954), was found to represent an easily recognizable widespread taxon with much shorter ascospores and SBs. The sharp separation between *O. vinosa* and *O. aprilis* was observed in a total of 366 (*O. vinosa*) and 228 (*O. aprilis*) collections reported here. A high molecular distance between *O. aprilis* and *O. vinosa* s.l. confirms the independence of *O. aprilis*.

More or less distinctive anamorphs were obtained in pure culture of certain species, particularly of sections *Helicoon* and *Arthrobotrys*, in cases when the teleomorphs hardly differed. Reverse cases of morphologically distinctive teleomorphs and hardly distinguishable anamorphs frequently occur mainly in sections *Habrostictis*, *Aurantiorubrae*, and *Hemiorbilia* of the genus of *Orbilia*, but also in *Hyalorbilia*. In these groups a culture with the anamorph can hardly be identified at the species level by morphology alone if the teleomorph is not present. Molecular studies usually indicate that in both cases the observed morphological characteristics are correlated with differences in their rDNA.

The *Orbiliomycetes* seem to represent a group in which species extinction during evolution comparatively rarely occurred. Most sections and series of *Orbilia* are rich in species and not easy to separate from each other. In fact, the different character states seem to occur in nearly all imaginable combinations. We have repeatedly discovered missing links that form, for instance, a connection between a 64-spored and an 8-spored taxon, or between a species with long spore tails and another with very short tails. The spectrum of character states and their combination perpetually increased with every newly detected species. However, an earlier hypothesis turned out to be erroneous, which considered slight differences between closely related taxa to be due to comparatively few changes in the genome. On the contrary, rather high differences in parts of the rDNA were often observed between closely related taxa.

Similar problems are known in some helotialean genera, such as *Mollisia* (Fr.) P. Karst. (Greenleaf & Korf 1980, 'an excercise in frustration') or *Tympanis* Tode (Ouellette & Pirozynski 1974 citing Seaver 1953: 'there are about as many interpretations of the genus as there are workers on the group'). Another example is *Unguiculariopsis* Rehm, an apparently large genus of xerobiotic taxa which are much more common than currently believed. In a majority of collections of *Unguiculariopsis* which we have studied, a convincing morphological species concept was very difficult to acquire, and many of our specimens could not be identified with Zhuang's (1988) monograph.

ITS Barcode. Molecular data offer a valuable additional tool to clarify species concepts, but they need to be handled with care. Apart from the frequent problem of contaminant DNA (Gams et al. 2012b), some species are highly constant while others strongly vary in the ITS rDNA, the currently used fungal barcode. For this gene region, no 'stringent upper limit for intraspecific variability, such as the canonical 3% threshold, appears to be applicable with the desired outcome throughout the fungi' (Nilsson et al. 2008). Jeewon et al. (2016) recommended 'for practical purposes' a threshold of 1.5% as tentatively indicative for a new species, but Nilsson et al. (l.c.) showed in their tab. 1 that 20% of the tested 4185 fungal species varied more than 3% in this gene region. Some species of some groups of fungi, e.g. *Dothideomycetes*, *Eurotiomycetes*, or *Sordariomycetes*, are not clearly resolved at the species level using ITS rDNA, in which case protein-coding genes could be used as an alternative barcode (Hongsanan et al. 2018).

Within *Orbiliomycetes* a comparatively high interspecific distance is observed in the ITS rDNA, which generally ranges at ca. 4–16% among members of a subgroup of a series, although their infraspecific variation is often very low (Tab. S2). An unexpectedly high ITS distance of 16–16.5% was noted in three species pairs, in which virtually no or only slight morphological differences could be seen, apart from a different apothecial colour in case a teleomorph is known: (1) between *O. xanthostigma* s.str. and *O. leucostigma* s.str., which were considered to be conspecific by most authors; (2) between *O. tremulae* and *Dicranidion inaequale*, which share a morphologically identical anamorph; and (3) between *O. cejpii* s.str. on *Salix* and *Sorbus* and *O.* cf. *cejpii* on *Fagus*, which show only slight deviations in apothecial colour and ascospore characteristics.

Despite such high distances between closely related taxa, an ITS variation above 1.5–3% could already be taken as a hint that different species are involved, particularly in cases of highly constant subclades. However, we never found distances in this range to be coupled with clear morphological differences, so we preferred to apply a broad species concept in such a case. But even ITS distances below 1.5% may be disputable. For instance, variation of 2–6 nt (0.4–1.1%) and 3 gaps is observed within *O. aurantiorubra* between samples on *Fabaceae* and non-fabaceous hosts (*Salix*, *Ulmus*, and *Rhamnus*) (Tab. 69, Tab. S2, Phyl. 14). A tendency to shorter spores in the *Fabaceae* group appears to support distinction, but sharp separation of the many collections of *O. aurantiorubra* based on spore length proved impossible, and the affiliation of rare hosts (*Acer*, *Euphorbia*, *Frangula*, *Fraxinus*, *Prunus*) remained unclear because of absent DNA data. The single sequence of a *Frangula* sample (H.B. 7278, with long spores) refers it to the *Salix-Ulmus* clade, but another *Frangula* sample (J.P.P. 29241) was short-spored.

The infraspecific variation of numerous species ranged at only 0–0.2(–0.6)%, e.g., *O. xanthostigma* s.str., *O. leucostigma* s.str., *O. aurantiorubra* s.str., and *O. tremulae*. A low ITS variation of 0–0.8% was even observed between samples from different continents (Europe and eastern Asia), as exemplified by *O. tremulae*, *O. xinjiangensis*, and *O. zhongdianensis*, whereas particularly *O. xanthostigma* and *O. leucostigma* (s.l.) developed various strongly deviating genotypes in continents other than Europe. *O. oligospora* showed a worldwide variance of 1.3–3% by forming various more or less homogeneous cryptic lineages, some of which included samples from more than one continent.

In contrast to the typically low infraspecific variation in *Orbiliomycetes*, remarkably high variation was observed among European samples of *O. xanthoguttulata* (0.6–3.5%) and *O. eucalypti* (4–11.5%) (Tab. S2), and the observed subclades did not show a clear geographical correlation or host specificity. Similar examples of cryptic speciation are observed in various nematode-trapping taxa, such as *O. auricolor*, *Arthrobotrys musiformis*, and *Gamsylella cionopaga*.

Infraspecific ranks. The question of recognizing infraspecific levels was variously discussed. For instance, R.P. Korf (pers. comm.) tended 'not to use *varietas* at all, believing that *forma* is the appropriate rank for simple variants that seem to differ in only a few genes, and *subspecies* as appropriate for geographically or ecologically isolated populations that seem not to be interbreeding'. A different opinion was advocated by Huhtinen (1990a) who suggested to apply the varietal rank to ambiguous, unsettled cases, such as collections which mainly differed in the presence vs. absence of croziers. In this concept, varieties are no more than a provisorium in the lack of a better solution and also lack of enough collections. In the meantime, molecular research on, e.g., *Hyaloscyphaceae* showed that taxa differing mainly in the ascus base are sharply separable by rDNA data, and also differences in apothecial colour may correlate with striking deviations in the genome (example: *Orbilia leucostigma* and *O. xanthostigma*).

In the present study we have avoided the application of infraspecific ranks, for the following reason: although the usage of infraspecific taxa emphasizes minor morphological differences and the difficulty to separate between them, the infraspecific rank needs some definition which can hardly be provided. The application of infraspecific ranks forces taxonomists to group two or more taxa as, e.g., subspecies of a species, and this method does not warrant that closely related species are then sharply delimited by their morphology. As an extreme consequence, a large series of taxa would be reduced to a single species. Since we did not perform interbreeding experiments and our molecular research still lacks data on various critical taxa, many of the species accepted in this monograph are to be considered as tentative.

Generic concepts and higher taxa. – **1**. **Taxonomic rank**. Baral et al. (2017b) saw three possibilities to classify the taxa within *Orbiliomycetes*: (1) the generic name *Orbilia* is used in a wide sense to contain a majority of species of the single family *Orbiliaceae*; (2) the generic name *Orbilia* is used in a moderate sense to comprise two subgenera, *Orbilia* and *Ovoideae*, while, e.g., *Arthrobotrys* would include *Neodactylella* and four predacious subgenera; (3) the generic name *Orbilia* is used in a narrow sense with *Ovoideae* as a separate genus, and the genus *Arthrobotrys* would include only taxa with adhesive nets.

In the past a narrow concept has been applied to the anamorph of the class but a broad concept to the teleomorph. As a result, many more generic names exist that are based on anamorphs (Baral et al. 2017b). In the broad concept, most of these genera fall into synonymy with *Orbilia*.

As an advantage of the broad concept, which was chosen in the present monograph, species with critical relationship can be accomodated without doubt in the genus *Orbilia*; a disadvantage would be that the currently used generic names of nematophagous taxa (*Arthrobotrys*, *Dactylellina*, *Drechslerella*, *Gamsylella*) fall into synonymy of *Orbilia*, where they are recognized at the series level. As an advantage of the narrow concept, which would be in concordance with the current trend in fungal classification, the close relationship of a species is recognizable from the generic name; a disadvantage would be that some of the accepted genera are only recognizable by cultural or molecular methods.

Based on a proposal to evaluate the rank of a taxonomic group by the concept of temporal banding according to the geological age estimated from fossils, a suggestion to revise the classification of *Lecanoromycetes* was made by Kraichak et al. (2018). This concept implies that each rank is represented by a period range (temporal band). The authors proposed to assign the ordinal rank to groups diverging in the range of 176–194 myr before present, and families in the range of 111–135 myr. When applied to *Orbiliomycetes*, this concept would raise sections of the present monograph to ordinal level and genera to classes. However, the temporal banding approach neglects the fact that, depending on the group, evolution took place with a very different speed. When considering changes in morphology as the benchmark for taxonomic units, this method may at best be useful within a given group by chosing a scale that is appropriate to it. Therefore, Lücking (2019) proposed that ranking of taxa should follow integrative principles that best reflect their individual evolutionary history.

2. **Paraphyly**. Frequently our phylogenetic analyses resulted in monophyletic groups which reflect very well our morphological criteria. In many other cases, however, they resulted in paraphyletic groups, and in cases of strong morphological evidence we preferred to put more weight on morphology than on molecular data. For instance, *Orbilia vinosa* and *O. aprilis* rarely fell together in a clade in our analyses, which is supported by a strong genetic distance (21–22.5% in ITS, 7.5% in LSU). Nevertheless, their ana- and teleomorphic features are so similar that we have placed them in the same series *Hesperideae*, which formed no less than four different clades with unresolved relationship. Another representative paraphyletic group is the non-predacious series *Neodactylella*, from which the four monophyletic predacious series of section *Arthrobotrys* appear to have evolved. Another example concerns series *Lentiformes* and *Phanosomates* which constitute the two main subgroups of section *Lentiformes*. These two series are sharply distinguished by spore body morphology, but each of them formed a paraphyletic group based on available rDNA sequences. We maintained their distinction because we believe that the different SB types emerged from a common ancestor within each series, contrary to what the tree topology suggests.

Paraphyletic groups are a natural consequence of evolution and require acceptance in the classification of organisms (Zander 2008). Davydov et al. (2010) exemplified this when accepting the monophyletic genus *Lasallia* Mérat and the paraphyletic *Umbilicaria* Hoffm. When trying to apply a strict monophyletic concept, the morphologically well-defined genus *Umbilicaria* would need to be split into numerous genera, for which no morphological support was seen. We agree with Zander (2007) and Schumm & Aptroot (2019), who wrote that the evolutionary process that leads to new species (speciation) must involve paraphyly, by which an ancestral species may remain virtually unchanged and paraphyletic after a budding speciation event; by extension, paraphyly must also be expected among genera and families. The high importance of morphology in classification is expressed in the following quotation from Zander (l.c.): ‘Even if many organismal structures have unknown function, the morphology as clue to phenome/environment interaction should characterize the taxon’.

Etymology. Facing the huge number of species now recognized within *Orbilia*, we nevertheless tried to prefer names that refer to the typical features of the fungus. A convenient solution for giving characteristic names was found in the use of a prefix that indicates the number of spores. This method is exemplified on p. 57–58 (Fig. 41 and Tab. 6) by three new taxa that deviate in spore number from the closely related old taxon *O. euonymi*.

New names introduced in this monograph are also influenced by the history of the species when it was first discovered, which often resulted in more or less inappropriate names. We mostly decided to continue usage of such names that we previously gave them because they appear on many of our notes, and name changes would have caused confusion. For example, the spores of *O. delphinus* in the first collection studied resembled more or less a dolphin, unlike in some later collections, whereas spores of later detected new species resembled more obviously a dolphin. So we refrained from transferring the epithet to a taxon with more obviously dolphin-like spores.

Such historically born, more or less inappropriate names are also a consequence of nomenclatural rules and taxonomic progress, resulting in illogical names that were erected when the species diversity and variation was little explored. We must, therefore, content ourselves with the inevitable consequence that species are named *coccinella* and *rubella*, although dozens of other species have the same colour, or *euonymi* and *eucalypti*, although later collections revealed that these species occur on a very wide range of host plants. In cases when the morphological features of our new taxa did not provide enough peculiarities, we nevertheless continued to create names based on hosts and colour, or used collector's and geographical names.

We early refrained from erecting new names for anamorphs which we obtained in pure culture of described teleomorph-typified species. Herein we followed the recommendation of Art. 59A.3 (McNeill et al. 2006) which recommends that 'authors should avoid the publication and use of binary names for anamorphs when the teleomorphic connection is firmly established and there is no practical need for separate names'. The increasing possibility to clarify the whole life cycle of fungi with molecular methods and the increasing data from molecular environmental extracts supported the practice of using only one scientific name for one species (Rossman 2009).

Regarding priority, the switch to one name for one fungus posed various problems. A proposal by Gams et al. (2012a) to use, e. g., *Orbilia orientalis* as holomorph name when the genus *Orbilia* is adopted in a wide sense, instead of combining the older *Drechslerella brochopaga* in *Orbilia*, was not approved by the new Code (Turland et al. 2018), which gave anamorph names equal priority. Not approved was also a proposal by Hawksworth (2014: prop. 15 Art. 59) to regard the erection of a new species for the teleomorph of an existing anamorph name as a new combination, which was forbidden under the old Code. Art. 59 was replaced in the new Code by Art. F.8 on fungi with a pleomorphic life cycle, which implies (Note 2) that all legitimate names for the different morphs of a fungus have equal priority. Here, Note 3 treats names that were proposed simultaneously for teleo- and anamorph of a single species. They are necessarily heterotypic, which means that they are always typified on different elements, even if they are preserved on the same piece of substrate under a single voucher number. For such not infrequent cases of equal priority, Rossman (2014: 86) suggested to simply adopt that name which stands in the desired genus, but Art. F.8 does not treat this situation in detail.

The main problem in *Orbiliomycetes* is that many species with clearly different teleomorphs possess anamorphs that hardly differ at all. For this reason, we have frequently been unable to unequivocally clarify the identity of existing names of anamorphs, particularly if type strains and molecular data on them are lacking.

Documentation, descriptions, accuracy of observation

How long should descriptions be? Many taxa of *Orbiliomycetes* published over the past centuries have been so inadequately described that their identity can hardly be determine without studying the type specimens, a circumstance being experienced in many groups of fungi (Dayarathne et al. 2016). In our opinion, species descriptions should be comprehensive and detailed. Even though long descriptions may hide the important details, they help in making potentially distinctive characters available for future work, when new taxa will be discovered, new characters detected, and new taxa concepts developed. A large scope of reported characters will help to settle taxonomic problems with difficult groups. Furthermore, comprehensive descriptions aid in the construction of synoptic keys. Reading long descriptions consumes much less time than reexamination of inadequately described type material.

For each species the scope of variability known at present should be presented in a monograph. This only works well when more or less all characters of a fungus that are visible under the light microscope are described, and when data from several collections are illustrated. On the other hand, it is recommended to exclude any unreliable information from descriptions. This mainly concerns redundant characters which are present more or less across a taxonomic unit. Huhtinen's (1990a) monograph on *Hyaloscypha* and allied genera provides an exemplary standard for a sound ascomycete taxonomy in which detailed drawings from different collections were supplied for most of the treated taxa.

Users of a monograph should not simply try to identify their collections with one of the accepted taxa. We recommend to get acquainted with a species by trying to collect it repeatedly and to study it several times before expecting a trustable determination. Furthermore, we recommend to make notes, macro- and microphotographs, or small sketches of a majority of the studied collection in order to explore the individual variation. Brief documentations of the reliable data of the collections under investigation are the minimum demand. By simply applying a name to a fungus, workers often overlook the bad taxonomic exploration of a given taxon.

About illustrations. The crucial focus of this study was to provide detailed drawings of the micromorphology, especially of the teleomorph, and that from several collections of each taxon, following the conviction that 'a good figure is better than a full page of letter-press' (Lange 1935). The frequent absence of meaningful and exact illustrations is the most time-consuming obstacle of any efficient taxonomic work. 'Even the most painstaking and carefully worded description will often fail to give that clear and exact idea of the varying colours and forms of a mushroom which a good portrait will give at a glance' (Lange l.c.). Particularly those older authors who were using a microscope (e. g., Karsten, Fuckel, Rehm, Höhnel, Kirschstein), were used to describe new species without providing visual data. Although Svrček supplied drawings to nearly every taxon he described as new to science, the value of his revision of the 81 taxa being described by Velenovský in *Orbilia* (Svrček 1954) is greatly diminished by the absence of any illustration. The practice of publishing characteristics of fungal records without visual information, a feature typical of the 19th century but sometimes even practised within the past decades, makes constructive taxonomic work extremely difficult.

Drawings require appropriate magnification rates in order to permit proper illustration of the discernible microstructures. It is further recommended to use a constant scale for the same element within a taxonomic group, because this highly facilitates comparison among the drawings. However, it is not advisable to draw all kinds of elements at the same scale. As a general rule we suggest to draw medium-sized ascospores at a scale of 3000 ×. Due to the sometimes very small spores and minute details of the spore bodies in *Orbilia*, a drawing scale of 4000 × for ascospores seemed to be more appropriate within *Orbiliomycetes* and was, therefore, consistently used in the present study. The same applies to the ascus apical structure. For the often large conidia a scale of 2000 × was used instead. Drawings should be reduced to around 30–70 % when printed, which will not result in any loss of information.

Microphotographs are generally closer to reality than drawings but not always as easy to interpret. They sometimes provide limited possibility to arrange the elements, e.g., asci and paraphyses in the context of the hymenium. Asci are usually separated by squashing, therefore, photographs often show them in the dead state. Photographs are inferior to drawings regarding the limited depth of focus, e.g., when elongated spores are obliquely oriented within the asci or when spores lie in several layers inside polysporous asci. This disadvantage can be overcome by taking a series of subsequent digital photographs of a single ascus with different focus. However, such image series can profitably be viewed only on a computer. Photographs are suitable to figure complex excipular textures in median section, also free ascospores and conidia, or isolated hymenial elements, but may also yield good results for asci and paraphyses in situ, either in the living state (in water) or in the dead state, particularly when staining the entire ascoplasm by iodine.

Drawings are never free from a certain degree of imagination and arbitrariness. The role that fantasy may play in descriptions and drawings is exemplified by the fact that, e.g., polyspory, inverse spore orientation, and spore bodies have frequently been ignored in *Orbilia*. These characteristics have often been overlooked when studying dead herbarium material, but workers have also ignored them in studies of fresh collections because they appeared to be abnormities. Unexpected deviations from the general situation with ascomycetes may easily be neglected intuitively.

One example of the inaccuracy of drawings concerns paraphysis septation. Desiccation-sensitive species of *Orbilia* are characterized by paraphyses having the terminal cells much longer than the lower cells. Nevertheless, Velenovský's (1934) drawings hardly account for this fact but, instead, the author put the septa arbitrarily. This became obvious during revision of his type material, but also when comparing his drawings published in 1934 with those of his manuscript. For instance, on his manuscript plate of *O. acuum* the three figured paraphyses show either none or just one basal septum, whereas on pl. 11 fig. 22 Velenovský (1934) put four septa to each of the three.

In our opinion, the characters of every collection we are about to study needs to be annotated in a descriptive way, preferably in combination with either pencil drawings or photographs. Whenever collections show slight micromorphological deviations, microscopic images should be taken, following the suggestions of Huhtinen (1990a: 46) to illustrate such variation of a species from different populations. According to Huhtinen, 'authors of monographs tend to illustrate one, preferably 'ideal' specimen of a species, giving a simplified picture of the situation in nature and excluding undesirable, but inevitable, variation'. We have frequently illustratesd collections from different hosts or geographical areas, even if they did not distinctly deviate. This was also Huhtinen's idea who wrote about his depicted populations: 'In this paper equal attention is paid to stability and variation'.

Apart from rarely encountered taxa, we have documented the micromorphology of a species from a minimum of 2–4 populations. Huhtinen's monograph supplies illustrations from (1–)2–4(–6) collections for each taxon (exceptionally 7–9). Despite the richness of illustrations in Huhtinen's publication, the author published only a selection of the whole set of his annotations and drawings. 'The great majority of the over 1700 collections were depicted in detail' (Huhtinen 1990a: 85). In the present monograph we decided to present nearly all of the drawings, considering the fact that words cannot substitute illustrations. The complete set of drawings, photographs, and annotations are accessible online (IVV).

Resolution limit, **accuracy of measurements**. In the descriptions we have evaluated measurements smaller than 10 µm with an accuracy of ~0.2 µm, since we believe that it is possible to estimate such values and that it is obligatory to measure with an error < 3% for an element above ca. 3 µm diam. Measuring at an exactness of 0.5 µm is inacceptable for elements smaller than about 4–6 µm. This is obvious when doing drawings to a scale above 1000×. At 2000× a measurement error of 0.5 µm causes a deviation of 1 mm on the drawing sheet and severely alters the shape of small spores. In our experience, a microscope magnification of 1500× allows more precise direct measurements of small spores compared to 1000×. Most measurements were gained in the present study under 1500× using a measuring scale with a 1:1 calibration, therefore, the published values behind the point have no mathematical origin.

Filaments or membranes of the living cytoplasm such as the tonoplast or the filum of spore bodies have a thickness of much less than 0.1 µm. They can be seen with the LM under bright field, although the resolution limit of the visible light (~0.2 µm) should forbid observation of such minute structures. However, the limit of resolution indicates at which minimal distance two lines or points remain discernible. For the recognition of small objects the crucial parameter is the recognition limit (for a detailed account on this topic see Françon 1967). According to Clémençon (1974: 249), dots of 0.032 µm diam. or lines of 0.002 µm width are still recognizable under the LM. Also Miettinen et al. (2006: 213) subjectively estimated distances of 0.1 µm with a 1-µm-grid eyepiece, using phase contrast and a viscid mountant (CB in lactic acid) in which the spores stay still.

In the mycological literature, calibration and measurement errors are frequent and show in the worst case a deviation of 10–30 percent or more from the true values. Examples of such errors are found in the works of, e.g., Boudier (differences between text and scale) and especially Velenovský (see p. 190–191).

Vital taxonomy, differences between living and dead cells

The present monograph, including the dichotomous key, is based on a taxonomy that combines persistent and transient (vital) light-microscopic characters. This means that predominantly and preferably recently collected specimens were examined in the living state. During our up to 40 years lasting microscopic work on various groups of non-lichenized ascomycetes, we became more and more aware of the extraordinary taxonomic value of vital characters in many groups of both disco- and pyrenomycetes. Differences in morphology between living and dead cells can virtually be found in every fungal species. Taxonomically important vital characteristics also occur in most groups and concern both anamorphs and teleomorphs. The study of living collections of ascomycetous fungi enormously increased our knowledge in various ways, including desiccation tolerance and spore discharge mechanisms.

One of the aims of this monograph was, therefore, to assess the taxonomic impact of vital characters in the *Orbiliomycetes*, particularly that of the spore body (SB). Baral (1992) gave a detailed account on vital taxonomy, which represents an over a hundred years old knowledge favoured by authors like E.

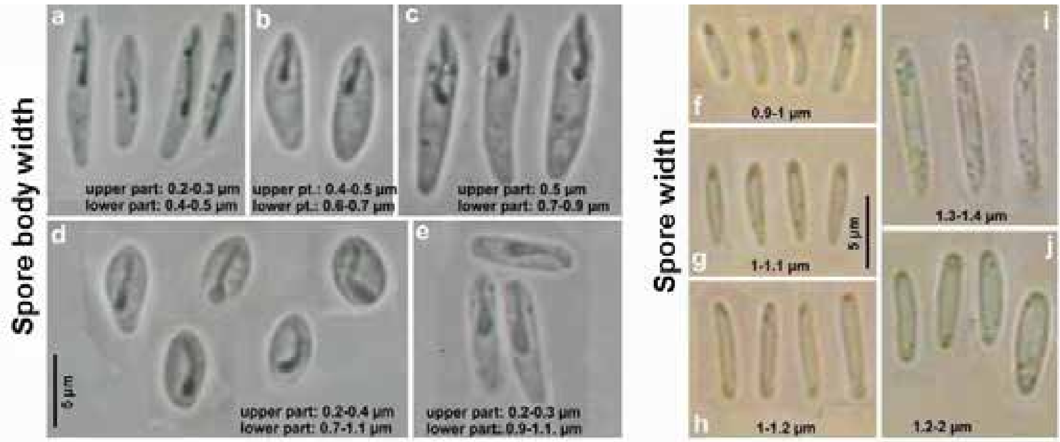


Figure 2: Accuracy of measurements. — **a**. *Orbilia flavidorosella* R.T.L. 10122202; **b**. *O. cylindrosoma* R.T.L. 13083101; **c**. *O. carpoboloides* R.T.L. 13032901; **d**. *O. gambelii* R.T.L. 13083001; **e**. *O. vitalbae* H.B. 9681; **f**. *O. epipora* H.B. 8186; **g**. *O. alba* H.B. 9051a; **h**. *Hyalorbilia inflatula* H.B. 8885a; **i**. *H. juliae* H.B. 8894a; **j**. *H. polypori* H.B. 9211.

Boudier and J. Lagarde (Baral l.c.: 336). In *Orbiliomycetes*, vital taxonomy permits to achieve significantly higher confidence levels in species identification and delimitation based on the teleomorph, to a rate inaccessible by traditional herbarium taxonomy. A monograph of *Orbiliomycetes* based solely on herbarium material would inevitably have resulted in less than half of the species accepted as distinct in the present study.

Vital taxonomy means to base descriptions and illustrations on the living state concerning all kinds of cells of the holomorph. Characters provided by living cells mainly concern plasmatic structures, which are usually completely invisible in the dead state, irrespective of which method is applied. In our simultaneous studies on other groups of ascomycetes, two types of plasmatic organelles were found to be of high taxonomic relevance in both the *Helotiales* and *Pezizales*: lipid bodies (LBs) in ascospores, and refractive vacuolar bodies (VBs) in paraphyses, sometimes also in hairs and cortical excipular cells.

In the taxonomy of *Orbiliomycetes*, LBs in spores and conidia play a subordinate role, and the presence of VBs in the paraphyses of *Orbilia* is more or less restricted to hygrobiotic taxa, except for the xerobiotic genus *Amphosoma* which is characterized by multiguttulate VBs. Yet, two further types of vital characters turned out to have high taxonomic importance, mainly at the species level: the spore bodies (SBs) in the ascospores, and a peculiar type of cytoplasmic bodies (SCBs) in paraphyses and excipular cells. SBs show a high morphological diversity in shape, especially between higher taxonomic units, but little variation within a species. SCBs are mainly important in their crystalloid subtype and are present only in a part of the species, thus serving as a key character in many groups, mainly at the species level. Therefore, SBs and SCBs allow in combination with persistent characters quite a clear and rapid identification of many taxa of *Orbiliomycetes*.

A frequent belief is that vital taxonomy is impracticable because of the unavailability of fresh material. Yet, vital taxonomy does not necessarily mean to study fresh collections (see p. 30–31). On the contrary, living cells can often be found in herbarium material that was dried some months or even years ago. On the other hand, fresh specimens may contain a varying, sometimes rather high amount of dead cells, even if studied at the day when collected. Hence, doing vital taxonomy requires the capability to distinguish between living and dead cells. The use of oil immersion is obligatory in vital taxonomy, and self-evident regarding the often very small structures in this group of fungi.

A widespread usage is to mount a specimen's fragment, irrespective of being fresh or dry, in a lethal mountant such as MLZ, CB$_L$, or KOH. To put fresh apothecia in such a medium is actually equivalent to the study of hundreds of years old herbarium specimens, and it is actually the intention of this usage to achieve a compatibility between fresh and herbarium material. Vital characters are completely overlooked by this method, as they can only be observed when using water with a very low concentration of salts or other ingredients (we recommend tap or rain water as standard mountant).

All who use this monograph must be aware of the demand **to study collections in water mounts and within a period of time during which the cells (asci**, **paraphyses**, **ascospores**, **excipular cells**, **conidia) remain viable**. Otherwise, neither SBs in the mature ascospores nor SCBs in the cells of paraphyses and ectal excipulum can be seen, and the keys will not work. Even the evaluation of spore numbers within asci is hampered when studying dead specimens, especially in taxa with narrow spores, and also ascospore size and shape in the dead state will be difficult to assess, since free spores are often rare and those within the asci usually very difficult to see.

Dead herbarium specimens can often only tentatively be identified. A frequently given advice to provide two dichotomous keys, one based on vital characters, the other on persistent characters, was abandoned in view of the many problems we already had in elaborating an operative key to the numerous taxa and infrageneric groups based on the full scope of morphological characteristics. For the identification of dead specimens we suggest to use our Tab. S3 (Morphological characteristics) by restricting the search to persistent characteristics, which should permit to exclude a vast majority of the taxa.

Huhtinen's (1990b) demand that 'at least one of the depicted populations should represent living specimens mounted in water' is a first approach to a better taxonomy, but does not permit exploration of the variability of vital characters. Huhtinen actually studied only a small percentage of fresh collections as he (1990a: 85) admitted that 'fresh material was available for 50 % of the taxa' only, and 'most of the observations were made on material in CB [CB$_L$] and MLZ'.

Vital characters are bound to the living state and cannot be preserved other than by documentation. Therefore, it was argued in personal communications that such transient characters, particularly of the teleomorph, are less useful for taxonomic work. However, this view neglects the taxonomic importance attached to the shape of chloroplasts and other cytoplasmic structures in living algal cells. Vital characters of fungal anamorphs obtained in pure culture can usually be studied over a very long period of time, if the cultures are still sporulating. Nevertheless, morphological analyses from pure cultures have often been made from dead cells, either due to careless preparation methods or intentional application of lethal mountants. TEM studies on spore bodies and SCBs yield remarkable results, thus offering a possibility to study these organelles from material placed in the living state in fixation solutions. However, the effort is enormous, and artifacts can frequently not be avoided.

Contrary to vital taxonomy, cultural studies became a well-established part in mycological systematics, despite the fact that they require fresh collections. Nevertheless, anamorphs are often unavailable in specimens deposited in herbaria or cannot with certainty be connected to a teleomorph. So, how to determine a taxon for which the anamorph is asked for in a key, if the specimen in question is dead herbarium material? One of the reasons why pure cultures became well-established in mycology was that this routine work served as the only proof for anamorph-teleomorph connections prior to the era of molecular research.

Taxonomic concepts arising from the study of herbarium specimens are based on a reduced set of morphological characters, comparable to the study of fossil organisms. While palaeontologists dream of the possibility of reanimation of extinct species in order to complete the limited knowledge about these organisms, fungal taxonomists are either unaware of the severe changes during cell death, or ignore these effects by arguments such as unavailability of living specimens during their free time.

A possibility would be to speak of a ‘species complex’ for those groups of taxa which are distinguishable by vital characters but hardly so by persistent characters alone. There is, however, no good reason (at best a practical one) to give more taxonomic weight to characters which are stable under the conventional method of air-drying, and molecular data has variously confirmed the value of vital characters in the past decade.

For instance, spore numbers in asci are stable in dead material but sometimes represent the only difference between closely related taxa, whereas spore bodies (SBs) often characterize higher taxonomic units. Shape and insertion of the SBs turned out to belong to the most important characteristics regarding recognition of infrageneric groups. The application of terms like ‘species complex’ for taxa which are difficult to delimit without vital characters would lead to artificial groupings. Quite distant taxa may be confused in the dead state due to a similar spore shape though containing very differently shaped SBs, whereas more closely related taxa with a concordant shape of SBs may differ in persistent characters such as spore size and shape. In the most extreme case, confusion at the level of the class occurred when neglecting vital characters, e. g., in the genus *Pithyella*, which comprised members of both *Orbiliomycetes* and *Leotiomycetes* (see p. 208–209).

As a consequence of this, we doubt the importance that is currently attached to the preparation and maintenance of fungal herbaria. In our experience, morphological work exclusively based upon herbarium material is more an obstacle against a sound and well-founded fungal taxonomy. Fact is that most of the preserved herbarium specimens remain unexamined over a very long period of time, and also usually lack any documentation by the collector, including the fresh apothecial colour. Progress in knowledge about variation and delimitation of taxa is much accelerated when specimens are continuously documented, preferably in the living state, and presented in articles, monographs, or other media such as websites or internet forums. Only when we shift our focus on the documentation of collections instead of merely their preservation, natural taxa concepts can be worked out in a reasonable period of time.

Doing vital taxonomy results in a much higher complexity of character combinations, thus requires a more time-consuming work on each collection. Illustrations need more patience, and descriptions become longer, but the taxonomic conclusions based on these data have a much higher relevance. On the other hand, microscopic work on old specimens is often more difficult and consumes more time than documenting fresh material, an experience also expressed by Svrček (1976: 116). As an example, a very time-consuming task with dead specimens is to discern thin-walled hyaline spores inside the asci, although in living material such spores are seen at a glance.

A frequently heard argument that favours monographs on herbarium specimens concerns the impossibility of microscopic study during an expedition to remote areas of the world. Especially tropical mycology is said to prohibit any such research due to the very high temperatures and atmospheric humidity. Undoubtedly, such climatic conditions involve serious technical problems. Our impression is, however, that it is rather a matter of willingness for making vital studies, to avoid giving up a method practised over decades. In our experience, workers focused on herbarium material are indeed generally unaware of the characters that they lose when treating their fungi with lethal mountants.

Tropical regions undoubtedly require high expense for a thorough study of vital characters of hygrobiotic, desiccation-sensitive taxa, similar as arctic regions do. Boreal, temperate, and subtropical climates hardly cause any problems if taxonomists have the possibility to use working rooms for immediate microscopic study. Mailing specimens from other countries and continents is problematic with such taxa which must be preserved in a way that they retain their hydrated state and are not exposed to mechanical pressure. Mailing between countries of western and northern Europe is hardly problematic since mails are usually only 2–3 days on route. Sending fresh specimens in rather cheap express air mails from other continents turned out to be difficult, but was successful in some cases (e. g., from USA or China to Germany).

In contrast to hygrobiotic fungi, vital studies on xerobiotic, desiccation-tolerant taxa, to which by far the majority of species in this monograph belong, is most convenient because such specimens are collected in the dry state and remain viable over quite a long time. The problems that these taxa frequently impose are those of their minuteness, scarceness, and intermingled growth, which requires collecting of enough amounts of substrate and to search for them under the dissecting microscope. Frequently, the different taxa discovered on a single branch cannot adequately be split into separate herbarium specimens.

As a herbarium taxonomists, one tends to be unaware of how frequent many species are, and how many species exist which have not yet been catalogued and preserved in herbaria. During our monographic study we have never been in want of living material. This was mainly due to the frequent expeditions to semihumid or semiarid areas of southern Europe, Northern America, and Australia by one of us (G.M.), and the enormous desiccation tolerance of most of these species, allowing to study them within a period of 0.5–2 or even 3–4 years. Many further collectors have contributed in sending living collections from Europe, Macaronesia, or China. Mailing hygrobiotic species in the dry state a few weeks after collecting proved to be an acceptable compromise, allowing to study the ascospores of many Chinese collections in the living state.

The ease to collect ascomycetes in the field and the longevity of many desiccation-tolerant taxa fixed the focus of our work on vital research, and relegated herbarium studies with their often only weak or ambiguous results was of subordinate importance, restricted predominantly to type specimens of previously described taxa.

As one of the consequences of vital taxonomy, we advocate the simultaneous research on a broad scope of taxa, including those outside the monographed group, despite the disadvantage that publication is delayed. Especially in the Northern America and Australia we came across a lot of ostropalean, helotialean, and dothidealean discomycetes growing in close vicinity with *Orbiliomycetes*. Many of them we have studied in detail in the living state, and notes and drawings of them can be found on our homepage (IVV). Their immediate documentation turned out to be important because we frequently experienced that several of these species did not show up a second time by now, and a later restudy of the dead material would mean a serious loss of data.

Monographic work based on vital taxonomy requires a strategy completely different from herbarium taxonomy. The availability of recent collections, i.e., the knowledge about how to find apothecia in the field, is of major interest in regard to taxonomic questions such as clarification of species limits, whereas the maintenance of a herbarium, though valuable in various ways, is of subordinate importance.

Arguments pro herbarium taxonomy. Traditional monographs are usually restricted to a few years and, therefore, put their focus on the study of dried personal collections and those deposited in public herbaria all over the world. The advantages are convincing: (1) a collection can be studied at any time and as often as wanted if plenty enough; (2) several specimens of a variable taxon, being collected in different years at different places, may simultaneously be compared; (3) a given species is usually easily located in a herbarium but often difficult to find in the field; (4) a taxonomic study can be planned and finished within a reasonable period of time; (5) due to the restriction on persistent characters, all characters of a specimen can be seen and verified or rejected by later workers at any time. Argument (5) is particularly important concerning type material.

The use of lethal clearing agents such as KOH, MLZ, CB_L and others has several advantages: (6) the preparation becomes clear and transparent; (7) living collections get compatible with herbarium material in their microscopic appearance; (8) viscous media (MLZ, CB_L) suppress annoying trembling and drifting of free spores; (9) MLZ stains iodine-reactive structures, whereas IKI was avoided by most mycologists during a long time because it scarcely improves the aesthetical appearance of a preparation.

Regarding the difficulty of detecting discomycetes in the field (argument 3), reasons to rely on herbarium material may involve arguments such as: (a) the worker has not enough time or experience to undertake field work, especially concerning very remote areas; (b) many fungi form their apothecia only a few months per year; (c) undescribed species are assumed to occur only far away from the worker's laboratory; (d) a high number of fungi are regarded as rare.

Herbarium taxonomy sounds convenient and easy. Fresh collections are put straight on the dryer in order to be studied at any occasion. Apothecial fragments are consistently mounted in lethal agents irrespective of the living versus dead state of the cells. The worker must not rack his brains about differences between living and dead cells, such as the following: why do some cells contain many small droplets whereas others a few large drops or none at all. In herbarium taxonomy water is actually not very often used as a mountant, instead, the above-mentioned agents are preferred to mask disturbing structures of the dead cytoplasm, or various stains are applied to improve visibility of microstructures. As a consequence, microscopic illustrations performed by herbarium taxonomists usually refer to dead elements, irrespective of whether the illustrated specimen concerns old type material or a recent collection.

Arguments pro vital taxonomy. The study of living cells includes not only taxonomic but also developmental, cultural, physiological, and ecological aspects. Taxonomic aspects involve: (1) achievement of more natural concepts at species or higher level due to a higher complexity of character combinations; (2) higher contrast and transparency of living cells, better visibility of septa, spores inside asci, spore sheaths, easier recognition of spore numbers, abortion of spores, inverse spore orientation; (3) awareness of striking effects concerning cell size, shape, and contents during killing: shrinkage and artificial flattening, changes in curvature, imbibition (swelling) of walls and sheaths, loss or coalescence of cytoplasmic guttules, invisibility of nuclei; (4) awareness of severe changes in spore arrangement inside asci; (5) correct interpretation of colours (original colour of apothecia, location of pigments, oxidative colour changes of VBs); (6) recognition of hemiamyloidity which may severely change in material older than ~30 years; (7) easier performance of free-hand sections of apothecia due to cell turgor. Developmental aspects comprise: (8) recognition of development stages of asci and spores, which is important for a precise definition of ascospore maturity, in order to answer questions such as: (a) occur features like septa, wall pigments and ornaments, or cell contents in immature, mature, or overmature spores? (b) are true ascoconidia present (conidia produced on ascospores before spore discharge), or are the conidia only formed on overmature ascospores? Cultural aspects involve (9) morphology of different organs formed in pure culture, including establishing anamorph-teleomorph connections. Physiological aspects include (10) function of asci and their apical apparatus in regard to spore discharge. Ecological aspects involve (11) recognition of desiccation and frost tolerance.

The annoying drift of free spores in water has also an advantageous aspect: it permits to obtain a three-dimensional image of spores and their SBs, for example, if spores or SBs are helicoid, or SBs subapically to laterally attached. Sometimes freely floating living mature asci can be seen rotating slowly along their longitudinal axis, which permits viewing of the arrangement of the contained spores from different sides.

Documentations of recent collections are nowadays presented and discussed in internet forums (like AscoFrance or PilzePilze), and experts can give their suggestions. Herbarium taxonomy produces huge amounts of unexamined specimens which require high efforts of maintenance, but with slow progress in knowledge. Voucher specimens may get lost, apothecia destroyed by arthropods, fragments put back in the wrong envelope, or specimens may contain a mixture of very similar, easily confounded species. Such mixed populations are much easier revealed when enough apothecia of a specimen are studied in the living state, compared to the study of dead material or by molecular methods.

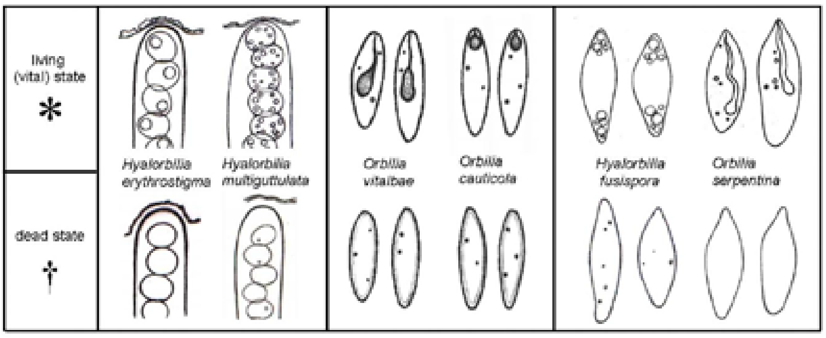


Figure 3: Spore bodies as a species marker, exemplified by three pairs of species with a similar spore size and shape, but very different plasmatic inclusions (upper row). In the dead state these transient structures get completely lost (lower row).

History of vital taxonomy in *Orbiliomycetes*. The first to perform vital studies on teleomorphs of *Orbiliomycetes* were Patouillard (1892), Rolland (1901), and Chenantais (1918), who presented drawings of ascospores with obvious spore bodies (see Fig. 151). The asci and paraphyses in their drawings were dead, however, or uncertain concerning their vitality. Velenovský (1934) favoured vital observations, but only rarely depicted spore bodies in the spores (Figs 154: 4; 156: b), and almost never the spores inside the asci, which indicates that he mainly studied spores and asci in the dead state. Svrček, in his many papers on inoperculate discomycetes, repeatedly studied living specimens, but among the orbiliaceous taxa this mainly applies to his *Orbilia cryptocarpa* (= *Hyalorbilia polypori*, see Pl. 65: 9). Only when *Orbilia septispora* Baral (1989) was described in the living state and the study on vital taxonomy appeared (Baral 1992), the number of papers on *Orbiliomycetes* which included living elements distinctly increased (see p. 201).

The studies by Drechsler (1936–64) on numerous anamorphs of mainly nematode-trapping *Orbiliomycetes* were done on specimens grown in agar cultures, and his detailed microscopic drawings leave no doubt that they were done in the living state. Also other papers on orbiliaceous anamorphs sometimes present living elements, particularly those of Chinese workers from 2005 onwards. Orbiliaceous anamorphs only sometimes provide transient characters of taxonomic importance, for instance SCBs in the conidia of *Hyalorbilia*, but the applied method seriously influences conidial dimensions (see p. 28).

Taxonomic value of spore bodies. The *Orbiliomycetes* are a famous example of the high taxonomic value that morphology and especially vital taxonomy provides. This mainly concerns the spore bodies (SBs), a conspicuous, refractive cell organelle in the mature ascospores, which is unknown in any other class of *Ascomycota* and, therefore, easily permits to recognize a discomycete as belonging to this group of fungi. The high amount of collections with viable spores studied in this monograph allowed us a thorough exploration of both diversity and intraspecific variation of spore bodies. As a result, the SBs turned out to be a feature of high diagnostic value comparable to that of spore shape. Among the ca. 480 taxa examined in the living state, we found a very high diversity in SB morphology on the one hand, and a pronounced intraspecific consistency on the other hand, which both indicate a high biological importance of this organelle.

Spore bodies are mainly diagnostic for higher taxonomic units. This is in contrast to spore shape which is more diagnostic at the species level. In fact, similar spore shapes often occur in very distant groups. Fig. 3 exemplifies this with three pairs of species: the left cell shows two probably closely related species, the middle cell two which belong to different sections of subgenus *Habrostictis*, and the right cell an example of two species that belong to different genera. In the dead state the two species of each pair may easily be confounded by spore morphology alone. Therefore, if only dead herbarium material is available, or if lethal mountants are applied to the living specimen, confusion is predictable.

Many of the here circumscribed sections or series are to a certain degree defined according to shape and attachment of the SBs (for a survey on the various types see Fig. 4). In numerous cases, delimitation between otherwise very similar species turned out to be possible merely on the basis of differences in spore body morphology. There exist many examples of often very distant species which have ascospores of quite a similar size and shape, whereas their SBs are very different. Without information on SB morphology, a collection often remains undetermined. For the same reason, type material can often only tentatively be classified. Some species are so far only known from dead material, without any information on shape and size of the SBs, and are, therefore, difficult to place in a proper infrageneric group.

Quite a complicated group, even for a vital taxonomist, concerns those *Orbiliomycetes* with comparatively small subglobose to ellipsoid-fusoid or ovoid to clavate ascospores and 8-spored asci (Fig. 4). Though in some cases showing a different size and also shape, distinct differences are mainly found in SB morphology, particularly because size and shape of spores of a given species usually show a higher variation than that of SBs. Therefore, these taxa are often difficult or even impossible to distinguish with dead herbarium material, although they belong to three different genera (*Orbilia*, *Hyalorbilia*, *Lecophagus*), and within *Orbilia* to four different subgenera or sections. The contents of the living spores permit rapid recognition in most of these cases, however.

Six of these species have ellipsoid-fusoid to ovoid-clavate spores of *4–8.5 µm length and are shown in the upper row (Fig. 4: a–f). The lower two rows (Fig. 4: g–q) present species with broadly ellipsoid to subglobose spores of *2–5 µm length. Apart from the 16-spored *O. pleioeuonymi*, all species have 8-spored asci. However, not all of them are clear-cut because of more or less strong variation, which also affects the spore bodies to some extent. Two further examples similar to Fig. 4 but with cashew-shaped or tailed (sperm-shaped) spores are shown in Fig. 49.

Another example regards the six known species of *Orbiliomycetes* with black-olivaceous apothecia (Fig. 5). Although these have more or less differently shaped ascospores, spore shape is again rather variable in some of the species and, therefore, of limited value. In contrast, the shape and number of spore bodies show only little intraspecific variation, and almost all species possess their unique SB shape and size. In most of them the SBs are broadly affixed to the spore apex: *Amphosoma atroolivaceum* differs from the remaining in having SBs at both spore ends, *Orbilia purshiae* differs from *O. patellarioides* in SBs with angular to acute internal protrusions, and *O. atrolentiformis* from both mainly in narrower spores. *O. pileosoma* has ovoid spores with very thin and broad, plate-

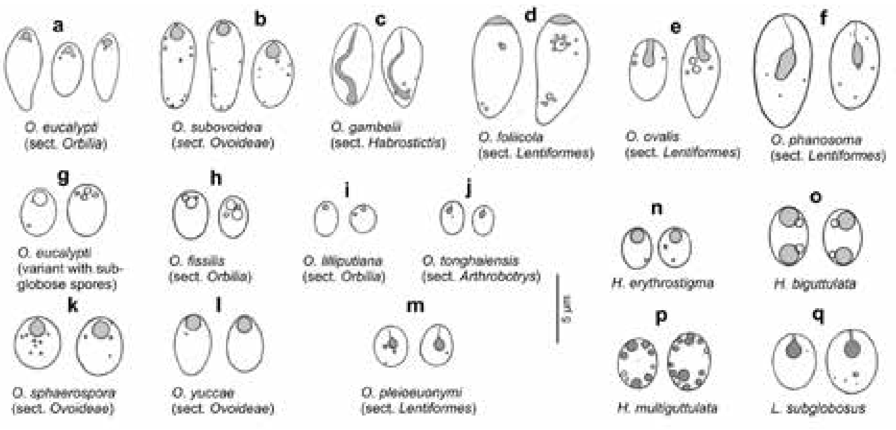


Figure 4: Living ascospores of some selected, mainly 8-spored species of *Orbilia*, *Hyalorbilia*, and *Lecophagus* with partly very different spore bodies (tinted in grey) but a rather similar spore shape. SBs were not seen with certainty in the variant of *O. eucalypti* with subglobose spores and in *O. fissilis*, at least their larger guttules are LBs.

like SBs and deviates in 16-spored asci. *O. olivacea* sharply differs in having ellipsoid to tear-shaped SBs with a narrow attachment to the spore wall. A monographer working with dead material would most probably overlook the autonomy of some of these species, apart from the fact that a relationship of these black apothecia with *Orbiliomycetes* is quite impossible to recognize in the dead state.

Based on the differences in SB morphology, these six species obviously do not form a monophyletic group within the *Orbiliomycetes*. They fit very well three quite distant groups of *Orbiliomycetes*, which otherwise include pale-coloured, whitish to reddish apothecia. *Orbilia patellarioides* matches the light orange *O. lentiformis* (series *Lentiformes*) in having a large lens-shaped spore body at the spore apex, and our molecular data supports this relationship. *O. olivacea* differs from the other five dark-coloured species in the absence of an ascus apical thickening and appears to be related to section *Ovoideae* of subgenus *Orbilia*. The genus *Amphosoma* is characterized by two vital characters: (1) ascospores with a spore body at both ends, (2) paraphyses and marginal excipular cells containing conspicuous guttules (VBs). Mainly because of these two features, *A. atroolivaceum* is undoubtedly closely related to the pale-coloured members of *Amphosoma*.

Another nice example of two species with a very similar spore size and shape concerns the North American *O. cucumispora* and the South European *O. cercidicola* (Fig. 6). The two species sharply differ in SB shape, also in the type of SCBs in the excipular cells. The difference in apothecial colour between the two species (pink vs. orange) becomes obscure in old herbarium material, and only the isodiametrical vs. elongate marginal excipular cells appear to be diagnostic between the two species when dealing with dead material alone, besides ecological differences.

Recognition of the living versus dead state of fungal cells. Both living and dead cells often occur within an apothecium (see p. 30–31), therefore, the recognition of the living vs. dead state of individual cells is essential for the application of vital taxonomy. This requires some exercise, but once accustomed to the involved diagnostic features, the state of the cells will mostly very easily and quickly be recognized, even without applying vital stains. Examples of the characteristics of living and dead cells are given in Figs 7–10, 24–25, 52–53, 67 (see also Baral 1992: 339 ff., figs 1–14, 15f–g, 16f–g, 21–22).

The main characteristics of dead cells are: (1) detachment and increased refractivity of the cytoplasm (Fig. 7: d–f), (2) distortion of regular lipid patterns in cells with high lipid contents, (3) loss of SBs (Figs 7: b, d; 9: c–d), (4) loss of VBs, (5) loss of SCBs (Figs 9: a–b; 87: g–h), (6) shrinkage of cells (Figs 7: a–b, d; 8), (7) inflation of the apical thickening of the ascus wall (Fig. 31). These more or less striking alterations can easily be induced in living cells, either by mechanical pressure, by briefly heating the slide, by drying out and rewetting in the case of desiccation-sensitive cells, or by adding lethal mountants to the preparation.

A differentiation between living and dead cells is also possible using vital stains (basic dyes or other cytoplasmic stains like phloxine) which serve as a proof for vitality (Fig. 7: a–c; see also Baral 1992: 340). The entire cytoplasm of dead cells is stained by these agents due to a loss of semipermeability of the plasmalemma, whereas in living cells

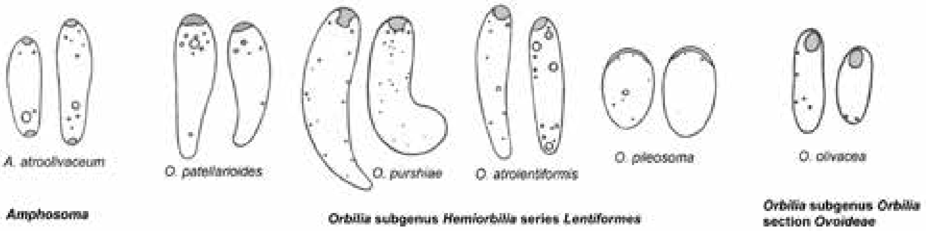


Figure 5: Living ascospores of the six known species of *Orbiliomycetes* with black apothecia. The spore bodies (tinted in grey) differ in size and shape and occur either at both spore ends or only at the apical end, in correlation with the generic affiliation of the species.

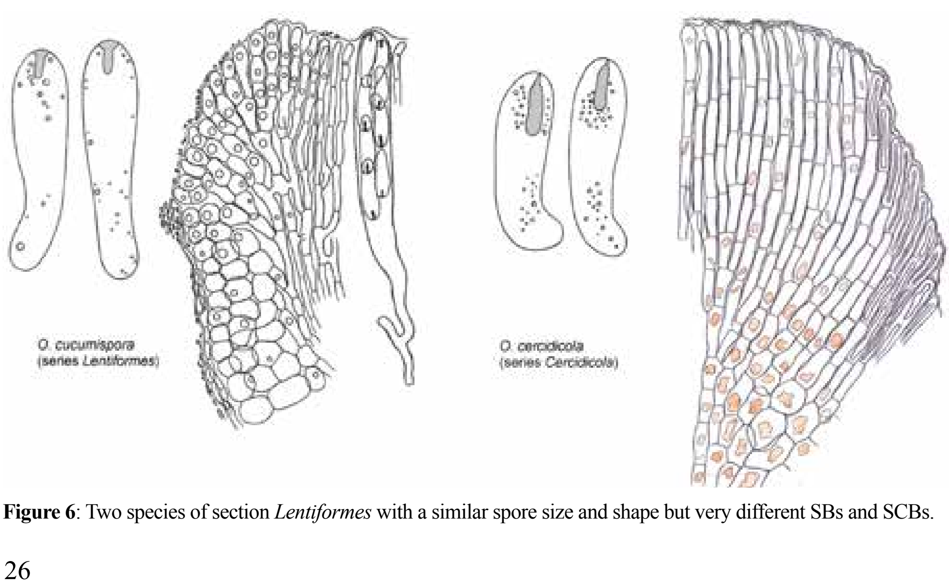


Figure 6: Two species of section *Lentiformes* with a similar spore size and shape but very different SBs and SCBs.

only the vacuoles (including VBs and SBs) are stained through accumulation (in the case of basic dyes such as CRB).

Vitality of individual cells can usually be recognized on microphotographs of unstained fungal cells made under oil immersion. However, images taken with Nomarski interference contrast are sometimes difficult to interpret because the strong contrast lowers the resolution and masks the cell contents, especially those situated close to the cell wall. Some of such images on our plates are, therefore, unclear as to their living state.

The living or dead state can often also be recognized by drawings. For instance, a number of figures in Huhtinen's (1990a) monograph clearly show living elements including turgescent asci, namely figs 36, 62, 150, 175, 180, 212, 231 and 255. Only those parts of these figures show living elements which Huhtinen marked by 'H_2O', and even here some of the depicted cells are clearly dead. For example, his fig. 231b shows three dead spores with large non-globose oil drops. In order to be precise, drawings made from aqueous mounts should be marked by a sign that indicates the living or dead state. As a further example, Scheuer (1988: pl. 12b) figured only one out of 153 ascomycetes in the living state (*Psilachnum acutum*).

Drawings or photographs made from KOH mounts sometimes have the appearance of viable material, particularly if the oil drops, which are well seen in that medium, did not form large aggregations by fusion.

Shrinking effect. When cells die in the hydrated state, they irreversibly lose turgor and thereby often show a more or less strong decrease in size (without collapsing) by losing water mainly from the vacuoles, though they remain surrounded by plenty of liquid. Thereby, the rate of shrinkage depends on the strength of turgor of the intact cell, and on the elasticity of the cell wall. Irreversible shrinkage is induced by lethal mountants, such as 50 % chloral hydrate (in MLZ), 99.5 % lactophenol (in CB_L), or 1–5 % KOH, also by mechanical influence, or by applying heat. All these treatments irreversibly destroy the semipermeable properties of the plasma membranes (see Baral 1992: 340 ff.).

The effect of shrinkage is most pronounced in asci, particularly in those ascomycetes which are capable of forcible discharge, whereas ascospores, paraphyses, excipular cells, or conidia have usually a lower turgor and less elastic walls, and sometimes do not noticeably shrink at all, although exceptions occur. That asci strongly shrink is a consequence of their ability of active discharge: forcible spore ejection requires a highly elastic ascus wall. At full turgescence, ample vacuolar water is present in the lower half of the ascus. Even though authors drew attention to this striking property of fungal cells (e. g., de Bary 1887: fig. 6, Huhtinen 1985a: 18, Baral 1992: 345, Matočec & Focht 2000: 75), the mycological community neglects the effect. Very rarely authors indicate whether their measurements refer to living or dead asci, while it can usually be assumed that they were gained from dead asci, according to the prevailing usage of studying herbarium specimens or placing fresh specimens in lethal mountants.

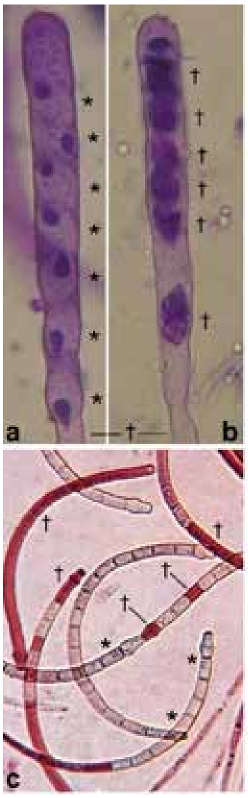


Figure 7: Recognition of the living state of cells: living cells are unstained in cytoplasmic stains (except for vacuoles and spore bodies), whereas dead cells exhibit a deeply stained cytoplasm which is often detached from the cell wall; SBs in dead ascospores strongly lose contrast or get entirely invisible). — **a–b**, **d**. living and dead spores inside dead asci (*Orbilia arizonensis*, **a–b**. H.B. 8002a, in CRB: SBs in living spores deep blue-violet; **d**. H.B. 4566, in H_2O); **c**. living and dead cells occurring mixed in multiseptate ascospores (*Ophiobolus acuminatus*, from Erb & Matheis 1983 fig. 119, in phloxine); **e**. paraphyses with dead terminal cells and living lower cells (*Orbilia commarosa*, H.B. 7302b, in H_2O); **f**. living and dead ascospore (*O. megaocculta*, H.B. 6775, in H_2O).

Particularly within the *Orbiliomycetes*, considerable differences in size between moderate and full turgescence complicates **ascus** measurements (see Figs 24, 43: d). Fully turgescent asci of *Orbilia* spp. have roughly a 1.5 × higher volume compared to asci with moderate turgescence. An evaluation of data from 12 species revealed an ascus volume at moderate turgescence of only 60–75 % of that at full turgescence. Asci of moderate turgescence show again a roughly 1.5 × higher volume compared to dead, non-turgescent asci, showing a shrinkage during killing of likewise 60–75 %. The volume difference between full turgescence and complete loss of turgescence lies at about 40–55 %. Differences in ascus length and width are in the range of 10–15 % when asci shrink for ~25–40 %, and in the range of 20–25 % when asci shrink for ~45–55 %. Depending on the species or genus, the shrinkage factor may differ somewhat between length and width: for instance, a living ascus of 100 × 10 µm may measure in the dead state 80 × 8.5 µm, or 85 × 8 µm. These values of shrinkage more or less concur with those observed in other classes of ascomycetes, such as *Leotiomycetes*, *Lecanoromycetes*, *Pezizomycetes*, and *Dothideomycetes*.

The percentage of shrinkage is best evaluated from a single ascus by applying lethal agents, or during spore discharge. The above values of shrinkage were mainly evaluated by comparing measurements of living and dead asci from several collections. In a few species (e. g., *O. sarraziniana*, *O. luteorubella*, *O. rosea*) hardly any shrinkage (or only 5–10 %) in ascus length could be noted, although data from numerous collections was available.

Not only ascus turgor determines ascus size. Dead asci which contain living spores are often slightly wider than those containing dead spores because the living spores are wider and

Figure 8: Shrinkage of asci and elongation of pars sporifera (in water). Left: living state, right: dead state; both asci contain living mature spores (*Orbilia ocellata*, H.B. 9151a).

may press against the lateral ascus wall. Therefore, dead asci should be measured preferably after adding killing agents like KOH. Also the ascus stipe is distinctly thinner in the dead state. Since asci scarcely shrink in length in the region of the stipe, ascus stipes appear in the dead state seemingly longer in comparison with the upper part of the ascus. Similarly, perforations in croziers increase in the dead state because their arches shrink in thickness.

The stronger shrinkage of asci compared to paraphyses evokes that, in the living state, asci often protrude beyond paraphyses whereas, in the dead state, paraphyses protrude beyond asci. Living asci of *Hyalorbilia* may protrude 1–2 µm beyond paraphyses by lifting the overlying exudate, which dead asci never do. Similarly, in those species of *Orbilia* with spathulate to mammiform paraphyses, their tips may protrude 0–7 µm in the living state but 3–10 µm in the dead state. Fully turgescent asci of *Orbilia xanthostigma* project 7–10 µm beyond the hymenial surface (Fig. 45), while those of moderate turgescence are still slightly shorter than the paraphyses (see also Pl. 875: 15).

Living **ascospores** of *Orbiliomycetes* in water mounts are usually distinctly larger compared to dead spores mounted in any medium. (Figs 9, 52, 53: b; 67). An evaluation of data from 15 species of *Orbilia* revealed that the volume of dead spores is around 75–85 % of that of living spores, but sometimes only 60–70 % (e. g., *O. flavida*) or also 90–95 % (e. g., *O. cercidicola*, *O. sarraziniana*). Both length and width of dead spores lie in the range of about 85–98 % of the living spores. However, the spores often show a stronger shrinkage in width than in length, but sometimes also the reverse was noted.

Within the ascomycetes, shrinkage of ascospores varies considerably among the groups. In four species from four different genera of *Helotiales* examined, shrinkage varied between about 6 and 18 % in length, and between 7.5 and 25 % in width (Baral 1992: 345). These differences are probably mainly due to differences in spore wall elasticity among the genera: highly elastic spore walls provoke high degrees of shrinkage whereas inelastic walls may collapse when placed in high-concentrated media.

Shrinkage and collapsing is not only observed between living and dead spores, but also under dehydration without loss of viability, either by a high osmotic pressure in the surrounding medium, or by dehydration in dry air. Inside living mature asci the spores are often considerably smaller, especially narrower, compared to discharged spores, due to osmotic effects (Baral 1992: 350). Considerable spore shrinkage occurs, e. g., in the genus *Hymenoscyphus*: spore width inside turgescent asci is here around 85–90 % of free spores. Measurements of such compressed spores should, therefore, be avoided or separately stated.

Within the *Orbiliomycetes* we experienced that living mature spores inside asci of moderate turgescence generally did not noticeably deviate in size from recently ejected spores, or from living spores inside dead asci (see Fig. 8), obviously due to the comparatively low elasticity of the spore wall in this group of fungi. However, measuring dead spores inside dead asci was often troublesome and resulted in ambiguous values because of a problem in the exact recognition of the spore wall (see p. 11, also Fig. 10: d–e)

Inside fully turgescent asci the spores often collapse by dehydration and are usually quite obscured within the spore cluster that neither their shape nor their contents can adequately be studied (Fig. 43). In fully turgescent asci of the *Helotiales* collapsed living spores were never seen, apparently because of a more elastic spore wall.

Also **conidia** show a varying rate of shrinkage when treated, e. g., with KOH (Fig. 9: a–b). An evaluation on six species of the genera *Lecophagus*, *Hyalorbilia*, and *Orbilia* revealed a volume decrease of dead conidia to around (55–)70–80(–90) % of the volume of living ones. The linear decrease in size was thereby to around (80–)85–95(–100) % in both length and width, thereby shrinkage in width was sometimes a little higher than shrinkage in length.

If measurements did not markedly differ between living and dead conidia, this was either a result of variation between populations or, in the case of their width, a result of artificial flattening. Particularly cases of very broad conidia cause problems of artificial flattening, even in the living state: such conidia may get compressed by the cover slip as soon as the water beneath evaporates below a critical level. Thereby the width considerably increases, resulting in erroneous values. Adding enough water to living conidia instantly removes the effect.

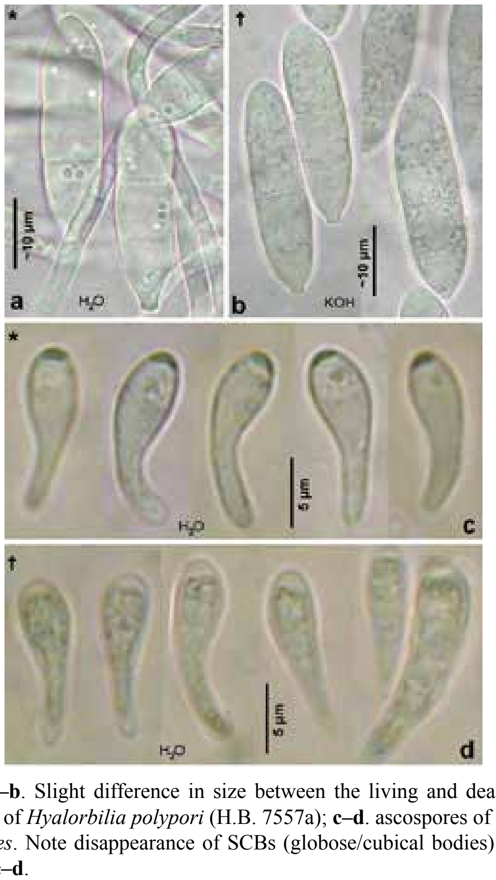


Figure 9: **a–b**. Slight difference in size between the living and dead state. a–b. conidia of *Hyalorbilia polypori* (H.B. 7557a); **c–d**. ascospores of *Orbilia patellarioides*. Note disappearance of SCBs (globose/cubical bodies) in **a–b** and SBs in **c–d**.

Shrinkage may also affect spore shape: curved (falcate or helicoid) ascospores in section *Arthrobotrys* are generally distinctly less curved in the dead state (in water or KOH) and, therefore, slightly shorter in the living state when measured in situ (see Fig. 52: c). The actual length is probably slightly longer in living spores but can only approximately be measured.

Vegetative (somatic) cells of paraphyses, excipulum, and anchoring hyphae also shrink to an often considerable extent when they die, therefore, measurements in the literature are also here generally smaller than from living samples. In an evaluation on 13 species of *Orbilia*, the volume of dead terminal cells of paraphyses was around (50–)60–75(–85)% of that of the living ones. Thereby, the length of the dead cells was around (80–)85–95(–100)% of the living cells, whereas the width showed a slightly stronger shrinkage to (70–)80–90(–95)%. Cells of the ectal and medullary excipulum and of anchoring hyphae usually shrink to a similar rate, for instance, cells at flanks for 20% in both length and width in *Hyalorbilia lunata*, or anchoring hyphae of *Lecophagus vermicola* for 7–16% in width.

Diagnoses of ascomycetes currently describe how the spores are arranged within the asci. Such descriptions are misleading, however, because **spore arrangement** strongly depends on ascus turgor (see also Baral 1992: 348). Despite the strong shrinkage of asci during turgor loss, the pars sporifera often elongates because of a reduced width of the asci, especially if the spore remain alive. During this irreversible rearrangement, biseriate spores often become more or less uniseriate, at least in the lower part of the pars sporifera. As a peculiarity of the *Orbiliomycetes*, the pars sporifera in the living asci distinctly contracts when the spore cluster is formed at full turgescence. At this stage the pars sporifera has a length of only 65–80 or even 50–65% of that at moderate turgescence, while in dead, non-turgescent asci it is about 110–120% of that at moderate turgescence. Yet, anomalous values of the length of the pars sporifera may infrequently occur, for two reasons: (1) if some of the spores abort prior to maturation, the pars sporifera is shorter than usual, (2) if a gap between the spores or especially between the ascus apex and the upper spores exists. Such gaps were consistently subtracted when the pars sporifera was measured.

Frequency of mature asci and ascospores. In the *Helotiales* or *Pezizales*, free ascospores often occur in rather high abundance when mounting a mature fresh apothecium in water. Spores are ejected from many asci within a few seconds or minutes in a lot of genera. But some genera behave similar as members of *Orbiliomycetes*: often only very few free spores are found in a squash mount, although plenty of mature living asci are present. In our experience, this physiological difference is somewhat correlated with desiccation tolerance: many desiccation-sensitive, short-living species (e.g., *Sclerotiniaceae*) readily liberate their spores, whereas predominantly xerobiotic species very rarely do so, sometimes even if IKI, an efficient stimulans for spore discharge, is added to a water mount.

Therefore, fresh mature apothecia of, e.g., *Hymenoscyphus*, *Lachnum*, *Mollisia*, or *Sclerotinia* are usually rather rich in free spores, whereas those of *Orbilia*, *Durella*, or *Calycellina* are often poor herein. However, in some collections of *Orbiliomycetes* free spores were encountered in considerable abundance in both fresh and herbarium material, irrespective of being desiccation-tolerant or not. Desiccation-sensitive discomycetes usually lose a lot of their mature spores via spore discharge during drying of a specimen, because dry air generally induces puffing. Yet, the paucity of spores in herbarium specimens of *Orbiliomycetes* can hardly be explained this way because we never observed simultaneous spore release in this group.

Visibility of spores inside asci. In recently collected apothecia the ascospores are seen with high contrast inside the asci without applying staining agents (Fig. 10: a, see also Fig. 57: c–d), if a number of rules are followed: (1) spores and preferably also asci must be in the living state, (2) tap water must be used as mountant, (3) oil-immersion (magnification 1000×, better 1250–1500×) must be applied, (4) any strong pressure on the cover slip must be avoided. An ordinary light microscope with a comparatively high numerical aperture (1.25) of the 100× objective is completely sufficient, no phase contrast or other equipment is necessary.

A frequent experience with dead herbarium material of *Orbiliomycetes* is that collections are thought to be immature since no spores are seen inside the asci (Fig. 10: b, see also Figs 24; 25: c right), and free spores can hardly be found. Nevertheless, such specimens are usually fully mature. Application of cytoplasmic stains or, alternatively, cell wall stains to a KOH-mount usually makes the spores better visible (Fig. 10: c–e) and demonstrates that mature asci are present in great number (see also p. 11).

Inappropriate preparation methods applied to dead material are apparently the reason, why the original descriptions of rather many species of *Orbilia* are either devoid of spore data, or incorrect concerning spore shape or spore numbers. Even workers who reexamined type material in the last decades were unable to emend such diagnoses. For example, Berkeley (1875) could not find any spores when describing *Peziza saccharifera*. In the present study of the type specimen, spores could be seen inside many asci in KOH+CR mounts, and its identity could be much more precisely resolved. *O. siculispora* is another example with a very characteristic type of narrow ascospore with an acuminate apex and a small, thickened basal part separated from the main part of the spore by a strong constriction (see Fig. 52: a). This characteristic spore shape could be seen in the holotype in a KOH+CR mount in- and outside asci, but was completely overlooked by Cash (1938) who obviously saw only the thickened basal part of the spores.

The reason why ascospores become invisible inside asci in dead material can be explained as follows: the refractive spore wall optically disappears on account of a dehydration of both asco- and sporoplasm (Baral 1992: 354). In the living state the ascoplasm is strongly hydrated and mainly represents a big vacuole that contains the spores (Fig. 25: a–b). The ascoplasm is, therefore, highly transparent and non-refractive, whereas in the dead state it becomes dehydrated at a considerable rate and, therefore, very intransparent and more or less refractive (Fig. 25: c, d left). The spores remain clearly visible inside the dead asci only in species with more rigid spore walls, for instance in the *Pezizales*. This phenomenon of invisible spores inside asci is a general one, and is also common in the *Helotiales*, if the spores have delicate and hyaline walls. Because of this effect, drawings of dead asci in the literature often do not show the included spores (see also p. 11).

Recognition of maturity – Definition of the term 'mature'. A general observation in all groups of sporulating fungi is that the features of the spores as seen under the light microscope

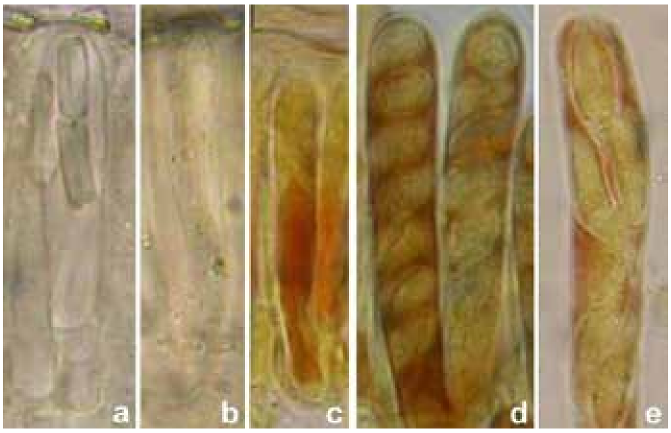


Figure 10: **a–e**: Mature asci of *Hyalorbilia* and *Orbilia* (**a**. living state in water, spores visible with high contrast; **b–e**. dead state (**b**. in KOH, spores hardly visible; **c–e** in KOH+IKI, spores better visible, glycogen stained red-brown, **d–e**: the unstained spore wall is difficult to locate, and a light zone may easily be mistaken for a spore sheath); **a–c**. *H. polypori* (**a**: H.B. 7943b, **b**: H.B. 7971, **c**: H.B. 7965b); **d**. *O. ophiosoma* (H.B. 8095d); **e**. *O. bicknellensis* (H.B. 5669).

change considerably during the different development stages of spore formation and germination. The observed changes concern characters of the cell wall (spore shape, size, septation, pigmentation, ornamentation, and sheaths) as well as those of the living sporoplasm (lipid bodies, spore bodies, nuclei, vacuoles, glycogen). It is, therefore, inevitable for accurate taxonomic work to compare spores at the same development stage. Although there is general agreement that the mature stage of a spore should be used in fungal taxonomy, the definition of the term mature strongly varies among authors. Concerning the ascomycetes, a frequent opinion is that only free ascospores can be considered to be mature. However, this thumb rule does by no means warrant exclusion of immature or overmature stages.

Spores actually do not change their appearance during the process of forcible ejection, apart from some water uptake by the sporoplasm and, therefore, a greater volume after ejection in a water mount. The opinion that spores inside asci are less mature than free spores originates from the study of herbarium specimens. Fact is that the focus on free spores offers only a slight chance to gain more compatible data. Free spores may actually be less developed than those within asci, since (1) free spores may have been squeezed out of broken or cut immature asci, and (2) spores inside dead asci can be overmature and may even germinate inside them. Although the study of herbarium specimens allows to recognize different maturity stages of ascospores, the terms immature, mature, and overmature can credibly be applied only if living asci are present.

Developmental changes in spore wall features such as formation of septa following nuclear divisions, wall pigmentation, and ornamentation are visible in both living and dead spores. Yet, developmental changes in spore contents need to be studied in living spores, due to the frequent confluence or optical disappearance of characteristic structures in the dead state. Changes in the cytoplasm during spore development concern the formation of LBs, glycogen, and vacuoles in many groups of ascomycetes, and, as a peculiarity of the *Orbiliomycetes*, the formation of spore bodies (Fig. 69). In our experience, all these structures in living spores do not allow precise definition of maturity, if only dead asci are present. For example, the occurrence of septa, or a high lipid content, do not necessarily mean that these spores are mature, in comparison with spores without septa or with a low amount of lipid in the same preparation.

Maturity of ascospores was redefined by Baral (1992: 375) who emphasized that the term 'mature' can only properly be applied if restricted to those spores being forcibly ejected from turgescent asci in a water mount. This definition requires living asci capable of active spore discharge. Mature asci are those which are turgescent enough to discharge their spores within some minutes or hours as a maximum. Such asci can be recognized by having a single large vacuole that includes the mature spores and ample water around and below them. Immature living asci contain immature spores and are recognized either by numerous small vacuoles, which are clearly visible particularly below the pars sporifera (Baral 1992: figs 15b, 16b), or by the abundant presence of lipid bodies in the ascoplasm (l.c.: fig. 43a).

This definition of maturity comprises also free spores a few hours after ejection. However, exposition of ejected spores to a humid condition for about 5–10 hours at room temperature may induce metabolic ageing processes such as swelling, consumption of the lipid content, formation of septa, or in the *Orbiliomycetes* retraction in length and increase in width of elongate SBs (Figs 11: e–f, 70) and eventually regression of the organelle. Especially in senescent apothecia such overmature spores are often found inside dead asci if the asci failed to manage spore ejection. If a rehydrated herbarium specimen contains only dead asci, it is generally impossible to determine whether these asci got dead during drying or how long they might have been already dead prior to drying. As a consequence, spore maturity cannot be estimated without the presence of living asci.

This definition of maturity of spores is in discordance with a current opinion which tends to use 'mature' for overmature stages, particularly for spores which are discharged when hyaline but later become brown. It must be noted, however, that such spore ageing may exceptionally occur even within living asci, particularly if apothecia are kept in a moist chamber over several days. Such cases of apothecial senescence are characterized by a high variation among the spores inside the living asci, in contrast to well-developed apothecia showing a high consistency in spore characters.

As a peculiarity of *Orbiliomycetes*, living asci undergo two subsequent development stages (see Fig. 24: E–F) which both may be termed 'mature'. The later stage of the two (F) shows maximum turgescence, with all spores dehydrated and sticking together in a cluster. However, since spores of the earlier stage (E) do not morphologically differ from free spores shortly after ejection, both may be attributed the same stage of maturity because, during turgor increase, the spores seem to undergo merely a reversible dehydration process.

Fresh and dry versus living and dead state. Desiccation-sensitive (hygrobiotic) apothecia are defined here by the inability of their asci to survive more than about one day or even less than one hour after complete drying. Therefore, in fresh apothecia of hygrobiotic species most cells are usually alive, and in dry apothecia most of them are dead. In contrast to this, apothecia of a majority of *Orbiliomycetes* are desiccation-tolerant (xerobiotic), and many other groups of fungi share this peculiarity. Xerobiotic taxa are usually collected in the dry, completely dehydrated state, in which all types of cells are still viable though dormant. Here the term fresh appears inappropriate because mature apothecia have endured a long-lasting period of repeated drying and

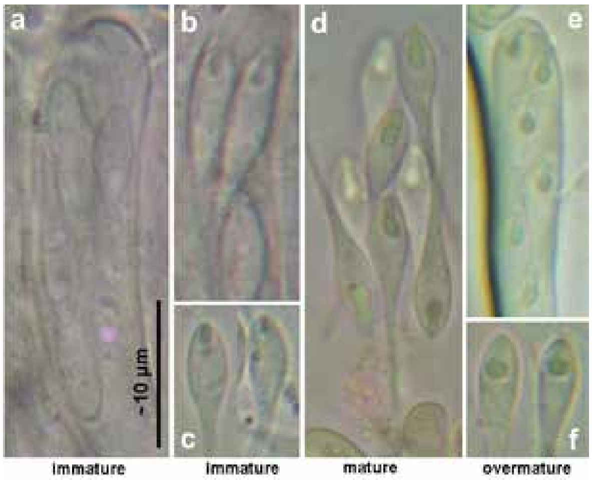


Figure 11: Immature (**a–c**), mature (**d**) and overmature (**e–f**) spores (**a**. inside living ascus, **b**, **e**. inside dead asci, **c**. liberated by pressure, **d**. shortly after active spore discharge, **f**. ejected probably a longer time ago). The development stage of the spores in **b–c** with their rather short and narrow SBs is evaluated from observations in other collections of this species, because such spores were here only seen inside dead asci. Those spores in **e–f** are estimated as overmature because such short and basally inflated SBs have never been seen inside living asci of this species. — *O. aristata* (28.X.2007, phot. P. Perz).

rewetting during their development. Depending on the climatic condition, this period may take several years. Vitality of such rehydrated apothecia is easily demonstrated by active spore discharge and subsequent germination on agar.

However, very recently collected fungi may contain a varying number of dead asci, irrespective of being desiccation-tolerant or not, or collected in the fresh or dry state, even if looking macroscopically sound and being carefully mounted. Of course, a few asci always lose turgor by mechanical influence when taking fragments out of the hymenium. For all these reasons, a water mount frequently contains both living and dead asci at the same time, and recognition of the living state is obligatory in order to restrict measurements and other data on either of the two states (see p. 26–27). An often occurring situation in water mounts is the presence of living spores within a dead ascus (see Fig. 25: c–d: states 2a, 2b), either because asci are more sensitive to mechanical pressure due to their larger width, or because ascospores tolerate desiccation for a longer period of time than asci do.

Particularly in xerobiotic species, some or all asci, paraphyses, or ascospores may be dead, although immediately examined after collecting. The external appearance of rehydrated apothecia of such collections thereby often does not deviate in the least from those in which most of the cells are viable. There is no doubt that the cells of such apothecia have been already dead in the field. Frequently, the excipular cells are still viable while most of the hymenial elements are dead. One could imagine that a longer period of drought or some other stress like frost may be responsible for these mortality effects. It can be assumed that ascomata with a viable excipular tissue are able to produce new asci during more favourable conditions. Sometimes the hymenial elements were dead only in a portion of the population, while the rest showed full vitality. Undoubtedly, the latter represent the younger portion of the population.

When collecting in temperate regions, all cell types of xerobiotic species often showed a certain sensitivity to repeated drying and rewetting. After rewetting for the first time, most cells were usually alive. Yet, after drying at room temperature and rewetting a second time some hours or days later, a major part of the cells were dead. In other cases, particularly in populations from semihumid to arid areas, no such mortality rates were observed after repeated rewetting and drying in the laboratory. A problem with the scanning of branches is that minute apothecia can hardly be detected without rewetting the entire substrate.

Consequently, microscopic study must be done immediately after detecting a population, otherwise valuable vital characters may get lost. The observed mortality is possibly avoided under natural conditions by longer periods of hydration.

Conservation of vital characters. A frequently raised question concerns the conservation of vital characters. Is it possible to preserve SBs or SCBs in herbarium specimens or permanent slides? After testing various methods, we came to the conclusion that conservation for light microscopic study is impossible. Fixatives such as formaldehyde, high-concentrated alcohol, or Carnoy's solution (a mixture of 96 % ethanol, chloroform, and glacial acetic acid) are lethal agents, which irreversibly destroy the refractivity of spore bodies or SCBs. Also when treating SBs with vital stains, such as CRB, they become irreversibly invisible when adding such lethal reagents afterwards.

However, ultrastructural studies have shown that SBs are clearly visible under the TEM when fresh specimens are fixed and stained (see Fig. 71). Likewise, Woronin bodies can very clearly be demonstrated with the TEM in fixed material, although in dead specimens they are impossible to see under the LM. Whether this method works also with dead herbarium material is unknown.

Experiments on the prolongation of vitality during long-term storage were not undertaken. As practised with the storage of dry seeds at -18 °C in the arctic seed bank on Svalbard, storage of dry apothecia of xerobiotic taxa at low temperature might extend the period of time during which they remain viable. Storage in mineral oil as practised for living cultures might offer another method of conserving vital characters, besides further techniques such as liquid nitrogen storage at ultra low temperature (Smith & Onions 1983), or storage in sterile water (Harris undated).

A method that extends the life span of a population of a xerobiotic species to a period of about 5 years imitates the sparse and occasional precipitation under natural condition. Such experiments were only exceptionally undertaken, thereby an extension from about 3.5 to more than 4.5 years was achieved in an Australian collection with ca. ten different species of *Orbilia* (see p. 159).

The loss of visibility of taxonomically important characters, such as spore bodies (SBs) and unstable plasmatic bodies (SCBs) in species of *Orbiliomycetes*, pertains also to the rules of the International Code of Nomenclature (ICN) regarding valid description of new taxa. According to Art. 40.5, 'the type of a name of a new species or infraspecific taxon of microscopic algae or microfungi may be an effectively published illustration (...) if it is impossible to preserve a specimen that would show the features attributed to the taxon by the author of the name'. Since plasmatic structures cannot be preserved by conventional methods of herbarization, the taxonomic value of illustrations is of particular interest in comparison with herbarium material. The application of Art. 40.5 on teleomorphs of *Orbiliomycetes* appears to fail because of the definition of 'microfungi', which implies the absence of multicellular sporocarps, although other definitions emphasize their invisibility with the naked eye. For instance, Barber & Keane (2007) included also minute ascocarps under the term 'microfungi'.

The main intention of Art. 40.5 appears to be that characteristics of certain algae or fungi cannot be preserved because of 'technical difficulties of preservation'. Hence, not their minute size is crucial, but their unstable microstructures cause the trouble. With this understanding, a majority of *Orbiliomycetes* fall in this category, as they become indeterminable in the dead state. Molecular techniques, which enable to distinguish cryptic or otherwise difficult species, might solve the problem in the future even regarding minute and sparse or even disappeared apothecia. In a few cases in which no apothecia remained after study and no piece of substrate was preserved, we rely on Art. 40.5 when describing new species based merely on illustrations serving as holotype.

MORPHOLOGY OF THE TELEOMORPH

General remarks. The apothecia (teleomorph) of the *Orbiliomycetes* provide a fairly large number of characters, particularly when including vital characters. These comprises elements of the sterile (vegetative, somatic) parts of the apothecium (anchoring hyphae, ectal and medullary excipulum, hairs, paraphyses, glassy processes, and exudate) and the fertile (generative) parts (asci, ascospores). Although included in the scope of the teleomorph, the anchoring hyphae at the base of apothecia correspond to the mycelial hyphae on which the anamorph develops. Many of these characters are more or less consistent within a taxonomic group above the species, hence they have no or limited value for species delimitation. The frequently observed morphological variation within a species often diminishes the taxonomic value of characters.

A remarkably high level of morphological diversity of microscopic features has developed in the *Orbiliomycetes*, which makes taxa recognition comparatively easy in many cases. This diversity is largely confined to a few elements of the teleomorph, the most important being the ascospores and their SBs. Tab. 2 gives an overview of the taxonomic relevance that the different characters can be attributed, as experienced in the present study.

Table 2. Selected characters of the teleomorph of *Orbiliomycetes* and their estimated taxonomic relevance for species delimitation in comparison with delimitation of infrageneric and generic groups (* = low, ***** = high). Characters which are more or less exclusively visible in the living state are italicized.

Element	Character	Species level	Infrageneric level	Generic level
Apothecia	size, shape, *colour*	**	**	**
Asci	shape and thickness of apical wall	*	****	****
	spore number in ascus	*****	**	**
	orientation of spores in ascus	***	**	*
	ascus base	-	**	*****
Ascospores	size, shape	*****	***	**
Spore bodies	*number, size, shape, curvature*	*****	*****	*****
Paraphyses	shape of apex	****	***	**
	distribution of septa	*	***	***
	branching at upper septum	*	**	**
Excipulum	size of cells near base	*	*	*
	type of marginal ectal excipulum	*	***	**
	presence of septate hairs or glassy processes at margin	***	***	**
SCBs	*type, colour*	****	***	**
VBs	*type, refractivity, colour*	**	**	***
Exudate	type, thickness, *colour*	***	***	***
Anchoring hyphae	width, wall thickness	*	-	***

Apothecia

Similar to other groups of *Ascomycota*, quite a large number of species of *Orbilia* or *Hyalorbilia* closely resemble each other in external appearance so that only their microscopic features allow identification at the species level. A few species are more or less characteristic in apothecial colour and shape, or their margins being hairy or toothed, which allows to suspect their identity in combination with substrate and geographical origin. As a further complication, macroscopical variation within a species is often comparatively high. Populations with very different colours may belong to the same species. For example, *O. sarraziniana* and *O. eucalypti* may occur with whitish, pale (or bright) rosaceous-lilaceous, or bright yellow-orange apothecia. Also *O. comma* occurs in pale cream or bright orange colours. However, whitish *O. leucostigma* and yellow *O. xanthostigma* were found to belong to two species, differing greatly in the ITS rDNA data, though growing sometimes intermingled. Populations varying between almost smooth and distinctly toothed apothecial margins (e. g., *O. flagellispora*, *O. austrocylindrica*) are considered by us to belong to the same species, whereas *O. aristata* with usually indistinct teeth and *O. subaristata* with very distinct teeth are separable also by their molecular data.

In some species the external appearance of apothecia permits recognition of their generic, infrageneric, or sometimes specific relationship. However, often such characteristics are quite insignificant, for instance in the case of small whitish apothecia, which may belong to either *Lecophagus*, *Pseudorbilia*, *Amphosoma*, *Hyalorbilia*, *Orbilia*, or even to a member of the *Helotiales*. Large apothecia of *Orbilia leucostigma* often closely resemble those of *Hyalorbilia inflatula* and are, therefore, easily confused.

Size. Mature hydrated apothecia of *Orbiliomycetes* show a wide range in size. The smallest taxa measure about 0.05–0.15 mm diam. and are, therefore, invisible with the naked eye. Such a size is not rare in desiccation-tolerant taxa. The prevailing diameters lie between 0.3 and 1 mm, and the largest species attain 2–3 mm, very rarely 4–7.5 mm (*O. alba*). Dry (living or dead) apothecia are distinctly smaller and range at (50–)60–75(–80)% of the fully hydrated state (see Fig. 12). Also when comparing fully hydrated apothecia, dead apothecia are slightly smaller than living apothecia: a test with KOH applied to fresh apothecia of *O. leucostigma* yielded (7–)10–13(–18)% shrinkage, i.e., a diameter of 1 mm was reduced to (0.82–)0.87–0.9(–0.93) mm.

Although apothecial size was found to vary considerably in many species, it can be attributed a certain diagnostic value. A tendency of desiccation-tolerant apothecia to a smaller size can be noted: on average, apothecia of desiccation-sensitive species of *Orbilia* and *Hyalorbilia* are distinctly larger. However, there exist many exceptions, and the reason for this tendency is unclear. For example, the highly desiccation-tolerant species *O. carpoboloides*, *O. siculispora*, *O. euphorbiae*, *O. denticulata*, and *O. anigozanthi* have rather large apothecia (~0.5–2 mm), whereas the desiccation-sensitive species

Pseudorbilia bipolaris, *Hyalorbilia ulmi*, *H. fomentarii*, and *Orbilia flavovacuolata* have rather small ones (~0.1–0.3 mm). Possibly, the depth of substrate decay influences apothecial size. Due to the often very long-lasting dryness and short periods of moisture, xeric substrate is often only superficially rotten, because only the outer layers of the host tissue are soaked with water and available as a nutrient source for the mycelium.

Gregarious versus scattered growth. The water relations in the inhabited substrate and the depth of decay might influence not only apothecial size, but also how dense apothecia grow in a population. Apothecia growing gregariously in more or less large populations are typical of desiccation-sensitive species. One of the most impressive examples is *O. epipora* (series *Neodactylella*) which densely covers large areas with thousands of apothecia. Other desiccation-sensitive species, e. g., *O. polybrocha* and *O. orientalis* (series *Drechslerella*), are usually found in small quantities, perhaps because they are adapted to nematodes as prey. Desiccation-tolerant species mostly grow in scattered to subgregarious populations, or gregariously in small groups. A few exceptions confirm this rule: at least two species, *O. pilifera* and *O. comma* (section *Aurantiorubra*), usually grow densely crowded over large areas of the inner surface of rotten bark detaching from *Ulmus* trunks.

Stipe and receptacle. Although the apothecia of a majority of *Orbiliomycetes* are more or less sessile, a short and broad, often hidden stipe is frequently present. Such short stipes are best seen in median section due to being immersed in the substrate, the covering biofilm, or hidden by the subiculum. The stipes are either obconical to cylindrical and thereby sharply differentiated from the receptacle, or ill-defined by forming an indistinct protrusion of the narrowed base. Sharply differentiated stipes are quite typical of the genus *Hyalorbilia*, but also of some species of *Orbilia*. As a rare exception, the stipes are as long as or even longer than wide (*H. erythrostigma*, *H. anonyma*, *O. aureocrenulata*, *O. pilosa*, *O. orientalis*). The comparatively small apothecia of many desiccation-tolerant species are broadly sessile and without any trace of a stipe, but also very large apothecia may be stipeless and broadly attached to the substrate (*O. anigozanthi*, *O. alba*). The length of the stipes ranges from usually 10–50 up to exceptionally 500–800 µm, the width from 40–70 up to 100–300 or even 700 µm.

The thickness of the receptacle at the junction with the stipe lies between ~35–60 and 150–280 µm, while the total height including the stipe may attain up to 300–800 µm. Receptacle thickness mainly correlates with ascus length and excipulum thickness, less so with apothecial diameter. For instance, *O. alba* has very large apothecia (2–6 mm diam.) but rather small asci, and the unstalked apothecia are comparatively thin (80–200 µm). In contrast, *O. pleistolilacina* has small apothecia (0.15–0.45 mm diam.) but very long asci, and the likewise unstalked apothecia are 180–270 µm thick. The thickness of the receptacle may either be rather equal from base to margin, or often gradually attenuates towards the margin, especially in *Hyalorbilia*.

Superficial vs. erumpent. Apothecia of desiccation-sensitive taxa grow mostly superficial on the surface of the substrate. In contrast, the base of desiccation-tolerant apothecia is often partially or entirely immersed in splits of the decomposed outermost zone of the host tissue. Sometimes the entire apothecia are immersed or hidden within clefts or holes in bark or wood, or are more or less embedded up to their mid flanks in a layer of algae and black yeasts mixed with remains of host tissue. An immersed growth may be simulated if apothecia grow on decayed erumpent pyrenomycetes. For example, apothecia of *O. carpoboloides* grow superficially on old perithecial stromata, which rupture through the periderm of the host long before the apothecia of the *Orbilia* appear.

Outline. Hydrated apothecia of *Orbilia* are usually more or less roundish in outline. Large apothecia often develop an undulating margin. An elliptical shape is observed when growing immersed in fissures of the substrate, due to limited space in lateral direction. When growing densely aggregated, the outline becomes irregularly shaped by mutual 'pressure'. On drying, the apothecia often become more undulating and irregular (Fig. 12: g–j), sometimes hysteriform (Fig. 12: c).

Disc. The hymenial disc is usually flat when hydrated, or may be slightly to strongly concave or convex. In large apothecia it is sometimes centrally depressed (umbilicate) or otherwise uneven. Young immature apothecia have frequently a concave disc, but certain species retain concave discs at full maturity: for instance young *O. carpoboloides* has cup-shaped or almost urceolate apothecia which later become saucer-shaped due to a still raised margin. In other species the apothecia soon develop flat discs which later become more or less convex.

When placing a median section of an *Orbilia* apothecium in water and adding a cover slip, a previously flat hymenium gets more convex due to heaviness of the cover slip. This pressure drifts hymenial elements more apart than excipular texture because of a looser cohesion of hymenial elements. Hymenial elements of *Hyalorbilia* are much more agglutinated in a gel, therefore, the effect is here much less pronounced. Reducing the heaviness of the cover slip, e. g. by adding ample water, reestablishes the natural condition.

Dry apothecia are more or less contracted and usually show a deeper colour than in the hydrated state (Fig. 12: i–j), sometimes even a change in colour (e. g., from yellow to red, Fig. 12: k–l). The hymenium becomes more concave and the margin is much more raised and incurved (Fig. 12: a–b). This is due to shrinkage of the hymenial elements in both length and width and contraction of the medullary excipulum, whereas cells of the compact ectal excipulum are less shrinkable. If the apothecia turn hysterioid in the desiccated state and the margin is hairy, the disc may completely be concealed (Fig. 12: c–d). Erumpent, basally immersed apothecia may deeply retract between the host fibres in the dry state and hereby become almost invisible (Fig. 12: e–f). Complete rehydration of dry, living or dead apothecia may roughly take between ~10 sec and 1 min.

Margin. The apothecial margin of *Orbiliomycetes* is usually more or less smooth and protrudes only slightly or not at all beyond the disc. In a comparatively small number of species the margin is conspicuously raised and often finely crenulate or sometimes strongly dentate or hairy (see p. 85 ff.). Species with such a feature were formerly placed in *Habrostictis*, *Hyalinia*, and *Orbiliaster*. Although most of the species with a hairy or toothed margin are desiccation-tolerant (Fig. 13: f–j), some are not, e. g., *Orbilia pilosa*, *O. polybrocha* (Fig. 13: l), *O. crenatomarginata* (Fig. 13: k), and *Hyalorbilia citrina*. As a rare abnormity, marginal elements were formed in the centre of the disc (e. g., *O. pseudoaristata*, Pl. 524: 2a, 3g, 4c).

Figure 12: Apothecia in dry state and after rehydration (all in living state, image pairs show the same apothecia and have the same scale); **a–b**. median section, showing increase in thickness and diameter during rehydration, change from cupulate to flat; **c–l**. apothecia in situ, changing size, outline, and colour. — **a–b**. *Orbilia aurantiorubra* in median section (H.B. 8130); **c–d**. *O. spermoides* (H.B. 7517), **e–f**. *O. cryptogena* (H.B. 8055a); **g–h**. *O. comma* (H.B. 8505), **i–j**. *O. trapeziformis* (H.B. 9139), **k–l**. *O. xanthoguttulata* (H.B. 7915b).

Pigmentation. Apothecia of *Orbiliomycetes* are usually light-coloured, varying from unpigmented (hyaline, whitish-greyish) to different shades of reddish (orange to rose or sometimes lilaceous) and yellowish (chlorinaceous, golden- to sulphur-yellow, ochraceous). A few species are dark-coloured (purplish-brown, dark purple-lilac, black-olivaceous). Pigments that occur in *Orbiliomycetes* probably belong to different groups of chemical compounds and are located in four different microstructures (see Tab. 10).

Apothecial pigmentation was found to show a high correlation with desiccation tolerance (Tab. 3). More or less colourless apothecia are typical of many desiccation-sensitive taxa, but also occur in desiccation-tolerant taxa of the genera *Lecophagus* and *Hyalorbilia*, and in some species of *Orbilia* and *Amphosoma*. *Hyalorbilia* has typically pale chlorinaceous apothecia. Reddish pigments are frequently observed in desiccation-tolerant species (Fig. 13: a, c–d, g–i), whereas they are rather rare in desiccation-sensitive taxa (*Orbilia rubrovacuolata* Fig. 13: o, *O. martinicensis*, *O. luteorubella, O. sarraziniana*). A few species are characterized by pinkish-lilaceous apothecia, e.g., the desiccation-tolerant *O. lilacina*, *O. plurililacina*, *O. myriolilacina*, and *O. pleistolilacina* (Fig. 13: d); among the desiccation-sensitive taxa, a pale lilaceous colour is typical of *O. rosea* and *O. sarraziniana*, and also occurs in *O. leucostigma.* A few species have bright golden-yellow-orange to ochraceous pigments, e.g., the desiccation-tolerant *O. xanthoguttulata* (Fig. 13: b), *O. pilifera* (Fig. 13: f), *O. suberis*, and *O. eucalypti*, or the desiccation-sensitive *O. xanthostigma* (Fig. 13: n), *O. xanthoflexa*, and *O. flavovacuolata*. Dark pigments are restricted to desiccation-tolerant species: blackish-olivaceous pigments occur in one species of *Amphosoma* (*A. atroolivaceum*), in some members of *Orbilia* series *Lentiformes* (*O. atrolentiformis*, *O. patellarioides* (Fig. 13: e), *O. purshiae*, *O. pileosoma*), and in one species of *Orbilia* section *Ovoideae* (*O. olivacea*); dark purple-lilac pigments occur in *Lilapila* spp. (Fig. 13: j) and *Liladisca*. An intermediate case is *O. polybrocha*, a desiccation-sensitive species with a medium (reddish-)brown colour (Fig. 13: l). The frequent occurrence of reddish pigments in desiccation-tolerant species is apparently a genetic adaptation to a higher UV-illumination in their habitats.

Natural colour variation and method-dependent deviations. The macroscopic apothecial colour exhibits more or less pronounced variation in shade and intensity within a spe-

Figure 13: Examples of apothecial diversity in *Orbiliomycetes*; **a–j**. desiccation-tolerant species, **k–o**. desiccation-sensitive species. — **a**. *Orbilia carpoboloides* (H.B. 9233), **b**. *O. xanthoguttulata* (H.B. 7915b), **c**. *O. delphinus* (H.B. 7892a), **d**. *O. pleistolilacina* (H.B. 8746b), **e**. *O. patellarioides* (H.B. 9173a), **f**. *O. pilifera* (H.B. 8145), **g**. *O. fimbriata* (H.B. 8838a), **h**. *O. flagellispora* (H.B. 8359a), **i**. *O. gemma* (H.B. 9020a), **j**. *Lilapila oculisporella* (H.B. 7063a), **k**. *O. crenatomarginata* (H.B. 9265a), **l**. *O. polybrocha* (H.B. 8317), **m**. *Hyalorbilia inflatula* (H.B. 8150), **n**. *O. xanthostigma* (H.B. 8536), **o**. *O. rubrovacuolata* (H.B. 8492a).

cies. Colour intensity often varies between pale, light, bright, or deep. Typically deeply pigmented species may even occur unpigmented, or vary in rather different colours (e.g., *O. eucalypti* Fig. 14: c, *O. comma*, *O. rubrovacuolata*, and *O. xanthoguttulata*). This variation may occur between different populations but also within a population.

For instance, collections of the *xanthostigma-leucostigma* complex comprise populations with pale to bright golden- or orange-yellow apothecia and those with whitish to pale chlorinaceous or lilaceous apothecia. The microscopic features are the same between these colour variants, hence we believed for a long time that the pale-coloured populations were albinotic forms due to the loss of yellow pigmentation. Likewise, in *O. sarraziniana* apothecial colour may vary between pale rosaceous-lilaceous and sometimes bright yellow-orange, and the typically bright red apothecia of *O. rubrovacuolata* may occur in a whitish-yellowish form. Molecular data have shown that *O. leucostigma* and *O. xanthostigma* represent two different species within Europe, while the colour variants observed in *O. sarraziniana* and *O. rubrovacuolata* are merely due to loss of pigments. In the collection of *O. sarraziniana* in Fig. 14: d–e we have the complex situation that morphologically the pinkish apothecia belong to *O. rosea*, while molecular data assign them to the associated rather rare orange form of *O. sarraziniana*.

Whether or not different species are involved in such colour variants is frequently not clear. Our present data provides evidence that intermingled growth of differently pigmented apothecia with a high microscopical similarity may result from independent populations of genetically different species. Within Europe, apothecial colour turned out to be diagnostic for distinguishing *O. leucostigma* (whitish) from *O. xanthostigma* (pale to bright yellow), and apparently also *O. rosea* (rosaceous) from *O. luteorubella* (yellowish-orange). However, populations with pale or otherwise intermediate colours are difficult to place if no molecular data is available or clear microscopic differences exist. In contrast, red European and whitish Macaronesian populations of *O. rubrovacuolata* turned out to be genetically conspecific. In the case of Fig. 14: d–e) we observed two populations which grew intermingled and differed sharply in apothecial colour and ascospore orientation: the orange form with upper spores inverted, the pinkish form with lower spores (mostly) inverted. Yet, molecular analysis revealed identical ITS sequences that refer both

Table 3. Frequency of apothecial pigmentation (predominant colour in fresh state) in different groups of *Orbiliomycetes* in relation to desiccation tolerance and sensitivity. The numbers of desiccation-tolerant (before slash) vs. desiccation-sensitive species (after slash) are given for each genus or section and include unnamed taxa (aff. or nom. prov.; see also Tab. S3). Apothecia are classified as desiccation-tolerant when surviving min. ca. 1–2 weeks, including their asci. Note frequent occurrence of reddish apothecia in desiccation-tolerant (xerobiotic) taxa and of whitish apothecia in desiccation-sensitive (hygrobiotic) taxa.

Genus/Section	Apothecia whitish(-yellowish)	Apothecia yellow(-ochre)	Apothecia orange-rose-lilaceous	Apothecia ochre-brown	Apothecia purple-lilac	Apothecia olivaceous-black
Liladisca	–	–	–	–	1/0	–
Lilapila	–	–	–	–	4/0	–
Amphosoma	4/0	–	1/0	–	–	1/0
Lecophagus	3/0	–		–	–	–
Bryorbilia	0/1	–	–	–	–	–
Pseudorbilia	0/1	–	–	–	–	–
Hyalorbilia	~11/16	~7/11	~2/0	–	–	–
Orbilia sect. *Lentiformes*	–	–	29/0	–	–	4/0
sect. *Hemiorbilia*	–	–	95/0	–	–	–
sect. *Aurantiorubrae*	~2/8	~11/2	~58/2	4/0	–	–
sect. *Helicoon*	~0/6	~1/7	~0/7	–	–	–
sect. *Habrostictis*	–	–	108/0	–	–	–
sect. *Ovoideae*	1/0	–	27/0	1/0	–	1/0
sect. *Orbilia*	~3/14	~4/4	~22/4	–	–	–
sect. *Arthrobotrys*	~5/30	~8/7	~8/3	~4/2	–	–

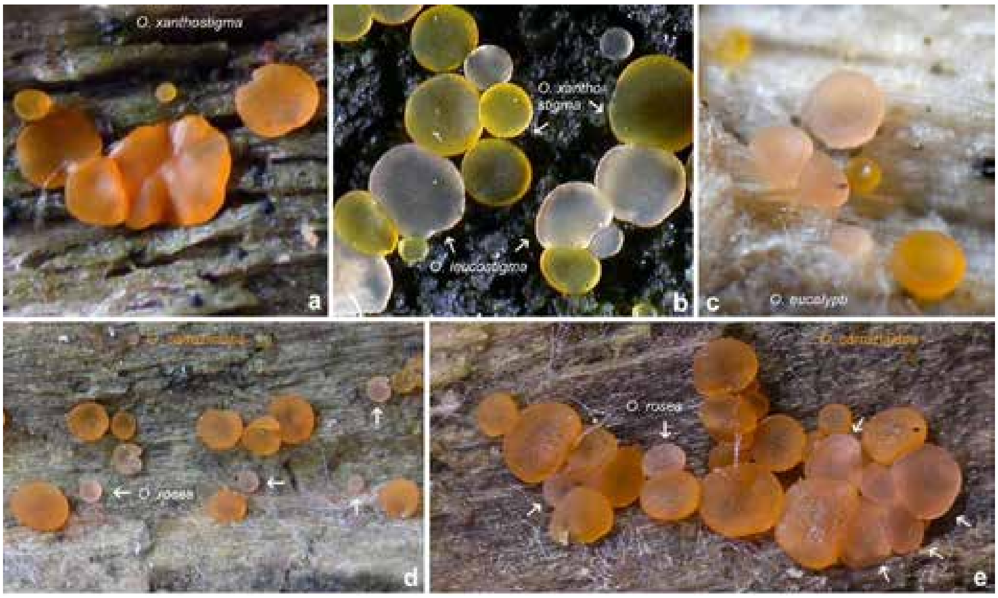


Figure 14: Colour variants within a species or between very closely related species. — **a–b**. *Orbilia xanthostigma* and *O. leucostigma* (**a**. orange *O. xanthostigma*, 10.X.2002, phot. P. Karasch, **b**. yellow *O. xanthostigma* (H.B. 7852a) intermingled with white *O. leucostigma* (H.B. 7852d); **c**. *O. eucalypti* (pinkish and orange form, P.P. 20100221, phot. P. Perz); **d–e**. *O. sarraziniana* (orange, H.B. 9691a) and *O. rosea* (pinkish, marked by arrows, H.B. 9691b).

variants to *O. sarraziniana*, although we consider the pinkish ones to belong to *O. rosea*.

Among desiccation-tolerant species, *O. eucalypti* s.l. is a famous example of variable colours. The species mainly occurs with light to bright yellowish-orange to rose-orange colours, but sometimes also in a pale cream or rose-lilaceous form, without showing a clear correlation with its somewhat variable microscopic characters. However, apothecial colour seems here to correlate somewhat with the habitat. Collections close to the ground had always whitish to light yellow apothecia. They tend to have smaller spores and are tentatively separated here under the name *O. tremulae*. Loss of pigmentation was rarely observed in three species with black apothecia (*Amphosoma atroolivaceum*, *O. patellarioides*, *O. purshiae*), in which whitish or orange colour variants occurred closely adjacent to the dark ones.

The reason for a partial or complete absence of pigmentation in usually brightly pigmented species could be sought in a reduced exposure to light. In fact, apothecia of the *xanthostigma-leucostigma* complex are always colourless when growing on the dark underside of a trunk, but usually bright yellow when more on the sides or on the top. In some populations, however, bright yellow and colourless apothecia grew like a mosaic intermingled on the upper side under the very same conditions (Fig. 14: b), which gave a hint that genetically different populations should be involved.

Dry apothecia usually exhibit a more intense colour due to a concentration of pigment during shrinkage. Thereby, light orange apothecia become bright or deep orange-red, pale chlorinaceous ones turn intensely honey-yellow, and yellow colours change to orange-ochre or orange-red, and rehydration reestablishes the paler colour (Fig. 12: g–l). However, this only works with recently collected samples. Apothecial colour fades in the herbarium with the years, therefore, yellow-orange or rosaceous-lilaceous colours eventually turn uniformly cream-ochraceous or whitish (Fig. 15: a–h, see also p. 101, Pigments).

Different types of light sources and different adjustments of white balance of the camera strongly influence apothecial colour on macrophotos. A higher fraction of ultraviolet enhances a greenish-yellow component (perhaps by autofluorescence) which is not seen under a lower fraction of UV (Fig. 15: i–l). Also white balance strongly influences the result. Automatic white balance may suppress an orange component which is seen when using a manual white balance (Fig. 15: m–n). However, the manual calibration of the white balance is problematic as it depends on the computer screen and its adjustment, while the automatic white balance may cause false colours if black and white regions are missing on the image.

Translucency. Fully hydrated, light-coloured apothecia are often more or less translucent, particularly in the central region of the disc, which allows to see the usually darker colour of the subjacent substrate. This translucency depends, however, on the presence of extracellular water in the medullary excipulum. Apothecia exposed to dry air will, therefore, get more and more non-translucent when gradually losing water, whereas rehydration rather instantly reestablishes maximum translucency. During dehydration, the intercellular spaces become air-filled at first in the centre of the apothecium, thereby the border against the surrounding water-saturated area is usually very sharp. A comparable effect is known as hygrophaneity in some *Agaricales*. A certain decrease in translucency appears to be provoked by rough hymenial exudates or protruding paraphyses.

Consistency. In the hydrated state, apothecia of *Orbiliomycetes* generally have a soft consistency which is often called waxy or waxy-gelatinous in the literature, and was currently used as a key character of the group. Yet, in our experience there is scarcely any difference in consistency to be observed between *Orbiliomycetes* and soft-fleshed *Helotiales*. Even high-experienced workers may sometimes confuse orbiliaceous and non-orbiliaceous apothecia by macroscopy. In fact, most members of *Orbilia* are characterized by the absence of a compact gelatinous tissue. A waxy-gelatinous consistency is typical of the genus *Hyalorbilia*, in which the hymenium is usually embedded in gel, and often also the ectal and medullary excipulum is medium to strongly gelatinized. Also in *Liladisca* and *Lilapila* the medullary excipulum is strongly gelatinized. In the dry state, both gelatinized and non-gelatinized apothecia become similarly tough, horny, and brittle.

There is some controversy about whether authors applied the term waxy (or ceraceous) to the consistency or the external appearance of sporocarps. Bresinsky & Besl (2003) pointed out that ‘ceraceous’ has been used by Fries probably more in the sense of external appearance of lamellae in *Hygrophoraceae*. In orbiliaceous fungi, however, Fries, Rehm, Höhnel, Nannfeldt, and Dennis clearly used waxy more in the sense of consistency: in combinations like waxy-gelatinous, but also by referring to

Figure 15: Variation of apothecial colour with the applied method. **a–h**. loss of colour during long-term storage; **i–l**. colour depending on the kind of light source; **m–n**. colour depending on the white balance of the camera. — **a–d**. *O. abutilonis* complex (**a**: holotype of *O. abutilonis*), **b**: *O. ficicola* (21.IX.2011), **c–d**: *O. siculispora* (H.B. 7824); **e–f**. *O. occulta* (isolectotype), **g–h**. *O. spermoides* (H.B. 7604d); **i–l**. *H. inflatula* (**i–j**: H.B. 7360, **k–l**: H.B. 8885a): **i**, **k**: illuminated by miniature LED; **j**, **l**: illuminated by Luxeon-LED; **m–n**. *O. flagellispora* (H.B. 8359a), illuminated by miniature LED, **m**: manual white balance (WB) on a pale cream paper, **n**: automatic white balance. All photos with Nikon Coolpix 4500 and Horizon macrolens.

the exudate over the paraphyses as 'waxy' and responsible for the coherence of the hymenial elements. Both senses of 'waxy' may apply to apothecia of some species of *Hyalorbilia* as well as *Orbilia*, but this characterization is quite vague and also applicable to certain *Helotiales*.

Apothecial ontogeny is frequently ignored in monographic studies, although apothecia at different stages of development usually occur in a population. Immature apothecia have frequently been left aside also in the present study, because they seemed to contribute little to taxonomy. It turned out, however, that some members of *Orbiliomycetes* greatly differ from the majority in ascoma development: the hymenium usually develops exposed at a very early stage, but in some desiccation-tolerant species it remains more or less completely enclosed by the overlying marginal excipulum and hairs during different stages of hymenial development, even when fully hydrated.

Van Brummelen (1967: 22–28, pl. 17) presented a scheme of the developmental types in *Ascobolaceae* (*Pezizales*). This involves (a) gymnohymenial ascomata that are permanently open from the beginning (including the archihymenial phase in which young paraphyses are not yet developed), with a semispherical peridium of excipular tissue present below but not above the ascogonium, and (b) cleistohymenial ascomata that produce a spherical peridium which covers the ascogonium also above. This covering tissue of the cleistohymenial type, which is formed in the archihymenial phase, remains closed during a shorter or longer period of time. Therefore, Van Brummelen distinguished three subtypes within the cleistohymenial type, according to the development stage at which the ascomata open: (1) opening in the prohymenial phase (young paraphyses present but no ascogenous hyphae), (2) opening in the mesohymenial phase (ascogenous hyphae present but no mature asci), and (3) opening in the telohymenial phase (at least a few mature asci present). Apothecia that open in the mesohymenial phase are again divided into early (no asci), mid (young asci, the first with beginning spore formation), and late (immature asci at different stages of maturation). Those ascomata that open in the telohymenial phase were perithecioid, and in some cases the ascomata even remain closed until they disintegrate. The term cleistohymenial seems to be somewhat inappropriate when applied to the prohymenial subtype, because the hymenium is formed here just when the peridium opens at the top, and is thus never enclosed by a covering tissue. Since the first appearance of ascogenous hyphae is difficult to see, the prohymenial phase is not easily delimited from the early mesohymenial phase.

In an ontogenetic study of apothecia from various groups of inoperculate discomycetes based on microtome sections, Bellemère (1968: 542–550) treated in detail only a single species of *Orbilia* (unidentified, possibly *O. aurantiorubra*). Since the terminology of the French school is quite different from the Anglo-American terminology of apothecial elements, we here provide a list of relevant terms of both schools (Tab. 4). Virtually all taxa studied by Bellemère can be classified in the cleistohymenial type, because the archihymenial phase includes

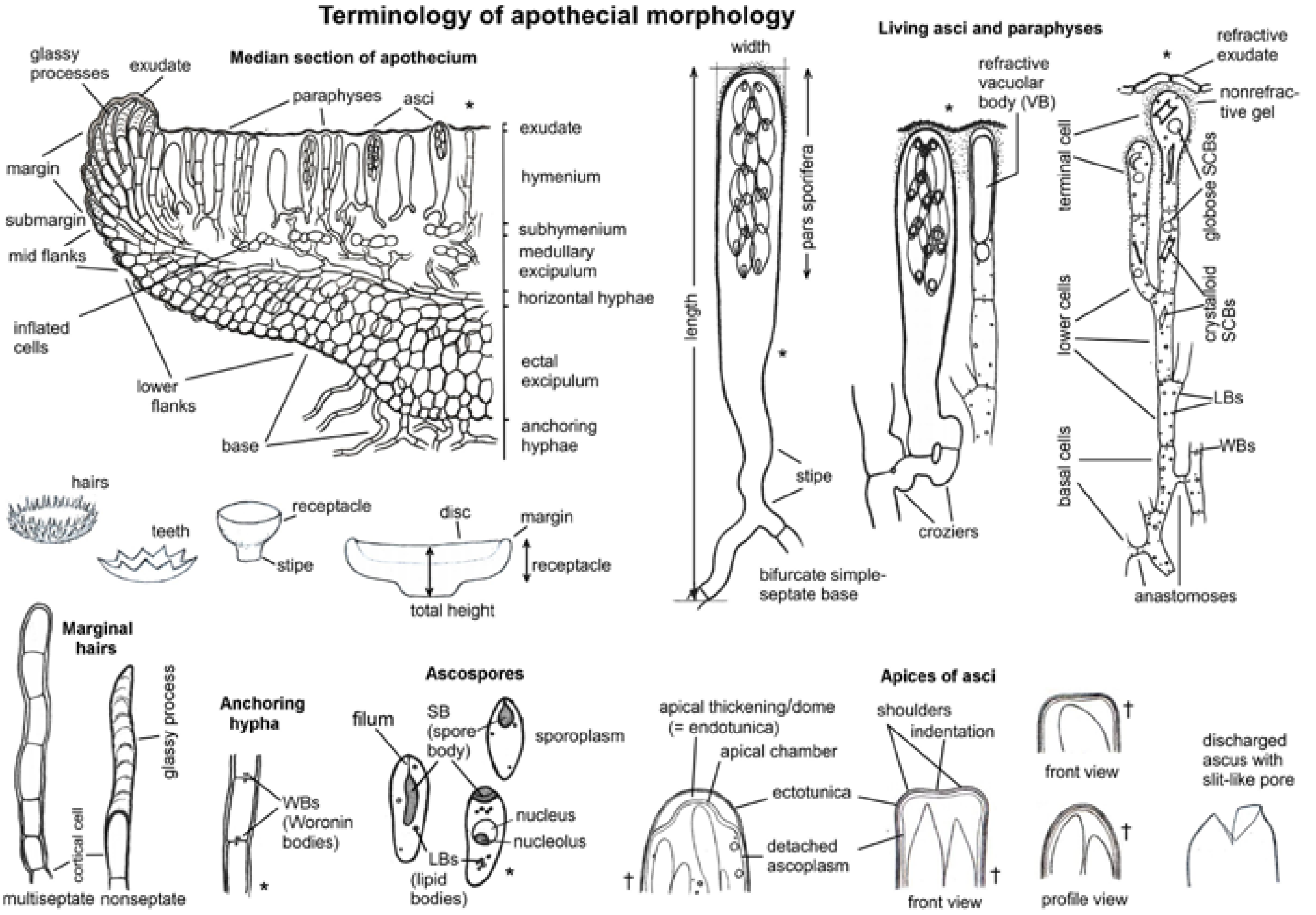


Figure 16: Schematic overview and terminology of elements of the teleomorph in *Orbiliomycetes.*

a stage at which the 'carpocentre' (young medullary excipulum with ascogonial elements) is completely covered by a peridium of ectal excipular tissue. This applies also to the orbiliaceous species investigated by him (Fig. 18), which can be classified as subtype (1), i. e., opening in the prohymenial phase.

Our studies in *Orbiliomycetes* indicate that the prohymenial subtype might actually represent the general case in *Orbilia* and perhaps also *Hyalorbilia*, however, we were so far unable to detect apothecial initials of the archihymenial phase on the natural substrate. Subtypes which open in the meso- and telohymenial phase occur in at least three species, all of which having septate marginal hairs. In *O. siculispora* (Fig. 17: a–b) the hymenium is completely covered by a tissue of cortical elements and opens in the early mesohymenial phase when the spores are not yet recognizable in the asci. *O. pilifera* also appears to belong to this subtype. *O. carpoboloides* (Fig. 17: c) opens in the late meso- and the telohymenial phase when many asci already attained maturity. Here, the hymenium of the as yet closed apothecium lines also the covering tissue which later represents flanks and margin, with the asci and paraphyses oriented upside down (Fig. 17: c).

Also Nannfeldt (1932: 97) observed in *O. carpoboloides* (as *Habrostictis rubra*) that the hymenium is entirely covered for a long time by an overlying tissue which finally lacerates to form triangular marginal lobes. This situation of a hymenium that almost entirely lines the internal cavity of the closed apothecium also occurs in *Cenangium ferruginosum* as reported by Bellemère (1968: fig. 66D), though in *Cenangium* the apothecium seems to open already in the early mesohymenial phase.

Apothecial initials of the archihymenial phase as observed by Bellemère (1968) in *Orbilia ?aurantiorubra* (and Descals et al. 1999 in *O. rosea*) are subglobose and measure about 50–90 µm diam. (Fig. 18: a: A–B). They develop either superficially or sometimes beneath a layer of host tissue (Fig. 18: b). The initials are composed of an ectal excipulum of small isodiametric cells. Like a hollow sphere, this tissue forms a compact layer around a less dense central tissue ('carpocentre') of slightly smaller cells (Fig. 18: b).

The central tissue of apothecial initials, which represents the early medullary excipulum, consists of vegetative paraphysogenous plectenchyma and, more in the centre, of slightly wider ascogonial cells, from which the generative ascogenous hyphae emerge. These two types of tissue systems stain differently, according to Bellemère: the walls of the paraphysogenous cells stain in Vert lumière (Methyl green), whereas the ascogonial cells, ascogenous hyphae, and young asci are more strongly eosinophilous.

In the prohymenial phase, in which the initials usually attain a size of ca. 100 µm, the carpocentre differentiates into a lower layer of paraphysogenous plectenchyma and an upper layer composed of a palisade of young paraphyses. About at this stage the ectal excipulum ruptures at the top of the apothecium. However, this rupture is difficult to observe: the pore-like opening remains rather small at the beginning, and free-hand sections are almost impossible. During further growth (Fig. 18: a: C–E) the cells of the ectal excipulum more and more increase in size, especially in the basal part. The ascogenous hyphae grow upwards and reach the hymenial base where they form ascus

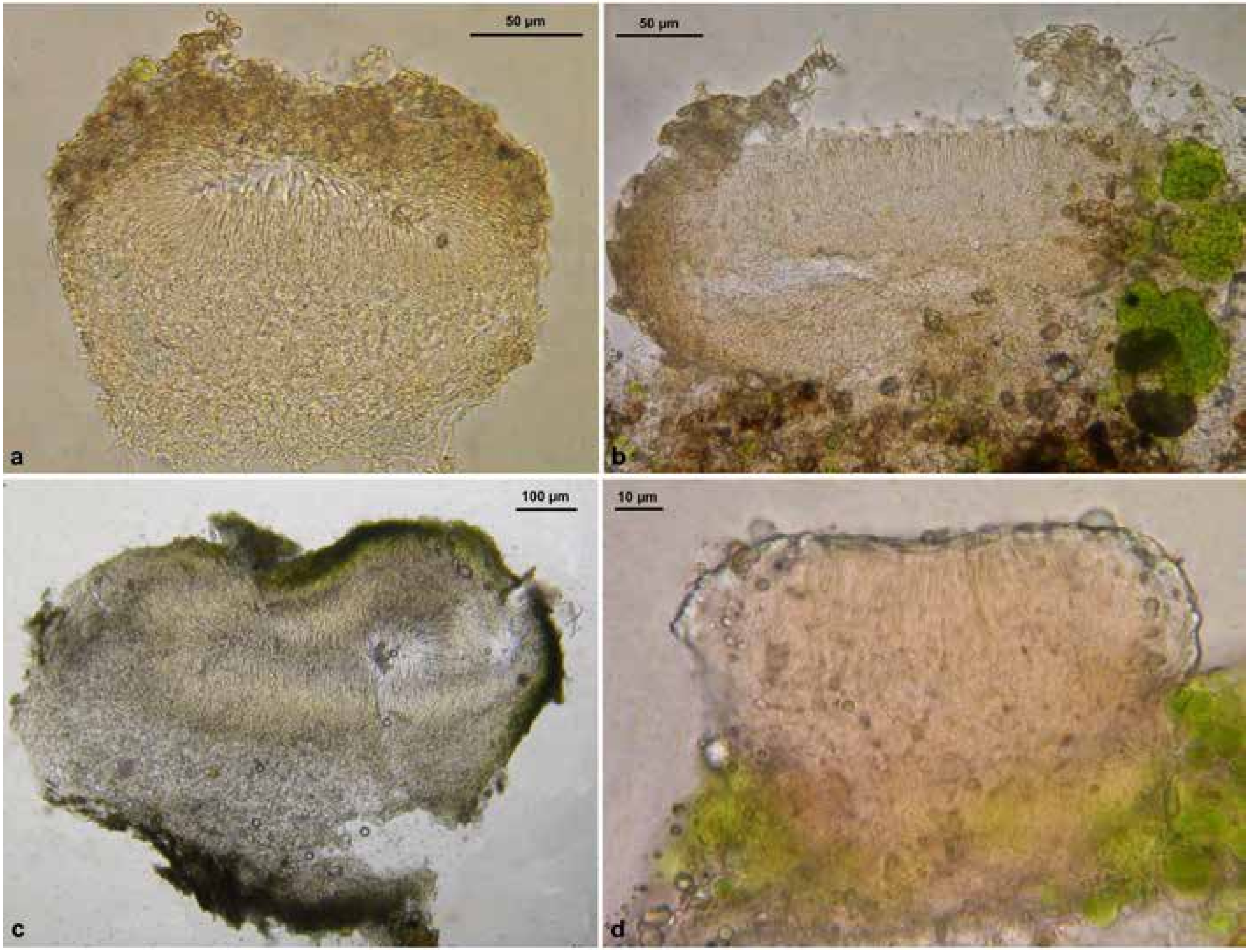


Figure 17: Apothecia in median section, belonging to three species of *Orbilia* and three different subtypes of cleistohymenial development. — **a**. young apothecium of *O. siculispora* (H.B. 8121, prohymenial phase), with marginal excipular tissue and hyphae covering the young hymenium; **b**. more developed apothecium of *O. siculispora* (mesohymenial phase), with exposed hymenium; **c**. mature apothecium of *O. carpoboloides* (H.B. 9233, late meso- to telohymenial phase), the covering layer bears inside a mature hymenium with the asci and paraphyses oriented upside down; **d**. young apothecium of *O. aristata* (H.B. 9226a, pro- or early mesohymenial phase); the paraphyses are already covered by thick exudate.

initials. In the medullary excipulum below the paraphysogenous system, some voluminous cells are found (~10 µm diam., referred to as 'inflated cells' in the present study). They are highly vacuolated. and their wall is stained by Methyl green while being surrounded by a clew ('peloton') of eosinophilous ascogenous hyphae (Bellemère 1968: 547).

In the late mesohymenial phase (stage F in Bellemère's study), a basal layer ('podium hypocentral') between medullary and ectal excipulum differentiates, which is without ascogenous hyphae. This layer represents the lower part of the medullary excipulum, but is sometimes difficult to delimit from the ectal excipulum. Particularly in desiccation-tolerant species

Table 4. Terminology of vegetative and generative apothecial elements.

French school (Bellemère 1968)		Anglo-American school (present monograph)
c	conceptacle	ectal excipulum
pl	plancher du conceptacle	basal ectal excipulum
a, r	amphithecium, revètement amphitécioïde	ectal excipulum at flanks and margin
pd	podium hypocentral	lower part of medullary excipulum
ca, cg	carpocentre, complexe paraphysogène	central tissue of apothecial initials, hyphal system in upper part of medullary excipulum that gives rise to paraphyses (stained by Methyl green)
pt, mp	parathécium, manchon parathécioïde	thin layer of horizontal hyphae delimiting medullary from ectal excipulum
cr	couronne parathéciale	continuation of 'parathecium' at upper margin by forming a transition between marginal ectal excipulum and hymenium (growth zone)
fd, fp	filaments descendants, filaments paraphysoïdes	periphysoids
e	épithécium	exudate
t	toit du conceptacle	part of ectal excipulum that protrudes like a roof beyond margin
aa, ha, as	appareil ascogonial, hyphes ascogènes, asques	ascogonium, ascogenous hyphae, asci (eosinophilous)
s'	partie basilaire de l'appareil sporophytique	basal part of ascogenous hyphae (eosinophilous)
pI, pII	paraphyses primaires, paraphyses secondaires	primary and secondary paraphyses

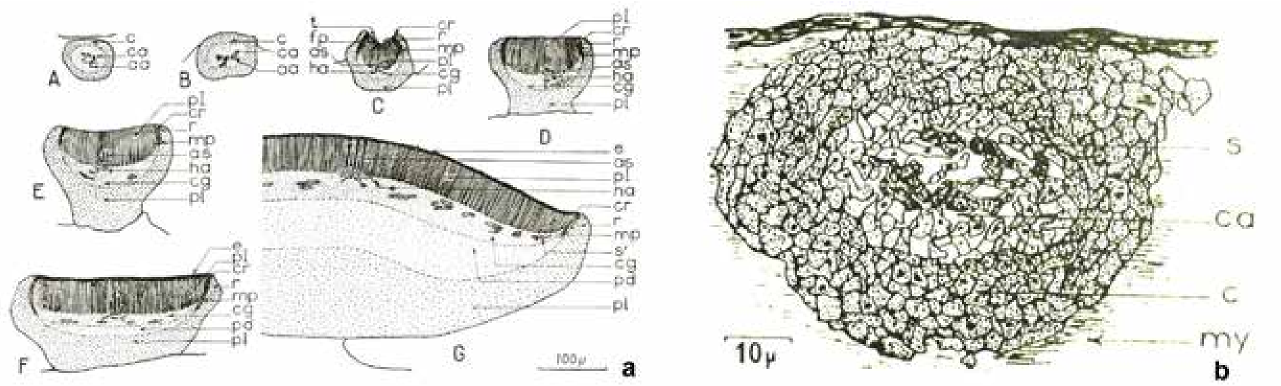


Figure 18: Apothecial development in *Orbilia ?aurantiorubra* (Bellemère 1968: figs 51–52). — **a** (fig. 51). **A–B** = archihymenial phase, **C** = pro- or early mesohymenial phase, **D–F** = mesohymenial phase, **G** = telohymenial phase (in Van Brummelen's terminology); the dark elements in the upper medullary excipulum in **D–G** are ascogenous hyphae (for the abbreviations see Tab. 4); **b** (fig. 52). archihymenial phase, apothecial initial covered by host periderm; c = conceptacle (= ectal excipulum), ca = carpocentre (= medullary excipulum), s = ascogonial cells.

of *Orbilia*, a thin layer of hyphae forming a textura porrecta ('parathecium' in Bellemère's terminology) may occur which sharply separates ectal and medullary excipulum, but this was not observed in Bellemère's specimen. Bellemère pointed out that the exudate over the paraphyses attains its final thickness at stage F (Fig. 18: a), but we have seen fully developed exudate in *Hyalorbilia* and sections *Hemiorbilia* and *Aurantiorubrae* also in the prohymenial phase (Fig. 17: d).

Sexual reproduction. Details about gametangiogamy in *Orbiliomycetes* have very rarely been investigated. Bellemère (l.c.) described the ascogonial cells as having the shape of a small dense clew (Fig. 18: b). Descals et al. (1999: fig. 9) observed hyphal coiling around 3-septate spermatia during formation of apothecial initials in *Orbilia rosea* (as *Orbilia* sp.). An accidental observation in *Hyalorbilia orbiliicola* (Fig. 19) shows helicoid gametangial branches which probably conjugate similarly as in *Ascodesmis* (*Pezizales*) as reported by Claussen (1905, in Gäumann 1964: fig. 191) or in *Talaromyces* (*Eurotiales*) as reported by Emmons (1935, in Gäumann 1964: fig. 132).

We have not conducted studies with single spore isolates, therefore, we have no results on mating types in *Orbiliomycetes*. Yet, a few literature reports give hints that heterothallism occurs. Descals et al. (1999: fig. 9) obtained apothecial initials in a monoconidial isolate of *Orbilia rosea* which showed fusion between microconidia and receptive hyphae of the same colony, but these initials did not reach maturity. Another, apparently multiconidial isolate of that species developed mature apothecia (l.c.: fig. 8). Guo et al. (2009b) found in their studies about sexual reproduction capacity of orbiliaceous anamorphs that none of the 65 single conidial isolates of apparently over 60 different species produced apothecia, and also some multiascospore isolates did (8 out of 20 isolates, about 5 out of 10 species). The ascospore cultures originated from apothecia collected in the field, whereas the conidia were taken from cultures isolated from soil, dung and plant substrate.

Guo et al. (l.c.) speculated that those strains obtained from conidia belonged to a genotype that might have lost the ability of producing a sexual phase, and that such loss of sexual reproduction is frequent in nature. In our opinion, apothecial reproduction was perhaps only suppressed because of a missing mating type in the single conidium isolates. The authors obviously did not test cultures gained from single ascospores, nor cultures gained from single conidia grown in multiascospore isolates: possibly such cultures would likewise have failed to produce apothecia. In the case these tests will show the predicted results, we may conclude that heterothallism was the reason for the failure of apothecium production. Webster & Descals (1979: 420) emphasized the usefullness of preparing multispore cultures along with cultures derived from single spores: 'If ascomata or basidiomata develop in [multispore] cultures, but fail to develop in cultures derived from single spores, this may indicate that the fungus is heterothallic.'

Growth rate, **age of apothecia**. The growth rate of apothecia was roughly evaluated in some species by placing them in a water-tight box at ~18–22 °C. Young apothecia of *Hyalorbilia* *inflatula* (IVV: H.B. 9041a) and *Orbilia leucostigma* (IVV: H.B. 10003) increased in diameter by 25–38 µm per day, evaluated during an observation period of 4 days. When starting from hypothetical initials of ~100 µm diam., this corresponds to an age of 7–12 days for adult apothecia with a final diameter of 0.3 mm, or 30–40 days with a final diameter of 1.5 mm in diam. However, the growth rate decreases with apothecial size. In *Orbilia* cf. *cotoneastri* (IVV: H.B. 9051b) apothecia showed a growth rate of (32–)60–65 µm diam. per day, evaluated during an observation period of 7 days, during which apothecia increased, e.g., from 0.33 to 0.76 mm in diam. Desiccation-tolerant apothecia showed a lower growth rate when kept under continuous moisture at room temperature: apothecia of *O. aristata* (H.B. 9406a) and *O. subtrapeziformis* (H.B. 9406b) grew only by about 5–10 µm in diam. per day. Apothecia would then attain a diameter of 0.3 mm after ~20–40 days.

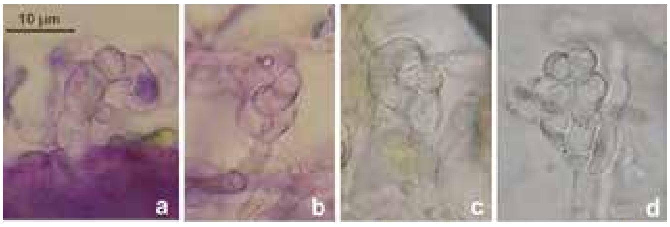


Figure 19: Presumed gametangial branches in *Hyalorbilia orbiliicola* (H.B. 9077b), formed at the apothecial margin of immature *Orbilia eucalypti*, on which *H. orbiliicola* grows as a parasite.

However, continuous conditions of warm temperature and high moisture are exceptional on xeric substrate, even in a cold-temperate humid climate, therefore, desiccation-tolerant apothecia in the natural environment attain a much higher age.

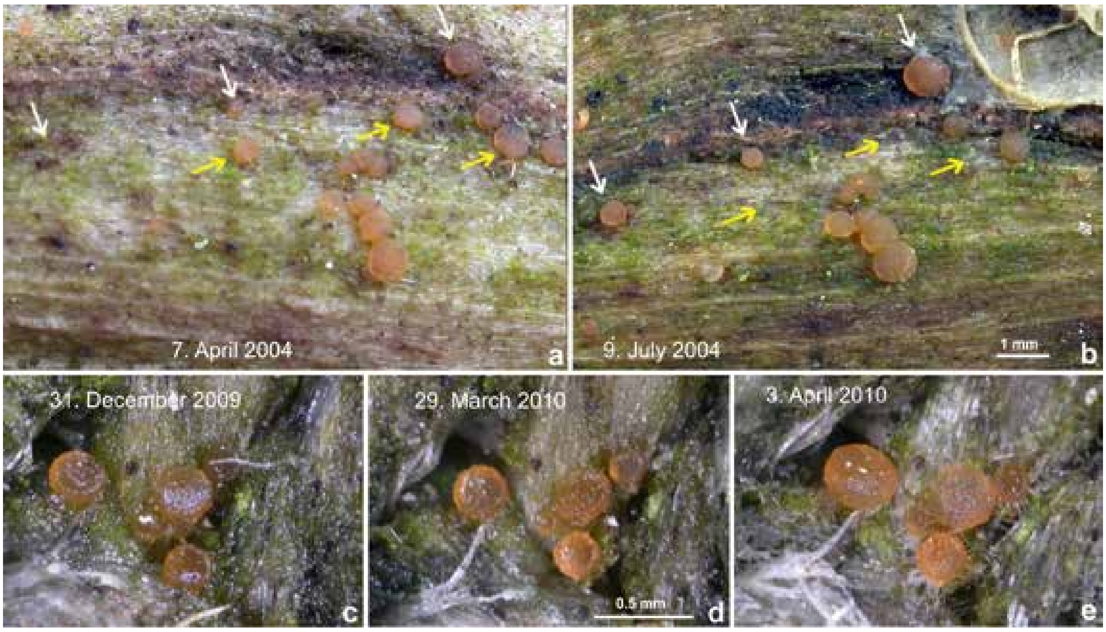


Figure 20: Apothecia of *Orbilia* on xeric substrate in our garden in Pfrondorf (Tübingen) monitored during several months (living state). — **a–b**. *O. trapeziformis* on a decorticated branch of *Juglans* (H.B. 7508c); some apothecia were consumed by animals (yellow arrows), while small apothecia strongly increased in size (white arrows); **c–e**. *O. aristata* on a rotten rope (H.B. 9226a); apothecia survived the winter without showing noteworthy growth, **e**. 3 days after transfer into a Minigrip closure bag kept at room temperature.

Apothecial growth of *O. trapeziformis* under field conditions, with alternate moist and dry periods during 3 months in early summer, can be seen in Fig. 20: a–b. A growth rate of 150–270 µm in diam. in smaller and 50–140 µm in more adult apothecia was observed, which results for the smaller ones in an average rate of ~1.5–3 µm diam. per day. However, in the winter season apothecial growth stagnates: *O. aristata* did not increase in size in a field experiment during a period of 3 months, though frequently moistened by rain and snow (Fig. 20: c–d). However, when transferred to a moist chamber at room temperature, apothecia increased by 55–85 µm in diam. during less than 3 days, which is ~20–30 µm per day (Fig. 20: e).

From this and other field observations we conclude that apothecia in temperate humid areas on xeric substrate attain an age of about 1/2–1 year. In a semihumid subtropical (mediterranean) climate they may grow up during the moist winter months, survive the following dry summer in a dormant state, and resume growth next winter. In semiarid to arid regions there can be no doubt that apothecia attain an age of around 5–10 years, during which period they experience only very rare and short intervals of hydration. There is always the possibility, however, that invertebrates consume some apothecia of a population. This was the case in the experiment with *O. trapeziformis* (Fig. 20: a–b): during June three of the observed apothecia disappeared (yellow arrows), while at the end of July only a few apothecia remained (not shown).

Asci

Ascogenous hyphae and development of asci. The situation of ascus bases in *Orbiliomycetes* is rather complicated, therefore, it seems justified to give a short survey on croziers in ascomycetes in general.

Very similar as with the presence or absence of clamp connections at the secondary mycelium of basidiomycetes, two very different main types of septation can be observed in the generative ascogenous hyphae of ascomycetes: (1) the individual cells are connected by croziers which separate adjacent cells by two septa; (2) the ascogenous hyphae are simple-septate, with a single septum between each cell. Therefore, asci arising from croziers have usually two basal septa (Fig. 21: 1), whereas asci arising from simple septa have usually one basal septum (Fig. 21: 4). However, simple-septate ascus bases may possess two or sometimes three basal septa, but then the ascus base is bi- or trifurcate (Fig. 21: 5), whereby a younger ascus emerges from the base of the older ascus, not from the crozier of the ascogenous hypha.

In contrast to basidiomycetes, the presence vs. absence of croziers has received comparatively little attention in taxonomic treatments in most groups of ascomycetes, including lichenized groups, with a few exceptions. For inoperculate discomycetes it was mainly White (1942, 1943, 1944), Berthet (1964b), Arendholz (1979), Huhtinen (1990a: 66), Hengstmengel (1996: 192), Baral (e.g., 1992: 354, 1997, 1999, 2015 etc.), Baral & Marson (2001), and Baral et al. (2009), who have emphasized and discussed the taxonomic value of the ascus base. Huhtinen (l.c.) and Hengstmengel (l.c.) gave a detailed history on the relevant literature on croziers and clamps (see also below).

Croziers are formed during conjugate or sometimes sequential nuclear division (mitosis) of the dikaryon in the terminal cell of an ascogenous hypha. A lateral outgrowth is formed at the apex or some distance below, which curves downwards. After the two nuclei of the dikaryon performed mitosis, each of the two resulting nucleus pairs are separated by a septum (Fig. 21: 1c, 2a). Thereafter, the downwards curved outgrowth fuses with the stalk cell. As a result, two septa occur between the young ascus and the supporting ascogenous hypha. In simple-septate ascus bases only one septum occurs that separates adjacent cells of the ascogenous hyphae (Fig. 21: 4, 5).

A special type of simple-septate hyphae is termed pseudoclamps in basidiomycetes (Clémençon 2009: 155, fig. 1E). A fully agreeing equivalent of pseudoclamps as seen with the LM is often observed in ascomycetes (Fig. 21: 6): a short lateral downward protuberance or hook emerges at the base of the young ascus, which neither fuses with the stalk cell nor does it give rise to a further ascus. Such ‘pseudoclamps’ are typical of some taxa of *Pezizales* (Berthet 1964b: pl. XII fig. 5, pl. XIII figs 4–5, *Humaria* and *Helvella*) and *Helotiales* (e.g., Berthet 1964b: pl. XI fig. 7, *Lachnellula*; Baral 1984, Baral & Matheis 2000, mainly *L. abietis* and *L. splendens*; Huhtinen 1987b, Baral

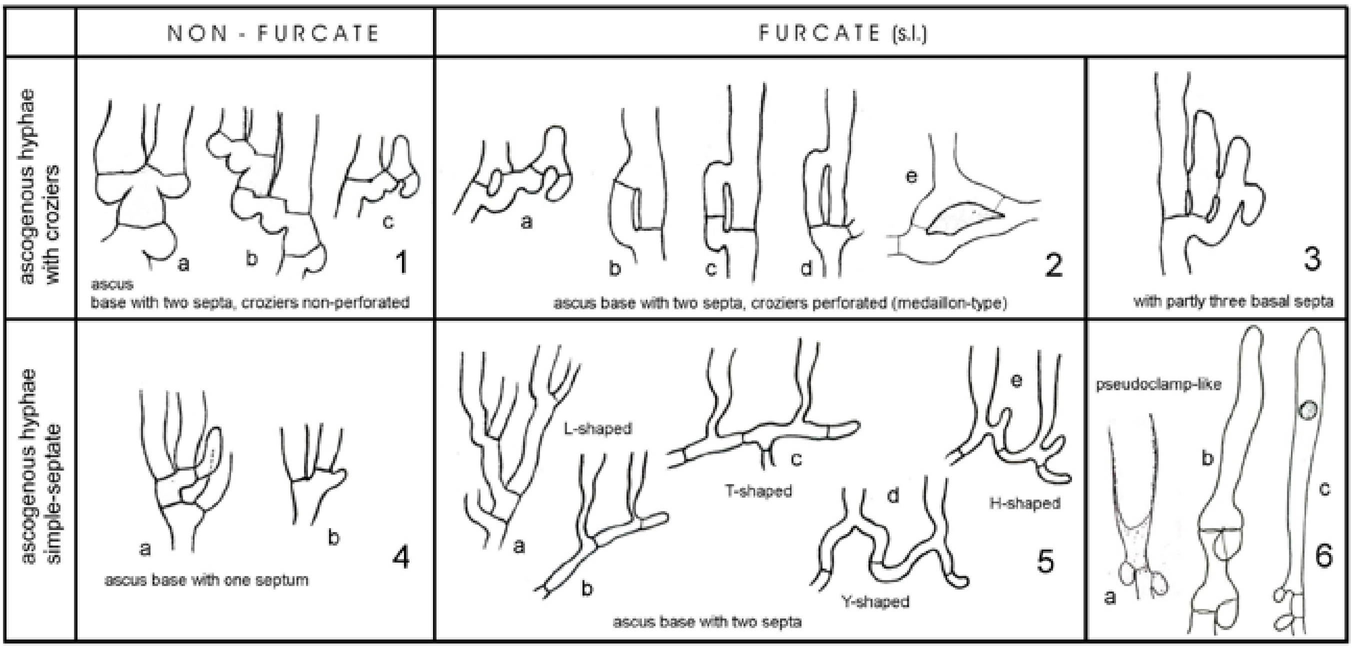


Figure 21: Survey on the different types of ascus bases occurring in ascomycetes. — **1–3**. croziers, **4–5**. simple septa, **6**. pseudoclamp-like. Within *Orbiliomycetes* types **1–5** occur. Drawings schematic, except for **2e** (*H. fusispora*, H.B. 8408), **3** (*H. erythrostigma*, H.B. 6605), **6a** (after Baral & Matheis 2000, *Lachnellula abietis*, as 'crozier-like, not rejoining'), **6b–c** (after Berthet 1964b: pls XI–XII, as 'pleurorhynque à crochet libre', **6b**. *Helvella elastica*, **6c**. *Trichoscyphella calycina* s.auct. = *Lachnellula* ?*subtilissima*).

1993a: 9, *Protounguicularia transiens* [= *P. barbata*]). In the *Orbiliomycetes* pseudoclamp-like ascus bases have so far never been observed, but upward protuberances that similarly do not further develop occur in the H-shaped type of furcate ascus bases (Fig. 21: 5e).

Like pseudoclamps, pseudoclamp-like ascogenous hyphae occur with or without a septum between protuberance and mature ascus. They are often misinterpreted as croziers, especially when the asci are detached, but can then be distinguished from true croziers by the protuberance having a rounded end (Huhtinen 1990a: 67). However, they may rarely occur mixed with croziers in some species of some genera (e. g., Baral & Matheis 2000, *Lachnellula*).

Ascogenous hyphae with croziers are probably generally dikaryotic in all groups of ascomycetes. Simple-septate ascogenous hyphae, in contrast, were shown by Weber (1992: 68) to be either purely monokaryotic, or mixed with dikaryotic cells, depending on the species of *Helotiales* investigated. In the former case all cells of the ascogenous hyphae contained only one nucleus, and these nuclei had always the double relative DNA content (= diplontic), in comparison with closely related taxa that possessed croziers. In the latter case, a mixture of diplontic monokaryons and haplontic dikaryons occurred, and this represented the majority of studied species. But even in species with croziers some diplontic monokaryotic cells were rarely noted (Weber l.c.).

Up to now, the alternative terms 'pleurorhynque' (pleurorhynchous) and 'aporhynque' (aporhynchous) are used instead of 'croziers' and 'simple septa', mainly by French mycologists. This usage traces back to Chadefaud (1943) and Berthet (1964b), who applied them to both operculate and inoperculate discomycetes. Although authors have asserted that these alternative terms are largely equivalent (Huhtinen l.c.), Chadefaud's original concept referred to dikaryotic hyphae in both cases: in the aporhynchous case the cells are wide enough to permit conjugate division of the dikaryon without forming a crozier. Therefore, simple-septate, purely monokaryotic ascogenous hyphae are not aporhynchous, and appear to have been unknown to Chadefaud.

Chadefaud (1943) separated a further type ('acrorhynque'), which he described for *Tarzetta* ('*Pustularia*') *catinus*. It is characterized by a terminal uninucleate cell which does not further develop nor fuse with the uninucleate basal cell, and one or several dikaryotic cells between basal and terminal cell. The dikaryotic cells give rise to asci, while the terminal and basal cell remain uninucleate.

In taxonomic treatments dealing with the ascus base, nuclear numbers in ascogenous hyphae are usually unknown, therefore, a classification in Chadefaud's sense is not easily practicable. From the above it is evident that not all simple-septate hyphae are aporhynchous. Chadefaud's illustration of *T. catinus* is reminiscent of the situation of simple-septate ascogenous hyphae in the *Helotiales* as well as *Orbiliomycetes*. Yet, it also resembles the pseudoclamp-like case, because the terminal cell in the acrorhynchous type strongly resembles the protuberance of pseudoclamps.

Although not fully understood from their genetical background, the two character states croziers and simple septa provide a valuable tool for the delimitation of taxonomic entities in the ascomycetes. In the *Pezizales*, for instance, all studied members of *Sarcoscyphinae* appear to be simple-septate (e. g., Berthet 1964b), whereas *Morchellaceae* and *Helvellaceae* comprise taxa with and without croziers (Berthet 1964b, Häffner 1987). Similarly, many genera in the *Helotiales* include species with and without croziers (e. g., White l.c., Huhtinen l.c., Hengstmengel l.c.). A comparable variation between presence and absence of clamps is known within different genera of *Agaricales* (Tehler 1988: 244).

For instance, in *Hyaloscypha*, *Hymenoscyphus*, or *Lachnum* (*Helotiales*) the ascogenous hyphae frequently differ between very closely related taxa in this respect. In such cases, dividing a genus according to ascus base features would result in highly artificial, polyphyletic groups. Huhtinen (l.c.) found that roughly half of the accepted taxa of *Hyaloscypha* lack croziers. He merely applied the varietal rank to taxon pairs which sharply differed in the ascus base but only gradually in other features, whereas Baral (1999) used the species rank for similar cases in *Helicogonium* W.L. White. However, populations with and without croziers were accepted by Baral (l.c.) in *Helicogonium orbiliarum*. The two character states may exceptionally even occur within a single apothecium (rarely seen in *Proliferodiscus pulveraceus*, Baral ined., or *Pyrenopeziza mercurialis*, Huhtinen 1990a: 66).

From the above it is clear that the crucial difference between croziers and simple septa is linked to the presence vs. absence of a junction between terminal (ultimate) and basal cell. On the basis of detached asci alone it is, therefore, quite impossible to distinguish between croziers with or without a large perforation (medaillon-type), a simple-septate bifurcate ascus base, or the pseudoclamp-like type. In detached non-furcate asci the presence of croziers is more or less recognizable, especially in the turgorless state, by a swollen base with two usually closely adjacent truncate zones which are often oriented to each other at an obtuse angle, whereas a simple-septate, non-furcate ascus base without downward protuberance possesses one truncate basal end which represents the single septum of the ascus.

In the basidiomycete *Schizophyllum commune*, which has heterokaryotic hyphae with clamps, it was shown that monokaryotic hyphae, being artificially prepared from isolated protoplasts, were simple-septate. Homokaryotic hyphae (with two identical nuclei) were also simple-septate but sometimes formed pseudoclamps (Wessels et al. 1976). Later research revealed that mutations in certain genes may result in pseudoclamp formation of usually clampless hyphae (*Coprinus*, Murata et al. 1998).

Situation in the *Orbiliomycetes*. In contrast to *Helotiales*, in which many genera are heterogeneous in regard to crozier formation, the two large genera of *Orbiliomycetes* behave consistent in the ascus base. In all 34 species of *Hyalorbilia* with a known teleomorph recognized here, the asci arise from croziers with or without perforation (Fig. 21: 1–3). Also the genera *Liladisca*, *Lilapila*, and *Pseudorbilia* possess croziers without perforation. Asci of *Amphosoma* (4 spp.), *Bryorbilia* (1 sp.), and *Orbilia* (about 450 spp.) arise from simple septa (Fig. 21: 5), with very rare exceptions of perforated croziers in single asci (like Fig. 21: 2). All these genera are separated by a number of characteristics, therefore, the presence versus absence of croziers in *Orbiliomycetes* has a high significance at the generic level, a view which is supported by molecular data. The small and very uniform genus *Lecophagus* is exceptional within the class in showing either simple-septate ascus bases (as in Fig. 21: 4) or non-perforated croziers (as in Fig. 21: 1), depending on the species.

The nuclear conditions in the ascogenous hyphae have so far apparently never been explored in the *Orbiliomycetes*. We have observed nuclei in ascogenous hyphae only in *Lilapila oculispora*, in which a dikaryon was once seen in unstained living cells (Pl. 29: 2).

Ascogenous hyphae with croziers. Asci arising from croziers always possess two septa at the base, and frequently their stalks are comparatively short and thick. Normally, the two septa are closely adjacent, without a perceptible central perforation of the crozier (as in Fig. 21: 1). This corresponds to the current situation in the *Helotiales* and *Pezizales*. In some taxa of *Hyalorbilia* the croziers are sometimes of the ‘medaillon-type’, i. e., they form an arch over a smaller or larger, round to slit-like perforation, and the ascus base then looks more or less bifurcate, with the two basal septa somewhat distant from each other (Fig. 21: 2). Such perforated croziers are also known from a few genera of *Helotiales* such as *Lachnellula*, *Trichopeziza*, or *Perrotia* (Baral 1984, Baral & Matheis 2000). In rare cases, the perforation may be so large that the asci look prominently bifurcate (*H. fusispora*, Fig. 21: 2e), and only the arch-like connection between the two branches distinguish such a crozier from simple-septate ascus bases of *Orbilia*.

An aberrant type of croziers is characterized by a vertical septum above the perforation (Fig. 21: 3). This septum separates two adjacent asci and resembles an anastomosis though it has a different origin: a hook-like protuberance grows out of the upper part of the arch. Contrary to the normal crozier type, this protuberance later forms two septa, a vertical one between the new and old ascus, and a horizontal one at the place of fusion with the basal cell. Finally all asci except for the first have three septa at their base. This type of croziers was only observed in *Hyalorbilia anonyma* (Pl. 132) and in one collection of *H. erythrostigma* (Pl. 126: 6).

Ascogenous hyphae without croziers. Simple-septate ascus bases possess either one septum as observed in *Lecophagus* (Fig. 21: 4), or two or more septa which is the typical case in *Amphosoma*, *Bryorbilia*, and *Orbilia* (Fig. 21: 5). In the frequent latter case the stalk divides into two or more legs or branches of rather variable length. Each of these branches terminates in a single septum (or sometimes in a blind rounded end), thereby each branching point lacks septa, at least for one of the two branches. The ends of the branches may point in different directions.

Contrary to perforated croziers, the legs do not form a closed ring, instead, one of the two legs gives rise to a further ascus. Thus, the asci are connected to each other with their basal legs like a chain (Fig. 21: 5), and with some dichotomous branches they form a complex tree-like structure. As stated above, such chains formed by connected ascus bases are in contrast to ascogenous systems with croziers, in which several asci emerge from a single basal cell. Yet, in simple-septate ascogenous systems medaillon-shaped true croziers with an elongate perforation have occasionally been observed in a few asci of a few species (*Amphosoma resinicola*, Pl. 34: 1b, *O. cardui*, Pl. 906: 2b, *Orbilia epipora*, Pl. 901: 4b, *O. geijerae*, Pl. 784: 1b, *O. polybrocha*, Pl. 1003: 1b).

Often, one of the two legs of an ascus is very short or even absent so that the ascus base appears unbranched. In this case the missing leg is usually reduced to a septum at the lateral wall of the ascus stalk a good distance above the base of the other leg (Fig. 22: a, d). The presence of two septa is only obvious here if the connecting hypha is not broken, or not hidden behind the ascus stalk.

If two legs point downwards, the ascus base is currently termed bifurcate, in the present work also h- to (inversely) Y-shaped (Fig. 21: 5d, 22: f–j). Irrespective of whether the two legs form a narrow or wide fork, they do not fuse at their base to form a ring. One or both legs are sometimes divided in turn, resulting in trifurcate or higher-branched types (without septa at their branching points). A special case in which only one leg is branched results in a characteristic H-shaped base (typical of section *Orbilia*, Fig. 22: k–m). Here only those two legs

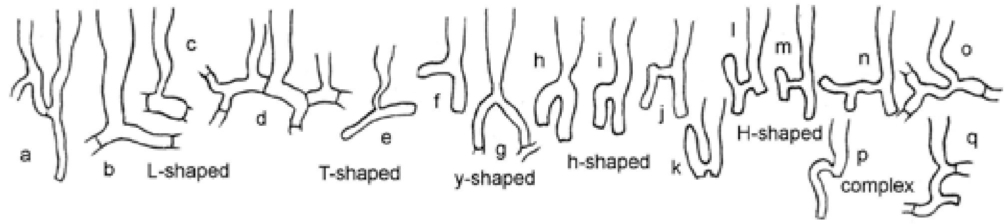


Figure 22: Different types of simple-septate ascus bases as they occur in *Amphosoma*, *Bryorbilia*, and *Orbilia* (schematic illustration).

oriented downwards are connected to adjacent cells (Fig. 21: 5e), whereas the third, upward oriented leg has a blind rounded end and does not give rise to further asci, even when the ascus achieves full maturity.

If the two legs are ± horizontally oriented, the ascus base looks L- (Fig. 22: b–d) or (inversely) T-shaped (Fig. 22: e). Such bases are quite frequent in *Orbilia* but can hardly be termed furcate. They are typical of, e. g., section *Helicoon*, and here the basal part is often distinctly thicker than the flexuous stalk (Fig. 22: c).

Simple-septate ascus bases strongly vary and usually represent several of the above-mentioned branching types within an apothecium. Actually, most species of *Orbilia* vary between furcate (Y and h) and non-furcate (L and T), with various intergradations, and each series and section shows this variation. Furthermore, the ascus stalk above the branching point varies in thickness and length (from entirely absent to very long), also in being often more or less irregularly flexuous, which results in rather variable ascus length values. Due to this striking variability, we did not make too much effort of presenting these various types in the drawings of a single species. Anyway, there are some tendencies recognizable: e. g., desiccation-tolerant species generally possess only L-, T-, Y- and h-shaped ascus bases, whereas the H-shaped type in combination with other types is characteristic of desiccation-sensitive taxa of series *Orbilia* and section *Arthrobotrys*, while rarly seen in desiccation-sensitive taxa of sections *Helicoon* and *Aurantiorubrae*.

No fundamental differences seem to exist between the furcate or otherwise branched ascus bases in *Amphosoma*, *Bryorbilia*, and *Orbilia*, compared to the simple-septate, usually unforked ascus bases seen in *Lecophagus* and in many species of *Helotiales*. Species of *Helotiales* and *Pezizales* without croziers usually have only one basal septum per ascus. However, in some groups the asci often have an L- or T-shaped base: they emerge from a straight, horizontal, oblique or vertical hyphal basal part ending up in two septa, the terminal septum giving rise to a further ascus (similar as in Fig. 21: 5a–b). Such cases were reported for the *Pezizales* by Berthet (1964b: pl. XI fig. 21, XII figs 6, 7, 13, 27, XIII figs 3, 9, 16, 17). Furcate bases as in *Orbilia* almost never occur in the *Helotiales*, but do occur, e. g., in some *Phacidiales* (*Helicogonium*, Baral 1999: 5), *Pezizales* (*Morchellaceae* and *Sarcoscyphinae*, Greis 1940, Berthet 1964b: pl. XI figs 22, 25, XIII figs 13–15; Greis 1940) and the *Saccharomycetales* (*Dipodascaceae*, *Lipomycetaceae*).

Phylogenetical considerations. – **Ascus base within *Pezizomycotina***. Our molecular phylogenetic analyses show a scattered distribution of croziers and simple-septate ascogenous hyphae within the *Orbiliomycetes*. Simple-septate ascogenous hyphae are typical of the genera *Amphosoma*, *Bryorbilia*, and *Orbilia* (Phyl. 1). Croziers are consistently present in the genera *Hyalorbilia*, *Liladisca*, *Lilapila*, and *Pseudorbilia*, and in some *Lecophagus* spp. A similar mixed occurrence of croziers and simple septa is known in other groups of *Pezizomycotina*, particularly in *Pezizales* and *Helotiales*. Here the croziers represent the predominant situation, whereas in *Orbiliomycetes* the simple septate ascus base is much more frequent.

This scattered occurrence of croziers and simple septa in various rather unrelated groups of *Pezizomycotina* indicates that one of these two morphologies represents an apomorphy with a polyphyletical origin, given that restoration of a lost character did not happen. Especially due to the more complicated shape of croziers and their genetic background of conjugate nuclear division of the dikaryon, it seems more probable that those species with simple septa have developed from ancestors with croziers, i. e., simple-septate ascogenous hyphae would then represent the apomorphic character state in all those taxonomic entities which comprise both morphologies (Fig. 23). This hypothesis is also shared by Cain (1948: 165) for ascomycetes in general, and is supported by a phylogenetic analysis of pezizalean genera by O'Donnell et al. (1997) (see also Baral 1999: 22).

A special type of simple-septate ascogenous hyphae, in which the ascus base shows a characteristic bifurcate shape, occurs, besides *Amphosoma*, *Bryorbilia*, and *Orbilia*, in a few very unrelated groups of *Ascomycota* (see above), which supports the polyphyletical origin of this character. As an example, some species of *Helicogonium* possess asci with a bifurcate, simple-septate base. These asci closely resemble those of *Orbilia*, especially section *Hemiorbilia*, where even the ascus apical wall thickenings look very similar. Yet, an evolutionary link can be excluded because ascospores of *Helicogonium* never contain spore bodies and their anamorph is phialidic and often develops directly from ascospores by budding. *Helicogonium* was tentatively placed in the tribe *Calloriopsideae* of *Leotiaceae* s.l. (Baral 1999: 20), for which later the new family *Helicogoniaceae* Baral was proposed (see Jaklitsch et al. 2016).

The two large genera *Hyalorbilia* (with croziers) and *Orbilia* (without croziers), which are both in a process of rich speciation, serve as an example which contradicts a theory advocated by Huhtinen (1990a: 67). The author observed that in *Hyaloscypha* (*Helotiales*) several 'taxon pairs' mainly differ in the ascus base which he thought to offer 'one of the first morphological signs of divergence'. He, therefore, separated these taxa only at the varietal level, and considered the frequent presence of such variation among closely related taxa of a genus as an indication for a rather 'active evolutionary stage' of the group. Genera lacking almost in total taxa with simple septate ascus bases (*Hamatocanthoscypha* and *Phialina* in his monograph) he thought to possibly represent older groups with a 'longer evolutionary history' in which 'the capacity for divergence has decreased'. This theory implies that those species with simple-septate bases are the more primary ones which in some groups disappeared during evolution, a view which is in conflict with the here presented hypothesis. The situation in the *Orbiliomycetes* hardly allows to apply Huhtinen's theory, as the largest genus *Orbilia* is consistently without croziers and, nevertheless, shows a high number of taxa in the process of divergence.

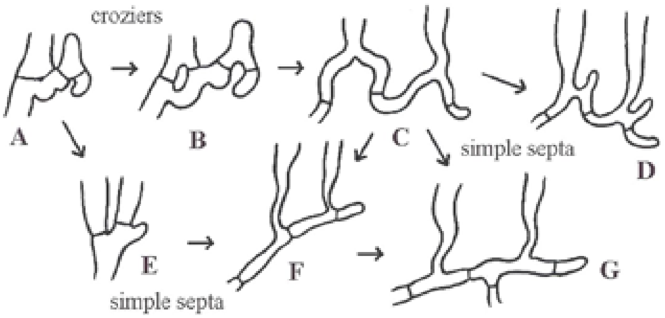


Figure 23: Hypothetical phylogeny from croziers to simple septa in *Orbiliomycetes*. — **A–B**: croziers (*Liladisca*, *Lilapila*, *Lecophagus* p.p., *Pseudorbilia*, *Hyalorbilia*), **C–G**: simple septa. Simple-septate ascus bases either unbranched, with one basal septum (**E**, *Lecophagus* p.p.), or branched, with two or more basal septa, Y-, L-, T-, H-shaped (**C–D**, **F–G**, *Amphosoma*, *Bryorbilia*, *Orbilia*).

Ascus base in other subdivisions of *Ascomycota*. When taking the whole *Ascomycota* into consideration, the first true croziers appeared, to the present knowledge, in the *Orbiliomycetes*, which branched off at first in the six loci ML analysis of Prieto & Wedin (2013). Only two subdivisions of more primitive ascomycetes, *Taphrinomycotina* and *Saccharomycotina*, separated earlier. True croziers in these two subdivisions appear to have never been reported. The asci of *Taphrina* are consistently without any kind of basal protuberances, and the asserted presence of a dikaryotic vegetative mycelium similar as in *Basidiomycota* (Martin 1940, see also Gäumann 1964: figs 182 ff.) was later rejected (see Landvik et al. 2003: 1028). Likewise, the ascogenous hyphae of *Neolecta* are always simple-septate and never showed any basal protuberances (Redhead 1977, Landvik et al. 2003, see also Baral IVV: H.B. 7428). Both genera have multinucleate hyphae in which nuclei form pairs and give rise to asci. The paired nuclei are apparently daughter nuclei, which might explain the absence of croziers (Landvik et al. l.c.).

In those genera of *Saccharomycotina* with a mycelial phase, the situation is less clear because an ascogenous system is in total absent, instead, the gametangium directly transforms into an ascus. In self-fertile taxa the subbasal conjugation branch of the ascus forms an arch with a smaller or larger perforation, similar to a crozier (*Endomyces*, Guillermond 1909, in Gäumann 1964: fig. 104; Helfer 1991: fig. 7). Redhead & Malloch (1977) observed in *Endomyces* crozier-like appendages which strongly resemble pseudoclamps, and the authors believed this to be degenerated croziers. However, Gäumann unmistakably spoke of male and female branches in this genus. Because of this similarity of the conjugation branches of anisogametangiogam (heterogam) taxa, it seems possible that all the ‘croziers’ reported in *Endomyces* concern the stage of conjugation or a reduction hereof.

Gäumann (1964: 113) emphasized that, in the phylogeny of ascomycetes, the genus *Myriogonium* Cain (= *Helicogonium*), which he accepted as belonging to the *Dipodascaceae* of *Endomycetales*, represents the first case of ascogenous hyphae with repeated crozier formation, i. e., the formation of croziers in a chain during mitotic divisions of a dikaryon. Yet, the genus is certainly not related to the *Saccharomycotina* but belongs in the *Pezizomycotina* (see p. 44).

Clamps of basidiomycetes. A long historical discussion about pro and contra of using different terms in asco- and basidiomycetes lasts up to now (see, e. g., Tehler 1988: 244). One of the asserted differences lies in the place where the hook-like outgrowth starts (apically in croziers, laterally in clamps), following the situation reported by Claussen (1912) in *Pyronema*. Yet, laterally outgrowing hooks were, e. g., figured by Björling (1942, in Gäumann 1964: fig. 249) in *Sclerotinia* and can actually often be seen in members of *Helotiales* (e. g., in *Hymenoscyphus*, Hengstmengel 1996: figs 4a, 5b). On the other hand, more or less terminal hooks were described in some basidiomycetes, e. g. in *Sebacina* (Rogers 1936). Another opinion stresses the restriction of dikaryons and croziers to the ascogenous hyphae in contrast to clamps which occur in the entire vegetative hyphal system of basidiomycetes (extended dikaryophase; see, e. g. Esser 1982: 545, Tehler l.c.). An ultrastructural difference lies in the presence of a dolipore in basidiomycetes in contrast to a simple pore with Woronin bodies in ascomycetes.

Authors doubting homology of croziers and clamps as established by Kniep (1915) were, e. g., Savile (1955: 76), who was fully convinced of a convergent evolution of croziers and clamps, by suggesting that basidiomycetes evolved from a taphrina-like ancestor lacking clamps, and Tehler (1988: 244) who supported Savile’s opinion. Authors postulating homology were many, including Rogers (1936), and also Hengstmengel (1996: 192), who concluded that there is general agreement about this topic, as both structures perfectly coincide in any respect of their cell wall morphology. Therefore, he suggested avoiding different terms in the two fungal divisions and to use the term clamps also in ascomycetes.

Homology of clamps and croziers would imply that a common ancestor of asco- and basidiomycetes existed which possessed this morphology. Clamps in *Basidiomycota* occurred apparently for the first time in some groups of *Ustilaginomycotina* (Begerow et al. 2014) and *Pucciniomycotina* (Aime et al. 2014). It was asserted that some groups of *Ustilaginomycotina* have croziers rather than clamps because the septa lack dolipores (Moore 1972), whereas the only group of the subphylum having dolipores (*Tilletiales*) lacks clamps (Begerow et al. 2014). A common ancestor for all *Basidiomycota* having clamps without a dolipore is thus imaginable.

In *Ascomycota* as well as *Basidiomycota*, taxa with simple septa and/or ‘pseudoclamps’ frequently occur as close relatives to taxa with croziers or clamps. This coincidence seems a further proof that the two divisions did not independently develop this morphology but inherited it from a common ancestor. The problem is that there is so far no case of crozier formation known in *Taphrinomycotina*, and in *Saccharomycotina* no ascogenous hyphae exist. The theory of a homology between croziers and clamps implies that the two latter subdivisions have lost croziers and/or ascogenous hyphae. The detection of a taxon with true croziers in this basal group could help clarifying the question.

The oldest fossil with clamps dates in the Visean of the Mississippian period of Carboniferous (~330 myr ago, Krings et al. 2011). This might correspond to the earliest diversification of *Pezizomycotina* which took place about 550–350 myr ago (see p. 133, Molecular clock).

Ascus maturation. During an early phase of maturation, the ascus elongates until it reaches almost the level of the paraphyses. In this phase the ascus is uninucleate. The large fusion nucleus is usually clearly visible in living material by its thin, slightly refractive nuclear membrane and a distinct homogeneously refractive nucleolus (Fig. 24: A–B, see also p. 96–97).

During meiosis the fusion nucleus divides into 4 nuclei. Additional mitotic divisions result in 8 or up to 128 nuclei, depending on the species. These nuclei and their nucleoli are much smaller and usually very difficult to see without applying nuclear stains. Asci up to this development stage are named 'young' in Verkley's (1995) terminology, whereas asci in which the ascospore wall is formed are referred to as 'immature'.

Four different states of mature asci in regard to the mixed occurrence of living and dead asci and spores. Herbarium specimens are either dead in all parts, or they are still viable in regard to all of their cells or often only a part of them. A possible vitality of dried material can be recognized under the light microscope after rehydration (see p. 26 ff.). Vitality depends on the desiccation tolerance of the species, i. e., the period of time the individual cells withstand dryness, also on the condition of the apothecia when collected.

The different cells of an apothecium may differ in their strength of drought tolerance, therefore, it is a normal case that living and dead elements are found side by side when a rehydrated apothecium is examined. But also apothecia collected in the fresh state may show dead cells. This phenomenon is of special interest concerning mature asci, which generally show a less pronounced tolerance than the spores within, or sometimes no tolerance at all. As a consequence, we need to distinguish four main states of mature asci, three of which being regularly found in preparations (Fig. 25). These four states correspond to the four possible combinations of living and dead asci and spores. However, intergradations may occur in which only some of the spores within an ascus are viable (see Figs 7: d, 25: c). In addition to this, the increase in ascus turgor from moderate to full turgescence provokes distinct changes in ascus size and spore arrangement.

State 1 (Fig. 25: a–b): A **living ascus** contains **living spores**. At normally occurring **moderate turgescence** of asci (state 1a) the cytoplasm (including vacuoles) of both ascus and spores is non-refractive and thus transparent. The spore wall and also the refractive SBs are distinctly visible. At this stage of development, the spores well correspond to ejected spores in regard to their shape and size, due to a more inelastic spore wall. State 1a is, therefore, the taxonomically most suitable one, and our illustrations of asci predominantly refer to it. For recognition of maturity of spores, this state is even superior to free spores since the latter, and also living spores inside dead asci, may either be immature, or may have undergone an ageing process, during which the SBs become considerably shorter and thicker by losing much of their taxonomic reliability.

Some minutes prior to discharge, the asci attain **full turgescence** (state 1b). At this stage of development the spores form a more or less compact spore cluster. The spores are usually considerably dehydrated and thereby shrink or collapse, the sporoplasm becomes somewhat refractive and less transparent, and the SBs rather obscure. The ascus vacuole attains its highest volume. Such maximum swollen asci show the highest contrast between spores and ascus vacuole, but are quite rarely seen in preparations.

State 2 (Fig. 25: c–d): A **dead ascus** contains **living spores**. Asci of this state have irreversibly lost their functionality. The ascus vacuole lacks a high percentage of its water due to damage of the plasma membrane. In the most frequent case the ascoplasm becomes refractive and intransparent (state 2a). The sporoplasm is transparent and the SBs are very clearly visible. The spore wall cannot be differentiated from the surrounding ascoplasm due to a similar refractivity index.

Such asci are frequently seen in recently dried material of desiccation-sensitive species, or in a few months or years old collections of desiccation-tolerant taxa, because of the limited tolerance of mature asci. The spores are no longer in their original arrangement but often occupy the whole length of the wider part of the ascus.

In a small number of dead asci the spore wall may nevertheless be clearly visible (Fig. 25: d: state 2b). In this case, the cytoplasm outside the ascus vacuole is apparently so strongly reduced that the area between spores and ascus wall remains transparent despite a high water loss. Asci of this type appear to derive from those which were fully turgescent when still alive (Fig. 25: a–b: state 1b). This would explain why asci of state 2b are only found in a comparatively small number, and also why such asci do not show the glycogen reaction typical of dead mature asci of state 2a and 4a.

State 3: A **living ascus** contains **dead spores**. This situation is very rarely found, especially in desiccation-tolerant species, perhaps due to some stress regarding water or nutrient availability while still in the field. It is in conflict with the general observation that spores exhibit a higher desiccation tolerance than asci do. Such asci may attain full turgescence and eject their functionless spores. A state 3b cannot be distinguished because in the compressed spore cluster the

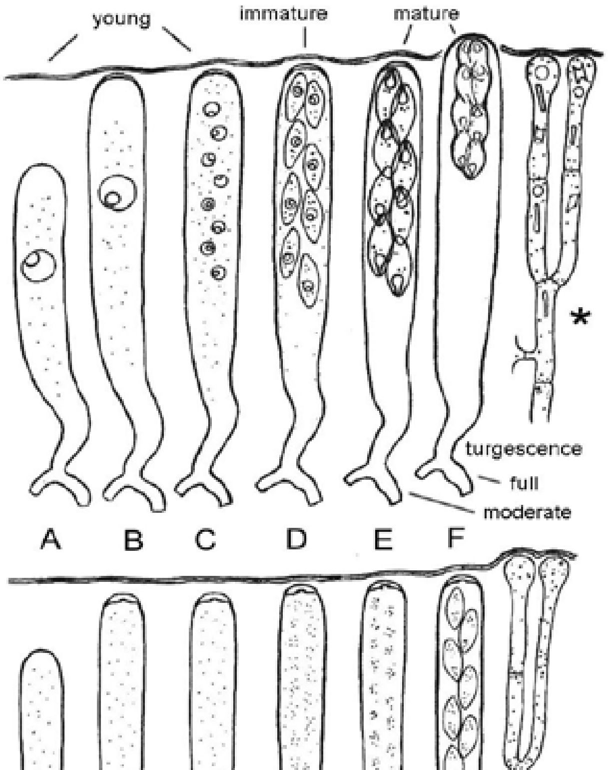


Figure 24: Schematic illustration of ascus ontogeny in the living (above) versus dead state (below).

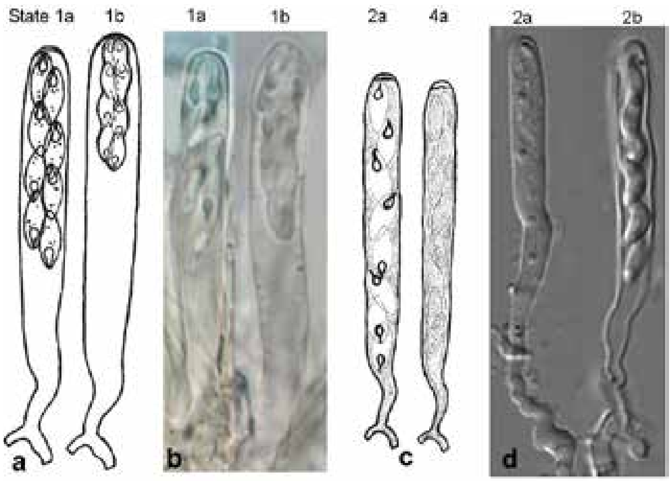


Figure 25: Different states of a mature ascus. — **a–b**. living asci (state 1), **1a**: at moderate turgescence, **1b**: at full turgescence; **c–d**. dead asci (state 2 and 4); 2a–b: containing living spores; 4a: containing dead spores; in 2a the ascoplasm is refractive and only the sporoplasm and SBs are clearly visible, whereas in 2b the ascoplasm is non-refractive, therefore also the spore wall is clearly visible. — **a**, **c**. Schematic drawing of fictive species, **b**. *Orbilia vitalbae* (phot. R. Tena), **d**. *O. neocomma* (phot. Z.F. Yu, DIC).

spore contents are too indistinct to decide whether the spores are alive or not.

State 4 (Fig. 10: d–e, 25: c): A **dead ascus** contains **dead spores**. In the more frequent case (state 4a), both asco- and sporoplasm are refractive. The SBs lost their refractivity and are usually completely invisible. The spores are invisible or very difficult to discern in mountants like H_2O (Fig. 25: c) or KOH, but they usually become clearly visible when applying cytoplasmic stains to a KOH mount, such as IKI, MLZ, CB_L, or phloxine, because the spore wall thereby remains unstained (Fig. 10: d–e). Alternatively, the spore wall may become discernible in some species when staining with CR.

As with state 2b, in a few asci the dead spores may very clearly be visible including their cell walls (state 4b). Asci of state 2b and 4b appear to originate from fully turgescent asci, which can be concluded from the absent glycogen reaction.

Ascus wall, **type of apex**. Light-microscopic observation allows to recognize three main ascus types within the *Orbiliomycetes*, based on external shape and internal wall thickening of the ascus apex (see Fig. 27). These three types often coincide with other features of the teleomorph, which supports their taxonomic value. Our molecular analyses confirm that ascus apex morphology provides a valuable tool in the classification of genera and infrageneric groups within the class (see Tabs 57, 63).

Five electron-microscopic studies (TEM) on the ascus apex of *Orbilia* came to our notice. What can be seen with the TEM in these studies well corresponds to results gained with the LM, and supplies only little additional information. Four of them (Bellemère 1977, Benny et al. 1978, Liu 2006, Kumar et al. 2012) present a comparatively primitive ascus apex, characterized by a continuously thin ascus wall that lacks any clear ring or pore structure. Although each of these authors studied only a single species with the TEM, thin-walled asci were believed to be typical of the genus, which was also supported by LM-studies, e.g., by Bellemère (1968: fig. 50).

In the present study about 73% of the species assigned to *Orbilia* possess asci with such a thin-walled, more or less truncate apex, whereas in the remaining 27% of the taxa the apex is abruptly thick-walled to a varying extent, due to a swollen endotunica that is often provided with an apical chamber. This ascus type was first reported by Baral (1994: fig. 2), and a new subgenus *Hemiorbilia* was proposed for it. In his unpublished TEM study, Müller (1998) treated two species with this ascus type (Fig. 29), besides one with a truncate thin-walled ascus apex.

Although our monograph favours the study of living cells, ascus apical apparati need to be studied primarily in the dead turgorless state (see also p. 50, Influence of ascus turgor). Here the differences in wall thickness and shape between the three main types are much more evident, whereas in living asci neither shoulders nor pronounced wall thickenings can be seen. Nevertheless, living turgescent asci should simultaneously be studied whenever available, in order to recognize the rather strong differences to the dead state, and to avoid misinterpretations in regard to spore discharge.

Ascus wall layers. With the TEM, Bellemère (1977: fig. 7A–B) found the ascus wall of *Orbilia leucostigma* (section *Orbilia*) to be four-layered (Fig. 34: a–b), whereas Benny et al. (1978: figs 6, 8) and Kumar et al. (2012) found in *O. sarraziniana* and *O. tenuispora* (section *Helicoon*) a two-layered wall (see Fig. 34: c–d). Both subgroups of *Orbilia* have an ascus apex of the truncate-shouldered type without apical thickening. Bellemère's two outer layers ('couche a' and 'couche b') appear to correspond to the darker outer layer of Benny et al. and Kumar et al., who found this layer to be comparatively thicker in the shoulder region. Verkley (1992–95) found a two-layered ectotunica (as 'outer layer') in many *Helotiales*, and referred to it as 'outer and inner stratum of the outer layer'. He likewise observed that the endotunica (as 'inner layer') may also be composed of two strata, of which the inner one is often most reactive. Possibly, the four strata observed by Verkley in the *Helotiales* correspond to the four layers described by Bellemère in *Orbilia*.

When transferring these results to our LM observations on more or less thick-walled ascus apices in *Orbiliomycetes*, we conclude that Bellemère's two outer layers correspond to the refractive outer part of the ascus wall here referred to as ectotunica (also termed 'ectoascus', 'exotunica', or 'exoascus', see also Baral 1987a). In species without apical thickening we usually could not clearly differentiate an inner layer (endotunica, also termed 'endoascus') in the apical region, although Bellemère's 'couche c' obviously represents a very thin low-refractive endotunica.

Thick-walled ascus apices occur in most members of subgenus *Hemiorbilia* and in some of section *Ovoideae* (subgenus *Orbilia*). Here the endotunica forms the main part of the strongly swollen apical thickening. Two species with such asci, *O. vinosa* and *O. aristata*, were studied by Müller (1998, see Fig. 69): ecto- and endotunica strongly differ in electron-density, but sublayers within each of the two main layers are not noticeable.

Bellemère's 'couche d' looks on his pl. 7A as if it represents the plasmalemma of the ascus. However, our LM-studies in *Orbiliomycetes* with apically thickened ascus wall show, particularly regarding species with large asci, that the inner boundary of the endotunica is visible in turgorless asci as a thin medium refractive layer, suggestive of Bellemère's 'couche d'. This layer is distinctly enhanced in contrast when stained with CR_{SDS} (Fig. 30: b).

At the ascus apex outside the ectotunica a layer is often found which is currently referred to as 'periascus'. This represents an excretion of the ascus wall and is, therefore, treated here under 'excretions, gel on asci and paraphyses'. In species with black apothecia the periascus may carry an olive-brown pigment.

Concerning the terminology around the apical thickening see also p. 49 (Apical thickening of the ascus wall).

Amyloidity and dextrinoidity. All parts of the ascus wall including the ascogenous hyphae consistently lack a positive (hemiamyloid or euamyloid) iodine reaction in all species of *Orbiliomycetes* examined. Even after KOH-pretreatment, both IKI and MLZ did not provoke any blue reaction at all (see Baral 1987b).

A few literature reports of amyloid (blue) ascus apices in *Orbiliomycetes* are erroneous and some of them might be explained by the presence of yellow pigments in the paraphyses staining blue-green with iodine. Three of the four species of *Orbilia* treated by Thind & Sharma (1980) were said to have amyloid ascus apices (in MLZ). Yet, reexamination of one of their material (*O. curvatispora*, = *O. auricolor*) proved that the asci are inamyloid. Likewise, amyloid ascus apices were reported by Starbäck (1899) for *Orbilia caudata* ('very faintly') and by Cash & Corner (1958) for *O. fici* (= *O. blumenaviensis*), but reexamination of their type material indicated the contrary. Also Vesterholt (in Hansen & Knudsen 2000) stated the asci of *Hyalinia rubella* (= *Orbilia rubella* s.l.) to have an amyloid pore.

In other cases, predominantly in the older literature, reports of blue iodine reactions of asci are coupled with further discrepant features, which indicate that the species belongs to the *Helotiales*. For example, Nannfeldt (1932: fig. 40c, n. 3849) included an unidentified species in *Orbilia*, although he stated on his herbarium label 'Asci I+'. Reexamination revealed that it probably belongs to the genus *Cistella* Quél. (IVV: H.B. 7328).

A faintly reddish reaction was inconsistently observed in a few species of subgenus *Hemiorbilia* section *Lentiformes* (*O. pileosoma*: Pl. 156: 1c), *Hemiorbilia* (*O. junci*: Pl. 389: 1c, *O. vibrioides*, several spp. around *O. myrioobliqua*: Pl. 375: 2e): the comparatively thick apical wall (type A) showed an inconsistent reaction in MLZ (especially when pretreated by heated KOH). In IKI (with or without KOH-pretreatment, or when pretreated by H_2SO_4, Fig. 30: d) no clear reaction could be observed. This reaction fits the definition of dextrinoid (Baral 1987b: 424). In *O. pileosoma* it was very clearly perceptible as a light red stain, whereas in *O. junci* and *O. myrioobliqua* it was only pale red. Only some of the collections of *O. pileosoma* and *O. myrioobliqua* showed the reaction, whereas others were completely negative. Within the discomycetes this reaction seems to be a rare though possibly overlooked feature of inamyloid apical thickenings.

Shape of the pore prior to dehiscence. Bellemère (1977) saw a very minute apical indentation of the endotunica that resembles an apical chamber (Fig. 34: b). This could, however, also be interpreted as a structure that emerged by somewhat irregular, wave-like swelling of the endotunica. A slight apical chamber appears to be visible also on Benny et al.'s (1978) TEM section in front view (truncate-shouldered aspect, Fig. 34: c). What Kumar et al. (2012: fig. 11) reported as electron-light zone (EZ) between apical ascus wall and ascoplasm appears to concern plasma detachment rather than a wall structure.

The presence of an apical chamber was frequently seen under the LM in species with an apical thickening (section *Lentiformes* p.p., section *Hemiorbilia*, section *Ovoideae* p.p.; Figs 28–29). This chamber is formed by an indentation of the endotunica in the central region of the apical thickening. It can also be seen in living asci, but it occurs inconsistently within a preparation, irrespective of the living or dead state (Fig. 31). Since the truncate-shouldered asci are thought to have evolved from ancestors with a hemispherical thick-walled apex, (see p. 254, Plesiomorphic characters in *Orbiliomycetes*), thin-walled apices might well possess some remains of both apical thickening and apical chamber.

Shape of the pore after dehiscence. Benny et al. (l.c.: fig. 7) and Kumar et al. (2012: fig. 13) observed that dehiscence results from a tearing of the thin-walled, flattened apical region between the more thick-walled lateral shoulder areas, but the spatial shape of the pore could not be seen. Our observations with the light microscope showed that the asci of *Orbilia* open by a comparatively large slit- or fissure-like pore. However, although quite clearly visible under the LM, emptied asci with an opening lying in a favourable orientation are not easy to detect. Slit-like pores of emptied asci were so far only seen in a few species of *Orbilia* sections *Lentiformes* (*O. patellarioides*: IVV: H.B. 9173a, *O. atrolentiformis*: Pl. 152: 1c, *O. pileosoma*: Pl. 157: 1n–o, *O. myriolentiformis*: Pl. 177), *O. flavida* (IVV: 23.V.2018), *Hemiorbilia* (*O. junci*: Kohlmeyer et al. 1998: fig. 8, *O. allantoobliqua*: IVV, *O. velutina*: Pl. 282: 1t, *O. occulta*: Pl. 355: 4d, *Habrostictis* (*O. spathulata*: Pl. 640: 1c), and *Orbilia* (*O. renispora*: Pl. 882: 3e). Apparently, the asci of all species of *Orbilia* do open by a more or less large slit-like pore, irrespective of having or lacking shoulders, an apical thickening, or an apical chamber, but this needs confirmation from further taxa from different series.

It is not fully clear whether the slit in truncate-shouldered asci runs from one shoulder to the other, or transversely between the shoulders, neither in *Orbilia*, nor in *Taphrina* (Fig. 39: m–o) and *Neolecta* (Fig. 39: j). However, in *O. renispora* the former appears to be the case when comparing Fig. 3d and 3e in Pl. 882. In *Pseudorbilia* the asci appear to open by a pore, which is ± round in outline and tends to be lateral (Fig. 26: d–f). In *Lilapila* a slit-like apical pore was indistinctly seen, while in *Hyalorbilia* no observations on the apical pore were made so far.

Thakur & Zachariah (1989: fig. 2 E–F) saw with the SEM a round pore with an operculate opening mechanism in the ascus apex of an *Orbilia* (*O.* ?*cardui*) which they obtained in pure culture of *Dactylella rhopalota*. Also Descals et al. (1999: fig. 7, *Orbilia rosea*) illustrated an ascus with an operculum; however, this feature is not further mentioned in the text and seems quite unlikely to represent the typical way of how these asci open during discharge.

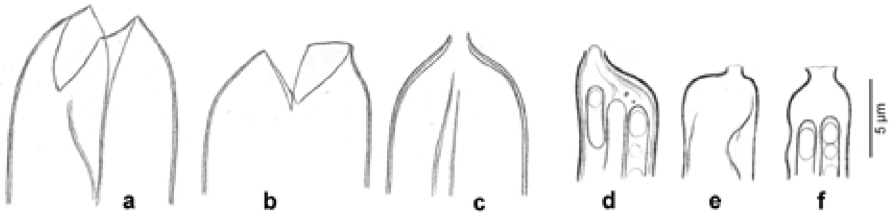


Figure 26: Apex of emptied asci. **a–c**. opened by a large slit-like pore (fissurate, *Orbilia myriolentiformis*); **d–f**. opened by a small, ± lateral, apparently roundish pore (poricidal, *Pseudorbilia bipolaris*).

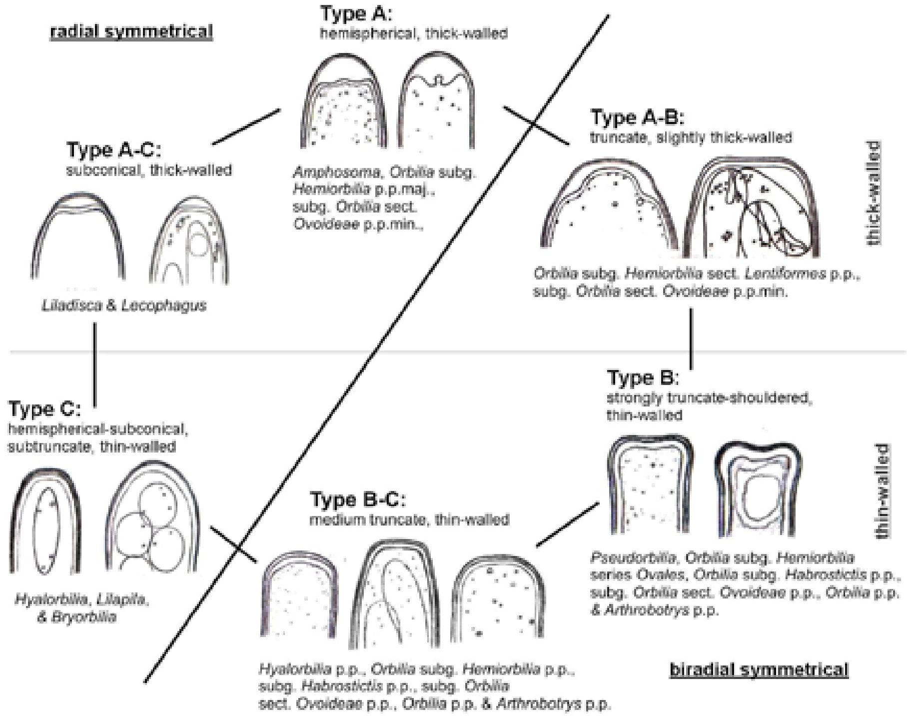


Figure 27: The three main ascus types (**A–C**) known within the *Orbiliomycetes*, and three intermediate types (all in the dead turgorless state).

Type A. **Hemispherical apex with apical thickening** (**Figs 27–32**). Asci of this type occur with a high continuity throughout subgenus *Hemiorbilia*, which represents about 25% of the members of *Orbilia*, but are also present in some members of subgenus *Orbilia* section *Ovoideae*, furthermore in the genus *Amphosoma*. The asci of *Liladisca* and *Lecophagus* (Figs 27 top left) belong to a reduced type that forms a transition to type C. Thick-walled asci are so far only known in the large group of desiccation-tolerant taxa, and their neglection is one reason why they remained unreported in the *Orbiliomycetes*. In other groups of ascomycetes, inamyloid ascus apical wall thickenings comparable to those of *Orbilia* are quite frequent. They are found, for instance, in many genera of *Ostropomycetidae*, or in some of *Leotiomycetes* such as *Calloria*, *Claussenomyces*, *Gelatinopsis*, or *Leotia*. Many of these discomycetes are desiccation-tolerant. Asci of subgenus *Hemiorbilia* resemble also those of the desiccation-sensitive genus *Thelebolus* which, however, differ in a more or less con-spicuous subapical reinforcement of the ectotunica (Fig. 32).

Apical thickening of the ascus wall. In the dead turgorless state the ascus apex of type A is distinctly thick-walled. The ascus wall appears as two-layered when viewing dead asci under the LM (oil-immersion) in water, KOH(+CR), or MLZ. It consists of a thin, firm, refractive ectotunica of quite equal thickness, and a more or less thick, soft, non-refractive endotunica. In the lateral ascus wall the endotunica is often very thin and, therefore, hardly perceptible, but it is abruptly inflated in the apex area. The inflated, thick-walled apex region is referred here to as apical thickening, following the terminology of Verkley (1992: 5). In other studies it was termed 'apical dome' (dôme apical, Bellemère 1977) or 'tholus' by lichenologists. In the present study the term apical dome is used as an equivalent of apical thickening. In the central part of the apical thickening the endotunica usually shows a more or less distinct indentation from below which is termed apical chamber (terminology following Verkley l.c.; in earlier studies also 'ocular chamber' or 'oculus', Bellemère 1977).

Three-dimensional shape. In contrast to the truncate-shouldered type B, one of the characteristics of type A is that the shape of the apex in the dead state does not or only slightly depend upon the viewing direction (Baral 1994: fig. 2). In the living state the ascus apices appear perfectly hemispherical due to the ascus turgor, whereas in the dead state the shape is sometimes broadly conical and/or subtruncate in front view but hemispherical in profile view.

Staining properties. Apical thickenings in *Orbiliomycetes* are unstained in iodine reagents, except for very rare cases of a faint dextrinoidity (see p. 48, Amyloidity). In CR_{SDS} the inner layer which constitutes the main part of the apical thickening, stains distinctly and homogeneously pinkish-red (Fig. 30: a–b). This congophilous reaction seems to occur in all *Orbilia* species with ascus apical thickenings (sections *Lentiformes*, *Hemiorbilia*, *Ovoideae*). It was detected in *O. vinosa* in 2009 by I. Wagner (pers. comm.) when routinely enhancing contrast with Congo red that contained SDS, and was later verified for a number of species of section *Hemiorbilia*. Actually, the reaction requires the presence of SDS, whereas CR alone does not provoke a perceptible stain, even if pretreated with KOH. The reaction is obtained immediately or at least within a few minutes, but only when exposing to a high concentration of CR, either by placing directly in a drop of undiluted CR_{SDS}, or by adding ample solution to a water mount. Presence of KOH strongly diminishes the reaction. Staining of empty, basally opened asci gave the best results.

The region stained by CR_{SDS} is restricted to the endotunica of the apical thickening, which gets entirely and homogeneously red without a perceptible ring-like structure. CRB stains the same region light violet-lilac. When adding KOH to a CRB mount, the stain of the endotunica became very distinct in *O. pleistoobliqua* (Fig. 30: c). A strong stain of the endotunica in CRB was seen also in *Amphosoma macrosporum*. No reaction of the external gel or the ectotunica is obtained in CR_{SDS}, whereas CRB also stains the external gel.

A comparable congophilous reaction could be obtained in the ascus apex of *Neolecta vitellina*. Although thin-walled when mounted in water, pretreatment with heated KOH induced a pronounced apical wall thickening which stained light red in CR (Fig. 39). In comparison with *Orbilia*, where the reaction is usually homogeneous in the entire apical tickening including the region above the apical chamber, the stained area in *Neolecta* forms a distinct apical ring because of a very deep indentation by the apical chamber.

When treated with H_2SO_4, the endotunica strongly swells, also the ascus apex gets more truncate, sometimes even shouldered (*O. aristata*, not so in *O. angustoobliqua*). After neutralizing with KOH, CR$_{SDS}$ stained a ring-like structure ~1 µm diam. deep red, whereas the rest of the endotunica appeared in a pale red (Fig. 30: e). The position of the ring-like structure strongly varied from central to peripheral, or from above to below.

No clear ring structure could be seen with the TEM in *O. vinosa* and *O. aristata* (as *O. occulta*), the two species with apical thickening treated by Müller (1998, Fig. 29). Verkley (1995) observed ring structures by TEM in a few genera of *Helotiales*, in which no amyloid ring structure is visible under the LM (in IKI). Verkley (1995: 17) used the silver-based PA-TCH-SP procedure, which he found to be 'by far the best method for a taxonomic study of the apical apparatus, also because conventional staining procedures (uranyl acetate, lead citrate) do not contrast the walls in ascomycetes'. Müller (1998) used only the conventional method and, perhaps therefore, he did not observe a ring structure in *Orbilia*.

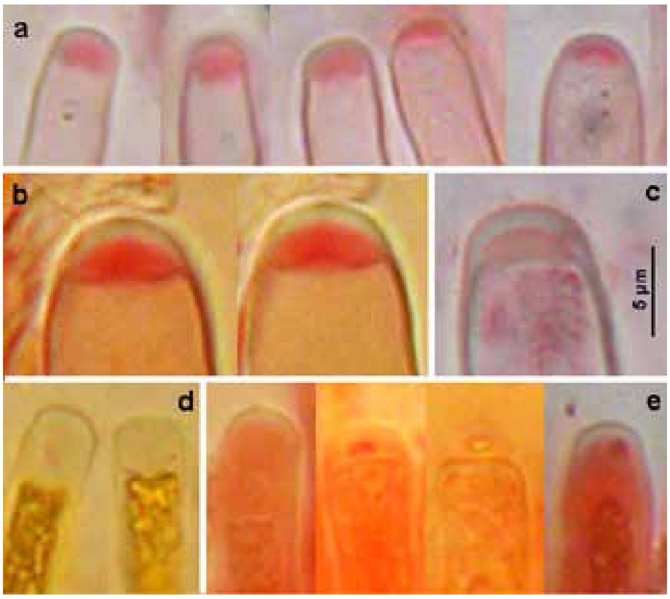


Figure 30 (Type A): Staining of ascus apices in CR$_{SDS}$, CRB, and IKI (dead state). — **a–b**. inner part of apical dome (endotunica) staining directly red in CR$_{SDS}$; **c**. endotunica and thin outer gel layer staining light lilac-violet in CRB+KOH; **d–e**. apical dome strongly swollen after H_2SO_4 treatment (lower end of thickening marked by adjacent ascoplasm), **d**. in IKI (hardly staining reddish), **e**. in CR$_{SDS}$ (partly with irregularly situated ring-like, distinctly red structure, apex sometimes slightly truncate. **a**, **d–e**. *O. aristata* (H.B. 9226a); **b**. *O. angustoobliqua* (H.B. 9050a); **c**. *O. pleistoobliqua* (H.B. 8727c).

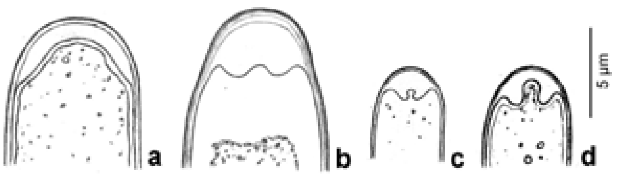


Figure 28 (**Type A**): Young asci with a ± hemispherical apex and an apical thickening with differently shaped apical chamber (dead state). Size and shape of the apical chamber and surrounding annular protrusion strongly varies between and within a species (**a**. *O. megahesperidea*, **b**. *O. myriooblique*, **c**. *O. vibrioides*; **d**. *O. euonymi*, all here assigned to subgenus *Hemiorbilia*).

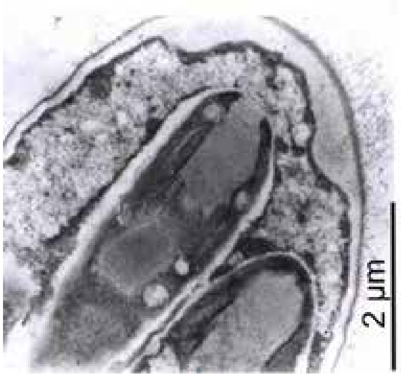


Figure 29 (**Type A**): TEM section of ascus apex showing apical wall thickening with wide apical chamber (dead state). The ectotunica is visible as a dark grey outer line, the endotunica with broad apical chamber as a thick pale grey region below, and the surface of the non-detached ascoplasm as a black irregular inner line (*Orbilia vinosa*, Müller 1998: fig. 13, V.1998, G. Marson, Luxembourg).

Influence of ascus turgor and maturity on the thickness of the apical dome. A frequently overlooked fact is that the ascus apical thickening, or more exactly the endotunica, is an expansible layer that behaves like a sponge (Fig. 31). In living asci the endotunica is comparatively dehydrated due to compression caused by the ascus turgor. For this reason it is rather highly refractive, but easily overlooked because the total wall in the apical region is often not much thicker than laterally. In the dead state the endotunica more or less strongly increases in thickness through imbibition of water and thereby becomes low-refractive. Particularly the inner boundary of the endotunica is highly refractive and rich in contrast in living asci, as opposed to the situation in dead asci. The effect is universal across the *Ascomycota* and was referred to as 'imbibition effect' (Baral 1992: 351).

In sections *Hemiorbilia* the total thickness of the apical wall increases during turgor loss to about 1.5–2.5 ×, e.g., by briefly heating a water mount. Mounting in KOH or H_2SO_4 often results in further imbibition of the endotunica, causing an increase of 2–3 × (KOH) or up to 4–10 × (H_2SO_4) in comparison with the living state (see Fig. 30). The apical chamber often gets narrower during wall imbibition, while its inconsistent presence is perhaps due to different viewing directions.

When comparing dead (or living) asci in the same mountant, the height of the apical thickening varies with the development stage of the asci. Apical thickenings are generally formed at a rather late development stage of the young ascus, i.e., during meiosis of the fusion nucleus or shortly before (see also Verkley 1992–95). At the end of meiosis, when the two unit membranes are formed around each nucleus, the apical thickening attains its maximum height (*Helotiales*, Verkley 1993: 42). This stage of development forms the transition from the young ascus to the immature ascus in Verkley's terminology. During the formation of the ascospore wall in the immature ascus, the apical thickening usually gradually decreases, either only slightly or rather strongly. This phenomenon of decrease in height can be observed in both living and dead asci. In the living asci it can be explained by the increasing ascus turgor, whereas in the dead turgorless asci the phenomenon is thought to be the result of increasing formation of cross-links in the wall matrix, resulting in an endotunica which is less able to swell. In the dead state, the apical wall of immature asci of *Helotiales* and *Orbiliomycetes* is usually about 1.5–2 × thicker than that of mature asci.

Considerable differences in thickness of the apical wall of dead, especially immature asci may occur between different taxa. Those with a thin apical dome (e.g., *Orbilia* subgenus *Hemiorbilia* section *Lentiformes* p.p.) form a transition to the hemispherical thin-walled ascus type, particularly if the apex tends to be truncate. The thickest apical domes known in the *Orbiliomycetes* occur in the immature asci of series *Vibrioides*, measuring immature †(2–)3–4(–6) µm in height. The small apical domes in *Lecophagus* (type A–C) did not show significant height differences between immature and mature, or between living and dead asci.

Difficulties in discerning apical thickenings with the LM. Apical thickenings are easily overlooked or misinterpreted under the LM in water or KOH mountants, due to the often very low refractivity of the endotunica in the dead state. Usually, the dead ascoplasm is more refractive than the endotunica, therefore, care must be taken not to confuse structures of the cytoplasm with those of the ascus wall. Since in dead asci the ascoplasm is usually detached from the wall to a very variable extent, apical thickenings may be reported thicker than they actually are. Because of the detachment, two very close or more or less remote lines can usually be seen: the lower of these two lines constitutes the border of the ascoplasm, the upper the border of the endotunica (Fig. 31: b, d). Drawings showing just one line (usually that bordering the dead ascoplasm which is more conspicuous) are no proof for the presence of an apical thickening.

As will be shown below, plasma detachment in taxa of *Orbilia* with thin-walled ascus apices (ascus type B and B-C) is very often stronger in the apex region compared to the lateral wall, which easily misleads to recognize an apical wall thickening where there is no such thickening at all (see Fig. 36: b). For example, in Spooner's (1987) drawings of species with thin-walled asci [*Orbilia flexispora* (fig. 22C), *O. juruensis* (fig. 24C, E), *O. delicatula* (fig. 21A, E), *O. auricolor* (fig. 19B), *Hyalinia crystallina* (fig. 26C)] the asci appear apically thick-walled, and hardly differ from a drawing of a species with undoubtedly thick-walled ascus apices [*O. vinosa* (fig. 25A)]. It is, therefore, recommended that drawings of apical thickenings indicate these different layers: (1) the outer and inner boundary of the ectotunica in larger asci by two lines, (2) the inner boundary of the endotunica by one line, and (3) the outer boundary of the detached ascoplasm by one line. In doubtful cases, TEM research would help in demonstrating the presence of rather thin apical thickenings, particularly in species with small asci. The inner boundary of the swollen endotunica is best seen when the ascoplasm is strongly detached from the apical wall, e. g., in asci which are broken below. In such a case the ascoplasm may have escaped through the opened base. In unbroken but dead, shrunken mature asci the apical thickenings are often rather compressed and poorly visible due to the closeness and pressure of ascoplasm and spores against the ascus wall, particularly if the spores are still viable and turgescent.

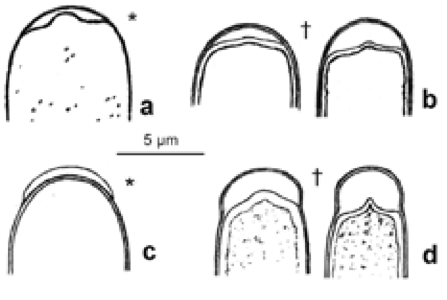


Figure 31 (**Type A**): Apices of immature asci of *Orbilia* subgenus *Hemiorbilia* section *Lentiformes* (*O. euonymi*, **a–b**) and section *Hemiorbilia* (*O. subaristata*, **c–d**). The inner layer (endotunica) of the apical wall strongly swells in dead asci by imbibition due to the loss of ascus turgor. In living as well as dead asci the apical chamber is not consistently seen.

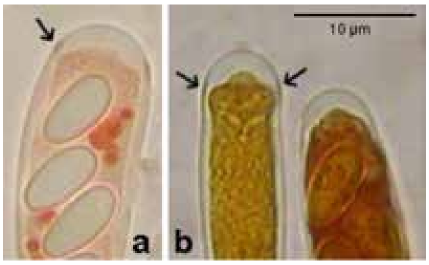


Figure 32 (**Type A**): Asci of *Thelebolus microsporus* (*Thelebolales*, H.B. 8829b) resemble the the hemispherical, thick-walled asci of *Orbiliomycetes*. Note subapical reinforcement of the ectotunica (arrow). Dead state (**a**. in CR, **b**. in IKI).

Intermediate type A-B. **Truncate-shouldered apex with apical thickening** (**Fig**. **27**). In a number of taxa of series *Lentiformes* and *Phanosomates* (section *Lentiformes*, subgenus *Hemiorbilia*) and section *Ovoideae* (subgenus *Orbilia*) both thin- and thick-walled apices occurred within a single apothecium, also truncate asci with distinct apical thickenings were observed. This illustrates the difficulty to draw a sharp limit between the different ascus types.

Type B. **Truncate-shouldered apex without apical thickening** (**Figs 27**, **33–35**). Asci of this type, together with the intermediate type B-C, occur with a high consistency in the two large subgenera *Habrostictis* and *Orbilia* of the genus *Orbilia*. They represent about 73 % of the whole genus. The same type of apex characterizes the small series *Ovales* of section *Lentiformes*, and also the monotypic genus *Pseudorbilia*. Truncate-shouldered, thin-walled asci occur in both desiccation-tolerant and -sensitive taxa. This ascus type is quite extraordinary within the ascomycetes and is otherwise only known from a few non-orbiliaceous genera (*Neolecta*, *Taphrina*, Fig. 39).

Apex shape depending on the viewing direction. This type of ascus apex has a biradial symmetrical shape (Fig. 33) which strongly depends on the viewing direction. In front view the apex appears truncate, often shouldered and centrally indented, whereas in profile view it looks hemispherical or subconical. During a rotation by 90° around the longitudinal axis of an ascus a truncate shape changes to a rounded shape. Therefore, only about half of the asci in a preparation look truncate. The orientation of the asci is obviously accidental in the context of the hymenium, therefore, asci with truncate and rounded apices are found in close association and equal frequency.

The simultaneous presence of truncate and rounded ascus apices may be misinterpreted at first glance as a morphological variation. Instead, every turgorless ascus has two shoulders, which is recognizable from those asci being oriented intermediate between front and profile view. Such asci show the phenomenon that, during focusing, the wall segment being in focus 'moves' from one shoulder to the other.

The biradial symmetry of the truncate *Orbilia* ascus was illustrated by Baral (1994, see Fig. 33: b) and Descals et al. (1999, Fig. 33: a), also by Liu (2006, Fig. 34: e). If only the truncate-shouldered aspect is shown, the ascus apex can easily be misinterpreted as a crater with a slight central depression. Instead, the ascus apex forms an obtuse ridge that runs from one shoulder to the other. This ridge is often somewhat depressed (indented) in the middle to form a saddle. In some asci or taxa the truncation is only slight so that the ridge is convex and the shoulders are less distinct, or the shoulders may project laterally. Such lateral protrusion provokes an abrupt widening at the ascus apex (Figs 34: c, 35: b), which is in contrast to most groups of ascomycetes in which the asci are apically narrowed.

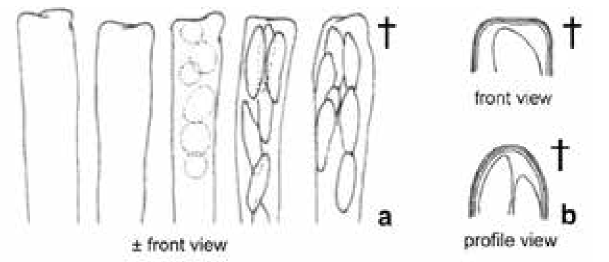


Figure 33 (**Type B**): Ascus apices in *Orbilia* subgenus *Habrostictis* as seen with the light microscope (dead state). Shoulders are visible only in front view. — **a**. *O. rosea* (Descals et al. 1999 fig. 8 A–F, as *Orbilia* sp.); **b**. *O. trapeziformis* (Baral 1994: 119: fig. 3d–e).

The two shoulders are the most prominent feature of this ascus type. Since central indentation and shoulders are only visible in front view, we have consistently figured the front view in our illustrations of this ascus type, but only exceptionally the profile view in addition.

Three of the five TEM-studies which treat this type of ascus apex each report the asci only in one viewing direction: Bellemère (1977, see Fig. 34: a–b) observed the asci in profile view and, therefore, figured an obtuse apex, whereas Benny et al. (1978: fig. 6, 8; see Fig. 34: c–d) and Kumar et al. (2012: figs 3, 9–11) found the apex to be truncate, sometimes slightly indented and with two shoulders, hence they observed the asci in front view. The biradial symmetry of the ascus is easily overlooked since TEM images are based on the study of ultra-thin sections, and spatial information is often not presented with this technique. Benny et al. (l.c.) mentioned the biradial symmetry of the ascal tip only indirectly by describing it as 'truncate with rounded shoulders'. SEM micrographs which show the spatial aspect of the shouldered ascus tips are unknown to us within *Orbiliomycetes* (two SEM-images in Pfister 1997: fig. 2 concern *O. blumenaviensis*, a species that lacks distinct shoulders), but were published for the genus *Neolecta*, which has a very similar type of ascus apex (see Fig. 39).

Apex shape depending on ascus turgor. Besides the fact that only those asci look shouldered which are oriented in front view, the shape of the apex highly depends on ascus turgescence (Fig. 35). Changes in ascus apex shape during the loss of turgor are generally observed in ascomycetes and, similar as with the shrinking effect, this feature is overlooked by many workers.

When studying recently collected specimens in water mounts, truncate apices are often only exceptionally found. The reason for this phenomenon is easily explained: due to their turgescence, living asci are much less truncate than dead asci, at any stage of development. The effect is provoked by the ascus turgor and the elasticity of the ascus wall. Only a very slight biradial symmetry can be noted in the living state, in which lateral inflation as well as central indentation are completely absent (Fig. 35: a, see also Baral 1994: fig. 3). The aspect of the taxonomically important truncate-shouldered apex is a result of ascus shrinkage in combination with an apparently higher wall rigidity in the shoulder region. The truncate-shouldered apex is most developed in basally broken (opened) asci. Sometimes only such artificially emptied asci are laterally inflated and apically indented. Moreover, the shoulders may be more prominent in water mounts compared to KOH.

Are the shoulders and the central indentation to be considered as artifacts of herbarium material? They become apparent indeed only when the asci lose turgor, either when they die prior to spore discharge or when they burst during discharge. However, shoulders are undoubtedly present also in the dry dormant state. Living asci lose all of their free water when apothecia are air-dried and thereby become laterally flattened (compressed) in their upper part. In order to study such asci, a section of an apothecium of *O. trapeziformis* was mounted in water and subsequently dehydrated by adding 96% ethanol, which changed the ascus apex from rounded to strongly truncate. However, the asci die in that medium, and a proper method to study the shape of dormant asci was not found. Asci of desiccation-tolerant species survive in a dry dormant state for a long time. Upon rehydration the shoulders instantly disappear with the increasing ascus turgor.

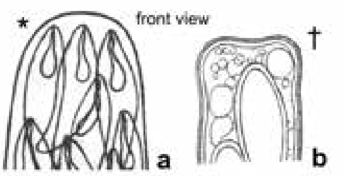


Figure 35 (**Type B**): Apex of mature ascus (**a**. living, **b**. dead state, both in front view). Shoulders appear only when asci lose turgor (*O. multidelphinus*).

When rehydrating dead, strongly flattened asci, they do not necessarily become circular in cross section, not even when heating a KOH mount, therefore, their width depends on the viewing direction, whereas dry living asci immediately reattain their circular outline in optical cross section when water is added (see also p. 9–11, Microscopic measurements).

Apex shape depending on maturity. In addition to the striking effect caused by turgescence, the shape of the ascus apex may slightly depend on ascus maturity: shoulders and indentation were sometimes found to be less developed in mature dead asci. In addition, living turgescent spores inside a dead ascus may prevent the elastic ascus wall from complete

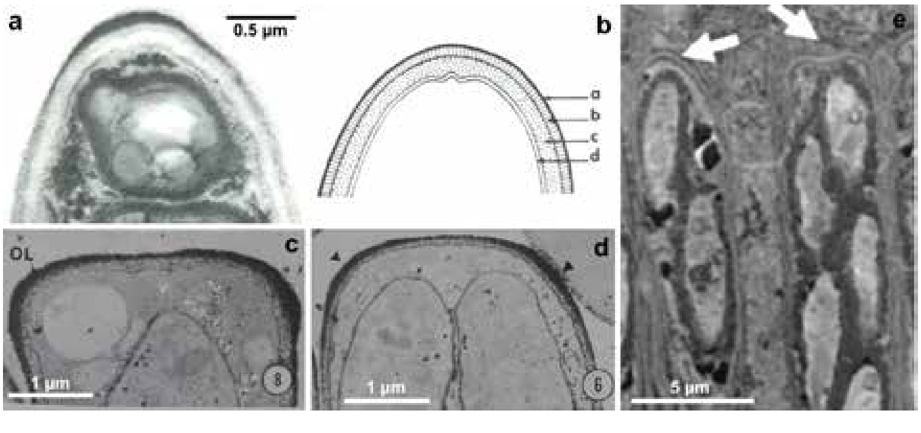


Figure 34 (**Type B**): Ascus apex in *Orbilia* as seen with the transmission electron microscope (TEM, dead state). — **a–b**. *O. leuco-/xanthostigma* s.l. (section *Orbilia*) in profile view (Bellemère 1977: 249, fig. 7 A–B, as *Orbilia* sp.); **c–d**. *O. sarraziniana* (section *Helicoon*), in front view (Benny et al. 1978: fig. 8, as *O. luteorubella*); **e**. *O. sarraziniana* (Liu 2006: 22, pl. 1 fig. C), showing the view-dependent aspect of the ascus apex (**left**: obtuse, in profile view; **right**: shouldered with indentation, in front view).

loss of its tension, resulting in the absence of either distinct shoulders or apical indentation.

Apex shape variation between taxa. Besides the three parameters vitality, maturity, and viewing direction, the apex of dead immature, tension-less asci differs between taxa with this ascus type: it varies from slightly truncate (with a convex apex) over strongly truncate (with a flattened apex) to more or less indented (Fig. 27, types B and B–C). Also the abrupt lateral inflation of the apex was not observed in every species. For instance, some taxa consistently lack both central indentation and lateral inflation irrespective of ascus maturity or other parameters, and are referred to as 'intermediate type B-C' here. On the other hand, prominent shoulders are sometimes only seen in a few asci of a preparation which contains only dead elements, therefore, their taxonomic value is limited.

Wall thickness of truncate ascus apices. One of the crucial characters of type B is that the ascus apex is thin-walled. Even in dead asci there is no apical thickening perceptible at any stage of development, whether studied under the LM (oil-immersion) or the TEM. The apical border of the detached ascoplasm can usually be seen in dead asci under the LM as a thin line a short distance from the ectotunica (Fig. 35: b). Under the LM the endotunica seems to be in total absent, whereas under the TEM a thin layer can be seen that does not expand in the apical region (Fig. 34: a, c–d).

Benny et al. (1978: figs 4, 6, 8, see Fig. 34: c–d) emphasized that the ectotunica is slightly thickened at the shoulders, compared to the central top and the sides of the ascus. This slight wall thickening was generally not seen by us under the LM in species with asci of type B, or rarely only very indistinctly. Bellemère's (1977) micrograph in profile view (Fig. 34: a–b) shows an apically thickened ectotunica, possibly because the section hits one of the shoulders. On his schematic drawing no such apically thickened ectotunica (layers a+b) is figured, and the endotunica (layers c+d) bears a very minute apical chamber that is not seen on the micrograph. Perhaps this drawing refers to a section across the centre of the ascus apex rather than the shoulders.

Intermediate type B-C. **Medium truncate apex without apical thickening** (**Figs** 27, **36**): Dead asci with medium truncate apices lacking apical indentation and often also lateral inflation may be considered as intermediate between type B and C. This type of apex is widespread within *Orbilia* subgenus *Orbilia*, and also occurs in some taxa of subgenera *Hemiorbilia* (series *Lentiformes* and *Phanosomates* of section *Lentiformes*), and *Habrostictis.* In some groups this type predominates (series *Abutilones* of section *Aurantiorubrae*, series *Microsomates* of section *Orbilia*, series *Dactylellina* of section *Arthrobotrys*). Rarely, type B-C is found in *Hyalorbilia*.

The dead ascoplasm is here often more detached from the apical wall than from the lateral wall (Fig. 36: b), and pretends a slight apical wall thickening. A thickened endotunica could, however, never be confirmed with certainty under the LM. However, in several species of section *Ovoideae* the apical endotunica of some of the dead immature asci was distinctly swollen, therefore, the present type can also be interpreted as intermediate between type A and type C.

Type C. **Hemispherical apex without apical thickening** (**Figs** 27, **37**): This rather primitive type of ascus apex characterizes the genus *Hyalorbilia* (Baral 1994: fig. 1), but is also found in *Bryorbilia* and the otherwise very different genus *Lilapila*. It is, however, not sharply differentiated from the intermediate type B-C.

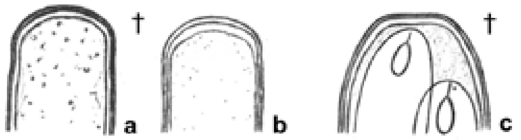


Figure 36 (**Type B-C**): Apices of dead asci in front view. — **a–b**. *Orbilia* section *Ovoideae* (*O. polyspora*, immature, slightly truncate); **c**. *Orbilia* section *Lentiformes* series *Phanosomates* (*O. tremuloidis*, mature, conico-truncate).

The ascus apex is more or less hemispherical in both the living and dead state. However, in the dead state it often tends to slightly or distinctly truncate (Fig. 37: b, h, resembling type B-C) or conical (Fig. 37: d, g, j). Whether the shape of the apex here also depends on the viewing direction is not clear. The apical wall is devoid of a thickened low-refractive endotunica, but sometimes the wall is thicker in the apex region compared to the lateral ascus wall (Fig. 37: b).

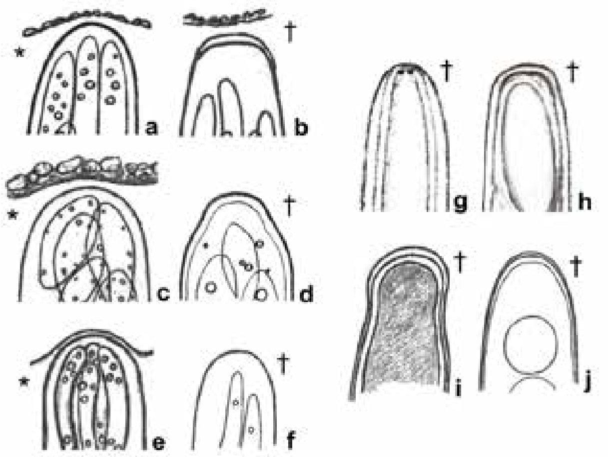


Figure 37 (**Type C**): Ascus apex in *Hyalorbilia* (living vs. dead state). — **a–b**. *H. juliae*; **c–d**. *H. latispora*; **e–f**. *H. helicospora*. Dead asci vary between truncate, conical, and hemispherical; **g–h**. *Bryorbilia arenicola*; **i**. *Lilapila oculispora*; **j**. *L. oculisporella* (**g** & **i**. immature asci).

Intermediate type A-C. **Subconical apex with a small lens-shaped apical thickening** (**Figs 27**, **38**): *Lecophagus* has subconical ascus apices (in the living state more hemispherical or slightly mammiform) with a rather small-sized, lens-shaped central apical thickening. The otherwise very different genus *Liladisca* shows quite a similar type of ascus apex which is, however, more distinctly conical.

In both genera the apical thickening appears to be devoid of a distinct apical chamber when viewed with the LM. Contrary to ascus type A, the apical thickening in *Lecophagus* scarcely gets thicker in the dead state, also it does not clearly decrease in thickness at maturity. Since *Liladisca* is only known from the old type collection, the situation in living asci could not be studied.

Non-orbiliaceous genera with a truncate biradial symmetrical ascus apex (**type B**, **Fig. 39**): Biradial symmetrical truncate ascus apices also occur in another subdivision of *Ascomycota*, the *Taphrinomycotina*. In the two genera *Neolecta* and *Taphrina*, which are assigned to two different classes within

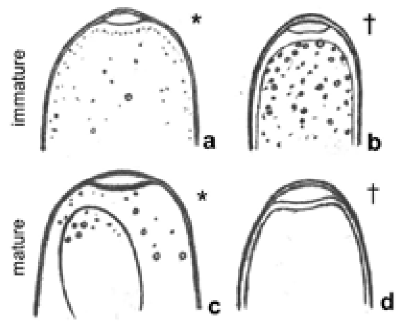


Figure 38 (**Type A-C**): Apex of immature (**a–b**) and mature (**c–d**) asci in *Lecophagus ellipsoideus*. Size and shape of the apical thickening scarcely depends on vitality or maturity.

this subdivision, the ascus apex is strikingly similar to that of type B of *Orbilia* (see also Landvik et al. 2003, Syrop & Beckett 1976: fig. 15). Landvik et al.'s SEM micrographs show for *Neolecta* two 'laterally-opposed horn-like protrusions' (Fig. 39: i) which, however, do not extend laterally. Their TEM micrograph in profile view (Fig. 39: k) shows a rounded-subconical ascus apex and a slight subapical thickening of the endotunica, but no shoulders. Shoulders could unexpectedly not be obtained in any of her TEM-sections, and even under the SEM the shoulders were rather rare and mainly seen in immature asci (S. Landvik pers. comm.). Shoulders were frequently seen by us under the LM in *N. vitellina* (Fig. 39: c), but are, as in *Orbilia*, only present in the dead turgorless state.

According to Landvik et al. (2003), ascospores in *Neolecta* are released through a slit across the thin-walled central region of the apex (fissurate type of dehiscence, Fig. 39: j). The subapical wall thickenings might prevent too irregular splitting during discharge (similar as the ring-shaped subapical wall thickening in the *Thelebolales*), but the authors mentioned also rupture at the subapical thickening (Landvik et al.: fig. 12). Since the shoulders are not further recognizable in opened asci, it remains unclear whether the slit runs from one shoulder to the other or transversely between the two shoulders.

We must be aware that this subapical wall thickening in *Neolecta* is only present in the dead state as a swollen endotunica, but of equal thickness with the adjacent wall in living asci. This is confirmed when studying fresh *N. vitellina* with the LM: the endotunica strongly imbibes water only when treated by heated KOH, and hereafter a ring-like structure that stained ± bright red in CR could be demonstrated (Fig. 39: e–h). This structure obviously corresponds to the subapical thickening reported by Landvik et al. (2003), who did not see a differentiated annular structure in their micrographs (Fig. 39: k). Increase in thickness of the endotunica when treated with KOH or H_2SO_4 and a more or less distinct congophily also occurs in ascus type A of *Orbiliomycetes* (see Fig. 30).

Like *Neolecta*, the genus *Taphrina* has a truncate to saddle-shaped ascus apex very similar to type B in *Orbilia*, judging from a TEM-study by Syrop & Beckett (1976, *T. deformans*) and an LM-study of a fresh collection of *T. pruni* (Fig. 39: l–o). Also in *Taphrina* the two shoulders are only present in dead asci. Similarly as in *Orbilia* the dead asci are widest at the apex when seen in front view. The ascospores are forcibly ejected through a very wide apical slit that runs laterally up to about 10 µm down on both sides (fissurate type of dehiscence, see also Syrop & Beckett l.c.: fig. 16). Again, the shoulders are not further recognizable in opened asci.

Landvik et al. (2003) compared the simple ascus apex types of *Neolecta* and *Taphrina* with their overall slightly thickened apical wall and a similar fissurate type of dehiscence with that of *Pertusaria* as described by Chadefaud & Galinou (1953), an ascus type reported also for various *Lecanoromycetes* by Chadefaud (1973: figs 9, 15, as 'déhiscence bivalve'). A similar fissurate opening mechanism was reported by David (1987) for *Epigloea* Zukal, but here an abrupt apical wall thickening with apical chamber and 'nasse apicale' was observed, although Döbbeler (1984) illustrated mature asci with an overall thin wall. Schoch et al. (2009) referred to this fissurate discharge mechanism as 'nonporicidal', in contrast to the poricidal mechanism through a round apical ring. Slit-like pores are also known from some other inoperculate ascomycetes, e.g., *Helicogonium* (*Phacidiales*, Baral 1999: fig. 5b) and *Deltopyxis* Baral & G. Marson (*Ostropales*, Baral & Marson 2012: fig. 5g).

Since the spatial shape of the biradial symmetrical truncate ascus apex (type B) is easily overlooked, it might well occur in some other groups of *Ascomycota*. Members of *Pezizales* or *Sclerotiniaceae* (*Helotiales*) are usually characterized by a more or less truncate ascus apex in the dead state (see, e.g., Van Brummelen 1981, Bellemère 1977, Verkley 1993). In *Coprotus* and *Kimbropezia* the truncate asci even appear to have shoulders or horns (Van Brummelen 1998a: fig. 12; 1998b: 261). The apex in *Desmazierella* is distinctly laterally inflated (Eckblad 1968: 115; see also IVV) very similar to type B of *Orbilia*. However, all these taxa with a truncate ascus apex are, to the present knowledge, radial symmetrical, i.e., they look truncate

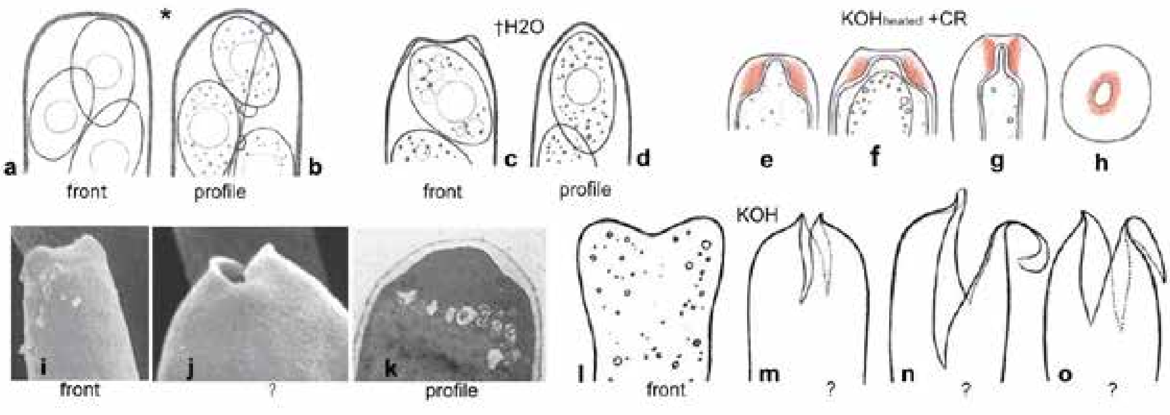


Figure 39 (**Type B**): Ascus apex of the shouldered type, with a fissurate opening mechanism. — **a–k**. *Neolecta vitellina*, **l–o**. *Taphrina pruni*. **b**. a tractus is visible in the living state; **e–h**. unopened asci in which pretreatment by heated KOH induced an apical wall thickening reminiscent of type A-B, enclosing a congophilous ring structure; **h**. top view; **j**, **m–o**. asci opened by a slit, in all of them the viewing direction (front or profile) is unclear. — **a–h**, **l–o**. after LM studies by H.O. Baral (ined.); **i–j**. SEM/**k**: TEM after studies by Landvik et al. (2003: figs 6–9).

irrespective of the viewing direction. However, the truncate ends of the ascospores of *Sarcoscypha* resemble the truncate asci of *Orbilia* in their pronounced biradial symmetry (especially in the dead state). Various authors thought that they vary between rounded and truncate but, in fact, they are saddle-shaped (Baral 1984: 126).

Phylogeny of the ascus apex. Asci with rather primitive apices, in which ring-like structures are absent and inner wall thickenings only slightly developed, represent either the original situation (plesiomorphy) within a group, or should have arisen by reduction as an apomorphy from a more complex structure.

The phylogenetic origin of asci with thick-walled apices within the *Orbiliomycetes* is difficult to determine. Their occurrence in different clades of *Orbilia* (sections *Hemiorbilia*, *Lentiformes*, *Ovoideae*) leaves the question open whether asci with thin-walled, truncate apices, which characterize subgenus *Habrostictis*, section *Orbilia*, and section *Arthrobotrys*, evolved by regression from the former, or represent a plesiomorphy within *Orbilia*. The striking similarity of the thin-walled, truncate apices of *Orbilia* with those of *Taphrina* and *Neolecta* led Kumar et al. (2012) to consider it as an ancient, plesiomorphic character. However, in *Neolecta* a distinct wall thickening with a congophilous ring structure could be induced by heating a KOH-mount (Fig. 39: e–g). The uniform and primitive ascus apex in *Hyalorbilia*, a genus which diverged rather early in the evolutionary history of *Orbiliomycetes*, would argue against the truncate ascus apex as a plesiomorphy within the class. However, also the small genus *Amphosoma* forms a rather basal group, judging from its predominant growth on coniferous substrate, the bipolar SB arrangement, and phylogenetic data. It unites characters of both *Hyalorbilia* and *Orbilia*, and might have maintained some morphologies of the common ancestor of the two genera, which would support our hypothesis that hemispherical, thick-walled apices are primary (Fig. 40). The ascus apices of *Liladisca*, *Lilapila*, and *Lecophagus* are rounded or conical and never with shoulders, either thin-walled or with a small wall thickening. The two former grow on conifers and all three undoubtedly represent rather basal groups. The similarity of the shouldered ascus of *Taphrina* and *Neolecta* could, therefore, be a feature which the common ancestors of *Orbiliomycetes* did not have but which has been reinstalled in some of its subgroups. The genus *Pseudorbilia* is interesting in this regard as it possesses shouldered asci but otherwise closely resembles *Hyalorbilia*, e. g., in having croziers and bipolar SBs.

Within the *Leotiomycetes*, some families consistently possess inamyloid asci (*Helicogoniaceae*, *Cordieritidaceae*) or almost so (*Tympanidaceae*). Species of *Orbiliomycetes* with black apothecia resemble some genera of *Tympanidaceae* not only macroscopically but also from their ascus structure, suggesting an evolutive connection between the two classes. However, molecular data indicate that the *Orbiliomycetes* are more related to the *Pezizomycetes* where they occupy a rather isolated position.

When adopting this regression hypothesis to the *Orbiliomycetes* in which amyloid asci are unknown, taxa with thin-walled apices could have evolved in different lineages from taxa with apically thick-walled asci. In some of these lineages the thin-walled asci are coupled with desiccation-sensitivity of the apothecia, whereas thick-walled asci were so far exclusively observed in desiccation-tolerant taxa.

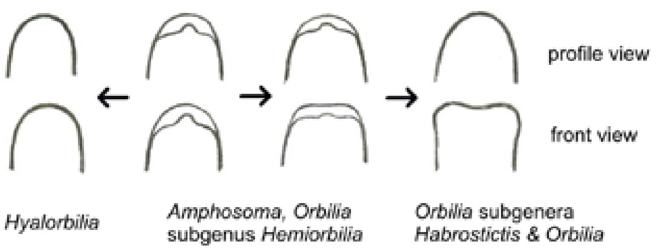


Figure 40: Hypothetical phylogeny of the ascus apex in *Orbiliomycetes* as seen in the dead state.

Wrinkling of the ascus wall or the ascoplasm. In dead asci mounted in H_2O or low-concentrated KOH (up to ~2%), the ascus wall in *Orbilia* rarely appear more or less strikingly transversely wrinkled, so that the asci look like warted, shrivelled or striate. The phenomenon was exclusively observed in very old herbarium material, e. g., in nearly all asci and even some paraphyses of the type material of *O. fibriseda* and *O. serpentina* (Pls 574: 2; 651: 2). This wrinkling may easily be mistaken for a taxonomic character. However, it depends on the mountant: when mounting in 3% or 5% KOH (unheated) the walls promptly turned smooth, whereas mounting in 2% KOH, even when very briefly heated, did not remove the striation. Of course this wrinkling is never seen in hydrated living asci.

The present observations with the LM leave some doubt about the origin of the phenomenon. At least in *O. serpentina* the observed wrinkling appears to result from a transversal folding of the peripheral ascoplasm (which is sometimes secondarily pigmented) rather than a wrinkling of the ascus wall. Due to the rarity of the phenomenon, the true nature of the striation could not be clarified, as it was never observed in any of the more recently collected specimens.

A similar wrinkling of the wall of dead asci is known in the genus *Sarcoscypha* (*Pezizales*, Van Brummelen 1975, Baral 1994). Here the asci get wrinkled during loss of ascus turgor, either after spore discharge or when the apothecia are dried, whereby the asci do not survive. That the observed wrinkling is provoked by shrinkage is obvious from the fact that living hydrated asci have always a smooth wall due to their internal turgor. Our observations in *Orbilia* and *Sarcoscypha* suggest that this wrinkling occurs only in some of the herbarium specimens of a given species and has little taxonomic value.

Amyloidity of the ascus wall. Since amyloid ascus walls have never been observed in any taxon of the *Orbiliomycetes*, a common ancestor with inamyloid asci can be postulated. The question whether an earlier ancestor of *Orbiliomycetes* possessed asci with amyloid walls remains up to now speculative. Molecular studies have shown that the *Orbiliomycetes* have early separated from the remaining *Pezizomycotina* (see Fig. 114). However, in the genus *Neolecta* which diverged even earlier and which belongs to the most basal groups of *Ascomycota* (*Taphrinomycotina*, Landvik et al. 1993, Schoch et al. 2009), the entire wall surface of the asci reacts hemiamyloid (IKI pale red, type RR, KOH-pretreated IKI pale blue; negative in MLZ, blue in MLZ after KOH; Redhead 1977, Landvik et al. 1993: 109, Baral ined.). Amyloid ascus structures are otherwise unknown in the *Taphrinomycotina* and *Saccharomycotina*. Hence, two possibilities seem plausible: (1) a common ancestor of all *Ascomycota* possessed amyloid ascus walls, or (2) amyloidity developed independently in different groups. We are unable to decide which of the two is the more probable scenario. The first option means that the *Orbiliomycetes* separated from the lineage leading to the remaining *Pezizomycotina* while still having amyloid ascus walls, but it is then difficult to understand why none of them survived. The second option would imply that hemiamyloidity, i.e., the KOH-provoked change in reactivity from red to blue, independently developed in different groups.

Spore number within asci, **polyspory**. Polyspory of asci, i.e., spore numbers higher than 8, was found in the present study to be a fairly frequent feature within the genus *Orbilia*, which occurred in about 30% of the taxa. Other genera of *Orbiliomycetes* displayed consistently 8-spored asci, with one exception, the 16-spored *Hyalorbilia pleioerythrostigma*. Regularly 4-spored asci, whether by an omitted mitosis or by abortion of spores, have never been noted with certainty in the class.

Within a given population, the number of spores of an ascus is highly constant, which indicates that spore number is genetically fixed. The observed spore numbers quite exactly follow the formula 2^n. The ascospores in *Orbiliomycetes* were found to be consistently uninucleate in the rare cases when nuclei could be seen. Polyspory in *Orbilia* is certainly always a result of mitotic nuclear division prior to spore formation, which can be concluded from the fact that neither yeast-like budding nor fragmentation of ascospores could be observed. In the terminology of Martens (1932), adopted e.g. by Barr (1991), this case is termed 'true polyspory'. Martens provided a detailed survey on polysporous ascomycetes, according to the three recognized types of polyspory (true polyspory, budding, fragmentation). Yet, in this systematic survey Martens did not mention the very sparse literature reports of polysporous taxa in the genus *Orbilia* known at that time.

Polysporous asci have been described in only four species of *Orbilia*. Two of them are 16-spored: *O. serpentina* (Patouillard 1892, 14–16 subulate spore bodies were seen in the asci) and *O. junci* (Kohlmeyer et al. 1998, 16-spored but often up to 8 spores aborted), and two are 32-spored: *O. paradoxa* Ade (1924, ?= *O. flavida*, '16–24-spored') and *O. polyspora* Grelet (1926; 'usually 24-spored'). Variation in spore number or numbers between 16 and 32 as indicated by the authors can be explained by the difficulty in counting the spores, particularly inside dead asci, but also by irregular abortion of spores or omission of mitoses. Polyspory in *O. serpentina* was obviously not fully understood by Patouillard (1892) since he stated the asci to be 'finally 8-spored'. The report of polysporous asci in *O. myriospora* (W. Phillips & Harkn.) Sacc. turned out to be erroneous: it refers to lipid bodies inside immature asci of a member of the *Calloriaceae* (*Helotiales*, see p. 1679). On the other hand, polyspory has been overlooked in several taxa (*O. coccinella*, *O. euonymi*, *O. flavida*) which were described as 8-spored, either in the protologue or in the current interpretation, but are, in fact, 16- or 32-spored.

Difficulty in counting the spores. Polyspory of asci in *Orbilia* has almost completely been neglected in the past, for the following reasons: (1) when dealing with dead material, the spores are difficult to discern within the asci (see Figs 24, 25: b); (2) if only some of the spores are still viable within a dead ascus, the living spores are much better visible, and the dead spores are easily neglected (see Fig. 7: d); (3) spore numbers of species with very elongate spores are often not easy to evaluate; (4) workers did not pay attention to spore numbers because they did not expect any deviation from the current situation of octospory.

When dead and living spores occur mixed within a dead ascus (case 2), the dead spores are often invisible because they do not contrast with the ascoplasm (Fig. 25: c). Mounting in lethal media such as MLZ, KOH+IKI, or KOH+CR may reveal the full spore number in such asci (Figs 10: d–e, 92: a). In any case, the study of dead herbarium material, perhaps in combination with inadequate preparation methods, was the reason why the three polysporous species were described as 8-spored in the literature. However, another possibility to explain different results of spore numbers is a mixture of several species in a collection (see p. 146–148).

High spore numbers are often difficult to count, especially if the spores are small and/or elongate. The presence of living spores (irrespective of whether mature or immature, or whether inside living or dead asci), enormously facilitates counting. Evaluating spore numbers is also often easier when counting the spore bodies instead of the spores, especially if the SBs are not very elongate and narrow. Such counting is further facilitated by selectively staining the SBs with CRB. Artificial flattening of the living or dead asci by pressure on the cover slip, e.g., through water evaporation, rearranges the included spores in ideally two layers which may aid in evaluating exact spore numbers of 64- or 128-spored taxa.

For species identification it is sufficient to roughly estimate spore numbers. E.g., when counting distinctly more than 32 spores, a sample may be classified as 64-spored. Another method evaluates spore numbers from the volume of the pars sporifera and that of the individual spores (see p. 9, Polyspory).

Spore numbers deviating from 2^n. Spore numbers that regularly deviate from the formula 2^n have never been observed in *Orbiliomycetes*. However, a small number of aberrant asci can sometimes be found within an apothecium, showing slightly reduced spore numbers, although all spores are in the living state and clearly visible. In such a case, one or several oversized spores can be found among the normal-sized ones. For example, in a species with regularly 16-spored asci, 1 or 2 spores inside a mature ascus may show a larger size, resulting in spore numbers of 15 or 14, respectively. Such larger spores contain also distinctly larger SBs. Rarely, such reduction results in a complete step downwards, e.g. from 32- to 16-spored asci. In this case, both types of asci are usually found in one apothecium, together with some asci with intermediate spore numbers and with the higher-spored asci distinctly prevailing. The opposite case, that a minority of asci of an apothecium deviate in a spore number higher than the majority, we have never observed.

Whether the oversized spores contain two nuclei or are formed by the occasional omission of a mitosis, could so far not be clarified. We consider problems in nutrition, or other external parameters, such as water supply or temperature, as possible factors that might disturb the regular process of mitosis and spore wall formation.

Taxonomic value of spore numbers. A lot of species here recognized in *Orbilia* are mainly or solely distinguished by their spore number. This raises the question whether such variation in the number of mitoses is a reliable character to be applied at the species or perhaps better at some infraspecific level. Species concepts become even more dubious in cases in which taxa with different spore numbers occur in close association on the same piece of substrate. However, we have found spore numbers to be generally highly constant within single apothecia and usually also within a population. Therefore, a high taxonomic value is attributed to spore numbers in the present study. It was also a practical reason at an early stage of this monograph, that populations with different spore numbers were consistently distinguished at some taxonomic level.

Barr (1991) discussed the question as to whether (true) polyspory in *Capronia* should be recognized at the genus level by separating 8-spored from polyspored taxa. She thereby relied, e.g., on results from members of *Valsaceae* (by Kern 1957 and Hubbes 1960, both cited in Barr) who reported that 'polyspory was a constant character in the specimens that they examined and cultured, that is that it was at least a character of specific value'.

Similar variation in spore numbers between closely related taxa is known from various groups of ascomycetes. Spore numbers are usually believed to be a constant character at the species level, though this seems not always to be the case in the genus *Thelebolus*, in which spore numbers of 8 up to > 2000 occur. De Hoog et al. (2005: 57) accepted, apart from three 8-spored species, only one multispored taxon, *Th. stercoreus*. Within a single sample of this species, spore numbers of 24, 32, 48 and 64 occurred, although spore numbers within a sporocarp appeared to be constant. In a monospore isolate of another population referred to the same species, spore numbers ranged from 128 up to 264, with an optimum close to 246.

Within *Orbilia*, the consistency and taxonomic value of spore numbers is supported by cultural results in a single species, *O. flavida*. This is the only polysporous taxon for which we obtained apothecia in pure culture (by adding sterilized natural substrate). The apothecia that developed there (H.B. 6716, Pl. 172: 4) fully concurred in their microscopic features with those that had grown in the field, e.g., concerning the consistently 32-spored asci and the spores with their lens-shaped SBs. This result confirms our hypothesis that features like spore numbers are generally not seriously affected by environmental conditions but are instead genetically determined.

A rather well-explored example is series *Microspermae* of *Orbilia* section *Lentiformes* (Fig. 41). The type species *Orbilia euonymi* has 32-spored asci and a wide and dense distribution within Europe, but also occurs in North America. A much rarer 16-spored European species (*O. pleioeuonymi*) differs in subglobose spores and wider SBs. A 64-spored species was discovered in Australia and China, and a 128-spored species rarely occurs in Europe. The spores of the latter two taxa do not markedly differ from *O. euonymi*, nevertheless, we preferred to attribute all four taxa specific rank, although their characters coincide to a high rate with those of the 32-spored populations. Even the anamorphs were found to show only little differences among the four species, apart from a slight reduction of conidial width with increasing spore numbers. Our species concept was confirmed when molecular data became available.

We have recorded quite a few similar cases of more or less similar species with deviating spore numbers, mainly from more or less desertic areas. In contrast to series *Microspermae*, the number of available collections of each species was here usually too low to explore their variation and to see which of the spore numbers are the predominant ones. Most of these mainly extra-European taxa described from just one or a few collections must be considered under this point of view. In the worst case, a here described taxon will turn out to represent a rare marginal derivative of a more common taxon which has escaped our notice.

Polyspory in *Orbilia* was found to be strictly confined to desiccation-tolerant taxa, but even among the 8-spored taxa about 75% are desiccation-tolerant (Tab. 5). Higher-than-average frequency of polyspory was encountered in samples from semiarid to arid regions (~70%, ca. 94 out of 137 polysporous taxa), while only 32 polysporous taxa (~23%) were observed in humid, mainly temperate climates, and 26% in each subhumid and semihumid regions. The 32 polysporous taxa in the humid zone are mainly from sections *Lentiformes* and *Habrostictis*. The proportion of polysporous to 8-spored taxa decreases significantly from arid to humid regions (1.8 in arid, 1.2 in semiarid, 0.6 in subhumid, 0.32 in semihumid, and 0.12 in humid regions). The number of 8-spored taxa in the two main humidity zones is about 325 out of 388 (84%) in humid and semihumid regions and 108 (28%) in arid to subhumid regions. Concerning the frequency of polysporous ascomycetes in arid climates see also p. 64, Advantages of spore cluster.

The occasionally observed variation in spore number within a single apothecium, which in some asci provokes a reduction down to half the typical values, appears to have a non-genetical basis as mentioned above. In apothecia of *O. euonymi* such abnormal 16-spored asci contain subglobose instead of ellipsoid spores with wider SBs, reminiscent of *O. pleioeuonymi*. Such cases of strong variation in spore number within an apothecium were only infrequently met in our study, therefore, the application of those names which are mainly defined by spore number was almost never a serious problem.

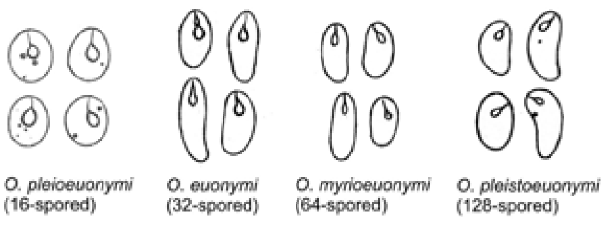


Figure 41: The four taxa recognized in series *Microspermae* differ mainly in spore number.

Because of the frequent absence of further distinguishing characters in taxa with a deviating spore number, one could

Table 5. Frequency of polyspory in *Orbilia* in relation to ascocarp desiccation tolerance and aridity of the geographic region. The table indicates the approximate number of species recognized in the present study, including undescribed (aff./cf.) taxa. Desiccation tolerance among the polysporous taxa was always medium (min. 1–2 months) to high (min. 0.5–1 year), whereas 8-spored taxa comprise a continuum from sensitive to highly tolerant. The number of tolerant 8-spored taxa in this table includes also those with a slight tolerance; subhumid includes a savannah climate.

	8-spored	16-spored	32-spored	64-spored	128-spored	total
desiccation-tolerant	294	58	42	30	7	431
desiccation-sensitive	94	–	–	–	–	94
arid	27	22	16	10	–	75
semiarid	58	26	19	21	4	128
subhumid	60	17	14	4	1	96
semihumid	110	17	10	4	4	145
humid	270	17	11	3	1	302

Table 6. Occurrence of polyspory in *Orbiliomycetes*. At present 137 polysporous species are known compared to 388 8-spored species. Numbers include undescribed (aff./cf.) taxa listed in Tab. S3.

	8-spored	16-spored	32-spored	64-spored	128-spored
used prefixes	octo-	pleio-	multi-, pluri-	myrio-	pleisto-
Liladisca	1	–	–	–	–
Lilapila	4	–	–	–	–
Amphosoma	5	–	–	–	–
Lecophagus	3	–	–	–	–
Bryorbilia	1	–	–	–	–
Pseudorbilia	1	–	–	–	–
Hyalorbilia	36	1	–	–	–
Orbilia sect. *Lentiformes*	15	3	6	6	2
sect. *Hemiorbilia*	64	10	8	11	3
sect. *Aurantiorubrae*	73	3	1	–	–
sect. *Helicoon*	20	–	–	–	–
sect. *Habrostictis*	48	31	19	10	1
sect. *Ovoideae*	18	6	4	1	1
sect. *Orbilia*	34	4	4	2	–
sect. *Arthrobotrys*	65	–	–	–	–
Total	**388**	**58**	**42**	**30**	**7**

assume that only slightly differences in the DNA exist between them, which might be restricted to the control of ascospore numbers. However, we generally found a rather high distance in the ITS region. For instance between *O. pleioeuonymi* and *O. euonymi* 6.5%, between *O. euonymi* and *O. pleistoeuonymi* 13–13.5%, between *O. flavida* and *O. ocellata* 7%, and between *O. sphaerospora* and *O. canadensis* 5%. Sometimes we observed populations with deviating spore numbers co-occurring on the same piece of substrate, and considered the possibility that they belong to a single species. From their different rDNA data, however, we must conclude that such mixed populations originate from independent colonization of the substrate.

Our molecular data on closely related polysporous species are rather sparse, and usually only a single sequence of each taxon was available for comparison. Future research on a wider scope of gene regions will perhaps answer the question whether closely related species with different spore numbers evolved by singular changes in spore number or by repeated changes in a polyphyletical process. Not only progression in spore numbers but also regression from higher to lower numbers probably occurred during evolution.

A system of prefixes was often applied when creating new names for closely related species (Tab. 6). For example, *Orbilia euonymi* has 32-spored asci, and a series of allied species is named *O. pleioeuonymi* (16-spored), *O. myrioeuonymi* (64-spored), and *O. pleistoeuonymi* (128-spored).

Inverse orientation of spores. Ingold (1954, 1971: 45) stated that the inverse orientation of a heteropolar ('bipolar-asymmetrical') spore 'never appears to occur'. Likewise Nannfeldt (1982: 165) thought that 'heteropolar spores (almost?) invariably are oriented in one way only' (with the wider spore end above). We can actually agree to these observations for the majority of hygrobiotic ascomycetes. Ingold's and Nannfeldt's statements are incorrect, however, regarding many xerobiotic ascomycetes but also many hygrobiotic *Orbiliomycetes*.

Inverse spore orientation in *Orbiliomycetes*. Particularly in the genera *Orbilia*, *Lecophagus* and *Liladisca*, inverse spore orientation is quite a consistent feature. In all the numerous species of *Orbilia* in which spore length exceeds ascus width, a varying percentage of the spores within an ascus is oriented inversely, i.e., with the 'lower' end towards the ascus apex, whereas the remaining spores are 'ordinarily' oriented. This is not only so in species with a heteropolar spore shape, but also in those in which the 'upper' end of the spore is only recognizable by the presence of a spore body (see p. 69 ff., SBs). But even in the genera *Hyalorbilia* and *Amphosoma*, in which the spores are predominantly homopolar in shape and the SBs occur at both spore ends, inversely oriented lower spores of a heteropolar shape were sometimes seen.

The number of inversely oriented spores in asci of a given apothecium varies to a more or less high extent, but some differences between taxa are obvious. In most of the species, about 35–65% inverted spores represent the general case [series *Phanosomates* and *Hesperideae*, subgenus *Habrostictis*, sections *Orbilia* and *Arthrobotrys*]. For species with 8-spored asci this means that 3–5 spores are inverted, while 1–2 or 6–7 inverted spores exceptionally occur. In contrast to this, many taxa of series *Lentiformes* and all of series *Hemiorbilia* show a more or less strong preference for only 1–3 spores inverted (except for the possibly misplaced *O. megaocculta*). Very exceptionally, a few asci were observed in which all 8 spores had an ordinary (*O. patellarioides*, *O. lentiformis*, *O. spermoides*, *O. aviflagellata*, *O. aviaristata*, *O. pseudoaristata*) or an inverse orientation (*O. lentiformis*, *O. ovoidea*, Pl. 766: 1b). In two species (*O. fimbriata*, *O. pseudoflagellispora*) the asci contained all spores with an ordinary orientation (Pl. 352: 1b), except for a few asci in which the lowermost spore was inverted. A maximum variance of (0–)1–5(–8) inverted spores was noted in *O. lentiformis*, and (2–)3–6(–8) inverted spores in *O. ovoidea*. In 16-spored taxa about 6–10 spores are usually inversely oriented, and also in 32-, 64- and 128-spored taxa many inverted spores occur in every ascus (Fig. 42: c).

In most taxa the inversely oriented spores tend to be grouped at the lower end of the pars sporifera, whereas the upper spores are those with an ordinary orientation (Fig. 42: a). In a rather small number of 8-spored species, the upper spores are those which are inversely oriented, either consistently (*O. pseudobrevistipitata*, *O. bomiensis*, *O. spirillospora*), or predominantly (*O. sarraziniana*, *O. spathulata*, *O. wannerooensis*). In these species usually all 8 spores point with their 'upper' (SB-containing) ends towards the middle of the pars sporifera (Fig. 42: b). Benny et al. (1978) figured this situation with the TEM in *O. sarraziniana* (Fig. 71: a). The authors were obviously fascinated by this striking arrangement of the SBs. However, they had only a slight idea of the widespread occurrence of SBs in *Orbiliomycetes*, and accidentally studied a species with an unusual spore arrangement. Also Liu's (2006) TEM-image of the same species (Fig. 71: b) shows inverse orientation of the upper spores and their SBs. So far this rare case never occurred in asci with more than 8 spores.

The inverse spore orientation is often rather regular not only within an apothecium but throughout the populations of a species. However, particularly in species with polysporous asci and/or a homopolar spore shape there is often slight if not considerable disorder, so that the inverted spores are not strictly confined to the lower part of the pars sporifera but occur more irregularly distributed within an ascus (Fig. 42: c). In the descriptions this case is referred to as 'mixed orientation'.

In those species in which ascus width exceeds spore length, the spores may be oriented in all directions, i. e., some of the spores have a more or less horizontal or oblique orientation (Fig. 42: d). Yet, an orientation parallel to the longitudinal axis of the ascus may also here be predominant if the spores are elongate, which forces them to lie more or less parallel in order to facilitate formation of the spore cluster (Fig. 42: c). So, even in this example, in which the rather short spores are homopolar in shape and the asci multispored, a majority of the lower spores tend to be inversely oriented.

Spore orientation is completely irregular in those species in which the spores have a more or less circular outline, or their length/width ratio is distinctly below 2. If such spores are more or less flattened, either by their semicircular shape (e. g., *O. leucostigma*) or when round spores are laterally flattened (*Lilapila* spp.), they may be arranged like coins in a pile, the SBs thereby pointing sideways (horizontal orientation). Likewise, in *O. corculispora* with heart-shaped spores (Fig. 42: d) the spores are oriented in such a way that the SBs tend to point in lateral direction.

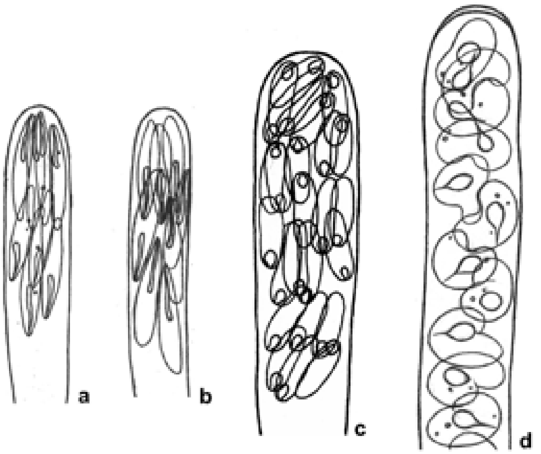


Figure 42: Spore orientation in living asci. — **a–b**. spores longer than ascus width, inverse orientation of lower (**a**. *Orbilia rosea*) or upper spores (**b**. *O. sarraziniana*); **c–d**. spores shorter than ascus width, orientation inverse for lower spores (**c**. *O. multiaustrocylindrica*) or irregular (**d**. *O. corculispora*).

Spore orientation in herbarium material, literature reports. The situation of inverse spore orientation is easily seen when studying living spores, due to the very conspicuous SBs in the spore apices. In dead herbarium material, spore orientation is often very difficult to evaluate in species with a homopolar spore shape, and even if the spores are distinctly heteropolar, the shape of the spores is not always clearly observable inside dead asci (see p. 29). Hence, literature reports of inverse spore orientation are rare due to the current method of studying herbarium specimens.

Only a few reports of inverse spore orientation in *Orbilia* prior to 2000 came to our notice. Three refer to living specimens: Patouillard (1892b) depicted subulate SBs in 16-spored asci of *O. serpentina*, some of them clearly inversely oriented (Fig. 151: 1). Baral (1989: pl. 4) figured an 8-spored ascus of *O. septispora* with 3 inverted lower spores (see Pl. 683: 2) and (in Rubner 1996: 94, fig. 48d) an 8-spored ascus of *O. elegans* (as *O. auricolor*) with 5 inverted lower spores (see Pl. 961: 1). Four reports refer to dead specimens (all with 8-spored asci): Drechsler (1937a: 458, fig. 18 R) described and figured inverse orientation of 1–4 lower spores in an unidentified *Orbilia* (possibly section *Arthrobotrys*). Ellis & Ellis (1985: fig. 1202) illustrated three lower of seven figured spores in *O. comma* inversely oriented. Galán et al. (1994: fig. 60) depicted three of six spores with an inverse orientation in *O.* (*Hyalinia*) *flagellispora*. In Pfister's (1994) illustration of a collection referred to *O. fimicola* (= *O. auricolor*), ~3–5 lower spores are somewhat indistinctly drawn with their acute lower ends pointing upwards.

When illustrating asci of *Orbiliomycetes*, authors have repeatedly figured all spores of an ascus with ordinary orientation. For example, Rolland (1901, three asci of *O. hesperidea*) and Chenantais (1918, one ascus of *Hyalinia ulicis*) illustrated all 8 living spores with their SBs oriented upwards (see Fig. 151: 2–3). Likewise, Starbäck (1899, *O. caudata*), Spooner (1987: 185, fig. 25 A, *O. vinosa*), Graddon (1977: fig. 17, *O. comma*), Birken (1984, *O. sarraziniana*) and Pop (1994: pl. 1 fig. 5) figured all (7–)8 dead spores with their tapered ends pointing downwards. In Spooner's drawing of *O. auricolor* (1987: 165, fig. 19 B), only one of the seven figured spores (above the lowermost spore) looks like being inversely oriented. Although asci without inverted spores occur only in a very small number of 8-spored species of *Orbilia*, we may assume that the above-mentioned illustrations were carried out with the belief that heteropolar spores are consistently oriented with their broader ends upwards. This was demonstrated when restudying the type material of *O. hesperidea*, *O. caudata*, and *O. comma*: all asci examined contained a varying number of inverted spores.

Inverse spore orientation in *Leotiomycetes* and *Pezizomycetes*. The phenomenon of inverse spore orientation in *Orbiliomycetes* strikingly coincides with that reported by Döbbeler & Poelt (1974) for *Bryodiscus* B. Hein et al. and by Döbbeler (1984: 208) for *Epigloea*. In *Epigloea*, Döbbeler found inverse orientation to be characteristic of all known species, though in some of them the feature is not easy to observe because of indistinctly heteropolar spores. Every ascus showed this phenomenon, without exception, and always the lower spores were those being inverted. The number of inverted spores in 8-spored species varied among the asci: mostly 4, but often also 2 or 3, rarely more. Döbbeler (1984) emphasized this peculiarity as extraordinary within ascomycetes, and could only refer to one further genus (*Bryodiscus*) in which the long, filiform-clavate ascospores in two of the three known species are in part inversely oriented.

Both *Epigloea* and *Bryodiscus* are obviously very distantly related to the *Orbiliomycetes*. In *Epigloea* the outer ascus wall layer reacts hemiamyloid. The spores are provided by large amounts of lipid and in some species by polar setulae. No SBs could be observed in a fresh collection of *E. urosperma* Döbb. (IVV: H.B. 6148b). In *Bryodiscus* the asci are gradually thicker-walled towards apex and react faintly euamyloid, while contents of the living spores are unknown. *Epigloea* stands in a family of its own with unclear relationship within the *Ascomycota*, and *Bryodiscus* is considered as a synonym of *Sphaeropezia* Sacc. in the *Stictidaceae* (Jaklitsch et al. 2016).

In the *Pezizales* the rarity of inverse orientation is mainly due to the rarity of heteropolar spores, besides the rarity of desiccation-tolerant taxa. Döbbeler (2004) reported inverse spore orientation in the desiccation-tolerant *Octosporella erythrostigma* (Mont.) Döbbeler. In this species the spore base is provided with an abrupt narrow tail, similar as in series *Hemiorbilia*. Our observations on this *Octosporella* confirm that mostly the lower spores are inverted. However, there is no distinct tractus to be seen in the living asci and the spores do no cluster near the apex, instead, they are distributed down to the base also at maturity. Moreover, neither Döbbeler nor we were able to detect any apical ascus structure like an operculum. Instead, the ascus wall seems to disintegrate with age. Apparently, the species is unable of forcible spore discharge and, therefore, does not require uniform spore orientation within the asci.

In *Leotiomycetes*, desiccation-tolerant taxa with slightly to distinctly heteropolar spores, such as *Patellariopsis dennisii* (I. Focht ined.; N. Matočec pers. comm.) or *Helicogonium* (*H. cyathiculae*, *H. mollisiophilum*, Baral 1999), may show a few of the lower spores with the narrower end directed towards the ascus apex. Also in *Durella atrocyanea* and *Patinella abietina* a few of the basal spores were found to be sometimes heteropolar and distinctly inverted (Baral ined.). *Ascocoma eucalypti* (*Phacidiales*) as described and illustrated by Swart (1986) has clavate ascospores with strongly eccentric septum and shows 3–7 of the lower spores inverted. On the other hand, other genera with desiccation-tolerant apothecia and distinctly heteropolar spores, such as *Patinellaria* (*Helotiales*) or *Patellaria* (*Patellariales*), never showed the phenomenon of inverse spore orientation.

Spore discharge. According to Landvik et al. (2003: 1029), active ascospore discharge is an ancient feature within *Ascomycota*, being first found in *Taphrinomycotina*. Spore discharge is a universal feature of various groups of discocarpous ascomycetes, such as *Orbiliomycetes*, *Leotiomycetes*, *Pezizomycetes*, or *Lecanoromycetes*. Exceptions are very rare and only known in taxa with more or less closed sporocarps, such as *Tuberales* and *Octosporella* (*Pezizomycetes*), or *Bicornispora* and *Unguicularia unguiculata* (*Leotiomycetes*). The phylogenetically oldest subdivision of *Ascomycota* in which active spore discharge occurs are apparently the *Taphrinomycotina* (*Taphrina* and *Neolecta*). Also many of the pyrenocarpous ascomycetes show active spore discharge, but various groups have lost this ability.

Our study showed that apparently all taxa of *Orbiliomycetes* are capable of forcible ascospore discharge. In a fairly large number of species of both *Hyalorbilia* and *Orbilia*, but also in *Lilapila*, we have observed fully turgescent asci in water mounts, and we saw active spore discharge from such asci into the water medium. Forcible instant spore discharge was observed in taxa with apically thick-walled as well as thin-walled ascus types. However, the process of spore discharge happens comparatively seldom, because fully turgescent asci occur usually in small number. But even if they occur abundantly, which is frequently the case in *Hyalorbilia*, spore ejection was only exceptionally seen in water mounts.

Spore discharge is used when obtaining pure cultures. Spores of *Orbiliomycetes* were forcibly ejected through the air within the Petri dish over the short distance between lid and agar in virtually all species of *Amphosoma*, *Hyalorbilia*, *Lilapila*, and *Orbilia* that we have tried to culture. The orientation of the apothecia was generally downward or laterally, but some inoculations were made with an upward orientation and likewise succeeded to land spores on agar.

The force that propels the spore cluster through the apical ascus pore originates from the osmotically generated hydrostatic pressure (ascus turgor) which increases during ascus maturation. Turgor is promptly released by bursting of the apical wall, obviously due to a preformed weakness zone. Complete ejection of all spores takes place in the blink of an eye (perhaps within 1/1000 sec) and cannot, therefore, be recorded with normal video cameras.

Active spore discharge requires a number of obligatory features, namely: (1) the ascus wall must be elastic, allowing volume increase during turgor increase; (2) the whole ascus wall must be permeable for water to enable water intake by the ascus vacuole; (3) water uptake is assumed to result from the transformation of osmotically inactive glycogen (see p. 96, Glycogen) in the ascoplasm to soluble sugar molecules; (4) the spores must be crowded at the top of the ascus (Baral 1992: figs 8–10).

Spore dehydration prior to discharge. In species with thin and/or elastic spore walls a further phenomenon supports discharge: the spores decrease in volume, either via shrinkage or collapsing. This is effected by partial dehydration, i.e., translocation of water from the sporoplasm to the surrounding ascus vacuole. The result of this process is a low spore volume in relation to a high ascus volume which is essential for an effective spore discharge. Shrinkage and collapsing of spores is caused by the raised osmotic pressure of the ascus vacuole that withdraws water from the spores.

If the spore walls are more or less elastic, the spores shrink to some extent prior to discharge during dehydration inside asci, particularly in width. This is quite a commonly observable feature in helotialean taxa (see also p. 28, Shrinking effect), which facilitates passage of the spores through the apical ring.

If the spore walls are more rigid, spore shrinkage is hardly noticeable, instead, the spores collapse inside the living asci when full turgescence is attained. Collapsing of spores is quite a frequently observable effect in *Orbiliomycetes*, especially in *Orbilia* (Fig. 43: a, c-d). It is not an artifact but a physiological process: the spores obviously cannot shrink to the required extent because their thin walls possess a too low degree of elasticity. The effect was particularly observed in species with globose or ellipsoid spores, and could not so far be seen in sections *Aurantiorubrae*, *Hemiorbilia* and *Arthrobotrys* in which the spores are mainly elongate and narrow. In *Hyalorbilia* deformed or collapsed spores were only seen in species with subglobose spores (*H. multiguttulata*), also spore shrinkage inside living asci could hardly be observed here. On the other hand, the subglobose spores of *Lilapila* were so far never seen to collapse.

Formation of a spore cluster. As a further peculiarity of *Orbiliomycetes*, the spores of an ascus stick together in the course of ascus turgor increase, apparently by adhesive remains of the ascoplasm around each ascospore. The resulting spore cluster forms a more or less compact projectile (Fig. 43: b, d), even in multispored asci. Thereby, collapsing of the spores allows a more tight packing which evokes that the pars sporifera is distinctly reduced in length and often also width. The refractive spore cluster exhibits an increased contrast to the large non-refractive ascus vacuole in which it is enclosed. The individual spores are often more or less indistinguishable within the cluster, also the SBs may become masked. The tight packing of the spores enables the spore cluster to be violently ejected as

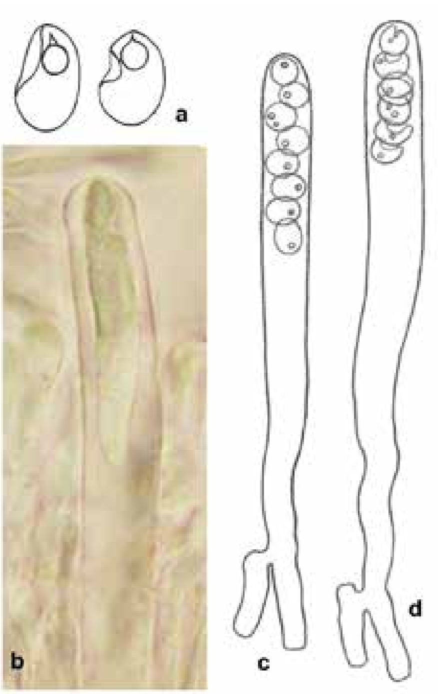


Figure 43: **a**. *O. octosporoides*, collapsed living spores inside fully turgescent ascus shortly before discharge; **b**. fully turgescent ascus of *O. vinosa*, with cluster of 8 dehydrated spores; **c–d**. *O. liliputiana*, mature living asci at moderate (**c**) and full turgescence (**d**), here with shortened pars sporifera and collapsed spores.

a single entity. This is confirmed when obtaining pure cultures, whereby each spore cluster produces a discrete spore heap on the agar (Fig. 44: a–b).

This peculiarity was observed in all our cultures of *Orbilia* and most of the other genera of *Orbiliomycetes*. *Lilapila* forms a very indistinct spore cluster inside turgescent asci, with a thin mucilage between the ± uniseriately arranged spores (Pl. 30: 1g). Also in *Hyalorbilia* the cluster is only indistinctly formed, but similar as in *Orbilia* the spores remain loosely coherent after discharge in a water mount (Fig. 44: d). Only in *Lecophagus* the spores were found singly or in pairs on the agar (*L. ellipsoideus*), and also spore clusters have not been seen in this genus, except for *L. subglobosus*: photos made by B. Coué (pers. comm.) suggest that the spores stick together and collapse somewhat prior to discharge (Pl. 50: 1g).

We conclude that in *Orbilia* the mature asci undergo two morphologically very different stages of development: (1) the stage of moderate turgescence with clearly visible individual spores, and (2) that of full turgescence in which individual spores are often hard to see (Fig. 24). Due to the absence of vital studies, literature reports do not account for the spore clusters in *Orbilia*. Because of the opposed orientation of the acute ('apiculate') spore ends in *O. sarraziniana*, Benny et al. (1978) assumed that the spores are discharged as a single entity. However, the authors did not study living asci under the LM, therefore, they could not prove their assumption.

When observing spore discharge from high-turgescent asci in a water mount, the spore cluster is brought to a halt at a distance of about 20–40 µm away from the ascus tip, due to the density of the medium. Shortly after discharge into water, the spores swell by water uptake and separate a bit form each other, though remaining loosely coherent for at least some minutes, apparently due to remains of ascoplasm (Fig. 44: c–e). These remains do not appear to consist of a mucilage as is infrequently observed in *Helotiales* ascospores, because such mucilaginous sheaths usually stain lilac in CRB, whereas the surface of ascospores of *Orbiliomycetes* did never stain in this basic dye.

Spore clusters are probably formed in every species of *Orbilia*, although we have seen them in only ~10% of the taxa recognized here. Photos or drawings of spore clusters in fully turgescent asci exist for the following sections: *Lentiformes* (*O. euonymi* Pl. 207: 1), *Hemiorbilia* (*O. aprilis* Pls 289: 1; 290: 1e, *O. breviclava* Pl. 322: 1e, *O. clavuliformis* Pl. 315: 6b, *O. graminis* Pl. 373: 2e, *O. myrioauris* Pl. 306: 2a, *O. octocorculispora* Pl. 296: 2m, *O. vinosa* Fig. 43: b; Pl. 262: 1b), *Aurantiorubrae* (*O. xanthoguttulata* Pl. 444: 10a, *O. pseudoaristata* Pl. 524: 5, *O. scolecospora* Pl. 464: 2b), *Helicoon* (*O. rosea* Pl. 529: 5, *O. sarraziniana* Pl. 538: 4c), *Habrostictis* (*O. gambelii* Pl. 721: 7d, *O. multihamulata* Pl. 590: 2f, *O. paravitalbae* Pl. 490: 2d), *Orbilia* (*O. battenii* Pls 840: 1; 841: 2a, *O. dryadum* Pls 870: 1–2; 871: 3a, *O. eucalypti* Pl. 857: 7, *O. fabacearum* Pl. 888: 1, *O. tremulae* Pl. 861: 5, 6, *O. xanthostigma* Fig. 45, Pls 875: 5, 15; 878: 4a, 7, *O. liliputiana* Fig. 43: d), and *Arthrobotrys* (*O. asomatica* Pl. 931: 1l, *O. multiformis* Pl. 958: 1a).

The particular phenomenon of a tight spore packing in combination with the partial invisibility or collapsing of individual spores could not be observed so far in any other class of *Ascomycota*, and appears to represent one of the unique characteristics of *Orbiliomycetes*. In all the many non-orbiliaceous inoperculate discomycetes which we have studied, the individual spores remain always clearly visible prior to discharge, and the spores are usually not ejected as a single entity but one after the other, frequently through an expansible amyloid apical ring. The difference between moderate and full turgescence in such taxa is only a gradual one, but also involves increase in ascus size, decrease in spore width, and also contraction of the pars sporifera.

Spore clusters similar as in *Orbilia* occur in multispored asci of some genera such as *Deltopyxis*, *Sarea*, and *Symbiotaphrina*. However, the spores do not collapse or become obscure prior to discharge here. As in *Orbilia* the asci open by a large slit-like pore, and the spores are ejected as a single entity by forming discrete heaps on the agar (for *Deltopyxis* see Baral & Marson 2012: fig. 5h–i). In ascoconidia-forming members of *Claussenomyces* s.auct., *Tympanis*, and *Helicogonium*, the conidia are included in 8 'balls' within the living asci, which are similarly ejected by forming 8 conidial heaps on the agar. Also

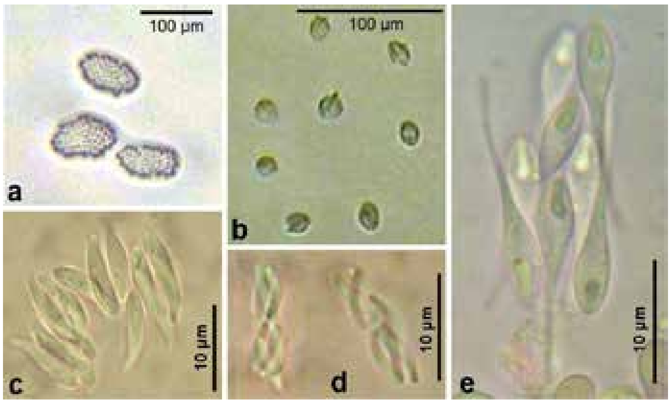


Figure 44: **a–b**. Spore clusters shot on agar, **a**. *Orbilia myriosphaera* (64-spored, H.B. 6679a), **b**. *O. obtusispora* (8-spored, H.B. 8691); **c–e**. loosely cohering clusters of 8 spores a few minutes after discharge from high-turgescent asci in water mounts, **c**. *O. quaestiformis* (H.B. 7592a). **d**. *Hyalorbilia tortuosa* (H.B. 7576), **e**. *O. aristata* (P.P. 20071028).

scolecosporous genera of *Ostropomycetidae* eject their very long, filiform spores as one entity in the form of an agglutinated parallel bundle, according to an unpublished observation in *Karstenia* sp. (IVV: H.B. 9272a).

In contrast to this, we have observed in various species of *Helotiales* with an amyloid ring that the spores arrive more or less singly on agar. This is also the case in those taxa with inamyloid asci in which the spores are successively ejected (e.g., *Durella connivens*, *D. atrocyanea*). Comparable observations were made by us in *Sclerococcum* (= *Dactylospora*, *Lecanoromycetes*), *Rhizodiscina lignyota*, and *Patellaria atrata* (*Dothideomycetes*).

The spore cluster in *Saccobolus* Boud. (*Pezizales*) differs from those of *Orbiliomycetes* in the eight individual spores firmly sticking together at a rather early immature development stage, i.e., prior to formation of the episporial pigment (Van Brummelen 1967: 40). The spores remain agglutinated during further maturation, also in the dead asci and after discharge.

Spore clusters similar to those of *Orbiliomycetes* were described for the 8-spored *Thelebolus microsporus* (*Thelebolales*), in which the spores are ejected as a single projectile (De Hoog et al. 2005: 64). A fresh specimen of this species showed a strikingly refractive, irregularly shaped gluing substance between the spores which stains bright rose-red in CR. With the help of this glue the spores may remain agglutinated after ejection in the same obliquely biseriate order as inside the living asci. However, dehydration and collapsing of the spores inside the high-turgescent asci was not observed. It appears that the spores are successively pressed through the pore and rearrange thereafter by means of the glue. Similar spore clusters held together after ejection by some gel sheaths or ascoplasm are known in *Podospora*, *Sordaria* (*Sordariales*), and *Dasyobolus* (*Pezizales*) (see Ingold 1933), also in *Unguiculella tityri* (Baral ined.). All these species are coprophilous, and the frequent occurrence of spore clusters in this ecological group might be indicative for a need for spore dispersal at high distances.

Tractus and nasse apicale. Neither of these cytoplasmic structures could be discovered with the LM (oil immersion) or the TEM in the mature asci of any member of *Orbiliomycetes*. This seems to support the isolated position of the class within the *Ascomycota*. Nevertheless, a structure must exist that draws the spores towards the ascus apex. Apparently this task is taken on by the remains of ascoplasm around the spores which hold them together in a cluster in the fully turgescent ascus. At earlier stages of ascus maturity these plasma remains cannot be seen, perhaps because they are more hydrated by connecting the spores only loosely together.

Tractus and nasse apicale are best seen in living asci. A nasse apicale is typical of various *Dothideomycetes* (e.g., *Gloniopsis*, *Patellaria*, *Pleospora*, *Rhopographus*, *Tubeufia*; Chadefaud 1942: figs 49–50; 1973: figs 8, 17, 19; Baral 1992: fig. 7). It was also reported for some groups of *Helotiales*, viz. *Belonidium*, *Incrucipulum*, and *Vibrissea* (Bellemère 1960, as 'manchon épiplasmique'; Baral 1987a: figs 17, 25; Leenurm & Raitviir 2000, as 'apical cap'). A tractus occurs as a general feature in the *Pezizales* (Chadefaud 1942: figs 56–66, 70–80), but was also observed in, e.g., *Leotia* (Chadefaud 1944: figs 15–18), *Lecanora* (Baral 1992: fig. 9a), and *Neolecta* (Fig. 39: b). A similar structure was seen in *Trichoglossum* by Verkley (1994). The tractus is affixed at the ascus tip and to each ascospore; it drags the spores upwards and holds them close to the ascus apex, while the nasse apicale perhaps functions as a reinforcement of the plasmalemma in the apex region that aids during spore passage. The presence of a tractus in *Neolecta* could indicate that the *Orbiliomycetes* early lost this microstructure. In polysporous asci a single tractus would actually seem unsuitable.

Frequency of fully turgescent asci. In desiccation-sensitive members of *Helotiales* and *Pezizales*, fully turgescent asci are often seen in mature apothecia in great number. Likewise, mature apothecia of *Hyalorbilia* often contain hundreds of fully turgescent asci. In contrast, in desiccation-tolerant discomycetes such asci are usually more sparse. Also asci of *Orbilia* that show the characteristic spore cluster are only infrequently seen, usually only a few in a section, although every successful ascus inevitably undergoes this stage of development.

The rarity of fully turgescent asci in *Orbilia* might be explained by the frequent desiccation tolerance of the apothecia, which are generally collected during dry weather. Immediately after rewetting they contain abundant mature asci at moderate but not full turgescence. Only when kept wet for some hours, a few asci may attain full turgescence and thereby project beyond the hymenium. However, even in those species of *Orbilia* which do not survive drying, full turgescence is often only observed when a section is kept for about 10–20 min in a water mount. Even if apothecia are submerged under water for some hours or days, the number of fully turgescent asci did not noticeably increase (tested with *O. sarraziniana*). Turgescent asci occurred in greater abundance only in a few cases, for instance in *O. xanthostigma* (Fig. 45).

In *Hyalorbilia* the difference between moderate and full turgescence is not as clear as in many species of *Orbilia*. Nevertheless, the abundance of fully turgescent asci in *Hyalorbilia* is a frequent feature and seems to correlate with the observation that the apothecia are comparatively short-lived, i.e., they survive only a short period of time in the dry state.

The paucity of fully turgescent asci in *Orbilia* is the reason why apothecia often shoot their spores rather sparsely on agar. It seems to be a general feature of desiccation-tolerant taxa including lichens, that 'comparatively few asci discharge at any one time' (Sherwood 1981: 32). But also in *Hyalorbilia* the obtained spore heaps on agar were often comparably few. Desiccation-sensitive members of *Helotiales* and *Pezizales* often discharge their spores in much higher quantities under the same conditions. The macroscopically visible 'puffing',

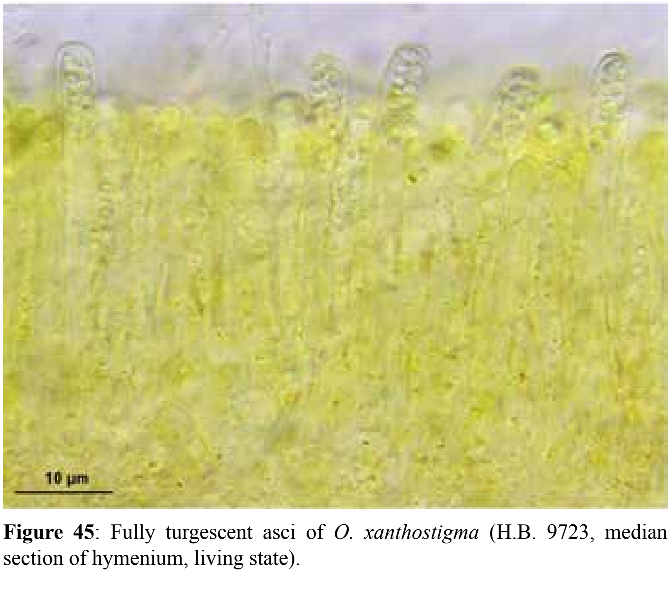


Figure 45: Fully turgescent asci of *O. xanthostigma* (H.B. 9723, median section of hymenium, living state).

whereby numerous asci simultaneously explode, being triggered by external influence (see Buller 1934), was never observed in the *Orbiliomycetes*.

The function of apical thickenings and truncate apices. Desiccation-tolerant ascomycetes grow in direct exposure to air currents or sometimes in the narrow interspace behind slightly detached bark of standing trees, therefore, long distance discharge does not seem to be important in this ecological group of fungi (Sherwood 1981). Amyloid apical rings are undoubtedly essential for long distance spore discharge due to their enormous elasticity (Baral 1987b: 432). Their absence in many desiccation-tolerant *Helotiales* can apparently be explained in such a way. Therefore, it is surprising that, among the desiccation-tolerant members of *Orbilia*, two very different types of ascus apices occur: those with apical thickenings and apical chamber, and those with truncate, thin-walled-shouldered apices. Judging from morphology, the former type appears to be more efficient in regard to active spore discharge than the latter type. However, the consistent absence of apical thickenings in desiccation-sensitive members of *Orbilia* is in conflict with this assumption. Experiments that assess discharge distances should be undertaken on representatives of the different ascus apex types.

A theory that tries to explain apical or lateral thickenings of ascus walls as an adaptation to a xeric environment in combination with long-lived apothecia (Nannfeldt 1932: 27; Chadefaud 1942: 59, 1973: 135f.; Dughi 1957), was considered as not convincing by Baral (1992: 353). Within *Orbilia*, however, this theory seems to be supported by the fact that all species with thick-walled ascus apices showed a more or less pronounced desiccation tolerance over several months or even years. On the other hand, many taxa with thin-walled ascus apices survive about the same periods of time in the dry state.

Theories that try to reconstruct the process of spore discharge are usually based on the morphology of the dead mature ascus as seen under the LM, TEM, or SEM, in comparison with the emptied ascus. Yet, in most orders of *Ascomycota* living turgescent asci differ greatly from dead asci. This is also the case in the two main types (A and B) of *Orbilia* asci (Figs 31, 35): asci with apical thickening are much more thin-walled in the living state, and truncate asci are almost hemispherical or only slightly truncate, without any trace of shoulders. This means that types A and B look rather similar in the living state and can hardly be distinguished. The strong difference in wall thickness and apex shape in the dead state might involve different pore structures of the emptied ascus. Yet, the few available observations in *Orbiliomycetes* disprove this possibility (see p. 48).

In *Orbilia* the apical chamber of the thick-walled ascus apex is often not perceptible in the turgescent state. One could conclude from this that the wall above the apical chamber is less expansible than the wall around, so that both wall areas have about the same thickness when compressed. However, in *Orbilia euonymi* (Fig. 31: a) the apical chamber could be seen in the living state, and also in the *Lecanorales* with a similar shape of apical thickening this chamber is very clearly visible in living asci, though lower and much wider compared to the dead state (Baral 1992: fig. 9).

During ascus explosion, the wall around the preformed apical fissure must be stretched in order to allow passing of the large spore cluster. Thereby, the apical thickening (the endotunica) probably elongates upwards. Such extensibility, sometimes in combination with a separation from the ectotunica, is known from groups with strongly expansible apical walls, such as the *Lecanorales* with a rostrate type of emptied ascus, but is also believed to occur, e. g., in *Thelebolus* (De Hoog et al. 2005: fig. 12f). Stretching and elongation of the thickened endotunica is probably a universal phenomenon in the ascomycetes, most developed in the fissitunicate ascus of the *Dothideales*, and appears to be the main function of this structure (see Baral 1987a: 127, 1992: 353).

Due to their elasticity and expansibility, apical thickenings appear to serve in preventing loss of water from the ascus when the spore cluster passes the pore. If this holds true, asci of the truncate-shouldered type should be less efficient in this respect so that the spore cluster is less forcibly ejected. The firm subapical wall of the thin-walled ascus type (Fig. 34: c–d) might restrict the apical opening to a short slit and thus avoid too much water loss. On the other hand, part of the ejected vacuole water undoubtedly remains attached to the spore cluster after discharge and increases its weight and, therefore, the distance to which the cluster is shot. Thick-walled ascus apices might be able to withstand a higher ascus turgor, but this has to be demonstrated experimentally.

Function of the inverse spore orientation. The inverse orientation of some of the spores within an ascus seems to support a more tight packing within the spore cluster. This applies, however, only to species with a heteropolar spore shape, with one end tapered or tailed. In species with long and thin spore tails there is a strong tendency of only 1–3 basal spores being inverted. Some asci of these species may even lack any inverted spores, and a few species (*O. fimbriata*, *O. pseudoflagellispora*) showed predominantly asci in which all spores were oriented with their tails downwards. Hence, the formation of a spore cluster does not seem to depend on inverse spore orientation. The orientation of all spores in the same direction probably represents a higher evolutionary level and becomes obligatory in species which eject their spores one after the other through an elastic apical ring.

Döbbeler (l.c.) imagined that the phenomenon of partial spore inversion in *Bryodiscus* resulted in cylindrical instead of clavate spore fascicles and, therefore, cylindrical instead of clavate asci which might serve in a more efficient spatial exploitation of the hymenium in concave (cup-shaped) hymenia, but in *Epigloea* he admitted that spore inversion could not be explained this way. We must remember, however, that Döbbeler's remark refers to dead shrunken asci in which the spores fill most of the ascus lumen. Considering the fact that living asci usually have ample water around the spores, we doubt that the shape of the spore fascicles in *Bryodiscus* necessarily influences the shape of the turgescent asci.

Whatever the advantage of spore inversion in *Orbilia* may be, the formation of a compact spore cluster appears to be a prerequisite for the evolution of a high diversity of different spore shapes, particularly concerning strong curvature. Inverse spore orientation might be a plesiomorphic character of a common ancestor of ascomycetes. Then it would now represent a relict which had not been abandoned with the emergence of heteropolar spores because of the ability to form a spore cluster.

Spores of desiccation-sensitive *Helotiales* are often slightly to strongly heteropolar in shape. When successively discharged, a heteropolar spore achieves greater initial velocity and consequently greater range during discharge (Ingold 1954). With its rather motionless air, the sheltered habitat of such fungi was suggested by Sherwood (1981) to require a more efficient spore discharge, and one could speculate that fungi of this habitat have abolished the unfavourable inverse spore orientation. But the opposite case, the loss of uniform spore orientation, could likewise have happened during evolution. This may well be so in those *Helotiales*, in which an amyloid ring is considered to be primary (Baral 1987b: 438), and inverse orientation could so far only be observed in genera with inamyloid asci.

Advantages of the spore cluster. The advantages of the spore cluster and the involved dehydration of the spores appear to be as follows:

1) A large compact cluster of spores is shot to a much greater distance compared to comparatively small single spores (Ingold 1933: 183 ff.).

2) A broad range of spore shape diversity could evolve in the *Orbiliomycetes*, because the individual spores do not require an aerodynamic design. The spore cluster has a concordant cylindric-fusoid shape, regardless of the individual spore shape.

3) All spores of a cluster are still held together when landing on the substrate. This kind of dispersal might avoid single spore mycelia during substrate infection, and provide a higher probability for an efficient colonization in case that species is homothallic.

The spore clusters of *Orbilia* appear to represent a strategy to achieve similar distances compared to those desiccation-sensitive *Helotiales* which eject single spores through an elastic amyloid ring. In desiccation-tolerant *Helotiales* with inverse spore orientation, spore clusters have never been observed in the living asci. Vital studies should clarify whether genera like *Epigloea* or *Bryodiscus* form spore clusters in the living asci. The *Orbiliomycetes* have possibly developed this type of discharge mechanism because the group as a whole has never possessed or very early lost amyloid ascus wall structures (see also p. 129–135).

Sherwood (1981: 31 ff.) postulated that discomycetes growing on branches exposed to air currents do not need efficient discharge mechanisms compared to those growing at the ground, followingly they were not subjected to strong selection pressure for aim or long distance trajectories. According to Sherwood, desiccation-sensitive ascomata are faced with problems of still air surrounding the substrate, whereas desiccation-tolerant ascomata are directly exposed to turbulent air and, therefore, need minimal distance trajectories for efficient spore dispersal. The situation found in *Orbiliomycetes* is in conflict with Sherwood's hypothesis. Desiccation tolerance is probably a plesiomorphic feature within the genus *Orbilia* (see p. 160). Nevertheless, the group appears to have developed an elaborate capacity of long distance discharge, and maintained this capacity also in desiccation-sensitive species. Since desiccation-tolerant species possess on average larger spores and also larger spore clusters due to the frequent polyspory, they are expected to achieve larger distances than desiccation-sensitive taxa.

Sherwood (1981: 25, 32) noticed the frequency of large, filiform or muriform spores as well as polyspory in desiccation-tolerant ascomycetes, combined with the absence of apical ring structures. Yet, she appears to have underestimated the efficiency of spore discharge in these fungi. Colonization of new substrate is possibly supported by invertebrates as vectors, for instance in semideserts with very scattered plants. Forcible discharge of a sticky spore cluster during moist periods should also be considered under this point of view.

Ingold (1933) drew attention to the efficiency of spore clusters ('spore masses') in long distance dispersal. Among the pyrenomycetes, the 128-spored *Podospora curvicola* attained 45 cm in vertical direction as maximum distance of discharge, whereas 8-spored species of *Podospora* and *Sordaria* attained 6–30 cm. In comparison, pyrenomycetes ejecting single spores attained a maximum of only 1–1.2 cm. Ingold also noted a correlation between the formation of 'spore masses' and coprophily: three very different groups of coprophilous fungi have independently evolved spore clusters, in which the spores are held together by gel sheaths, gelatinous appendages, or by the surrounding sporangial wall: *Dasyobolus* (*Pezizales*, maximum distance 30 cm), *Podospora* and *Sordaria* (*Sordariales*), and *Pilobolus* (*Mucorales*, maximum distance 200 cm).

The direction of discharge is governed in the three groups by a phototropic mechanism either of the individual ascus, the perithecial neck, or the sporangiophore. In the *Pezizales*, the protruding part of the asci is often bent towards the direction of light (Buller 1934: 264, Van Brummelen 1967: 36). No such phototropism of asci or ascomata could ever be observed in the *Orbiliomycetes*.

Ascospores

Ascospores of *Orbiliomycetes* provide the most diagnostic characters for species delimitation, which involves not only their size and shape, but also size and shape of the included spore bodies (SBs). In contrast to other ascomycetes, lipid bodies (LBs) turned out to have a rather low taxonomic value in this group. Due to their refractivity, SBs are very conspicuous cytoplasmic inclusions in the living ascospores when viewed under oil immersion, whereas they are hardly or mostly not at all discernible in dead herbarium material, irrespective of which staining agent is applied. Ascospores of *Orbiliomycetes* exhibit an extraordinary high diversity in shape, which appears unique among the *Ascomycota*. A similar diversity can be attested to SB morphology, which was found to better reflect phylogenetic lines than spore shape does. The high taxonomic value of ascospores lies in the combination of both characteristics. Many species or groups of species can readily be recognized merely by morphology of their living spores. Therefore, collections of *Orbiliomycetes* generally remain unidentified if no spores are found.

Spore size and shape. – Size. Ascospores of *Orbiliomycetes* are currently perceived as being extraordinarily small. However, there is actually a wide size range across the taxa. Living spores may range from *(1.8–)2.5–3.5 up to 20–25(–30) µm in (actual) length and from *(0.6–)0.7–0.9 up to 4–5(–6) µm in width. This diversity corresponds to a volume range of around 2–5 up to 150–250 µm^3, which means a maximum difference of over 100×. Desiccation-sensitive species tend to have rather small spores whereas those of desiccation-tolerant taxa comprise the full range of spore size, with a tendency to larger spore volumes if 8-spored and to smaller volumes if polyspored.

Curved spores pose a methodological problem when measuring their length. The direct distance from end to end (in situ) is easier to evaluate but subjected to higher variation,

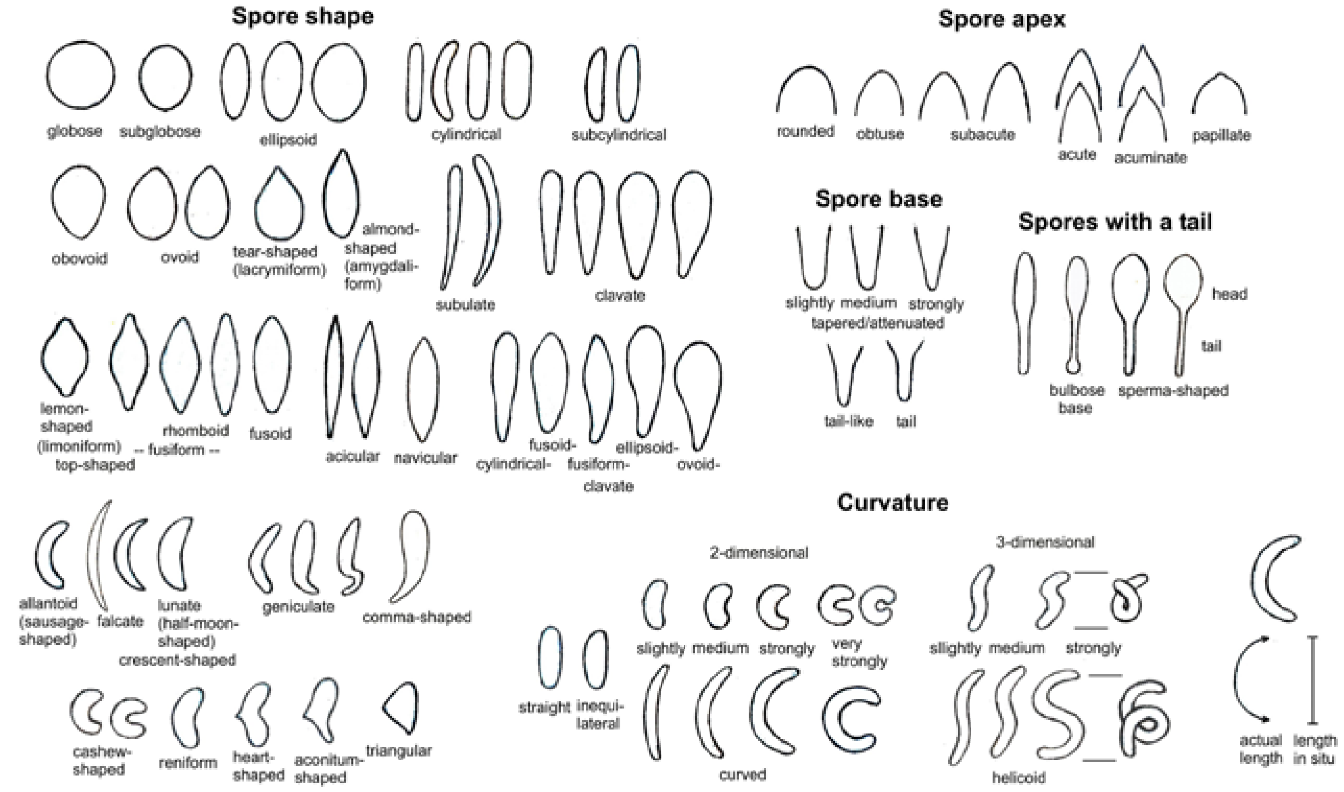


Figure 46: Different types of ascospore shapes occurring in *Orbiliomycetes*. Terminology following in parts De Hoog & Guarro (1995) and Hawksworth et al. (1996).

however, the actual length along the curvature yields more reliable information but can only be estimated or calculated by respecting spatial spore shape. The best is, therefore, to separately evaluate spore length in both ways (see p. 10, Microscopic measurements).

Shape. Spore diversity within *Orbiliomycetes* comprises virtually all types of spore shapes known in ascomycetes: globose, ovoid, ellipsoid, fusoid, rhomboid, clavate, sperm-shaped, tear-shaped, cylindrical, subulate, falcate, helicoid, comma-shaped, sausage-shaped, cashew-shaped, triangular, heart-shaped etc. (Fig. 46). This high diversity within the class as opposed to a rather low intraspecific variability suggests that spore shape diversity reflects some kind of ecological adaptation, rather than representing an accidental evolutionary product.

Many species of *Orbilia* possess more or less ellipsoid ascospores. Besides species with globose and subglobose spores they represent the more primitive type of spore shape (see Fig. 55). A more complex morphology is achieved when the spore ends become attenuated or pointed, which results in a fusoid or fusiform (rhomboid or navicular) shape. These types of spore shape often occur in very distant groups of *Orbiliomycetes*, therefore, confusion at the sectional up to generic level may occur when dealing with dead herbarium material, in which the spore bodies are invisible (see Fig. 3), also if ascus characters are neglected.

Similarly, vermiform to acicular ascospores occur in various, more or less distant taxa. For instance, falcate spores are typical of section *Arthrobotrys*, but also occur in sections *Helicoon* and *Hemiorbilia*, and even in *Hyalorbilia* (Fig. 47). Such spores may sometimes show a very slight helicoid twist. In other species the spores are distinctly helicoidally twisted (within the living asci but also after discharge). Helicoid spores are typical of series *Aurantiorubrae*, *Hyalinia*, and *Xanthoguttulatae* (section *Aurantiorubrae*, Fig. 48: a–d), but also occur in sections *Hemiorbilia* and *Orbilia*, and even in *Hyalorbilia* (Fig. 48: e–g). Helicoid spores in *Orbiliomycetes* are predominantly twisted like a right-hand thread. In this way they are tightly intertwined inside the asci. Only in three rather distantly related species (*O. spirospora*, *O. bomiensis*, *O. helicovinosa*) the spores are consistently twisted like a left-hand thread. Such helicoid spores are often incorrectly termed 'sigmoid' (e.g., by Spooner 1987) or 'spirally twisted' (e.g., by Velenovský 1934), terms which should better be restricted to spores curved in one plane, though the letter sigma resembles helicoid spores seen in side view. Falcate and helicoid spores are heteropolar in most species of *Orbilia*, i.e., their two ends deviate in shape and contain a spore body only in one end, whereas in *Hyalorbilia* they are homopolar in shape, and their SBs occur near both spore ends.

Sausage- to cashew-shaped spores exist in a few species of two rather distant sections (*Hemiorbilia* and *Orbilia*, Fig. 49: a–e). Such spores often form semicircles, and even almost complete circles occur (*O. subfabacearum*, Fig. 49: c). The rare case of warted spores occurs only in this spore type (Fig. 49: d).

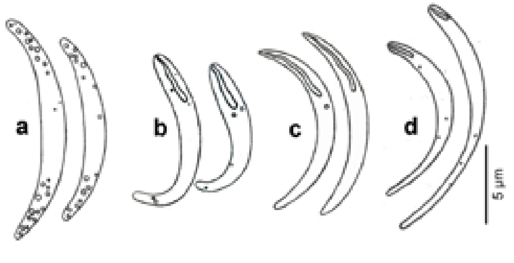


Figure 47: Falcate (sickle-shaped) spores as occurring in quite distant groups of *Orbiliomycetes* differ markedly in the living state by their SBs, while in the dead state they are easily confused. — **a**. *Hyalorbilia berberidis*, **b**. *Orbilia multicurvula* (section *Hemiorbilia*), **c**. *O. arcospora* (section *Helicoon*), **d**. *Orbilia* cf. *rubrovacuolata* (section *Arthrobotrys*).

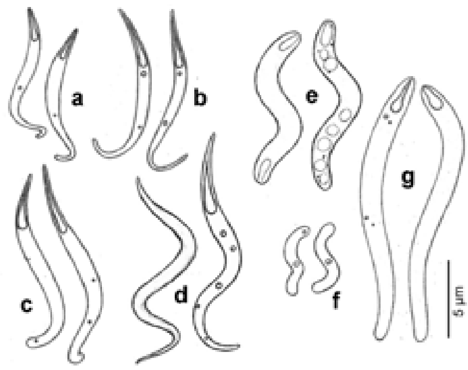


Figure 48: Also helicoid ascospores occur in very different groups of *Orbiliomycetes* (living state except for **e–f**). — **a**. *Orbilia pseudobrevistipitata*, **b**. *O. nemaspora*, **c**. *O. jugulospora*, **d**. *O. spirillospora* (**a–d**. section *Aurantiorubrae*), **e**. *Hyalorbilia macrohelicospora*; **f**. *O. spirospora* (section *Orbilia*), **g**. *O. helicovinosa* (section *Hemiorbilia*).

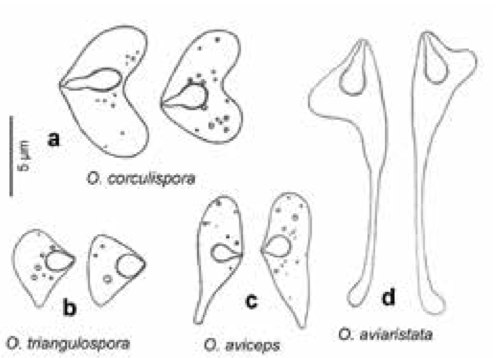


Figure 50: Extraordinary types of bilaterally symmetric spore shape (heart-shaped to triangular, SBs apically to laterally inserted). — **a**. series *Hesperideae*, **b–d**. series *Hemiorbilia*.

Spores with more or less long basal tails constitute quite a frequent type of spore shape. The tails are sometimes swollen and curved at their basal end. Such spores are typical of series *Hemiorbilia* (Figs 49: f, i; 50: d), but very similar spores occur in several more or less distant sections and series of *Orbilia* (Fig. 49: g, h, j–l). All these spore tails possess a lumen that contains cytoplasm along their entire length.

In an extraordinary type of ascospores the shape is asymmetrical and the spore apex with its large tear-shaped spore body is either in an apical or lateral position, resulting in heart-shaped or triangular spores (Fig. 50: a–b) or spores resembling more or less a bird's head (Fig. 50: c–d). Such spores occur in series *Hemiorbilia* and *Hesperideae* and appear to have evolved from symmetrical spores with apical SBs (see also under Spore body, p. 72). *O. aviaristata* and *O. aviflagellata* with their asymmetrical spore heads (Fig. 50: d) but apical SBs form a transitional type.

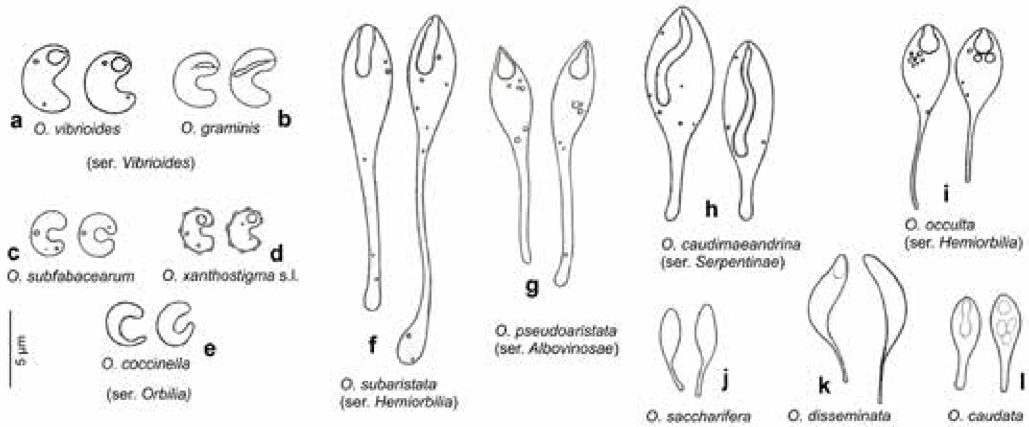
In quite a few species of *Orbilia* the spores have a seemingly aerodynamic shape. Their apex is tapered, often acute, and their base gradually attenuated or even provided with a tail, the widest part of the spore being above the middle. Yet, some of the spores are usually inversely oriented within the asci, and all spores are ejected as a compact cluster (see p. 60, Spore cluster). This provides sufficient evidence that the function of spore shapes in *Orbilia* must be explained differently (see p. 144–145, Preying on invertebrates).

Variation. Ascospore size and shape are usually quite valuable characteristics of a species, Yet, spore characters are sometimes overestimated in regard to species delimitation, and thought to be constant within a species. In our experience, variation in both size and shape seems to be a common phenomenon in many groups of ascomycetes. A more or less pronounced intraspecific variability was noted in almost every species of *Orbiliomycetes*, particularly between populations but also within.

Deviations in size and shape were particularly observed between collections from very remote areas, but sometimes also within a narrow area. They might in some cases be the result of external conditions rather than having a genetical basis. Frequently, however, such deviating populations raise the question as to whether they represent different species. For example, an extraordinary case of variation was observed between populations of *O. corculispor*a. Typically this species has heart-shaped spores, but sometimes it occurs in a form with more or less subglobose spores (see Fig. 65: b); intermediate spore types sometimes occur and would make a separation into two species difficult. In addition to this, typical populations vary among another between distinctly heart-shaped and kidney-shaped. Striking differences were sometimes also observed between parts of a single collection (Fig. 51: b–c). Whether such populations represent one variable or two separate species could not be clarified (see also p. 16 ff., Taxa concepts).

Spores may vary in size even within a single ascus. Such heterospory is known to occur commonly in the *Helotiales*: the lower spores of an ascus are slightly or even considerably longer than the upper ones. This phenomenon could be thought to provide a balanced discharge distance to all spores by compensating the declining turgor pressure during spore release. This assumption is based on Ingold's (1933)

Figure 49: Similar spore shapes in different series and sections of *Orbilia* (living state except for **e**, **k–l**). — **a–e**. reniform to semicircular spores; **f–l**. spores with tails.



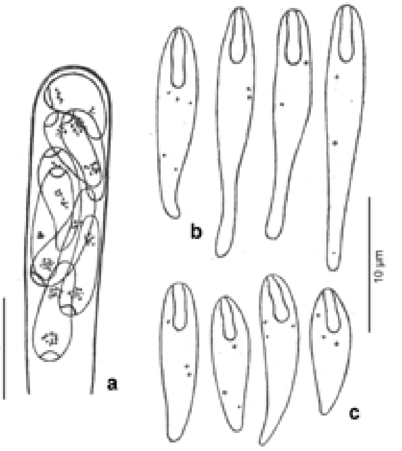


Figure 51: Variation in spore size and shape within an ascus (**a**) or a population (**b–c**). — **a**. Uppermost spore consistently shorter and wider and more curved than lower spores (*O. ocellata*); **b–c**. differences in spore length and shape observed in different subpopulations within an Australian collection of *O. hesperidea.*

observation that spores with a higher mass attain a higher distance. The lower, larger spores thereby compensate for loss of ascus turgor during spore discharge by a greater mass. In the *Orbiliomycetes* no such distinctly larger basal spores can usually be observed, instead, larger and smaller spores occur more or less scattered within the ascus. This is not surprising since here all spores of an ascus are ejected as a single cluster. It would not make any sense for an efficient dispersal to place the longer spores near the base of the pars sporifera. However, in series *Lentiformes*, and here particularly in 8-spored taxa, the uppermost spore is very frequently distinctly shorter and thicker and, furthermore, often strongly curved (Fig. 51: a). As this situation can regularly be seen in this series, such deviating spores are included in the description.

These deviations are considered to belong to the normal scope of variation, however, spores of abnormal size or shape may occasionally occur inside the living asci due to some possibly external influences. This concerns (1) spores of an abnormally large size but normal shape, which arise in asci with reduced spore numbers (see p. 56), or (2) spores of abnormal shape, generally more primitive than the typical spores of the species, for instance, normally ellipsoid spores are instead ovoid to globose, or spores with a tail or or tail-like base lack these markers. Both phenomena have occasionally been seen in a number of taxa, but usually only inside a few of the asci of an apothecium. In the case of abnormal shape, usually all spores of an ascus show this abnormity. Whatever causes such regression is unclear. We have consistently excluded abnormal spores from our species descriptions and keys if they occurred only exceptionally. In *O. eucalypti*, however, broadly ellipsoid to subglobose spores may occur in rather high frequency or sometimes strongly predominantly compared to the normal ellipsoid spores.

In those species of *Orbilia*, which mainly deviate from each other in spore number, the spores tend to be smaller with increasing spore numbers. However, exceptions confirm the rule: for instance, in series *Microspermae* a difference in spore volume is only seen between the 16-spored *O. pleioeuonymi* and 32-spored *O. euonymi* (Fig. 41). On the other hand, closely related species may markedly differ in spore size though having the same spore number (examples: *O. vinosa* and *O. aprilis*, or *O. pleiolentiformis* and *O. flavida*).

Terminology of spore ends. The partial inverse orientation of the spores in asci of *Orbiliomycetes* poses the problem of how to name the two spore ends. In most species the inversely oriented spores (with the SBs pointing downwards) are the lower spores of an ascus. In comparison with the *Helotiales* in which inverse orientation of some lower spores was rarely noted (see p. 59), we conclude that the SB-containing end of the spore, which is usually closer to the widest part of the spore, represents the 'upper' or 'apical' end, and the opposite the 'lower' or 'basal' end.

Of course, the terms 'upper' and 'lower end' applied to ascospores are somewhat incorrect because (1) ascocarps on the natural substrate often occur oriented in all directions, and (2) the spores within an ascus may also be oriented in two opposite or sometimes in all directions.

In order to avoid the first mentioned conflict, Domínguez de Toledo (1994) in her 'suggestions for describing and illustrating fungal spores' proposed the terms 'distal' and 'proximal' in order to characterize the poles of a spore. In her definition, the spore ends in fungi are determined either by their formation on sterigmata or conidiophores, or by their orientation within the asci, but not by their shape. 'Proximal pole' means the spore end by which a basidiospore or conidium is attached, or that end of an ascospore directed towards the ascus base. 'Distal pole' means the spore end directed away from the attachment. It must be noted, however, that some workers on pyrenomycetes, notably Eriksson (1967: 342), but also Webster et al. (1998) in *Orbilia*, conversely used 'proximal' for the broader ascospore end being oriented towards the ascus apex, and 'distal' for the narrower end pointing towards the ascus base (in pyrenomycetes with heteropolar spores we have so far never observed inversely oriented spores).

The second conflict mentioned above, the phenomenon of inverse spore orientation within asci, was obviously unknown to Domínguez de Toledo. However, she mentioned the case of rather short and wide spores, in which the spores do not show any regular arrangement within the asci. For this case Domínguez de Toledo concluded that the terms 'distal' and 'proximal' cannot be applied.

In our opinion, a clear reference to the two different poles is necessary for spores that are distinctly heteropolar in shape and/or cytoplasmic structure, even if the spores are irregularly arranged in all directions within the ascus. Based on the justified hypothesis that the differently shaped spore bodies in *Orbiliomycetes* are homologous organelles, we conclude that SBs provide a valuable tool for recognizing spore ends in *Orbiliomycetes* (see also p. 71–72).

We decided to continue the current usage of the terms 'upper/apical' and 'lower/basal' in reference to the terms 'ascus apex' and 'ascus base'. Thus, the 'upper end' contains the spore body. Thereby we refer to spores that point with their SBs towards the ascus apex as oriented 'ordinarily or upwards', and we name those spores as oriented 'inversely', 'inverted', or 'downwards' which point with their SBs towards the ascus base. In the case when SBs are absent or occur at both spore ends, the broader spore end is named 'upper end'. We also recommend arrangement of the spores on plates consistently with their upper end pointing upwards. In cases of homopolar spores with laterally inserted SBs (*O. corculispora*, *O. beatricis*, *O. fabacearum*) or when the spores are globose or flattened like a lens, no distinction can be made between upper and lower spore end, and also a distinction between ordinarily and inversely oriented spores is then more or less impossible. In such cases spore end terminology (including SB attachment) and spore orientation become ambiguous.

Shrinkage and collapsing during dehydration. Shrinkage and collapsing are universally observed effects of the living

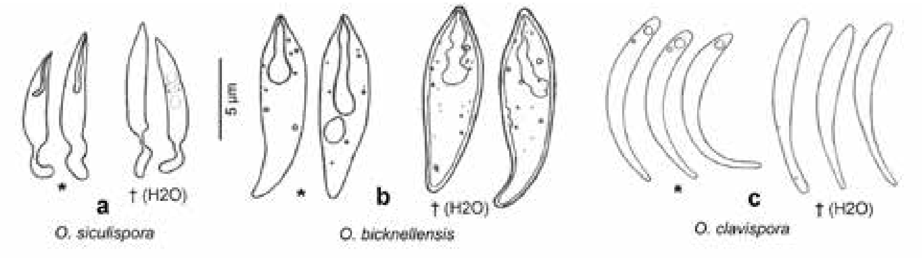


Figure 52: Spore shape may differ between the living (*) and dead state (†). — **a**. the basal constriction gets more pronounced; **b**. no change observed; **c**. falcate spores usually become distinctly less curved.

fungal spore and represent two types of response to dehydration (Baral 1992: 350, fig. 11). The two effects depend on whether the spore wall is elastic or not. Shrinkage and collapsing instantly disappear upon rehydration with water, if the spores are still alive. Due to the rapidness of the rehydration process, these effects of living spores are easily overlooked. The phenomenon has a general occurrence in ascomycetes with thin or thick but not too rigid spore walls, and is due to the high permeability of the spore wall to water (Baral 1992: 379). Shrinkage and collapsing is also observed when the asci attain full turgescence and the living spores thereby shrink or collapse (see p. 60).

The collapsed shape of dry dormant spores can be observed under the LM, either in air as medium, or when mounting dry spores in oil. Also the cells of conidia of *Orbiliomycetes* collapse in the dry state. This phenomenon was already observed with the first compound microscopes, according to a report by Loew (1867) who described the dry conidia of '*Arthrobotrys oligosporus*' as wrinkled and irregularly edged, with the protoplasm retracted from the cell wall. Collapsing is also often observed in SEM spore images.

Differences in shape between living and dead ascospores. When adding lethal media to water-mounted living spores, slight shrinkage and/or changes in shape usually occur (see p. 28). In *Orbiliomycetes* the spore wall shows quite a low elasticity, in strong contrast to the ascus wall. This can be concluded from the rather low values of spore shrinkage observed in this class, and from the phenomenon of collapsing. Nevertheless, minor changes in shape can be noted so that characteristic spore profiles may become enhanced or obscured in the dead state. For instance, spore tails or constrictions often become thinner (Fig. 52: a), and acute spore apices may either change to acuminate or subacute. In other cases spore size and shape remain quite unchanged (Fig. 52: b). Another, rather striking phenomenon concerns spore curvature: dead spores are frequently less curved than living spores (Fig. 52: c). This effect can be explained by a higher elasticity of the dorsal spore wall compared to the ventral wall.

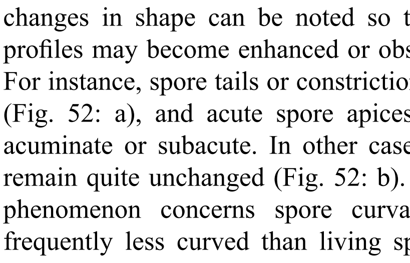


Figure 53: Collapsing of dead spores of *O. lentiformis*. — **a**. living spores, **b**. dead flattened spore, **c**. same spore after a 90° turn (all in H_2O). Living spores in the dry dormant state look quite similar as in **b–c**.

Living hydrated ascospores in *Orbiliomycetes* are usually more or less perfectly circular in optical cross section. In the dry state, however, they are more or less flattened or collapsed due to complete water loss, irrespective of being alive or dead. After rehydration in water, living spores reattain their original shape within a few seconds, while dead spores usually remain strongly compressed, and rehydration in KOH may but must not inflate them to their original shape. The width of such flattened spores in water was, e. g., 4.5–4.7 µm (Fig. 53: b) and after adding KOH it changed to 3.5–4 µm. Flattening of spores is easily overlooked under the LM, but becomes apparent when spores are floating in a water mount: after a turn for 90° the strongly collapsed middle part of the spores in the above example showed a width of only 1–2 µm (Fig. 53: c).

Lateral flattening was reported by Spooner (1987: fig. 26 D) for the narrow, somewhat subulate spores of *O. crenatomarginata* (as *Hyalinia crystallina*). Because of the helicoid spore shape, this flattening is only seen as a local constriction, the place of which depends on the viewing direction. However, such flattening apparently occurs quite rarely in such spores, as we have never observed it in series *Hyalinia* in the herbarium specimens studied.

Septation and germination. *Orbiliomycetes* have earlier been characterized as possessing non-septate ascospores, until a species was discovered with regularly (0–)1(–3) transversal septa while still within the living asci (*Orbilia septispora*, Baral 1989; Fig. 54: a). Until now, this species remains the only exception within the class, apart from very occasional spore septation within the living asci in one further species (*O. lentiformis*, Pl. 158: 2b).

During the process of germination, however, some species were found to produce one or sometimes up to three transsepta. Overmature spores can usually be obtained from senescent apothecia that had been affixed to the lid of the Petri dish and left for a few weeks. Except for *O. septispora*, spore septation was only observed in free spores or those inside dead asci. Septate overmature spores were noted in *Amphosoma* (*A. macrosporum*, *A. atroolivaceum*), *Orbilia* sections *Lentiformes* (*O. patellarioides*, *O. lentiformis*, *O. pleiolentiformis*, *O. phanosoma*, *O. cercidicola*), *Hemiorbilia* (*O. corculispora* Fig. 70: d), *Habrostictis* (*O. obtusispora* Figs 54: b, 70: c, *O.* cf. *quaestiformis*, *O. mesaverdiana*), and *Orbilia* (*O. austropleiomicrosoma*, *O. eucalypti*). Overmature stages of spores were mainly observed during such culture studies, because in *Orbiliomycetes* the spores frequently do not germinate in senescent apothecia on the natural substrate, even when kept in a moist chamber for some time. Only very rarely (e. g., *O. eucalypti*, P.P. 20061028–6, P. Perz pers. comm.; *O. austropleiomicrosoma*) abundant spore germination was observed on the natural substrate.

Phylogeny of spore shape. Globose to ellipsoid, homopolar spores probably represent the plesiomorphic type of ascospore within the *Orbiliomycetes*, whereas heteropolar spores as well as curved spores appear to be advanced, apomorphic features, particularly spores with a basal tail or a helicoid curvature. Nannfeldt (1982: 164) was similarly convinced that 'the change from radial symmetry to biradial or bilateral means a step of high

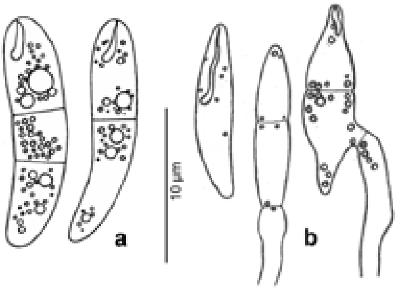


Figure 54: Septate ascospores in *Orbiliomycetes*, depending on maturity. — **a**. mature 1–2-septate spores of *O. septispora*; **b**. mature non-septate (left) and overmature, germinated, 1-sepate spores of *O. obtusispora*. Spores of *O. obtusispora* become septate only during germination, whereas those of *O. septispora* possess septa already during ejection, and do not get further septa during germination.

taxonomic and phylogenetic importance, a step from a more unspecialized and 'primitive' stage to a more specialized and 'advanced'. However, reverse evolutionary lineages may also have taken place. For instance, Rogers (1979) and Nannfeldt (l.c.) believed that the *Xylariaceae* which are characterized by homopolar non-septate ascospores developed from ancestors that had heteropolar 1-septate spores. We suspect that evolutionary steps in both directions (advance and reduction) have occurred within the genus *Orbilia*.

Spore wall, **surface and colour**. The ascospore wall of *Orbiliomycetes* is always thin (~0.1–0.2 µm), and varies only slightly in thickness among the taxa. Its surface is consistently smooth when observed under the LM at 1000–1500×, with a remarkable exception: the minute, cashew-shaped spores of the *xanthostigma-leucostigma* complex including the closely related *O. aureocrenulata*, possess a number of distinct warts on their dorsal but also laterally. These warts were described for the first time by Spooner (1987: fig. 21). Their presence was confirmed by us from numerous collections, and can quite easily be demonstrated on microphotographs (Fig. 56: e–f). Research with the TEM (Müller 1998) showed that they are protuberances of the spore wall which include the sporoplasm (Fig. 56: a–b). With the SEM a spatial image was obtained by Pfister (1997, Fig. 56: c–d). Mainly here it became evident that these protuberances also occur on the lateral side of the spore. For a possible function of these warts see p. 144–145, Infection by ingestion.

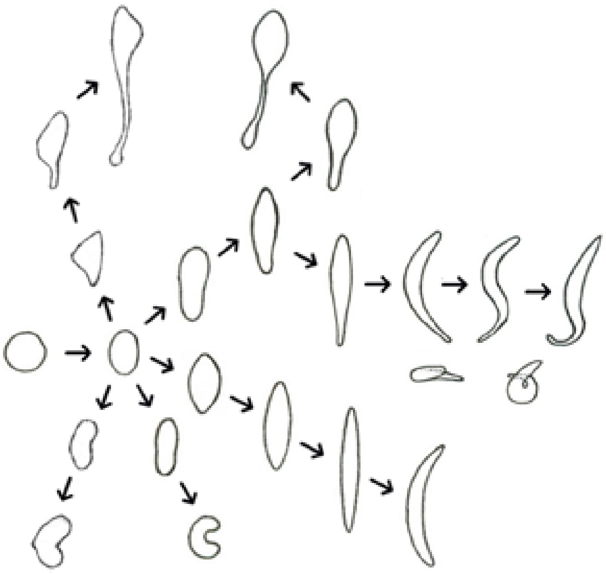


Figure 55: Hypothetical phylogeny of ascospore shape in *Orbiliomycetes*.

Non-cellular appendages such as setulae (previously called 'cilia') or slime caps have never been observed in the *Orbiliomycetes*. A peculiar spore sheath (a membrane that is shed when the spores are ejected into water, Baral 1992: 356, fig. 14) is rather frequently observed in the *Helotiales* but could never be seen in the *Orbiliomycetes*. There is not even a thin gel layer on the spore wall, as can be concluded from the absence of any colouration upon treatment with CRB. This is surprising since in all other elements of the holomorph, including often also the conidia, the wall surface is covered by a thin gel that stains faintly to intensely purplish-lilac in CRB (see p. 97–99).

The ascospores of *Orbiliomycetes* are always hyaline. Even during ageing and germination no natural colouration of the spore wall or the sporoplasm in the living or dead state was ever noted.

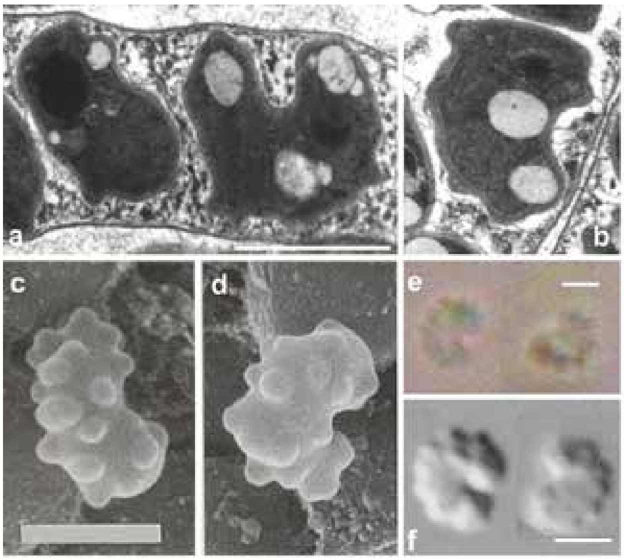


Figure 56: Warted ascospores of *O. xanthostigma* s.l., a rare case in *Orbiliomycetes*. The warts are caused by protuberances (bulging) of the spore wall and include sporoplasm. — **a–b**. Germany, VII.1998, TEM (Müller 1998: fig. 21 C, as *O. delicatula*), **c–d**. USA, H.B. 5165, SEM (Pfister 1997: fig. 2, as *O. delicatula*), **e**. Denmark, H.B. 8536, LM (bright field); **f**. China, 15.VIII.2003, LM (DIC, phot. M. Mo). Bar = 1.5 µm (in c & d: ~1.5 µm).

Spore body (SB)

Mature living ascospores contain conspicuous, hyaline, more or less strongly refractive cytoplasmic inclusions when viewed in water mounts under oil immersion, usually one per spore (Fig. 57). This curious organelle is consistently present in almost every species of *Orbiliomycetes*. No other group of ascomycetes is known so far to possess such a spore inclusion, which is referred to as 'spore body' (SB) here, a term introduced in an ultrastructural study by Benny et al. (1978).

SBs become invisible in media such as IKI in chloral hydrate (MLZ), lactic acid, Cotton blue in lactophenol (CB_L), KOH etc. by completely losing their refractivity. Frequently, no trace of the SBs can be discerned in dead spores with any of the methods that we have tested in the present study.

Only in a few, mainly small-spored taxa (*Hyalorbilia herbicola* p.p., *H. hergiswiliana*, *H. pleioerythrostigma*, *H. rotifera* p.p., *H. texensis*, *Orbilia asomatica*, *O. eucalypti* p.p., *O. subfabacearum* p.p.), the SBs are either absent, or too small to be discerned under the light microscope, or difficult to recognize among the similar-looking LBs that often accompany them. SBs are undoubtedly absent in *Orbilia asomatica* (section *Arthrobotrys*), a species which forms a rare exception within the large genus *Orbilia*: no trace of a spore body could be seen in the fully mature, rather large viable spores, whether ejected or in the living asci.

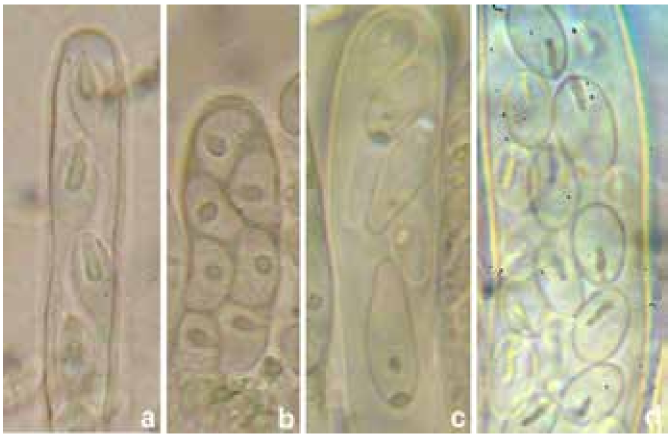


Figure 57: Four examples of different types of spore bodies (LM, oil immersion, bright field). — **a**. *O. aristata* (H.B. 8269b), **b**. *O. corculispora* (H.B. 8087a), **c**. *O. ocellata* (3.VIII.2008, phot. P. Perz), **d**. *O. multimacroasca* nom. prov. (#756). Living state, except for asci in **a–b**.

Size and shape. The size of SBs ranges among the species at (0.2–)0.4–2 in diameter for ± globose SBs and 2–10(–12) µm in (actual) length and 0.2–0.4 up to 1(–1.5) µm in width for elongate SBs. This diversity corresponds to a volume range of about (0.008–)0.05–10 µm^3, which implies a maximum divergence of up to ~200 × (or exceptionally 1.000)× between the smallest and the largest known spore bodies. Similar as ascospore size and LB diameters, SB dimensions have high taxonomic importance and, therefore, need to be included in descriptions. Similar as in curved spores, the length of curved SBs should be evaluated in two ways, i. e., straight length (in situ) and actual length (see p. 10, Microscopic measurements).

In addition to their size, SBs differ among taxa in a number of parameters which dictate their shape. These involve (1) length/width ratio, (2) width of upper end where they are attached, (3) width below attachment, (4) width of middle part, (5) width of lower end, (6) ratio between length of inflated and not inflated parts, (7) strength of curvature, and (8) place of attachment (apical, subapical, lateral). The ratio between SB volume and spore volume also varies considerably among the genera, subgenera, sections, and series. For instance, section *Orbilia*, but also *Hyalorbilia*, include taxa with very small SBs in relation to spore volume, despite the often comparatively small spores, whereas in series *Lentiformes*, or sections *Habrostictis* and *Hemiorbilia*, much higher SB volumes occur, and also the ratio between SB and spore volume is usually higher.

One of the main criteria to characterize the taxonomic groups within *Orbiliomycetes* is the shape of SBs (Fig. 58, see also p. 25). Lens-shaped SBs occur almost exclusively in *Orbilia* series *Lentiformes*, but also in *Lilapila*, *Pseudorbilia*, and *Amphosoma*, also in two species of section *Ovoideae* and in one of series *Microsomates.* Ampulliform to dumbbell-shaped or cylindric-subulate to tear-shaped, usually straight SBs occur in section *Hemiorbilia*. Elongate tear-shaped (subulate), straight SBs are typical of series *Hyalinia*, *Aurantiorubrae*, and *Xanthoguttulatae*, and tear-shaped SBs of series *Albovinosae*. Strongly elongate, worm-shaped to filiform or subulate, often flexuous to helicoid or uncinate SBs (sometimes resembling a question mark or a pig tail) are typical of subgenus *Habrostictis.* Stomach- to sausage-shaped or note- to lantern-shaped SBs mainly occur in series *Phanosomates* and *Microspermae.* Minute plug-shaped SBs are typical of series *Microsomates*, and ampulliform to christmas ball-like SBs of section *Ovoideae* and *Lecophagus*. Small globose SBs characterize series *Regales* and *Orbilia*, section *Arthrobotrys* p.p., and *Hyalorbilia*. Small rod-shaped SBs occur in series *Dactylellina*, *Gamsylella* and *Drechslerella* of section *Arthrobotrys*.

Attachment. Although sometimes seemingly unconnected, SBs are apparently always attached to the spore wall, either broadly as in the lens- or plug-shaped type, or by a more or less narrow connecting part. Often the connecting part is an extremely fine, tractus-like thread which is called ‘filum’ here.

SBs can be apically, subapically or laterally attached to the spore wall. Irrespective of their position in the spore and the position of the spore within the ascus, the point of attachment is referred to as the apical end of the spore body, which coincides with the spore apex in the majority of species, and the opposite as the basal end. As a consequence, in the case of lateral attachment the spore body apex points in a lateral direction.

Lens-shaped SBs may easily be mistaken for a thickening of the wall at the spore apex, due to their close and very broad connection to the spore wall. However, adding KOH to a water mount promptly makes the structure invisible, and the spore looks thin-walled at the apex, even if stained with CR afterwards.

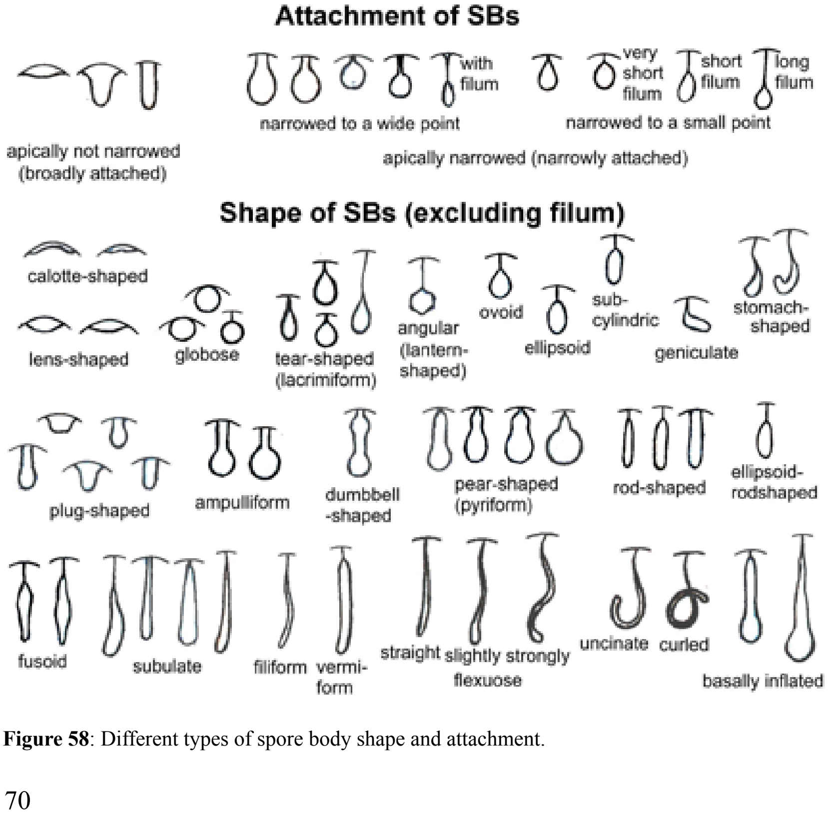


Figure 58: Different types of spore body shape and attachment.

However, the SBs are still present in the dead spores, though difficult to recognize. In water mounts the contrast is better (Fig. 67: j, o), and when cytoplasmic stains such as iodine or CRB are applied, the sporoplasm takes up the dye whereas the region of the SB remains unstained (Fig. 66: f).

SBs of section *Hemiorbilia* are apically often only slightly narrowed to a short and thick connecting part. Rarely the SBs are short-cylindrical to plug-shaped and broadly connected to the spore apex without any obvious constriction, e. g., in some species of series *Microsomates*. By far the major part of *Orbiliomycetes* have SBs with a more or less narrowed connecting part between inflated part and spore apex, thereby the thickness and length of this connecting part strongly varies between the series. In series *Phanosomates* (Fig. 59: a–c) and in some species of section *Habrostictis* the SBs consist of an abrupt basal inflation and a long and fine filum. Similar globose to ellipsoid SBs but with a shorter filum are predominantly found in series *Regales*, sections *Ovoideae* and *Arthrobotrys* (Fig. 59: d), and series *Orbilia*. In these four groups the filum is so fine that it is only exceptionally visible. In cases of a seemingly absent connection a very fine filum may sometimes become visible when staining with CRB. In *Hyalorbilia* a filum could only exceptionally be demonstrated (*H. erythrostigma*, *H. subfusispora*).

Ascospores containing a single SB. In the great majority of species only a single spore body is found in each spore, mostly at one of the two spore ends (Figs 57, 59). The SB-containing spore end is here consistently referred to as the ‘upper’ spore end (see p. 67). Such spores can be termed heteropolar with regard to their sporoplasm, although the spores may be homopolar in shape. Five genera of *Orbiliomycetes* include species with a heteropolar, asymmetrical sporoplasm: *Hyalorbilia* p.p.min. (*H. anonyma*, *H. erythrostigma*, *H. orbiliicola*, *H. ulmi*), *Lecophagus*, *Lilapila*, *Liladisca*, and *Orbilia*. Rarely the SBs are subapically to laterally inserted (Figs 50: a–c; 57: b).

Ascospores containing more than one SB. Contrary to the normal situation in *Orbilia*, the ascospores of the three genera *Amphosoma*, *Hyalorbilia* p.p.maj., and *Pseudorbilia* contain symmetrically arranged spore bodies, with one or up to about five SBs near each spore end. Such spores can be termed homopolar with regard to their sporoplasm, and also their shape is often homopolar in these taxa.

Species with a heteropolar sporoplasm may, as a rare abnormity, form two SBs, one at each spore end. Such exceptions were, however, only noted in about one out of a hundred spores, and so far only in a few desiccation-tolerant species, viz. two of series *Lentiformes*: *O. lentiformis* (Fig. 60: c) and *O. pleiolentiformis* (H.B. 7231d), one of section *Habrostictis*: *O. macrotrapeziformis* (H.B. 7284m), and several of section *Hemiorbilia*: *O. hesperidea* (Fig. 60: d), *O. aprilis* (P.P. 20060310), *O. montigena* (H.B. 9137b), *O. clavuliformis* (21. II.2010), and *O. myriofusiclava* (H.B. 8923b). In *O. lentiformis* two of the studied asci contained one abnormal and seven normal spores, while in the other species only free spores with this abnormity were seen. This phenomenon of abnormal spores appears to represent an evolutionary regression, supporting the idea that taxa with a heteropolar sporoplasm evolved from taxa with a homopolar sporoplasm (see Fig. 74).

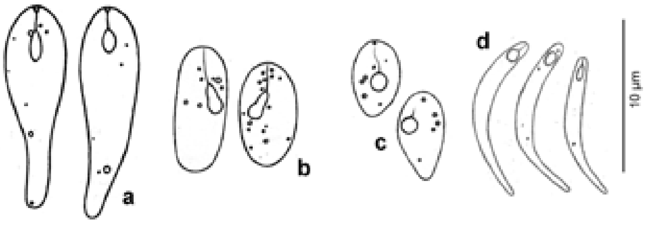


Figure 59: Spore bodies with a filum (**a–c**. series *Phanosomates*, **d**. series *Arthrobotrys*). — **a**. *O. magnifica* (with funnel-like attachment), **b**. *O. multiphanosoma*, **c**. *O. myriosphaera*, **d**. *O. auricolor*.

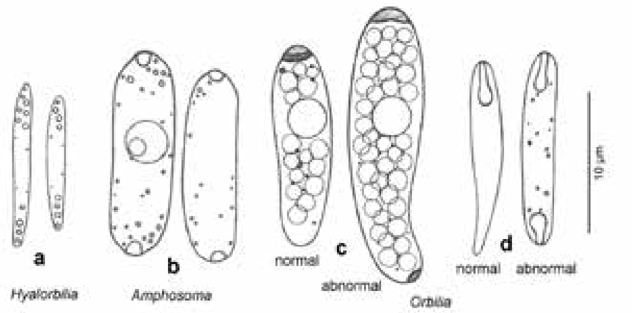


Figure 60: Homo- vs. heteropolar sporoplasm: SBs of *Amphosoma* and *Hyalorbilia* occur near both spore ends (**a–b**), whereas SBs of *Orbilia* occur at one end only (**c–d**, left), but abnormal spores may contain SBs at both ends (**c–d**, right). **a**. *H. juliae*, **b**. *A. macrosporum*, **c**. *O. lentiformis*, **d**. *O. hesperidea*.

SBs in ascospores with a heteropolar shape. In many species both the spore shape and the sporoplasm is heteropolar. In this case, the widest part of the spore is usually not exactly in the middle, and the SBs are mostly attached to that end which is closer to the widest part of the spore (Fig. 61 normal case).

Spore bodies provide a valuable means for defining the apical spore end (see p. 67). However, there are some exceptions to this rule. In a small number of species the phenomenon was observed that rare abnormal spores of an apothecium contained the SB in the ‘wrong’, i. e., narrower end of the spore (Fig. 61 abnormal case; observed also in *O. ovalis* Pl. 181: 4a and *O. coniferarum* Pl. 687: 2a).

A few further species or aberrant populations break this rule (Fig. 62: a, c, e): their SBs are consistently found in the acute end, whereas the opposite end is ± obtuse, with the widest part of the spore being predominantly closer to the obtuse end. In such a case, the spore shape misleads from an aerodynamical point of view to consider the obtuse end as the upper spore end and to arrange spore illustrations with their acute ends pointing downwards. The interpretation of the SB-containing spore end as the upper end is confirmed by closely related populations (Fig. 62: b) or species (Fig. 62: d), in which the widest part of the spore is closer to the SB-containing end. Obviously, spore shape is less important in regard to spore polarity than SB position.

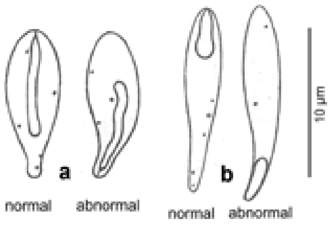


Figure 61: In species with a heteropolar spore shape the SBs are generally attached to the wider end of the spore, and only in abnormal spores they are attached to the narrower spore end. — **a**. *O. caudimaeandrina*; **b**. *O. pleionavajoana*.

SBs in ascospores with a homopolar shape. In ascospores with a homopolar shape, the upper spore end can only be recognized by the spore body that it encloses (Fig. 63). In such taxa, heteropolarity and inverse spore orientation is usually

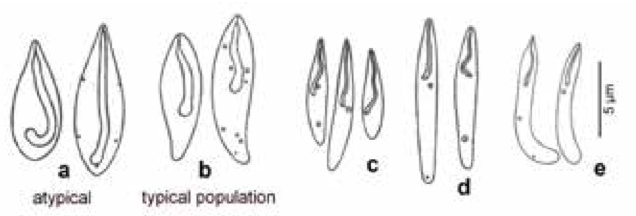


Figure 62: In a few taxa (**a**, **c**, **e**) the SBs are partly or predominantly attached to the narrower spore end. In closely related taxa or different populations (**b**, **d**) the SBs are predominantly attached to the wider spore end. In dead spores the two spore ends usually cannot be correctly addressed. — **a–b**. *O. maeandrina*; **c**. *O. sarraziniana*; **d**. *O. rosea*; **e**. *O. suberis*.

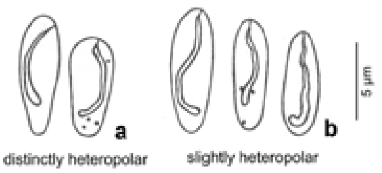


Figure 64: The spores of *Orbilia myrionamibica* are often distinctly heteropolar, but sometimes almost homopolar, SBs are attached to the wider but sometimes to the narrower spore end (right spore); in the dead state the upper spore end and consequently the spore orientation within the asci is quite impossible to determine in this species.

completely masked in the dead state (compare, e. g., Spooner 1987: fig. 20: *O. cunninghamii*, fig. 24: *O. juruensis*, fig. 28: *Habrostictis decipiens*; Haines & Egger 1982: *O. piloboloides*; see Figs 155–156), except for species with lens-shaped SBs in which the SBs often remain more or less perceptible in the dead state.

Frequently, not all spores of an apothecium are homopolar in shape. The lower end is often more or less variably shaped, whereas the upper end is generally more consistent in shape. As a consequence, spores which are ± strongly heteropolar in shape occur mixed with spores which are almost homopolar (example: *O. myrionamibica*, Fig. 64).

In a few species of *Orbilia* the definition of the upper spore end becomes more or less obscure because the SBs tend to be laterally attached (Fig. 65). In some of these species the SBs vary between apically, subapically or laterally attached (Fig. 65: a, c), while closely related species are known which have apically attached SBs. It can be assumed that the ancestors of species with laterally or subapically attached SBs possessed spores with apically attached SBs.

Such 'evolutionary migration' of SBs appears also obvious when comparing typical species of section *Hemiorbilia* with axially symmetric spores and apical SBs (e. g., *O. aristata*, *O. flagellispora*) with more rare cases of slightly (*O. aviaristata*, *O. aviflagellata*, Fig. 50: d) to strongly (*O. corculispora*, *O. triangulispora*, *O. aviceps*, Fig. 50: a–c) bilaterally symmetric spores with a subapical to lateral SB insertion.

The latter three species show a remarkable case of tripolarity in spore shape. The SB is affixed to a slight lateral projection of the spore which is predominantly oriented sideways within the asci. We see two possible explanations for this peculiarity: (1) the lateral projection represents the former upper spore end, or (2) the SB moved away from the spore apex to a lateral position. Surprisingly, both cases appear to exist, but in different series of *Orbilia*.

Case (1) is represented by species of series *Hemiorbilia* with strongly bilaterally symmetric spores (Fig. 48: b–c): the spore apex including the SB is pushed to a lateral position by a large, now apically positioned protuberance. This view is supported by the similarly but less strongly asymmetrical spores of *O. aviflagellata* and *O. aviaristata* (Fig. 50: d), in which the protuberance points in lateral instead of apical direction, whilst the acute spore apex with the SB still points upwards.

Case (2) is represented by members of series *Hesperideae* (*O. corculispora*, *O. octocorculispora* and *O. myrioauris*, Fig. 65: b–c), and similar cases occur in series *Orbilia* (*O. fabacearum*), ?series *Microsomates* (*O. beatricis* Fig. 65: a, e), series *Vibrioides* (*O. myriooobliqua*, Fig. 65: d) and others. In most of these species a migration of the SBs in whatever direction is beyond doubt. For instance sibling species of the latter three species (*O. cylindrospora*, *O. leucostigma*/*xanthostigma*, *O. paraobliqua*) have spores of a very similar shape but with the SB consistently positioned at the spore apex. In *O. fabacearum* and *O. myrioauris* we observe variation within apothecia (Fig. 65: a, c): usually, the SB is positioned at the lateral wall of the spore, but in a few spores the SB is attached more subapically, or even at the spore apex. Therefore, we assume that in these series the SB changed during evolution its place from the spore end towards the middle part.

In *O. corculispora*, evolutionary SB migration is suggested by rarely encountered atypical populations with ± ellipsoid to subglobose spores which usually more or less entirely lack the shape of a heart (Fig. 65: b): in these spores the SBs are either apically, subapically, or laterally attached, with a trend towards a lateral position in those spores with a slight bilateral symmetry. We presume that the ancestor of *O. corculispora* had subglobose spores which, during evolution, became more and more inequilateral and eventually got a deep indentation at one side and a protrusion at the opposite side, which resulted in the characteristic kidney- or heart-like shape. This process was accompanied by a lateral migration of the spore body.

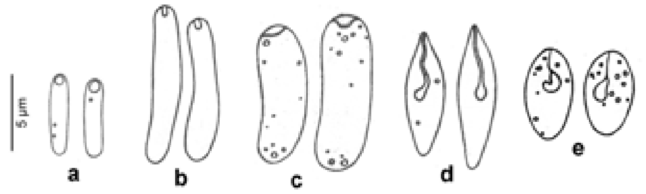


Figure 63: Spores with a homopolar shape but a heteropolar sporoplasm (**a**. *O. cylindrospora*, **b**. *O. microsoma*, **c**. *O. pleiolentiformis*, **d**. *O. carpoboloides*, **e**. *O. pluristomachia*).

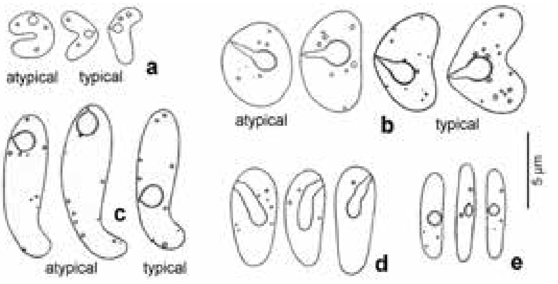


Figure 65: Rare examples of spore bodies being predominantly or consistently subapically or laterally attached. — **a**. *O. fabacearum*; **b**. *O. corculispora*; **c**. *O. myrioauris*; **d**. *O. myriooobliqua*; **e**. *O. beatricis*.

Behaviour of spore bodies during killing. From their refractive appearance under bright field illumination, SBs resemble lipid bodies, particularly when they are globose. Confusion with LBs is then easily possible, especially in species of series *Orbilia*, or in *Hyalorbilia*. Several small droplets are often found in the living spores of *Orbiliomycetes*, either scattered or near the ends, and only the use of a dye or a test with KOH reveals which of the droplets represent spore bodies.

When treated with KOH or CRB, SBs behave in a similar way as refractive vacuolar bodies (VBs) do, therefore, they have been included in the scope of this type of organelle by Baral (1992: fig. 37). The KOH test has been applied in the present study to a rather high number of species from various genera and subgroups of *Orbiliomycetes*, and also CRB was tested in quite a few taxa. The result was always the same, therefore, it can be assumed that SBs of all species behave this way.

KOH of different concentration (0.5–10 %) applied to a water mount rapidly kills the spores by destroying the semipermeability of the plasmalemma. SBs promptly and irreversibly become invisible under the LM by losing their refractivity, whereas LBs remain unchanged. The behaviour of SBs in acids is similar to alkali: if adding strong acids like nitric or formic acid, the plasmalemma is destroyed and the refractivity of the SBs disappears in the blink of an eye. In weak acids like diluted acetic acid (~5 %), the spores remain viable and the SBs unaltered for some time. Likewise, weak alkali such as diluted NH_4OH kill the spores only tardily when applied to a water mount. Mounting in CB_L (containing lactic acid or lactophenol) or MLZ (containing chloral hydrate) also promptly kills the spores and masks the spore bodies completely and irreversibly. Only SBs of the lens-shaped type may still be faintly perceptible in CB_L or MLZ.

The loss of refractivity, i. e., the optical disappearance of SBs, is not bound to the application of a chemical. When the spores die in the desiccated state during a longer period of dryness, e. g., in the herbarium, or when they die by briefly heating a water mount, also when strong pressure is applied to the cover slip, SBs and also VBs optically disappear in the same way, perhaps due to a raised pH when the plasmalemma, including the membrane around the SBs, loses its semipermeability. Therefore, VBs and SBs can properly be studied only in living cells mounted in water or other non-lethal media such as aqueous CRB (see also p. 31, Conservation of vital characters). Future TEM studies will undoubtedly greatly increase our knowledge on SB ultrastructure but the risk for obtaining artifacts is high with this technique, unless modern methods of cryofixation by high-pressure freezing are applied which conserve turgescence of the cells and their organelles.

Staining of SBs in living spores. Staining by metachromatic basic dyes (CRB or TB) yields a selective, spectacular, deep blue to violet or in some species at first turquoise stain to the SBs due to accumulation of the dye, whereas the rest of the sporoplasm remains unstained (Fig. 66). The same result of selective staining is obtained with VBs in vegetative cells, and probably the mechanism of accumulation of the dye is the same (see also p. 90–92). Aqueous Methyl blue (CB_a) and Neutral red (NR) likewise selectively stain SBs in the living spores (deep blue or bright orange-red, respectively), whereas Methyl blue in lactophenol (CB_L) kills the spores and destroys the SBs by staining the sporoplasm (similar as in Fig. 66: f).

The membrane that surrounds the refractive matrix of the SB is undoubtedly semipermeable and might have a composition similar to that of the plasmalemma, or to the tonoplast of vacuoles. VBs differ from SBs in the absence of a connection to the plasmalemma, and in staining more greenish-blue (turquoise) even at high concentration of CRB (see p. 90–92). CRB stains lens-shaped SBs (Fig. 66: e) much more quickly (within about a second) in comparison with narrowly attached SBs (often only after several minutes). The reason for this is probably that the stain intrudes through the spore wall into the matrix of lens-shaped SBs without passing any plasma membranes, whereas the delayed staining of narrowly attached SBs is due to a retarded intrusion, either through the fine attachment or through two membranes, plasmalemma and SB membrane. Staining of VBs in living paraphyses and excipular cells is similarly delayed, and here the cause of delay is unquestionably the passage of plasmalemma and tonoplast.

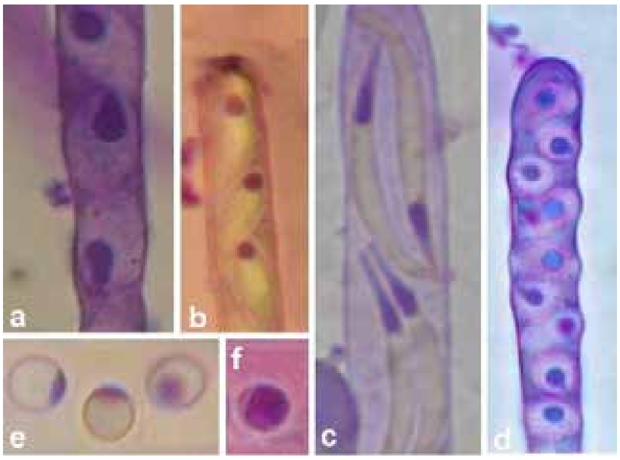


Figure 66: **a–e**. Living spores with spore bodies stained with Cresyl blue: SBs stain violet- to turquoise-blue, while the sporoplasm remains unstained; **f**. dead spore in KOH+CRB: SB remains unstained but sporoplasm stained deep purplish-violet. — **a**. *Orbilia arizonensis* (H.B. 8002a), **b**. *O. pilifera* (H.B. 8076a), **c**. *O. aurantiorubra* (phot. M. Hairaud, H.B. 8076b), **d**. *O. corculispora* (phot. J.P. Priou, J.P.P. 23138), **e–f**. *Lilapila oculispora* (H.B. 9162a).

SBs are formed by the invagination of the plasmalemma (see p. 74, Ontogeny of spore bodies). Therefore, the matrix of spore bodies is more or less exposed to the environment because it is mainly delimited by the spore wall but apparently not by a membrane. It is, therefore, possible that the SB matrix does not differ in its pH from the surrounding medium, and the accumulation of CRB in SBs could follow a mechanism different from that in vacuoles. However, the loss of refractivity of the SB matrix is probably due to a severe change in the pH inside the SB. SB refractivity gets irreversibly lost when destroying the semipermeability of the plasma membrane by applying acids or alkali, but also by applying heat or during long-term storage in the herbarium. This suggests some stabilizing influence of the intact enclosing membrane of the SB matrix on its refractivity and pH, or a closing membrane at the point of attachment.

Staining of living cells by IKI never caused a distinct accumulation of iodine in SBs, whereas VBs, particularly those in the *Helotiales*, frequently show a faint to strong red-brown reaction (Baral 1987b: 424, 1992: 364). VBs sometimes contain a pale to bright yellow or orange vacuolar pigment, whereas SBs are always hyaline. Moreover, hyaline VBs frequently turn yellowish to reddish-brown when the cells die, apparently through oxidation of phenolic compounds (Baral 1992). No such secondary pigment could ever be seen in dead spores of *Orbiliomycetes*.

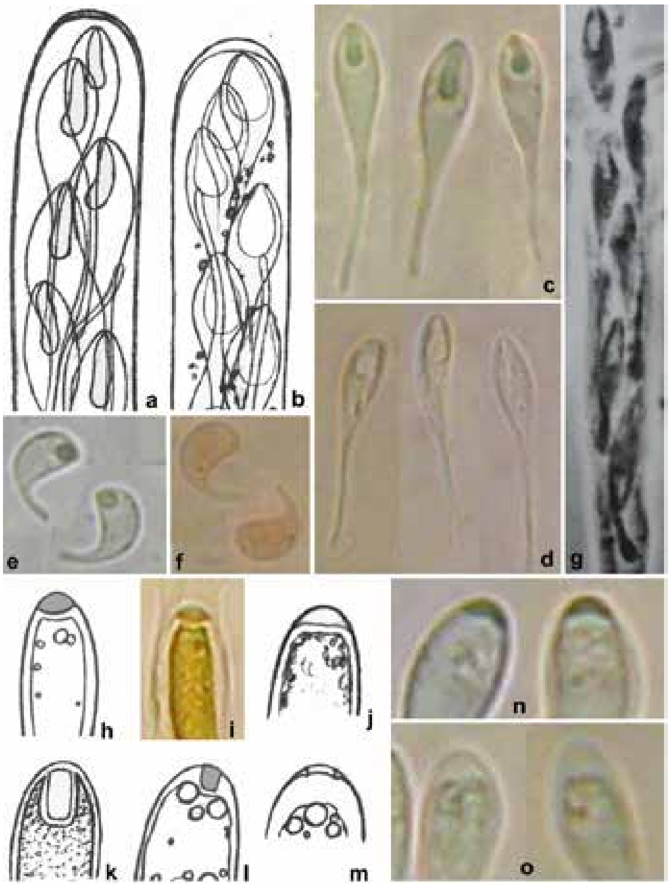


Figure 67: SBs in ascospores of *Orbilia* and *Amphosoma* in the living (**a**, **c**, **e**, **n**) and dead state (**b**, **d**, **f–m**, **o**); **f**. SBs invisible in the dead state; **b**, **d**, **j–k**, **o**. SBs remaining faintly visible; **h–i**, **l**. SBs remaining fully refractive; **m**. the SB has disappeared while a pore-like structure in the apical wall is visible. — **a–d**. *O. aristata* (**a**. H.B. 4156b; **b**. PRM 152468; **c**. PP 20071028, H.B. 7815b; **d**. H.B. 6992b, 5044a, 8359b; **e–f**. *O. myriomuscula* (H.B. 8697c); **g**. *O. flagellispora* (from Galán et al. 1994: fig. 68); **h–i**. *O. ocellata* (H.B. 5238, 9224); **j**. *O. lentiformis* (M, H.B. 5073); **k**. *O. cucumispora* (H.B. 5224a); **l–m**. *Amphosoma macrosporum* (H.B. 5181b); **n–o**. *O. patellarioides* (H.B. 9173a). — **a**, **c–e**, **h**, **j**, **m–o** in H_2O; **i** in IKI, **b**, **f** in KOH+CR; **k** in KOH+CB_L; **l** in lactophenol; **g** in MLZ (phase contrast).

The reason for the turquoise colour of CRB when accumulated in SBs or VBs is not fully understood. Possibly, chemical properties of the refractive matrix influence the colour of CRB (metachromatic effect) more than the pH of the water in the matrix does. The accumulation of CRB in SBs and VBs is not necessarily due to the ion trap mechanism of vacuoles: broadly attached (lens-shaped) SBs sometimes remain refractive although the spores are dead, and they were found to stain blue-violet irrespective of whether the spores are alive or not.

Shrinkage during osmosis. When adding a drop of high-concentrated sugar solution to a water mount that contains living asci and spores, not only the asci and spores shrink, but also the spore bodies. In *O. myriomuscula*, a shrinkage of the globose-ampulliform SBs by ~12–15% in both length and width was observed, resulting in ~30–40% volume decrease. This result demonstrates semipermeability of the SB membrane, and some kind of liquid nature of the refractive matrix. In the above sugar solution the width of a living ascus decreased by 18%. Observation of SBs in high-concentrated media is difficult, however, because of a strongly diminished contrast.

Spore bodies in dead spores. SBs are usually completely invisible in dead spores in any of the tested mountants (e.g., Fig. 67: f). However, in some species they could be seen as inconspicuous, non-refractive, transparent regions within the more refractive sporoplasm, sometimes in water mounts (Fig. 67: d), or when mounted in KOH, CR (Fig. 67: b), CRB, CB_L, phloxine, or MLZ (Fig. 67: g). This transparent region is not stainable by any of the tested staining agents. Despite a somewhat altered shape, the region clearly corresponds to the area of the refractive spore body. In water mounts the sporoplasm is more or less refractive and the transparent region of the SBs may sometimes be quite distinct by looking 'empty' (Fig. 67: d). Plasmatic stains, but also cell wall stains, preferably added to alkali-pretreated material, may sometimes improve the visibility of SBs in dead spores. Contrary to the living state, these dyes stain the dead, often somewhat granular sporoplasm (e.g., purplish-violet in CRB) whereas the region of the SBs remains completely unstained (Fig. 66: f). In cases of narrow or small SBs, however, often no trace of the previously so conspicuous SBs remains discernible, with rare exceptions (e.g., lectotype of *O. eucalypti*, Pl. 858: 1a).

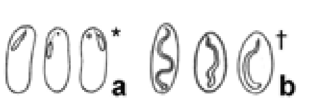


Figure 68: *Orbilia orientalis* (**a**. H.B. 7379, **b**. holotype), in H_2O: **a**. Living spores with short rod-shaped SBs with a delicate filum; **b**. dead spores with a worm-shaped helicoid structure of coagulated sporoplasm (SBs invisible).

In taxa with elongate SBs, the transparent region in dead spores is often shorter and wider than in living spores (see Fig. 67: a–d). This must be taken into account when comparing dead spores of one collection with living spores of another. A similar change in SB shape is observed when living spores get overmature (Fig. 70).

Our tests to preserve the refractivity of SBs in permanent slides or other voucher specimens were unsuccessful (see also p. 31, Conservation of vital characters). As a rare exception, however, some or all of the dead spores still contained SBs of the very same shape and refractivity as the living spores. This peculiarity was noted in some collections of species with broadly or narrowly attached SBs: *Lecophagus ellipsoideus* (Pl. 45: 2a), *Amphosoma macrosporum* (Fig. 67: l), *O. ocellata* (Fig. 67: h–i, see also Pl. 164: 3a), and *O. olivacea* (Pl. 806: 2a). Application of KOH irreversibly destroys refractivity of such SBs, and CRB stains them blue-violet similar as in the living state. Frequently, however, broadly attached SBs are low-refractive in the dead state (Fig. 67: j–k, o). In one case (*A. macrosporum*) the apical wall of a dead spore showed a pore-like aperture at the place where the SB was attached (Fig. 67: m).

The cytoplasm of dead spores is often coagulated by dehydration, showing an increased refractivity and a more or less strong detachment from the spore wall. In some cases the protoplast was so strongly dehydrated that it simulated SBs by forming rather regular, filiform, often flexuous structures. The effect was especially striking in the holotype of *O. orientalis* (Fig. 68: b). In many asci, all eight spores contained such a long, filiform, flexuous structure. However, undoubtedly conspecific fresh collections showed completely different, much shorter, rod- to tear-shaped SBs (Fig. 68: a). It can safely be concluded, therefore, that the observed filiform structure represents an artifact of the dead sporoplasm.

Ontogeny of spore bodies. In the course of spore maturation, SBs gradually increase in size and develop to their individual, species-specific shape. The ontogeny of SBs can rather easily be observed under the LM in living material (see the drawing of

Orbilia octosporoides, Pl. 793: 1a). A schematic representation of different SB types is given in Fig. 69. SBs develop very late in spore ontogeny, at a stage when the spores have attained their final size and shape. In comparison, LBs are usually formed much earlier, while at an early stage of development the spores are devoid of both LBs and SBs.

Those SBs which are apically narrowed to a point start as small dot-like initials. They either inflate to a broadly tear-shaped or globose drop (Fig. 69: b), or elongate more than they increase in width (Fig. 69: a), and such vermiform to subulate SBs sometimes exceed spore length by getting curled (helicoid or uncinate). Lens- and plug-shaped SBs start as similar initials, the former soon getting broader, the latter instead elongating (Fig. 69: c–d). SBs attain their maximum size and characteristic shape some time before the spores get dehydrated during ascus turgor increase.

In the course of SB development the refractivity of the matrix remains unchanged. Although SBs contain a liquid-like content surrounded by a delicate membrane, they have never been observed to show any migration during ontogeny when comparing different development stages, nor could any changes in their shape be seen whenever SBs in mature spores were monitored over a period of 5–10 min. When placing a water mount slide of an apothecial section in a moist chamber, SBs of immature spores inside living asci of *O. clavuliformis* were found to elongate for ~2–3 µm during about 1–2 days (e. g., from 1.5 × 0.8 µm to 4.5 × 1 µm).

As with LBs in spores of other groups of ascomycetes, SBs permit recognition of the development stage of living spores and consequently also that of living asci inside which they are found. When studying solely dead material, the question regarding spore maturity generally remains unanswered, i. e., it cannot be ascertained whether the observed spore characters (size, shape, septation, lipid contents) belong to immature, mature, or overmature stages (see p. 30, Recognition of maturity).

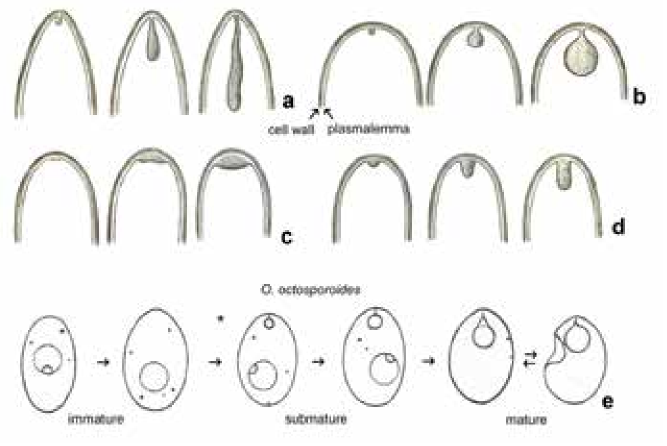


Figure 69: Schematic illustration of spore body ontogeny as seen with the LM in four different infrageneric groups of *Orbilia* (**a**. section *Habrostictis*, **b**. section *Ovoideae*, **c**. series *Lentiformes*, **d**. series *Microsomates*, **e**. *O. octosporoides* H.B. 5175b, section *Ovoideae*).

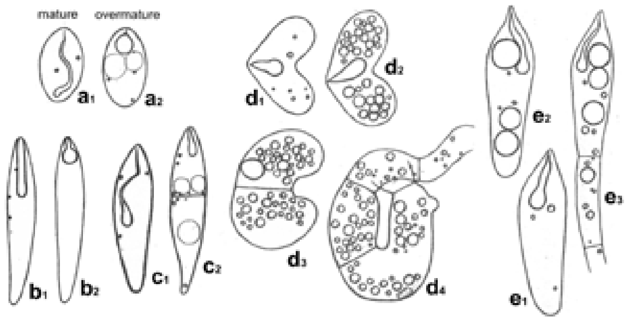


Figure 70: Mature (**1**) and overmature (**2**) ascospores observed in senescent apothecia (living state). SBs may change their size and shape before and during germination and LBs may increase in size. SBs often get shorter and wider (**a–d**), while lipid bodies sometimes strongly increase in size (**e**) and partly also in number (**d**). — **a–b**. from apothecia on the natural substrate, **c–e**. from apothecia kept at the lid of a Petri dish for some days. **a**. *Orbilia gambelii*: **b**. *O. vinosa*; **c**. *O. obtusispora*; **d**. *O. corculispora*; **e**. *O. carpoboloides*.

Spore bodies in overmature spores. At overmature stages a regression in the observed diversity of SB shapes is observed. Vermiform to subulate SBs, in particular, undergo severe changes during ageing. Often without noteworthy volume reduction, they become much shorter and thicker, i. e., broadly tear-shaped or even globose (Fig. 70: a–b). Only a short, more or less narrow apical part remains unaltered. These changes of elongate SBs are problematic because otherwise similar species may differ in showing consistently such short and thick SBs in mature spores. Examples are *O. vitalbae* – *O. caulicola* or *O. carpoboloides* – *O. pilifera*, the former of each pair with elongate SBs, the latter with globose SBs. Overmature spores often occur in collections, but can also be induced by incubation in a moist chamber. For instance, in *O. montigena* all short vermiform SBs changed to broadly tear-shaped in apothecia which were kept for a week inside a Petri dish. As a further complication, overmature spores with altered SB shape may exceptionally occur within the living asci. However, well-developed mature apothecia can be recognized by their abundant living mature asci that contain spores with SBs of a consistent size and shape. This conformity in SB shape allows to conclude that the spores are in a taxonomically reliable development stage.

When the spores germinate, SBs were observed to gradually decrease in volume until they completely disappeared (*O. corculispora* Fig. 70: d, *O. obtusispora* Fig. 70: c, *O. mesaverdiana* Pl. 673: 1a). Sometimes, however, SBs maintained their full size when germ tubes are formed (*O. carpoboloides* Fig. 70: e). LBs, on the contrary, may strikingly increase in number and size during germination in some taxa (Fig. 70: d–e, see also p. 89–90).

Cytological origin of spore bodies. Our light-microscopical and microchemical observations on spore bodies concentrate in the hypothesis that SBs are formed by invagination of the plasmalemma. Young SBs form a vesicle that increases in various, species-specific ways by genetic determination. From the beginning a substance of unknown composition is transported into the spore body, probably through the membrane of the young spore body. When inside the SB, the substance appears to change its chemical structure by becoming refractive.

As stated above, SBs behave very similar as vacuoles when treated with vital stains and lethal mountants. There is no doubt that both types of organelles are surrounded by a semipermeable unit membrane. Various TEM images have shown that vacuoles in general originate from small vesicles formed by invagination of the plasmalemma from which they finally separate. This process is related to endocytosis, by which cells absorb and engulf external substances (Weber 2002). In contrast to vacuoles, SBs remain attached to the plasmalemma, either broadly or by a more or less narrow point or filiform structure, for which spore bodies were considered to represent a special type of refractive vacuolar body (VB, Baral 1992: 363f., figs 34–37). The membrane that surrounds the large spore body of *O. vinosa* can be seen in Fig. 71: e as an electron-light line which at the spore apex clearly connects to the plasmalemma, suggesting an invagination process during SB ontogeny. TEM images of young stages of SB formation were not available, but our LM studies (Fig. 61) support this invagination process. Particularly when studying lens- to plug-shaped SBs in the dead state, the SB matrix is clearly seen as being located outside the detached sporoplasm Fig. 67: j–k, o, which is very obvious in the rare case when the matrix remains refractive (Fig. 67: h, l).

In SBs with a filiform upper part, the latter rarely enlarges like a funnel at the point of attachment (Fig. 59: a) which looks like an invagination. The filum is probably a very narrow tube composed of invaginated plasmalemma. Although lens-shaped SBs appear to be very different from those with a filiform part, the intermediate plug-shaped type (*Amphosoma*, Fig. 60: b; *O. cucumispora*, Pl. 179; *Orbilia series Microsomates*, Figs 63: b; 69: d) indicates that all types of SBs in the many groups of *Orbiliomycetes* represent a homologous structure that is formed by the same ontogenetic principle. SBs appear to be formed similarly as vacuoles, but the process of invagination never appears to result in a complete detachment from the plasmalemma. The more or less constant length of the filiform part suggests a connection of the SBs to the spore wall even in those species in which this connecting part is close to, or below the recognition limit of the light microscope.

SBs represent an extraplasmatic, sac-like organelle which contains a refractive hydrophilous substance. Whether SBs show a higher, equal, or lower osmotic pressure in relation to the surrounding sporoplasm is unclear. Probably the membrane around SBs is semipermeabile and elastic, because SBs shrink osmotically by water extraction (see p. 74, Shrinkage during osmosis). The ontogenetic similarity between SBs and vacuoles (including VBs) allows to speculate about a phylogenetic relationship between both organelles, and to consider SBs as a specialized type of vacuoles.

Literature reports of spore bodies based on LM observations. Despite their conspicuousness, reports of SBs, particularly those with a distinctly elongate shape, are extremely rare in the literature older than about 25 years. This is astonishing, because already 100–150 years ago light microscopes had a quality that permitted to resolve microstructures of < 0.5 µm diam. This quality is impressively demonstrated, e.g., by Patouillard's (1892b) microscopic drawing of subulate SBs in *Orbilia serpentina* (see Fig. 151: 1). That most workers of the 20th century failed to see SBs and consequently often also the inverse spore orientation, is a logical consequence of the prevailing method of herbarium taxonomy, besides the practice of applying too much pressure on the cover slip, or mounting fresh specimens in lethal solutions in order to obtain compatible results.

Although elongate SBs occur in a vast number of species, they have been reported in the older literature only in three desiccation-tolerant mediterranean species (*O. serpentina*, *O. hesperidea*, *Hyalinia ulicis*, see Fig. 151). Patouillard (1892a) described them as 'masses virgultiformes de protoplasma, réfringentes' (= rod-shaped refractive material of protoplasm). Rolland (1901) referred to them as 'gutta ovali', and Chenantais (1918) as 'guttula cylindrica nitenti sursum praedita' (= provided with an apical cylindrical shining guttule). Saccardo (1899: 802) even refrained from mentioning these bodies in his shortened diagnosis of *O. serpentina*, perhaps because he doubted their nature. He stated only 'sp[oris] intus granulosis' and the asci to be 8-spored, although the number of SBs drawn by Patouillard clearly indicates that the asci are 16-spored. Later, Saccardo & Sydow (1902: 767) and Saccardo et al. (1928: 1238) mentioned spore bodies when quoting the diagnoses of *O. hesperidea* and *H. ulicis*.

Ade (1924) described the polysporous species *O. paradoxa* with an apical 'spot-like' SB in each spore, but did not supply an illustration (the species is probably a synonym of *O. flavida* which has lens-shaped SBs). On his unpublished manuscript plates, Velenovský once (1925) illustrated subulate SBs in *O. sarraziniana* (as *O. luteorubella*, Fig. 156: b). The author possibly later doubted his observation, as he did not figure elongate SBs in any other specimen of *Orbilia*. SBs of a globose to ellipsoid shape have rarely been reported and figured in some species (usually as 'guttules'), e.g., in *O. comma* (Graddon 1977: fig. 17). The cytological difference between these and the associated, mostly smaller lipid bodies (LBs) was obviously unknown to all these authors.

TEM-studies of spore bodies. Obviously unaware of previous reports with the LM, Benny et al. (1978) found using transmission electron microscopy (TEM) in the mature ascospores of *Orbilia sarraziniana* (as *O. luteorubella*) an elongate, thick, electron-dense, membrane-bound structure of strong contrast and a length of up to three fourths of the entire spore, being attached to the inner wall at the acute, slightly acuminate spore end (Fig. 71: a). Since the function of this structure remained enigmatic, the authors applied the term 'spore body' as a neutral circumscription of the extraordinary organelle. In shape and contrast the organelle fully corresponds to the structure seen by us under the light microscope in living spores of that species.

The preparation procedure applied by Benny et al. (l.c.) comprised fixation in glutar-/paraformaldehyde and osmium tetroxide, and staining in uranyl acetate and sometimes also silver-methenamine. For examination under the LM, Benny et al. mounted their sections in CB_L, although they were dealing with a fresh collection. Obviously, the authors were unaware of the optical disappearance of SBs provoked by the freezing procedure in a cryostat and mounting in lactophenol Cotton blue, and believed that these structures can only be seen with the TEM. Whether the applied TEM fixation method maintains the exact ultrastructure of SBs is unclear. It appears possible that spore bodies as seen on TEM micrographs are comparable with non-refractive SBs in dead spores under the LM. SBs appear to receive high contrast under the TEM because their matrix, although having lost its refractivity, is selectively enhanced by the applied stains. Modern cryofixation methods are recommended here to avoid possible artifacts.

Benny et al. (l.c.) could not determine the function of spore bodies. On the basis of their TEM micrographs they came to the conclusion that SBs originate from mitochondria. The authors found SBs to become more and more opaque during spore maturation, being finally filled with a uniform, comparatively electron-dense material which showed a slight inhomogeneity (named 'cristae' by Benny et al., see their fig. 14). A membrane surrounds the spore body, but the authors did not state whether it was a double membrane typical of mitochondria. On their fig. 11 they reported rough endoplasmic reticulum in close contact

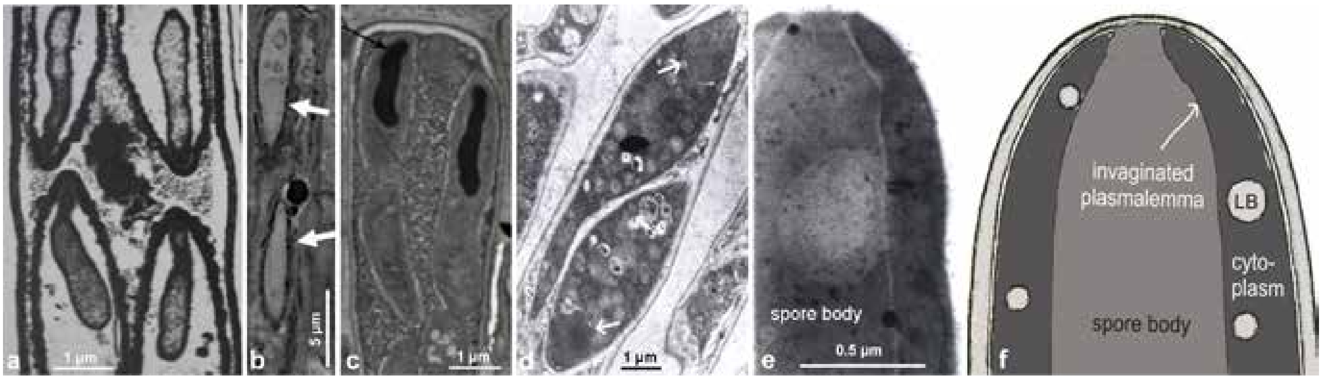


Figure 71: Ascospores with spore bodies as seen under the transmission electron microscope (TEM, arrows in **b** and **d** point to SBs). — **a**. *Orbilia sarraziniana* (Benny et al. 1978: fig. 17, as *O. luteorubella*); **b**. *O. sarraziniana* (Liu 2006: fig. 1D); **c**. *O. tenuispora* (Kumar et al. 2012: fig. 3, as *Orbilia* sp.); **d**. *O. aristata* (Müller 1998: fig. 21A); **e**. *O. vinosa* (Müller 1998: fig. 21B, spore apex); **f**. schematic representation of **e**. – Particularly **e** suggests that the SBs are formed by invagination of the plasmalemma as an extraplasmatic organelle remaining attached to the apical spore wall.

to the spore body. The spore wall was said to mature first at the spore apex by forming a distinctly thicker wall (as 'apiculus', see their figs 11–12), whereas the rest of the wall was said to attain this thickness at a later stage.

The connection between SB and spore apex is very clear on their fig. 17 (Fig. 71: a), but absent or only slightly perceptible in those micrographs at higher magnification. The reason for this is easily explained by the rather narrow connecting part which is difficult to hit in microtome sections. Since the spore inclusion is rather long in all of the micrographs presented by Benny et al. (l.c.), all these undoubtedly refer to more or less mature spores in which the SBs have attained their maximum length, contrary to the author's belief in different development stages. Benny et al. also stressed a close association between SB and nucleus. We consider this as a result of the length of the SBs and the narrow spore width. In species with wider spores and shorter SBs the nucleus is usually found a good distance away from the spore body (Fig. 93).

Liu (2006: 22, pl. 1 figs C–D) investigated asci and spores of *O. sarraziniana* with the TEM (see Fig. 71: b). The SBs are surrounded by a thin but distinct grey line, and their matrix appears almost as light as the sporoplasm. His TEM-procedure was very similar to that applied by Benny et al. (B. Liu pers. comm.).

Kumar et al. (2012) investigated another species of section *Helicoon* which, according to their molecular data, belongs to *O. tenuispora*. In their micrographs the SBs are shown as highly electron-dense (black) structures in the light grey sporoplasm (Fig. 71: c). Also Kumar et al. applied about the same fixation and staining procedure as Benny et al. (without silver-methenamine). The authors observed a mitochondrion at the apex of young spores which was later replaced by a spore body (A. Kumar pers. comm.). This was interpreted as a support for a mitochondrial origin of SBs (Kumar et al. 2012), a view followed by Pfister (2015).

Benny et al. (1978) and Kumar et al. (2012) did not study living spores under the LM, therefore, they overlooked that SB formation starts as a very small vesicle directly at the inner side of the apical wall of immature spores (Fig. 69). Such development of a gradually growing organelle is hardly concordant with the theory of a derivation from mitochondria, hence we are convinced that mitochondria do not directly develop into SBs. This was also the conclusion of Müller (1998) who applied a procedure similar as the above (without silver-methenamine) in his TEM-study on the ultrastructure of asci and ascospores of *Gyalectales* (*Ostropomycetidae*) and *Orbiliomycetes*.

Müller (l.c.) investigated three orbiliaceous species: *O. vinosa*, *O. aristata*, and *O. xanthostigma*. The two former taxa are representatives of section *Hemiorbilia*. Here the SBs are clearly visible as large, light grey areas within the more opaque sporoplasm (Fig. 71: d–e). They are surrounded by a thin transparent membrane and are broadly attached to the primary wall at the spore apex. The sporoplasm is completely absent at the place of attachment, where the spore body forms an aperture that is directly connected to the primary wall. At the place of attachment the lateral membrane of the spore body appears to merge with the plasmalemma, which would confirm the formation of SBs by invagination of the plasmalemma. However, Müller saw in *O. vinosa* at the place of attachment a thin membrane that seems to separate the SB matrix from the primary wall, and he could not exclude the possibility that this membrane is part of the plasmalemma.

Function of spore bodies. The chemical nature of the SB matrix is quite unknown, and about their function we can only speculate. The hypothesis that SBs are formed by invagination of the plasmalemma and their behaviour under staining indicate that they could have derived from vacuoles.

Benny et al. (1978) considered three possible functions of SBs: '(1) flotation and balance [of the spore] in a liquid environment before and during germination, (2) storage of waste products, and (3) storage of materials for use during germination'.

Possibility (1) implies a different, perhaps higher specific weight of the SBs. This seems to be confirmed when observing ascospores floating in a water mount. We have repeatedly seen that elongate spores of *Orbilia* tend to point with the spore apex downwards. However, this observation refers in part to spores with a slight or strong heteropolarity in shape, the widest part being nearer to the spore apex. Therefore, the observed effect might not only depend on the presence of a spore body. An interesting effect, though only rarely seen, was the adherence of the spores to large air bubbles (Fig. 72): the fusoid-clavate spores in the two species *O. mali* and *O. obtusispora*, in which the effect was so far observed, consistently adhered with their obtuse to subacute, SB-containing apical ends to the air bubble. The phenomenon might be explained by some difference in hydrophily between apical and residual spore wall. The rarity of the effect did not allow further experiments, e. g., whether it depends on the living state, or whether it vanishes when applying a detergent.

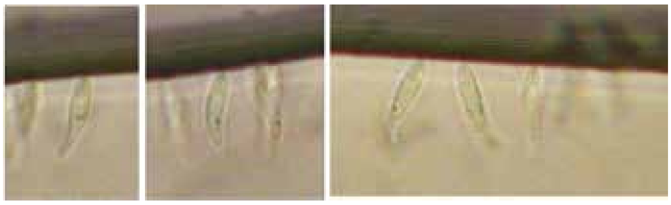


Figure 72: Living ascospores of *Orbilia mali* in water, adhering with their apex to a large air bubble.

Possibility (2) is not much convincing, since the body is so universal in the *Orbiliomycetes* and here completely restricted to the ascospores, that it is difficult to understand why other ascomycetes survive without such a structure. Concerning possibility (3) we must consider that storage products such as lipid and glycogen are not state-dependent, i. e., their presence can also be demonstrated in dead spores mounted in KOH (LBs), or by staining in MLZ (glycogen). In most of the species, SBs occur strictly at the spore apex, which is not that part of the spore where germination usually takes place (Fig. 70). With possibilities (2) and (3) the question remains open why the position of SBs is so fixed within a species, and why SBs remain connected to the plasmalemma.

The remarkably high refractivity of SBs during all stages of their development seems to suggest a metabolic substance that is accumulated within the organelle without undergoing further changes once it is transferred there. The fact that basic dyes accumulate within SBs does not necessarily indicate a more acidic pH inside the organelle. Unlike vacuoles, SBs seem to represent an open system connected to the environment by their attachment, although this connection might be closed by a membrane or plug. In any case, the sudden loss of refractivity when the spores die by mechanical influence strongly resembles refractive vacuolar bodies (VBs) in vegetative cells. The refractivity of VBs possibly originates from phenolic compounds which are known to lose their double bindings when the pH of the vacuoles increases (see p. 92).

Kumar et al. (l.c.) thought that the dense staining of SBs in basic dyes, such as Toluidine blue O, suggests that they might contain RNA, but it seems the authors did not take into account a vacuolar nature of the organelle.

The high morphological diversity of SBs that has evolved in the various taxa argues for a function important to the survival of the fungus. The predatory capabilities of some *Orbiliomycetes* tempted us to speculate that SBs might function as some kind of poison vial, whose contents paralyse small invertebrates when ingesting the ascospores. Another function might be in attracting animals in order to get swallowed from the apical spore end. A number of species of *Orbilia* with a peculiar ascospore shape support this idea, which implies that spores infect invertebrates via the ingestion tractus (see p. 144–145).

The long and filiform, flexuous and basally hooked SBs of many species of subgenus *Habrostictis* resemble somewhat the nematocysts of *Cnidaria* (medusas and polyps), or the injection (gun) cell of *Haptoglossa*, an endoparasitic oomycete that attacks rotifers (Barron 1980). However, the spore body of *Orbiliomycetes* is a soft and compressible structure surrounded merely by a cytoplasmic membrane, and there is no indication that SBs emerge as a whole through the spore apex.

The hypothesis that SBs might paralyse or poison motile organisms would shed some light on the high diversity in SB morphology among the taxa. The two main characteristics of SB shape are: (1) volume, and (2) ratio between surface and volume. There seems little doubt that these two parameters play some role in the life cycle of these fungi. The same two parameters are observed regarding the lipid content of living spores: number and size of globose LBs determine (1) the amount (total volume) of lipid and (2) their surface:volume ratio. The hypothesis is here that many small LBs are more rapidly degraded, whereas a few large LBs enable storage of higher amounts of lipid in a spore (Baral 2015: 284).

Undoubtedly, SB shape is genetically controlled. The simplest shape appears to be a sphere with a short apical connection, or a lens-like body. The stability of such a simple structure might be controlled by a slight difference in turgor, or by membrane properties. SBs with a more complex shape possibly need more elaborate membrane properties to stabilize their shape. Elongate SBs would then change to a globose shape in overmature spores by reducing the stabilizing properties of the membrane.

Vesicles found in trapping organs of *Orbiliomycetes* are thought to contain enzymes for the consumption of trapped invertebrates (see p. 116, 120). Although their size of ~0.1–0.3 µm should permit recognition under the LM, these organelles could not with certainty be seen in living traps. Possibly, their contents show only little refractivity though appearing electron-opaque in TEM micrographs.

Transient plasmatic inclusions in spores of non-orbiliaceous fungi. Despite a thorough search with the LM for spore bodies in numerous species of *Helotiales* and other ascomycetes, corresponding organelles that might be homologous have only very rarely been detected.

Globose refractive bodies of a similar behaviour upon treatment by KOH or CRB have been found in a few quite unrelated ascomycetes, for instance in the multiguttulate ascospores of a *Phaeohelotium* (as *Hymenoscyphus* cf. *sazavae*) and *Tubeufia paludosa* (Baral 1992: figs 34c, 35a), or in the multiguttulate conidia of *Symphyosirinia* (Baral 1994: figs 50–52, 63). The majority of droplets inside these propagules can be classified as vacuolar bodies (VBs). They disappear when KOH is added, and stain bright turquoise under vital staining with CRB, whereas adjacent, morphologically identical droplets (LBs) are KOH-resistant and not stained blue in CRB. In contrast to SBs of *Orbiliomycetes*, these VBs occur scattered inside the whole spore, with a variable distance to the spore wall.

The ascospores of '*Discinella*' *schimperi* possess two very large refractive VBs which touch the lateral wall but not the two spore ends (Fig. 73: a). This peculiar inclusion was also documented by Navashin (1888, tab. XV fig. 13, as 'biguttulate'). Similar as with SBs of orbiliaceous taxa, refractivity of these organelles is unstable in lethal agents such as IKI or KOH. Vital staining with CRB was not tested, but they might well be akin to SBs in their ultrastructure and chemistry. Although such big refractive spore vacuoles are very exceptional within the *Helotiales*, the presence of an amyloid ascus apical ring suggests a relation to this order, and in a phylogenetic

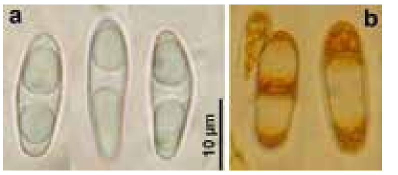


Figure 73: Ascospores of '*Discinella*' *schimperi* (H.B. 9386). — **a**. living state in water: two big refractive vacuoles (VBs) occur in each spore; **b**. dead state in IKI: the VBs instantly disappeared upon staining with IKI.

analysis of bryophilous ascomycetes (Stenroos et al. 2010) it clustered in a clade with, e. g., the genus *Pezoloma*.

Zhuang (1988: 93) reported for the globose ascospores of *Parencoelia myriostylidis* (*Helotiales*) a 'refractive equatorial plate' across the centre of the 'young' spore which disappeared upon treatment with KOH. This structure was observed in the nearly 100 years old type material and seems to be a feature of high consistency, as Zhuang depicted it in all 8 spores within an ascus. Vital studies should be performed to clarify the nature of this structure.

An interesting single, eccentric, refractive body (referred to as 'oil drop') reminiscent of SBs of *Orbiliomycetes* was described and figured by Barron (1985, 1991a) inside the conidia of several species of *Rotiferophthora* (in 1985 as *Diheterospora*). Since this genus of mitosporic fungi is predacious on rotifers and shows a diversity in conidial shape comparable to ascospore diversity in *Orbiliomycetes*, *Rotiferophthora* seems to be a candidate for a phylogenetic relationship to *Orbiliomycetes*. However, conidiogenesis is phialidic, and molecular data of two species demonstrates the group to belong to the *Clavicipitaceae* (*Hypocreales*, Sung et al. 2007), and particularly near another anamorph-typified genus, *Pochonia* (= *Diheterospora* s.str.), which preys on nematodes and has teleomorphs in *Cordyceps* (Zare et al. 2001). Regrettably, the bodies in *Rotiferophthora* conidia have not been tested with KOH or CRB (G.L. Barron in litt.), and cultures of two species kindly sent to us by S. Glockling did not produce conidia.

De Bary bubbles. When dealing with herbarium material, spores with thick rigid walls often contain eccentric, globose, refractive inclusions which represent a gaseous phase that originates from drying of the specimens. The bodies play a role in the desiccation tolerance of fungal cells, and are referred to as de Bary bubbles (DBBs, Ingold 1956, Dodge 1957). Due to the rather thin spores of *Orbiliomycetes* which collapse when drying out, DBBs do not occur in this class.

The presence of DBBs strongly depends on the method: DBBs are consistently absent in living specimens mounted in water. They are induced either when drying the specimen, or when adding dehydrating solutions (e. g., MLZ, lactophenol). When rehydrating dry living spores in water DBBs rapidly disappear, whereas when rehydrating dead spores they do not disappear (Baral 1992: 373). Uncritical reports of DBBs may, therefore, cause taxonomic confusion. For example, *Helotium zamurense* (≡ *Ascophanus zamurensis*) was described and illustrated as having ellipsoid ascospores with a single globose, eccentric guttule (Patouillard & Gaillard, 1889). Together with the reddish-orange apothecia the taxon resembles an *Orbilia* of section *Ovoideae*. However, the transfer to *Ascophanus* (*Pezizales*) by Svrček (1974), who saw this 'highly refractive large bubble' in some spores of the type, suggests that the bodies were DBBs.

Phylogeny of spore bodies. SBs are to be considered as a synapomorphy for the *Orbiliomycetes* in comparison with other classes of *Ascomycota* (Pfister 2015), because of their unique and almost consistent occurrence in all eight recognized genera with a known teleomorph. The high diversity in SB shape allows, in correlation with other characters, to speculate about phylogenetic lineages, along which SBs might have evolved. The phylogeny of SBs appears to follow two main parameters of storing the refractive substance under the premise of a constant volume occupied by this substance. (1) One parameter concerns the relation between surface and volume of the SBs: many taxa tend to increase the SB surface which results either in strongly elongated and curved SBs or in flattened SBs, whereas many other taxa minimize the SB surface which leads to tear-shaped or globose SBs. (2) The other parameter concerns SB attachment: taxa either tend to keep the width of the apical connecting part small, so that often only a very thin channel (the filum) remains, or they tend to have a wide connecting part, i. e., more or less broadly attached SBs.

Based on the hypothesis that vacuoles with a refractive content represent the evolutionary origin of SBs, the globose type with a short and narrow attachment should constitute the most primitive and ancient type of SB, as this would closely resemble a young vacuole which is yet attached to the plasmalemma. Two main evolutionary lineages would have evolved from the globose type of SB (Fig. 74). In one lineage the SBs tend to increase their width of attachment up to almost spore width, which leads to lens-shaped SBs; this SB type is typical of *Lilapila*, *Amphosoma*, *Pseudorbilia*, and *Orbilia* series *Lentiformes*. In the other main lineage the SBs tend to elongate, sometimes up to more than spore length, which leads to long, subulate to vermiform, often flexuous to curled SBs which are typical of sections *Habrostictis*, *Helicoon*, and *Aurantiorubrae* p.p. of the genus *Orbilia*. In both lineages the surface:volume ratio is strongly increased. Yet, only in the first lineage the entire SB surface borders on the cytoplasm. Judging from the consistent shape of SBs within a species, it can be concluded that these different parameters and also the absolute volume of SBs play a role in regard to SB function.

Another parameter concerns the number of SBs within a spore. The here presented phylogeny postulates that the multiguttulate spore with a bipolar arrangement of the up to about ten SBs per spore, which is typical of many species of *Hyalorbilia* and the monotypic *Bryorbilia*, represents the most ancient character state, i. e., a plesiomorphy within the *Orbiliomycetes*. This hypothesis presumes that the evolutionary direction was mainly characterized by a reduction in the number of SBs, which led at first to two SBs, one at each spore end, which is a characteristic pattern in the spores of *Amphosoma* and *Pseudorbilia*. In the large genus *Orbilia* the SB number was reduced to a unipolar arrangement with only one SB, which is usually situated at the spore apex, but the unipolar SB arrangement also occurs in a few species of *Hyalorbilia*. The direction of the evolutionary process from two SBs towards one can be assured by the rare observation in some species of *Orbilia* subgenus *Lentiformes* and section *Hemiorbilia*, in which a few (perhaps 1 %) aberrant spores with two SBs were sometimes seen, one at each end (Fig. 60: c–d). These aberrant spores appear to represent a regression to an earlier character state of SB arrangement, although the common ancestor of the

Figure 74. Hypothetical phylogeny of the spore body in *Orbiliomycetes*.

genus *Orbilia* is assumed to have already possessed spores with a unipolar SB arrangement.

An alternative hypothesis would consider the lens-shaped SBs as plesiomorphic, a view being supported by the fact that such SBs occur coupled with primitive ascus characters (hemispherical, often thick-walled apex), sometimes also with a bipolar arrangement of the SBs and with dark-coloured apothecia. Two presumably primitive features, lens-like shape and bipolar arrangement, are established in *Amphosoma* and *Pseudorbilia*, a small group of species growing predominantly on coniferous substrate, a phylogenetically old group of host plants.

Paraphyses

General remarks, **ontogeny**. In hymenia of mature apothecia the paraphyses generally occur with an equal abundance as the asci. When viewing under oil immersion in top view on the surface of the apothecial disc (water mount, living state, unsquashed), the distribution of asci and paraphyses is best seen. Especially in *Hyalorbilia* this is easy to observe due to the rather thin and translucent apothecia of that genus, and the wide, apically scarcely inflated paraphyses that contain pale chlorinaceous vacuoles (Fig. 75: a). Literature reports of sparse paraphyses usually refer to dead or overmature material in which the paraphyses are sometimes difficult to see, whereas reports of sparse asci refers to submature apothecia. The addition of IKI facilitates distinction between asci (which usually stain red-brown) and paraphyses (which remain unstained, Fig. 92).

As a common feature of most hymenium-forming ascomycetes, the paraphyses emerge from the vegetative hyphal system of the medullary excipulum separate from the ascogenous hyphal system. Due to the absence of a dikaryon in paraphysogenous hyphae, these never have croziers at their septa. As an exception, ascogenous cells in *Lophodermium* (*Rhytismatales*) are formed from anastomosing basal cells of paraphyses (Stephan 1971, Morgan-Jones & Hulton 1979).

The apices of paraphyses provide a valuable character at the species or higher level. However, their characteristic shape develops rather late in the ontogeny of an apothecium. Therefore, mature apothecia are required in order to properly estimate paraphysis characters. If only a few mature asci are found in a hymenium, the paraphyses have usually not yet developed their typical shape. Even in mature apothecia there are still some paraphyses to be found which are rather young; they are apically narrower and a bit shorter than the mature ones and should, therefore, be disregarded in descriptions.

The hymenium of young apothecia in the prohymenial phase merely consists of paraphyses, while the young asci are formed in the mesohymenial phase (see p. 37, Apothecial ontogeny). The hymenium is formed during the early prohymenial phase, thereby the paraphyses elongate and remain apically undifferentiated for a long time. They are early septate and often also branched at the base. Anastomoses between adjacent paraphyses are already present near the base. When the first asci are about to reach maturity, the paraphyses develop their typical characters: apices become swollen or beaked in some of the species, branching may extend to the upper part, also anastomoses sometimes occur more upwards, and cell contents (LBs, VBs, SCBs) appear or increase in size.

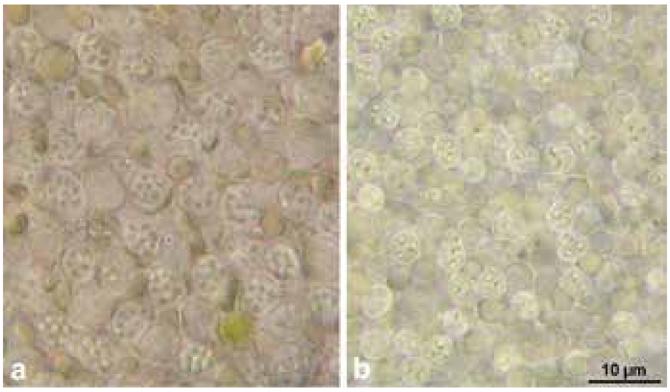


Figure 75: Hymenium of *Hyalorbilia* and *Orbilia* in top view (optical cross section, living state), showing mature asci (containing spores) intermingled with paraphyses (with pale chlorinaceous contents). — **a**. *H. juliae* (H.B. 7930, asci containing 8 spores in a parallel bundle); **b**. *O. luteorubella* (H.B. 9633a, spores in superimposed bundles, therefore only 3–4 spores visible).

Size and shape of apex. Although the lower parts of the mature paraphyses have a rather uniform thickness within the *Orbiliomycetes*, ranging at ca. *(1–)1.5–2.5(–3) µm, the width of the apex may vary considerably between taxa, ranging from *1.5–3 up to 3–5 or sometimes 6–8 µm.

Paraphysis apices have formerly been thought to provide a key character of the genus *Orbilia*. However, only about 40% of the species possess a more or less abruptly swollen, medium to strongly capitate (knob-like) or more gradually inflated (clavate or spathulate) apex which sometimes carries a beak on its top. The inflated knob-like apical part thereby has a diameter about two to four times of the lower part. The uninflated lower part shows in some groups a tendency to be narrowest directly below the inflated apex (often observed in section *Helicoon* and series *Orbilia*). In further ~30% species of *Orbilia*, medium to strongly capitate or clavate paraphyses occasionally occur besides the prevailing not or slightly inflated ones. Apically inflated paraphyses occur mainly in species with truncate thin-walled ascus apices, but even here they occur only in about 85% of the species.

Capitate to clavate paraphyses are more or less typical of sections *Habrostictis*, *Helicoon*, *Ovoideae*, and *Arthrobotrys*, and of series *Ovales*, *Aurantiorubrae*, and *Orbilia*, and also occur in some species of series *Lentiformes* and *Phanosomates*. Within each of these groups, paraphyses vary between slightly and strongly capitate, particularly when comparing different species (see Fig. 76, Tab. 62).

Eight small, more or less distant series within *Orbilia* (*Habrostictis*, *Regales*, *Abutilones*, *Albovinosae*, *Microsomates, Piliferae, Rubellae, Xanthoguttulatae* p.p.) are characterized by apices of a predominantly spathulate or even lageniform to mammiform (papillate to beaked) shape, and also some other series contain a few species with such paraphyses, e.g., *O. rhamni* and *O. fraxini* (series *Neodactylella*) or *O. anigozanthi* (series *Gamsylella*). However, paraphysis shape is rather variable within a species, e.g., apical beaks are not consistently present. Moniliform apices are taxonomically quite unreliable, as they occur only sporadically, mainly in species with capitate paraphyses with short terminal cells. In a few species of sections *Arthrobotrys* (*O. blumenaviensis*, *O. alba*) and *Orbilia* (*O. minutispora*, *O. guyanensis*, *O. umbilicata*, *O. spirospora*) the paraphyses are more or less lanceolate, showing gradually attenuated, obtuse to subacute apices. However, a sharp line between lanceolate and lageniform cannot be drawn.

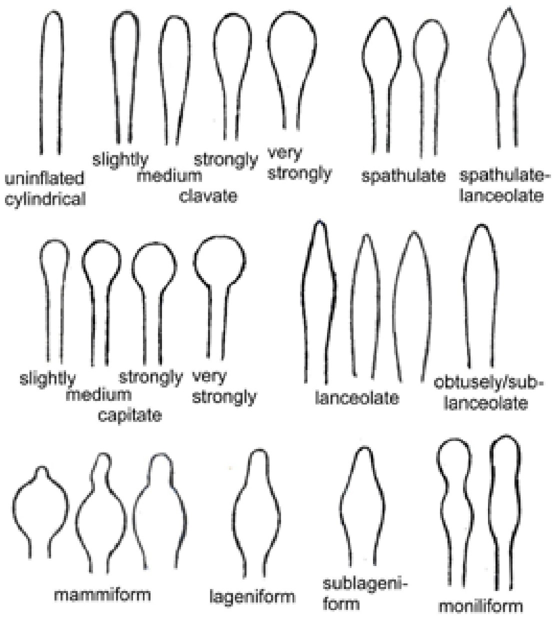


Figure 76: Different shapes of paraphysis apices in *Orbiliomycetes*.

The majority of species of *Orbilia* subgenus *Hemiorbilia* have paraphyses with more or less uninflated apices. Predominantly uninflated paraphyses are also typical of the genera *Hyalorbilia*, *Pseudorbilia*, *Lecophagus*, and *Lilapila*, whereas in *Liladisca* and sometimes also in *Amphosoma* (*A. macrosporum*) they are distinctly capitate.

Protrusion beyond asci. The tips of paraphyses are usually a few micrometres longer than the asci. However, when an ascus attains full turgescence, it usually protrudes above the paraphyses (Fig. 45). This is particularly the case in *Orbilia*, while in *Hyalorbilia* the asci at full turgescence are often more or less equal with paraphyses. Observations on protruding paraphyses or asci greatly depend on the living vs. dead state: upon adding lethal mountants, living asci shrink in length to a higher extent than paraphyses do. At moderate turgescence, asci of *Orbilia* are often slightly overtopped by the paraphyses, and even more strongly so in the dead state. However, in some cases the difference in protrusion between the living and dead state was not very clear, perhaps because the paraphyses shrink to a similar extent (e. g., in *O. pilifera*).

Remarkable protrusion beyond asci is mainly observed in paraphyses with a lanceolate or spathulate to lageniform or mammiform shape. Here the tapered or beaked apical parts protrude for 1–10 µm beyond the mature but not fully turgescent asci, resulting in a finely rough surface of the hymenium. Yet, a similarly strong protrusion occurs within series *Vibrioides* in which the paraphyses are rather undifferentiated.

Function of the apices of paraphyses. The capitate type of paraphysis apex may be mistaken as a glandular cell that excretes gelatinous or solid exudate. Yet, on the contrary, a rather strong trend can be observed in paraphyses with inflated apices showing diminished excretory activity, a correlation also observed by Velenovský (1934: 91). Thick clods of exudate are usually found over not or only slightly inflated apices, and are typical of, e. g., series *Microspermae* and section *Hemiorbilia* (Fig. 95: g), whereas capitate apices have generally low amounts of exudate, or even more or less completely lack exudates (e. g., various members of sections *Habrostictis*, *Helicoon*, and *Orbilia*, Fig. 95: h). Concerning excretion of gel, a similar negative correlation is exemplified by the genus *Hyalorbilia*, which is characterized by a continuous layer of thin granular exudate and a cohesive gelatinous matrix below, in which the usually more or less uninflated paraphyses are embedded (Fig. 95: d), whereas species of *Orbilia* with or without inflated apices have low amounts of gel around. The excretion of thick exudate from paraphyses with variable apical inflation (from uninflated to strongly capitate) is frequent in section *Ovoideae*.

Capitate apices of paraphyses occur fairly often in desiccation-sensitive species, but they are also typical of about 50 % of the desiccation-tolerant species. One of the functions of capitate apices might be to retain evaporation, i. e., to reduce water loss from the hydrated intercellular system of the apothecium. Undoubtedly, the tightly packed heads of paraphyses serve as some kind of protection of the young asci. They form a coherent layer, with more ore less small amounts of gel and exudate filling the minute gaps between the globose heads, thereby leaving only small openings for the ascus tips. These openings are widened when the asci attain full turgescence. However, cell walls are rather freely permeable for water, hence capitate apices cannot virtually prohibit dehydration. It can even be doubted that capitate apices of desiccation-tolerant species retard water loss at all. Among the desiccation-sensitive species, closely related taxa sometimes significantly differ in the strength of apical inflation. Thus, the function of capitate paraphyses remains unclear.

The ability to condense atmospheric humidity might be important, particularly for desiccation-tolerant taxa. We suppose that paraphyses with beaked or lanceolate apices and those with exudate caps (Fig. 91: i–l), as well as protruding cylindrical paraphyses in multispored taxa of series *Vibrioides*, favour condensation, and also the rough surface of exudate might assist condensation. Water that precipitates on a dry hymenium is rapidly soaked up by the hydrophilous exudate and rehydrates the cytoplasm of the collapsed cells beneath.

Septation. Paraphyses of probably all groups of sporocarp forming *Pezizomycotina* have septa, at least near the base, although drawings in publications often omit them. Septa are overlooked because they are difficult to discern in dead herbarium material unless cell wall stains are used (see p. 9). Some authors (e. g., Velenovský, see Fig. 154) have drawn septa of paraphyses quite arbitrarily. In most instances, septa become clearly visible in a squash mount of KOH to which Congo red (CR) is added, but in some cases even this method did not help. Cytoplasmic stains (IKI, CRB, CB_L, phloxine) added to a water mount of dead paraphyses occasionally yielded some good results. However, only the gap between the plasma portions of two adjacent cells can be seen while the septal wall remains invisible. Also adding cytoplasmic stains to KOH-mounts often did not allow us to see the septa.

In the living state, septa are mostly clearly visible, except for the quite rare case when the cytoplasm contains many small LBs which make septa difficult to discern. There is often a very slight constriction to be seen at each septum, which may help in detecting septa in difficult cases. However, this may be misleading since the individual cells have sometimes also slight constrictions in their middle part. Small portions of cytoplasm between vacuoles, but also rod-shaped SCBs, may be mistaken for septa when studying living paraphyses.

Although the length of the individual cells shows considerable variation within a species, a clear tendency within *Orbilia* concerning desiccation tolerance is obvious: in desiccation-sensitive species the terminal cell is generally (1–)2–4(–7) times longer than the lower cells, whereas in most of the desiccation-tolerant taxa the septa are more or less equally distributed from base to apex, the terminal cell being sometimes even shorter than the lower cells. Yet, much variation can be noted in the length of terminal cells. Because in desiccation-sensitive species the asci are generally comparatively short, each paraphysis possesses only a few lower cells, which are found near the level of the ascus base. In desiccation-tolerant species the asci are often rather long, and the long paraphyses with their short terminal cells multiseptate. However, in section *Aurantiorubrae* with only desiccation-tolerant species, the terminal cells are predominantly longer (often 1.5–3 ×) than the lower cells. In *Hyalorbilia* the terminal cells are always much longer (mainly 1.5–4 ×) than the few lower cells, irrespective of the rate of desiccation tolerance which is, however, never high in that genus.

Branching. Di- or sometimes trichotomous branching of the paraphyses occurs throughout the class. Paraphyses branch quite consistently only at the septa. Therefore, those paraphyses that have long terminal cells in combination with short asci show branching only near the ascus base. In taxa with short terminal cells and comparatively long asci, branching occurs not only near the ascus base but often also at the middle and sometimes upper level of the hymenium.

Due to the rather consistent occurrence within the *Orbiliomycetes*, branching of paraphyses in the lower part of the hymenium has little taxonomic value. In desiccation-tolerant species of *Orbilia*, branching at the uppermost septum appears to be of some taxonomic significance, being frequent in some species but rare in others. However, this feature was often found to vary strongly among collections, possibly depending on the age of the apothecia, therefore, its taxonomic value should not be overestimated.

The function of branching is apparently to fill gaps in the hymenium during apothecial growth. The general development of the apothecia from a concave to an eventually convex disc originates from both branching and apical inflation of paraphyses as well as from the formation of more and more asci.

Anastomoses. Anastomoses among adjacent paraphyses occur rather consistently throughout the *Orbiliomycetes* and have, therefore, hardly any taxonomic importance within the class. They are usually only found close to the level of the ascus stalk or slightly above, in taxa with large asci also at the middle level, and are usually provided with a vertical septum. Their function appears to be to increase mechanical stability of the hymenium.

Phylogeny of paraphyses. Phylogenetic considerations suggest that the equally septate, apically non-inflated type of paraphyses represents the plesiomorphic character state. This can be concluded from the fact that such simply constructed paraphyses are typical of various basal groups, particularly *Amphosoma*, *Lecophagus*, and *Lilapila*, but also *Orbilia* subgenus *Hemiorbilia*. Also in *Hyalorbilia* and *Pseudorbilia* the paraphysis apices are predominantly not or only slightly inflated, but here the terminal cells are generally much longer than the lower cells. Except for *Pseudorbilia*, all these genera are characterized by a hemispherical, often thick-walled ascus apex which is considered to be plesiomorphic in the present study (see p. 55). On the other hand, paraphyses with longer terminal cells and capitate or irregularly swollen apices occur in *Liladisca* and in *Bryorbilia*, two basal genera with unusual ascus apices of a conical shape.

When considering paraphysis septation, a comparison with the features of the marginal excipulum appear to be useful because the paraphyses (hamathecium) can be considered as ontogenetical descendants of the ectal excipulum. Mainly in desiccation-sensitive taxa the long terminal cells of paraphyses are in strong contrast to the short marginal cortical cells, whereas in many desiccation-tolerant taxa the length difference between the paraphysis terminal cells and the excipular marginal cortical cells is much lower. It seems conceivable that a low length/width ratio between paraphysal and excipular terminal cells is the plesiomorphic case, and it can be speculated that speciation within the *Orbiliomycetes* progressed towards paraphyses with strongly elongated terminal cells, particularly in desiccation-sensitive groups. This view is in concordance with the hypothesis that desiccation tolerance is a plesiomorphy within the *Orbiliomycetes*.

Ectal excipulum

The ectal excipulum constitutes from base to mid flanks the outer tissue of the ascocarp (Fig. 16) adjacent to the medullary excipulum and merges at the margin with the paraphysis palisade. Its development starts from the ‘conceptacle’ of the apothecial initial (see Fig. 18).

The cells of the ectal excipulum are usually larger and often also more tightly packed than those of the medullary excipulum. The two layers are frequently separated at the flanks by a more or less distinct, thin delimiting layer of textura porrecta, which consists of narrower cells and is, therefore, included in the medullary excipulum. In some species, especially of *Hyalorbilia*, *Liladisca*, and *Lecophagus*, but also in some taxa of *Orbilia* with large globose excipular cells, the border against the medullary excipulum is only very difficult to recognize. A layer of narrow hyphae covering the outer surface of the ectal excipulum may occur at the flanks or even up to the margin, e. g. in section *Habrostictis* (see, e. g., *O. trapeziformis* Pl. 592: 6f and *O. obtusispora* Pl. 595: 1f). At the base this layer intergrades with the anchoring hyphae and, therefore, it can be regarded as part of the latter. Living cells of the ectal excipulum frequently contain more or less distinct cytoplasmic inclusions (SCBs or LBs). The same inclusions usually also occur in the paraphyses, underlining the ontogenetic homology between paraphyses and ectal excipulum.

The individual cells are usually thin-walled and glued together by a thin refractive gel, but in various species of *Orbilia* and particularly *Hyalorbilia* the excipular cells tend to be slightly to distinctly thick-walled by a higher abundance of this gel (Figs 77: e–f). Also the genera *Liladisca* and *Amphosoma* p.p. are highly gelatinized in the ectal excipulum, and in *Lilapila* cap-like wall thickenings occur on the cortical cells (Pl. 29: 1h).

Layer thickness, **cell size**. The overall thickness of the ectal excipulum normally ranges at 20–50(–100) µm at the base, 20–30 µm at the flanks, and 10–20(–30) µm at the margin. Especially in large apothecia a basal thickness of 50–100 or sometimes up to 200–300 µm may be attained. Apothecial stalks of *Orbiliomycetes* are usually exclusively composed of cells of the ectal excipulum and are included in measurements of its basal height.

Excipular cell size provides some taxonomic value at the series level, but within a population it may considerably depend

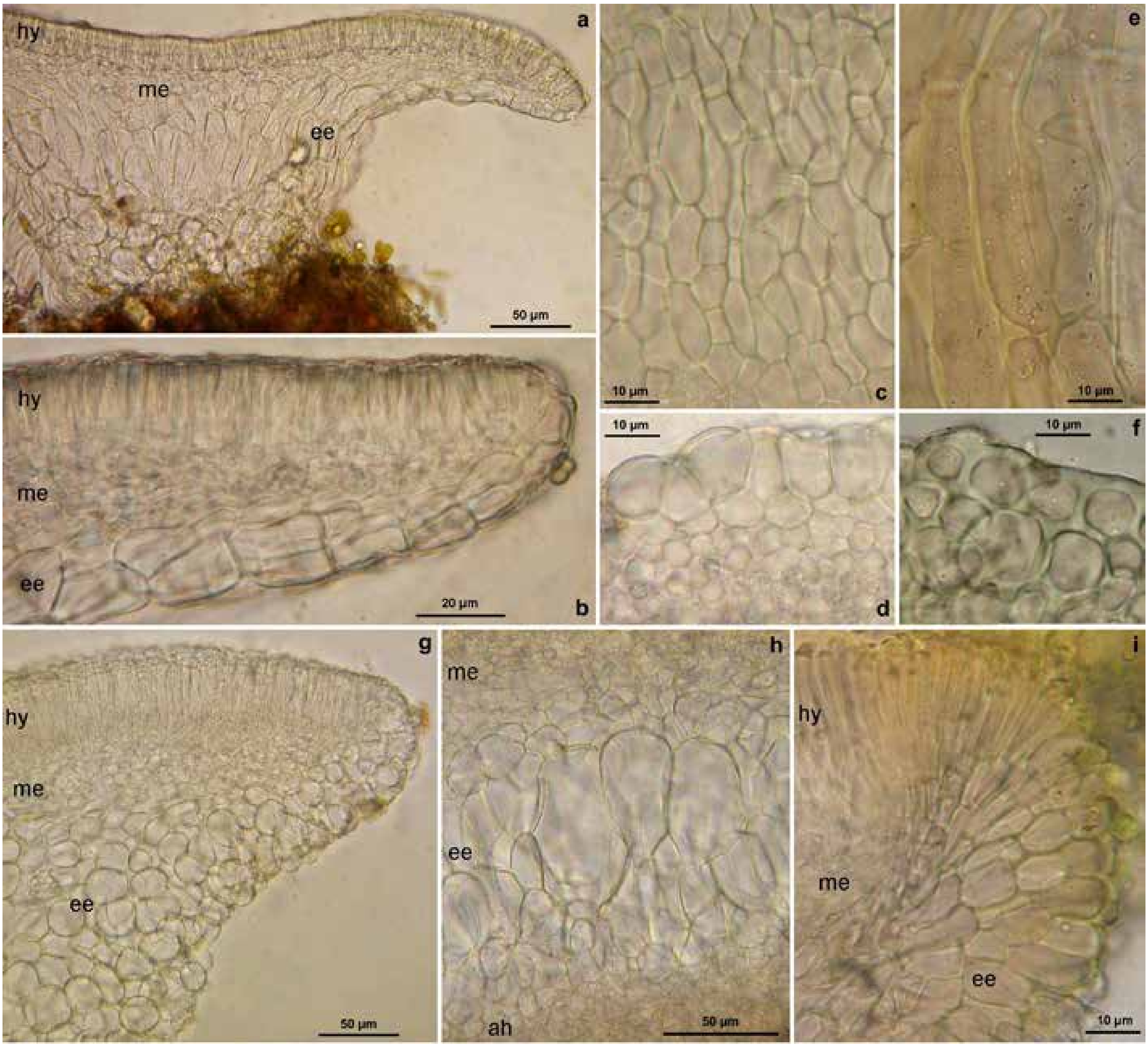


Figure 77: Ectal excipulum in median section (**a–b**, **g**. from base to margin, **h**. near base, **i**. at margin), external (surface) view at flanks (**c**, **e**), and top view on the margin (**d**, **f**). — **a**. vertically oriented, thin-walled textura prismatica in stipe (*Hyalorbilia inflatula*, H.B. 8882a); **b–c**. thin-walled textura prismatica oriented at a very low angle to the surface (*H. fagi*, **b**. H.B. 9105a, **c**. H.B. 7812); **d**. thin-walled subglobose marginal cells (*H. inflatula*, H.B. 8222); **e–f**. thick-walled (gelatinized) textura prismatica-porrecta and subglobose marginal cells (*H. citrina*, **e**. H.B. 8035, **f**. 8012); **g**. large-celled textura globulosa (*Orbilia auricolor*, H.B. 8898a); **h**. textura prismatica-globulosa with large, vertically elongated cells (*O. leucostigma*, H.B. 8259); **i**. margin of textura prismatica-globulosa oriented at a very high angle to the surface (*O. martinicensis*). — Living state except for **e–f** (in KOH); hy = hymenium, me = medullary excipulum, ee = ectal excipulum, ah = anchoring hyphae.

on apothecial size and maturity. Generally, cells near the base are much smaller in immature apothecia, but even if the asci are mature, cell size in small apothecia is sometimes only about half of that of large apothecia. Typical cell size of the basal ectal excipulum in *Orbilia* ranges at 8–20 × 5–15 µm. In contrast, many desiccation-sensitive species with comparatively large apothecia show a clear tendency to much larger cells (around 20–50 × 10–40 µm, Fig. 77: g vs. h). Velenovský (1934) referred to such an excipulum as ‘parenchyma grandicellulare’. Interestingly, species with large excipular cells and large apothecia have usually small asci and spores. Large excipular cells might function as a water storage vessel to retard hymenial desiccation during dry weather. However, large apothecia and excipular cells are also found in a few highly desiccation-tolerant species, e. g., in *O. anigozanthi*.

Cell shape, **texture types**. The individual cells of the ectal excipulum are either globose to angular (cubical), or more or less rectangular (prismatic) with a varying length:width ratio. They form a tightly packed tissue, of which two main types can be distinguished according to cell shape: (1) textura globulosa to t. angularis (lichenologists currently use ‘paraplectenchymatous’ for the earlier term ‘parenchymatous’): cells ± isodiametric though sometimes elongated vertically to the surface of the apothecium (Fig. 77: g–i; 78: e); (2) t. prismatica or t. porrecta (lichenologists currently use ‘prosoplectenchymatous’ for the earlier term ‘prosenchymatous’): cells elongated, parallel to the surface of the apothecium (Figs 77: a–c; 78: a).

A prosoplectenchymatous tissue at the flanks oriented parallel to the surface is typical of *Hyalorbilia*, but rarely also occurs in *Orbilia* (some species of section *Habrostictis*, particularly series *Habrostictis*; *O. cupularis* of section *Ovoideae*), though only towards margin. A paraplectenchymatous tissue at the flanks is typical of most species of *Orbilia*, but also of *Pseudorbilia* and *Lilapila*. The texture of *Bryorbilia* and *Lecophagus*, also in *O. sarcobati* of section *Ovoideae*, is somewhat intermediate, with angular to short-prismatic cells oriented oblique or parallel to the surface, respectively. In some taxa (e.g., *Liladisca* and *Amphosoma*) a textura angularis-prismatica oriented at a high (90°) angle at the lower flanks gradually changes its orientation near the margin to an angle of ~10–50° (Fig. 78: b–d).

In the prosoplectenchymatous tissue of *Hyalorbilia* the length/width ratio of the cells may considerably differ between taxa, ranging from only slightly longer than wide (textura prismatica-angularis to almost t. globulosa, e.g. in *H. erythrostigma*, *H. orbiliicola*, *H. polypori*, *H. lunata*, *H. sibirica*, *H. tortuosa*) to about 2–3× longer than wide (t. prismatica) or 3–6× longer than wide (t. porrecta). In one collection of *H. subfusispora* (Pl. 117: 3f) a t. globulosa as in *Orbilia* occurred.

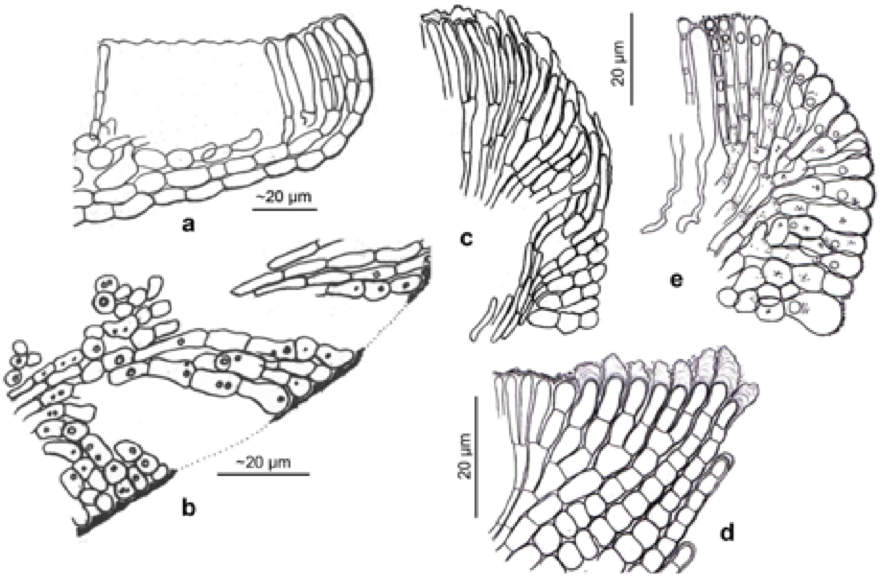


Figure 78: Different types of ectal excipulum at flanks and margin. — **a**. textura prismatica oriented parallel to the surface (*H. juliae*); **b**. lower flanks of t. angularis oriented perpendicular, mid flanks of t. prismatica oriented at ~40–50° (*Amphosoma atroolivaceum*); **c**. marginal excipular cells oriented at a rather high angle, but with the cortical hyphae curved upwards (*O. aristata*); **d**. margin of angular cells forming cell rows oriented at a low angle to the surface (*O. tenuissima*); **e**. ± clavate marginal cells oriented at a high angle to the surface (*O. sarraziniana*).

The cells of the paraplectenchymatous excipulum are either more or less angular (t. angularis) or tend to be globose (t. globulosa). The distinction between angular and globose cells is very gradual and, furthermore, state-dependent: the turgor of living cells provokes a more rounded shape whereas upon killing the cells become more angular.

Prismatic cells elongated vertically to the surface occur frequently in the paraplectenchymatous type, particularly in the more basal region of the apothecium (Fig. 77: h). Because of the prismatic shape, such a tissue is referred to as t. prismatica in the present study in spite of its vertical orientation. In *Hyalorbilia* a t. angularis of indistinct or sometimes vertical orientation is often present at the base, but this changes at the lower flanks to a t. prismatica oriented parallel to the surface. If there is a well-defined stipe, the cells form an upwards oriented t. prismatica parallel to the stipe surface (Fig. 77: a). Care must be taken, however, when doing median sections: if they do not run across the centre of the apothecium, a globular texture is simulated at the junction between receptacle and stipe, caused by tangentially cutting of a prismatic texture.

The hyphal origin of a paraplectenchyma is often not clearly discernible in an adult apothecium, in which it simulates a true parenchyma of higher plants. A vertical orientation, i.e., a connection of the excipular cells in a direction perpendicular to the surface, seems to be the general rule in *Orbilia*, even if the cells are isodiametric. Their growth at a high angle is obvious especially in the younger marginal region (Fig. 78: e). Here the thin t. porrecta of the medullary excipulum bends outwards into the ectal excipulum of angular to clavate cells oriented at a high angle to the surface.

Considerable variation in the structure of the ectal excipulum is usually observed within a species and even within a population. Therefore, the taxonomic value of the ectal excipulum should not be overestimated.

Marginal ectal excipulum. Whilst the structure of the ectal excipulum at the flanks (Fig. 78: a, b) is mainly useful for separating genera of *Orbiliomycetes*, that of the margin provides a number of different types which are characteristic of some sections or series of *Orbilia*. In many series the marginal cells are clavate to almost globose and oriented at a rather high angle to the marginal surface (see Figs 156, 78: e). However, a group within series *Neodactylella* deviates hereof in having rectangular, isodiametric to prismatic marginal cells that form characteristic cell rows at a low angle to the surface (Fig. 78: d). Some members of section *Habrostictis* show comparable marginal texture types, e.g., *O. carpoboloides* (see Pl. 568: 1f) (Spooner 1987: 192, fig. 28D, as *Habrostictis decipiens*), which Spooner believed to be diagnostic of *Habrostictis*. A similar margin is often found in section *Hemiorbilia*: the prismatic cells of the inner marginal excipulum are oriented at a high angle, whereas the hyphae of the cortical region bend upwards to run more parallel to the outside and often terminate in glassy processes (Fig. 78: c). In all species of *Hyalorbilia* the parallel layer of prismatic cells extends up to the margin (Fig. 78: a).

Phylogeny of ectal excipular textures. The two main types of tissues (proso- and paraplectenchymatous) at the excipular flanks, but also the variation at the margin require a hypothesis, which of the observed character states represents the old, plesiomorphic case. When considering a more complex texture as phylogenetically higher evolved, the parallel textura prismatica of *Hyalorbilia* would be more primitive than the vertical t. globulosa of *Orbilia*, based on two parameters, direction of growth and relation between cell length and width: (1) an ectal excipular texture parallel to the thin medullary layer of textura porrecta appears to be less evolved than a change in direction for 90°, and (2) isodiametric cells in a tissue appear to be higher evolved than prismatic cells which are typical of mycelial hyphae. On the other hand, the vertical cell elongation in the paraplectenchymatous ectal excipulum is a secondary phenomenon arising during the ontogeny of an apothecium.

The here presumed plesiomorphy in *Hyalorbilia* of a textura prismatica oriented parallel to the surface coincides with other presumably plesiomorphic features of that genus, such as homopolar ascospores with a homopolar spore body pattern, presence of croziers at the ascus base, and often uninflated paraphysis apices.

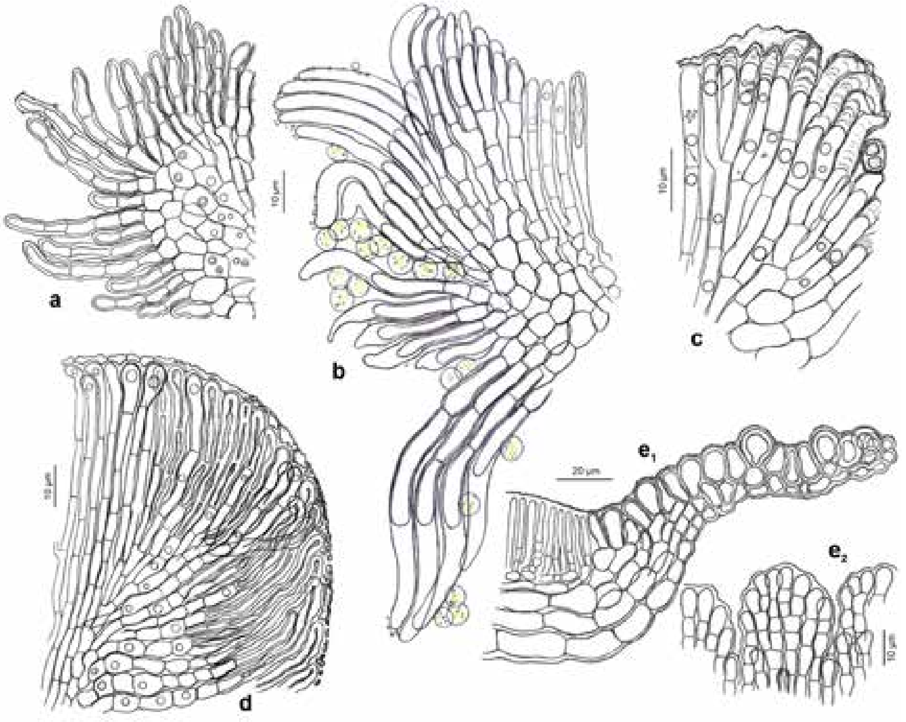


Figure 79: Structure of marginal excipulum (median section, **e**$_2$ in external view). — **a**. septate, thick-walled hairs (*O. phragmotricha*); **b**. septate firm-walled hair-like marginal hyphae terminated by glassy processes (*O. rubella*); **c**. similar as **b**, but cortical cells more compact instead of free (*O. flagellispora*); **d**. hair-like thick-walled hyphae forming a compact smooth margin (*O. ovoidea*); **e**. thick-walled ± isodiametric cells forming marginal teeth or lobes (*H. citrina*).

Hair- or tooth-like projections at the margin

Hair-, tooth- or lobe-like projections occur at the margin and often also the mid flanks in various groups of *Orbiliomycetes*. These projections may be of three very different kinds: (1) thin- or thick-walled hairs that are transversely septate when exceeding a certain length (Fig. 79: a); (2) solid (glassy), acellular processes of very different length, often with an internal stratification (Fig. 79: c); (3) a protruding compact texture of thick-walled, ± isodiametric cells (Fig. 79: e). Rarely types (1) and (2) occur in combination: the glassy processes emerge from the tips of septate hairs (e.g., *O. rubella*, Fig. 79: b, *O. octosporoides* (Pl. 793: 1g). All these types of marginal structures may easily confuse one into mistaking an orbiliaceous fungus as a hairy or toothed member of the *Helotiales*.

The two kinds of hair-like structures project either freely, or are more or less tightly agglutinated by some gel, and then either form more or less compact teeth or lobes, or sometimes a smooth margin. The latter is the case in *O. polyspora* and *O. ovoidea* (Fig. 79: d), and less developed in some other members of section *Ovoideae*, rarely in series *Phanosomates* (*O. myriosphaera*) and *Ovales* (*O. ovalis*): more or less elongated, thick-walled marginal hyphae are agglutinated to form a compact tissue that resembles a textura oblita. Contrary to those species with free hairs, the thickened wall in these conglutinate hyphae is composed of an inner wall layer that is able to swell, showing a distinct imbibition effect: only in the dead state the inner layer is thick and thereby of low refractivity, whereas the living cells have thinner and entirely strongly refractive walls. In *Hyalorbilia citrina* very thick-walled, ± isodiametric cells occur at the margin, which may form more or less prominent lobes or teeth (Fig. 79: e).

Septate hairs. More or less thick-walled septate hairs are typical of *Lilapila* and a few species of *Orbilia*, mainly of series *Rubellae* and *Drechslerella* (*O. pilosa*), whereas thin-walled hairs are typical of series *Habrostictis*, but also occur in series *Piliferae* (*O. pilifera*), *Abutilones* (*O. suberis*) and series *Hemiorbilia* (*O. fimbriata*). The latter species, in particular, is strongly reminiscent of a hairy member of *Helotiales*. The hairs in these species are usually free, but may also be somewhat conglutinate to form indistinct teeth. Hair size ranges from 20–30 up to 50–100(–200) µm in length and (2.5–)4–7.5(–10) µm in width. Very short (~7–20 × 2.5–5 µm) non-septate marginal hairs occur in a few species (e.g., *O. aethiopica*, *O. concoloris*, *O. pseudobrevistipitata*). The hairs are in most cases hyaline and smooth, or yellowish-ochraceous due to a thin exudate that covers the wall. Only in *Lilapila* are they densely punctate by a deep purplish-lilac pigment.

Glassy processes. In about 25% of the species of *Orbilia* a hyaline, solid wall substance is exuded from the tips of the cortical cells of the marginal excipulum. This wall material forms hair-like structures which vary in length from 1–10 up to 30–100 µm or more. In comparison, their width is rather consistent and ranges around 2–4(–5) µm, also the cell lumen below has a rather consistent size. The term 'glassy processes' is exclusively used here for the solid glassy matrix above the tip of the cell from which it is exuded. Earlier authors (e.g., Spooner 1987, Huhtinen 1987a) have classified this feature as hairs with a basal lumen and a solid, glassy, refractive apical part. In our opinion, the term 'glassy processes' facilitates description of septate hairs of varying length which are tipped by short to long solid parts. In some further species the solid parts attain only a length of 1–2 µm and are then easily overlooked. They are not included in the above 25%.

The processes are cylindrical, with a rounded or somewhat conical apex. They are more or less straight or somewhat flexuous, or they tend to be more or less strongly curved, especially when rather long, either under a wide arch, or sometimes only at their apices. Depending on the species, this curvature may consistently be oriented in one direction, either down-/outwards (Fig. 80: a–b) or up-/inwards (Fig. 80: c). The matrix of the processes somewhat differs in refractivity between the species, and often shows some kind of layering, referred to as 'stratified' in the descriptions (Fig. 80: d). Glassy processes are consistently without a central lumen.

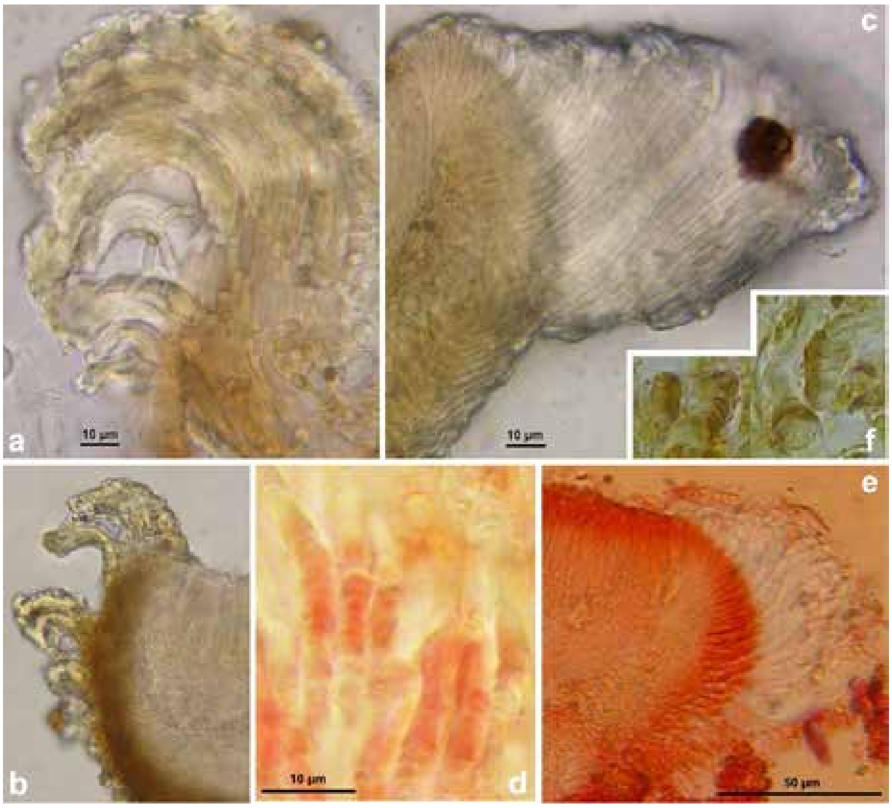


Figure 80: Glassy processes in *Orbilia* (median section of margin, except for **d** and **f**. squash mount). — **a–b**. curved outwards (*O. mirabilis*); **c**. straight or terminally curved upwards (*O. aviaristata*); **d–f**. chemical resistance and colourability (**d–e**. *O. aristata*, H.B. 9226a; **f**. *O.* cf. *puyae*): **d**. stained rose-red by CR_{SDS} after treatment with H_2SO_4 and then by KOH; **e**. glassy processes resist very strong H_2SO_4 treatment (heated); after adding KOH they were not stained by CR_{SDS}; **f**. stained in IKI after treatment with KOH.

In their microscopic appearance these processes resemble the glassy hairs of some *Hyaloscyphaceae*, particularly the genera *Olla* Velen. (= *Hyalopeziza* Fuckel p.p.) and *Urceolella* Boud. Indeed, a few species of *Orbilia* have been thought to be hyaloscyphaceous in the past (*Radotinea caudata*, Fig. 173, *O. albovinosa*, Pl. 520). Glassy processes are often agglutinated and, depending on their length, form either a minutely crenulate margin, or small to very large teeth-like structures. In a few species of series *Albovinosae* the very long glassy processes are less conglutinate and more or less free, therefore, the margin looks hairy or pubescent which strongly resembles apothecia of *Hyaloscyphaceae*.

The glassy matrix is insoluble in 10–20 % KOH, also in 30–60 % H_2SO_4, even when repeatedly heated. CRB, CB_L, or CR do not stain the matrix when applied to a water mount; only the surface is usually stained lilac or turquoise in CRB due to either a gelatinous sheath, or a covering exudate. Iodine reagents (IKI, MLZ) also yield negative results, even after pretreatment with KOH or H_2SO_4, though in one species (*O.* cf. *puyae*, Fig. 80: f) the glassy processes partly stained honey-brown by enhancing the stratification. CR_{SDS} stained the refractive matrix light pinkish-red to carmine if pretreated with KOH or H_2SO_4, but the results were somewhat inconsistent within the same collection (Fig. 80: d). Also a lilac-violet stain of the matrix in CRB was inconsistently obtained when adding SDS to an unpretreated CRB preparation. In contrast to *Orbilia*, the glassy hair matrix in *Olla* and similar genera often stains internally purplish-brown in IKI or MLZ (without KOH-pretreatment).

Glassy processes are sometimes difficult to recognize, especially when they are very short and covered by thick amounts of exudate. In this case strong squashing and subsequent staining with CR, IKI, CRB, or CB_L allows to differentiate between the unstained glassy matrix and the exudate that stains rose-red, red-brown, or blue, respectively. Alternatively, mounting in a drop of H_2SO_4 for a moment (and afterwards neutralizing the acid with KOH) more or less dissolves the exudate and allows to better see the resistant glassy matrix (Fig. 80: d–e).

In many members of series *Microsomates*, but also in some of sections *Aurantiorubrae* (*O. kingsiana*, *O. denticulata*, *O. xanthoguttulata*) and *Habrostictis* (*O. calyptrata*), small glassy caps occur not only on the excipular cells but also on the tips of the paraphyses. However, to clarify whether the interior of such refractive, firmly attached caps on the paraphyses are made up of a glassy matrix like those on the excipular cells, or entirely of exudate, proved difficult. In *O. xanthoguttulata* (Fig. 95: l) the caps obviously consist of an inner, thick, less refractive glassy wall matrix that does not stain in either CR or IKI, and a thin, strongly refractive covering layer of exudate that stains yellowish-brown in IKI and rose-red in CR. The exudate loosely covers the glassy matrix perhaps by a thin layer of gel between. The different nature of the two structures is best seen in IKI-mounts whereas in water or KOH the caps appear to consist of a single homogeneous layer. However, in *O. denticulata* treatment with heated 60 % H_2SO_4 dissolved the entire glassy cap on the paraphyses (Fig. 96: l).

Formation. The mode how glassy processes of *Orbilia* develop seems worth describing in detail. The more or less conspicuous hemispherical or subconical layering (stratification) of the glassy matrix is seen especially in mounts of KOH or acids (Fig. 80: d, f), even without applying stains. It consists of thin, low-refractive layers which occur ± scattered in the higher-refractive matrix. Upon strong pressure the processes may break at these layers. This layering could be interpreted as growth zones which indicate a discontinuous production of glassy substance. During formation, wall material is transported through the cell wall at the obtuse tip of the cortical cells and deposited externally on the wall, i. e., at the base of the growing glassy processes. Thus, the oldest wall material is found at the tip of each process. The cortical cells, from which the processes emerge, thereby retain their primal size during the whole growth period. The glassy processes, which thus grow in a basipetal manner, attain a length up to about ten times the length of the cortical cells.

Raschle (1977: 180) and Korf & Kohn (1980: 506) observed that the production of the glassy matrix in glassy-haired species of *Hyaloscyphaceae* 'proceeds from the apex backwards'. Such a process would likewise deserve the term 'basipetal', but it is fundamentally different: it means that the hairs at first attain their final length while they are still thin-walled, and later gradually deposit glassy substance to the inner surface of the cell wall by finally reducing their lumen to the cell base. The authors concluded that 'the glassiness thus appears to consist of secondary wall thickening'.

This is obviously true in species with hairs with a narrow central lumen (*Hyalopeziza*, *Urceolella*), but it might not be true in species without such a lumen (*Olla*, *Protounguicularia*). Here the glassy matrix appears to be deposited externally on the apical cell wall, resulting in a strong morphological similarity to glassy processes of *Orbilia* by showing an irregular outline of the glassy matrix and a cell wall bordering the base of the matrix. Like in *Orbilia*, the glassy matrix in *Olla* often shows an internal hemispherical or conical layering (see Baral & Marson 2005: *O. millepunctata*, *O. scrupulosa*), at which the processes may break. The chemical composition of the glassy matrix is obviously different between the two classes, because KOH-solubility and internal lumina (both typical of *Urceolella*), as well as amyloidity (typical of *Olla*) have never been observed in *Orbilia*. This seems to justify the assumption that the glassy matrices in *Orbilia* and the *Hyaloscyphaceae* are a result of convergent evolution rather than homologous structures.

Occurrence. Within the *Orbiliomycetes*, glassy processes are so far almost exclusively known in *Orbilia* (the single exception concerns *Hyalorbilia noduosa*), and here provide a valuable species marker. Very closely related species may differ in this respect (examples: *O. nemaspora* vs. *O. scolecospora*, *O. rectispora* vs. *O. cardui*, *O. sphaerospora* vs. *O. subsphaerospora*, the latter mentioned species always with glassy processes). Glassy processes are typical of many desiccation-tolerant species but also occur in a few more or less desiccation-sensitive taxa, e. g., *Orbilia crenatomarginata*, *O. cardui*, *O. polybrocha*, *O. desertorum*, *O. orientalis*. Formerly, glassy processes were used to define a separate genus *Hyalinia* Boud. (see p. 203), but the present work provides evidence that they occur scattered in various sections and series of *Orbilia*. Even within a species or species aggregate, populations with and without glassy processes were noted (e. g., *O. vinosa*, *O. aprilis*, *O. caudata*, *O. cardui*, *O. austrocylindrica*). Glassy processes are absent in section *Lentiformes* (with the exception of series *Ovales*) and section *Habrostictis* (with the exception of short glassy caps in *O. jurana*).

Function of marginal hairs, **teeth or lobes**. Like protruding paraphyses, an uneven margin might help in the condensation of atmospheric humidity. Thick-walled marginal cells or glassy processes could serve in protecting the apothecia from mycophagous invertebrates. The length of glassy processes might also be a response to a longer life span of the apothecia. In this concern they could serve as an UV-protection of the apothecia in the dry state, in which long processes may completely cover the disc. In some cases, closely related species differ in the length of the glassy processes. For instance, *O. subaristata* has longer processes and occurs in more thermophilous areas including the Mediterranean belt, in contrast to *O. aristata* which is absent in regions of such a high insolation. Similarly, *O. vinosa* is generally devoid of glassy processes, but a montane, mainly orosubmediterranean variant is characterized by such processes that form distinct teeth, perhaps as a result of cold temperature and short summers in the mountains and, therefore, a longer life span of single apothecia which are exposed to higher amounts of UV. On the other hand, many species of *Orbilia* that occur in subtropical desertic areas are devoid of glassy processes, although they are subjected to extremely high amounts of radiation in combination with a life span of single apothecia of probably several years.

Medullary excipulum

The medullary excipulum fills the space between hymenium and ectal excipulum of an apothecium. It develops from the 'carpocentre' of the apothecial initial (see p. 37 ff.). In *Orbiliomycetes* its thickness in mature apothecia varies from about 10 to 50, sometimes 100 µm. If the apothecia are stalked, the medullary excipulum may more or less extend down into the stalk. A separate subhymenial layer is rarely recognizable. In contrast to the ectal excipulum, the tissue of the medullary excipulum consists of a network of hyphae (textura intricata) among which inflated, more or less globose cells of varying abundance are interspersed in most species of *Orbilia*, being often aggregated in chains (Fig. 81: a–b). Hyphae and inflated cells form a texture varying in density between loosely interwoven with varying amounts of intercellular space and densely packed as in the ectal excipulum. The intercellular space is usually filled with water, but in a few species of *Hyalorbilia* and *Orbilia*, and in *Lilapila* and *Liladisca*, it is gelatinized (see p. 98).

The inflated cells vary in size among the species. Mostly they measure around *6–12 × 5–9 µm, but also sizes of *(3–)4–7 × 4–6 or up to (8–)11–20(–30) × 6–15(–20) µm occur. If the inflated cells are very abundant, the tissue takes the appearance of a t. globulosa (or t. angularis), and if the medullary excipulum is rather thick, the inflated cells may be crowded either below the subhymenium or close to the ectal excipulum. In both cases the medullary excipulum appears to be two-layered when viewed in median section. If the lower layer contains the inflated cells, the boundary against the ectal excipulum becomes rather indistinct.

A thin (~5–15 µm), more or less distinct layer of loose or dense, parallel hyphae (textura porrecta) is often found at the border between ectal and medullary excipulum at the flanks of various *Orbilia* species (Fig. 81: a). This layer ends up in the marginal growth zone of the apothecium from which the two adjacent tissues emerge by dichotomous branching of the hyphae: the ectal tissue on the outer (lower) side, and the medullary tissue on the inner (upper) side of the apothecium. This delimiting layer is considered to be a part of the medullary excipulum, because hyphal diameters and their sometimes loose texture correspond to the main part of the medullary excipulum.

The inflated, chain-like cells belong to the vegetative (haplontic) hyphal system and might serve in storing water. However, our tests on desiccation sensitivity indicate that these inflated cells exhibit almost the highest tolerance, which is only sometimes overtopped by ectal excipular cells or ascospores. In *Lilapila*, for instance, the ascogenous hyphae are quite easy to follow in the upper medullary excipulum, but did here not emerge from these cells. In *O. xanthostigma* they contain in the living state the same yellow VBs as the paraphyses (Fig. 81: b), while in most species they are without visible cytoplasmic inclusions. Bellemère (1968: 547) referred to these inflated cells as 'very voluminous cells 10 µm diam.', showing the cytoplasm strongly reduced (vacuolated), and the wall stained by Methyl green.

The hyphoid elements between the inflated cells seem to represent a mixture of vegetative and ascogenous hyphae. In *Orbilia* the ascogenous hyphae can hardly be recognized by morphology due to the absence of croziers, and also in *Hyalorbilia* with consistently present croziers they can usually be traced down only a short distance, while the paraphyses clearly emerge from inflated cells of the medullary excipulum.

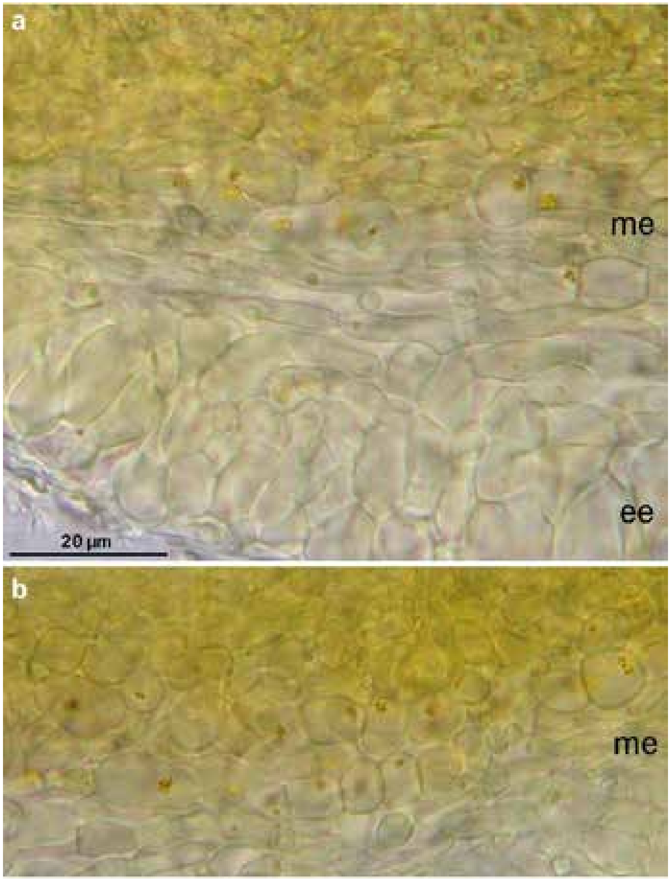


Figure 81: Medullary excipulum in *O. xanthostigma* (H.B. 7848), **a**. parallel hyphae near flanks; **b**. chains of inflated cells containing yellow LBs. ee = ectal excipulum, me = medullary excipulum.

There is some controversy in the terminology of the two excipular layers. In concordance with Durand (1901: 488, pl. 32 fig. 16, *Orbilia vinosa*) the complete tissue below the hymenium, except for a poorly developed subhymenium (as 'hypothecium') is named 'excipulum' in the present study. Durand distinguished between an outer layer of isodiametric cells, and a very sharply delimited inner layer of 'fine, closely interwoven hyphae', which corresponds to the medullary excipulum as here applied. Spooner (1987, *O. flexispora*) used the term 'medullary excipulum' only for the thin delimiting layer of t. porrecta, whereas the adjacent thicker layer above he termed 'subhymenium'. Nannfeldt (1932) used the term 'hypothecium' for the complete tissue between hymenium and 'excipulum' of globose or prismatic cells. We here use subhymenium only if there is a thin layer below the hymenium which clearly deviates in cell size or pigmentation from the main part of the medullary excipulum.

In those desiccation-sensitive *Orbilia* species with large isodiametric ectal excipular cells, these occupy the major part of the excipulum, and only a very thin layer of much smaller cells is to be found below the hymenium. The large-celled layer is sometimes assigned by authors to the medullary excipulum by restricting the ectal excipulum to the smaller cortical cells. This view was applied even to desiccation-tolerant species with rather small excipular cells, e. g., in *O. junci* by Kohlmeyer et al. (1998). We have usually not accepted this view, except for European species of section *Helicoon*, in which it seemed clear that the medullary excipulum attains a high central thickness by including many of the large globose cells. However, the boundary between ectal and medullary excipulum is often hard to see in the basal part of the apothecium.

Anchoring hyphae

The hyphae that emerge from the cortical excipular cells, mainly near the base of the apothecium (Fig. 82: e) but also at the flanks (here especially in *Hyalorbilia*, Fig. 82: a), attach the apothecium to the substrate and supply it with water and nutrients. Some of these hyphae might belong to the mycelium that gave rise to the initial stage of the apothecium, while the majority grew out of the excipulum at a later stage of apothecial development.

The anchoring hyphae have a diameter of about (1.5–)2–3(–4) µm in most groups of *Orbiliomycetes*. At the place where they emerge from the excipulum they may be thicker and sometimes tend to be moniliform or even form a paraplectenchymatous layer. A few species of *Orbilia* deviate in having wider anchoring hyphae (~3–6 µm), for instance, *O. auricolor*, *O. menageshae*, and *O. denticulata*. In contrast, in *Hyalorbilia* the hyphae are often ~3–6 µm wide (Fig. 82: a–c), sometimes up to 10 µm. Also *Lilapila* has comparatively wide anchoring hyphae [3.5–5.5(–6.5) µm], whilst the widest hyphae occur in *Lecophagus* [(5–)6–13(–17) µm].

Anchoring hyphae of *Orbiliomycetes* are generally hyaline and smooth. Only in *Lilapila* a rough thin layer of exudate was observed on the their walls. The cell wall is usually thin (†0.1–0.3 µm), but in some species it is sometimes or mostly thickened (†0.4–1 µm, in *Lilapila* up to †1–2 µm), particularly in those species with a gelatinized ectal excipulum.

The abundance of anchoring hyphae is sometimes typical of a species, but it usually varies considerably. Normally the hyphae are restricted to the base of the apothecium. Here they may occur rather sparsely, or they form a thin or thick (up to 100 µm) layer of loose or dense textura intricata (Fig. 82: e), which may laterally run out in more or less distinct hyphal strands. Sometimes, the intercellular space between the densely intermingled hyphae tends to be gelatinized. In quite a few desiccation-tolerant taxa the anchoring hyphae densely cover the flanks of the ectal excipulum by a thin layer of t. porrecta immersed in some gel. This layer may extend up to the margin, or even somewhat protrude beyond it, and then provokes a rough or finely crenulate, whitish appearance of the margin. In *Hyalorbilia* the anchoring hyphae are often rather long and straight and project more or less vertically from the excipulum by affixing the receptacle to the substrate.

If the anchoring hyphae occur abundantly, they can be recognized macroscopically around the apothecial base, especially in the dry state, as a white hyphal mat which may then be termed 'subiculum'. A conspicuous subiculum was ± inconsistently present in species with large, mainly desiccation-sensitive apothecia belonging to *Hyalorbilia* (e. g., *H. inflatula H. andina*, *H. japonica*, *H. arcuata*), *Orbilia* sections *Orbilia* (e. g., *O. dryadum*, *O. gaillardii*) and *Arthrobotrys* (e. g., *O. auricolor*, *O. neglecta*, *O. rectispora*), but also in some desiccation-tolerant species of sections *Aurantiorubrae* (*O. aethiopica*) and *Habrostictis* (*O. carpoboloides*). A certain macroscopic similarity between *H. inflatula* and *O. auricolor*, including their subiculum, led in the past to confusion of the two species.

Septation of anchoring hyphae is usually sparse, but in *Hyalorbilia* and *Lecophagus* a trend to more densely septate hyphae in relation to hyphal width can be noted. Living anchoring hyphae are usually without visible cytoplasmic

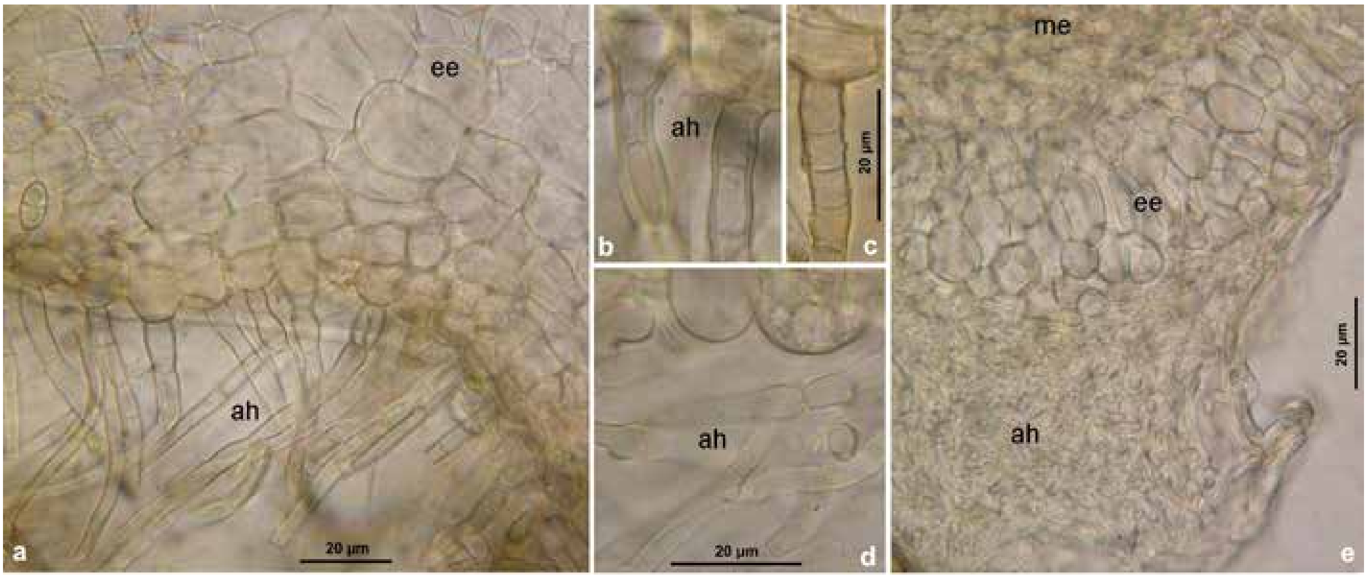


Figure 82: Anchoring hyphae emerging from cortical cells of the ectal excipulum. — **a**. *Hyalorbilia fagi* (H.B. 7934); **b**. *H.* cf. *japonica* (H.B. 8725b); **c**. *H. ulicicola* (H.B. 8357); **d**. *Orbilia anigozanthi* (H.B. 8831e); **e**. *O. eucalypti* (H.B. 7968). Living state except for **b** (in KOH); me = medullary excipulum, ee = ectal excipulum, ah = anchoring hyphae.

bodies. Remarkable inclusions (SCBs) occur only in a few cases (*Lecophagus*, *Hyalorbilia ulicicola*).

Cytoplasmic inclusions of the living cells

Within *Orbiliomycetes* a number of different cell contents can be seen under the LM in the living state in all types of cells and tissues of both anamorphs and teleomorphs. Although these cytological characters are usually transient, i.e., visible only in the living cytoplasm, they provide valuable and quite consistent features for the recognition of species or higher taxonomic entities. Because their visibility is confined to living cells, they have been overlooked by herbarium taxonomists and are, therefore, almost completely unreported in the literature. The most important organelle, the spore body (SB) inside the ascospores, is treated after the paragraph on ascospores, because its attachment to the spore wall is thematically interrelated to ascospore shape and polarity (see p. 69 ff.).

Lipid bodies (LBs). LBs are globose, strongly refractive, hyaline or pale to bright yellow-orange droplets with a diameter of about 0.1–4 µm or more. They are formed within the cytoplasm and are always to be found outside the vacuoles (Baral 1992: 357, for further literature see there). In the *Orbiliomycetes* they occur scattered and predominantly few in number and small in size in all types of cells, including ascospores and conidia. Examples of comparatively high lipid contents are shown in Figs 83–85.

LBs are very clearly visible when living cells are studied in a water mount. They are insoluble in 2–20 % KOH or 30–60 % H_2SO_4, even when heating the slide. Under vital staining with CRB, LBs remain unstained, in contrast to VBs which stain blue to greenish or purplish. Yet, LBs turn reddish when adding 0.5 % KOH to a CRB-mount (Baral l.c.), or when adding lactic acid or H_2SO_4 to either CRB or Réactif de Bailenger (Fig. 85: c). LBs are usually more or less invisible in dead herbarium material when mounted in media such as H_2O, MLZ, or CB_L, due to the masking effect of the dead cytoplasm around. They are, however, clearly visible when mounting dead elements in KOH. Although we recommend to mount dead herbarium material first in water in order to be able to search for living elements, or to see the natural colour of exudate, we later use to add KOH for swelling collapsed cells and for enhancing visibility of LBs.

Due to the prevailing study of herbarium material in all groups of fungi including lichens, the taxonomic value of LBs, particularly in ascospores and conidia, has very often been overlooked. The main reason for this lies in the fact that LBs tend to fuse in herbarium material, where they finally show a very irregular and variable pattern, but also because of the masking effect of the currently applied mounting media (MLZ, CB_L).

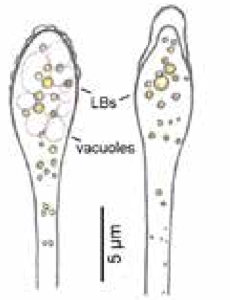


Figure 83: Yellow LBs in the living cytoplasm outside of inconspicuous hyaline vacuoles in paraphyses of *O. xanthoguttulata*.

LBs in asci and ascospores. Within the *Orbiliomycetes*, LBs in asci and ascospores are often very sparse and minute, or even absent. If present, they are formed at a rather late development stage when the asci or spores have almost attained their final size. Nevertheless, LBs in spores are present prior to the formation of spore bodies.

The absence of LBs in young ascospores is a frequent but not general feature of the *Ascomycota*. In certain groups of *Helotiales* and *Pezizales* the young asci are multiguttulate: they contain numerous small LBs around the fusion nucleus in the upper part of the ascus. After meiosis the usually eight spore nuclei are dispersed within this guttulate area. During spore wall formation, the double membrane between which the wall is later formed encloses besides the nucleus a certain amount of plasma that contains LBs. This peculiarity of a multiguttulate cytoplasm of young asci is only to be found in some of those species of *Helotiales* and *Pezizales*, in which the mature spores possess a high lipid content (example: *Pezicula*, Baral 1992: figs 42–43).

Multiguttulate asci have never been observed in *Orbiliomycetes*. Asci during and prior to meiosis are more or less devoid of LBs, also during spore formation the ascoplasm usually contains

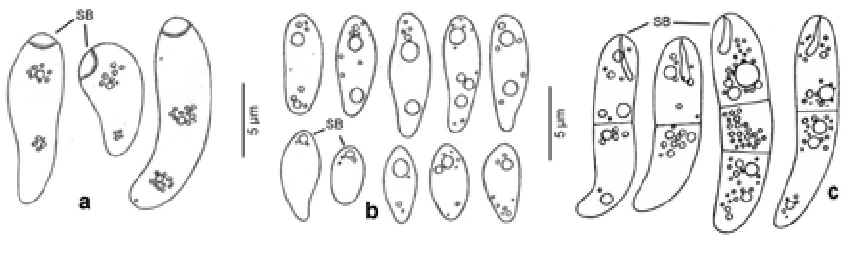


Figure 84: Ascospores containing globose, small to large LBs (living state, SB = spore body). — **a**. *Orbilia ocellata* (lipid content 1–2); **b**. *O. eucalypti* (lipid content 1–3); **c**. *O. septispora* (lipid content 2–4).

only some scattered small LBs. In some species of *Hyalorbilia*, however, a group of LBs 0.3–1.5 µm diam. occurs more or less regularly at the base of mature living asci (*H. berberidis*, Pl. 112: 5b, *H. fomentarii*, Pl. 110: 2b, also inconsistently seen in *H. juliae*, Pl. 106: 4b and *H. tortuosa*, Pl. 89: 1b).

Number, size, and arrangement of LBs within the living mature ascospores serve as a very important, albeit often neglected feature at the species or higher level in virtually all groups of fungi (Baral 1992: 359f.). Closely related species, or higher taxonomic entities may strongly differ in this regard. In order to have a measure for the relative lipid content of spores (in relation to spore volume), a scale ranging from 0 (no LBs visible) to 5 (maximum possible lipid content, excluding nuclear region) was introduced (Baral 1992: 363). This scale was adopted by various authors and was differently called. We here adopt the version OCI = oil content index introduced by Declercq in an unpublished key on *Hymenoscyphus* (2004).

Ascospores of *Orbiliomycetes* are characterized by a comparatively low lipid content that ranges from 0 to usually 0.5–1, rarely 2–4. Lipid body size is mostly ~0.1–0.5 µm, rarely 0.5–1.5 µm. Their colour is always hyaline. In contrast to SBs, LBs usually do not have a consistent arrangement within spores of this group of fungi. Therefore, and because of their rather uniform size and shape, the taxonomic value of LBs in ascospores of *Orbiliomycetes* is quite low. In those species with a higher lipid content, however, the LBs are usually arranged in two groups, or near the septa if spores are septate (Fig. 84). Examples of such higher lipid contents are known in series *Lentiformes* (*O. patellarioides*, *O. ocellata*, *O. cucumispora*), *Cercidicola*, *Orbilia* (*O. eucalypti*, *O. fissilis*, *O. guyanensis*), and *Serpentinae* (*O. septispora*), but such high lipid contents are not species-specific, instead, they occur sometimes only as an exception, possibly due to some external influence (e.g., in *O. eucalypti*, Fig. 84: b, see also p. 1357).

As a further complication, the lipid content in ascospores of *Orbiliomycetes* was found to increase either more or less strongly (Fig. 70: d–e) during ageing or not at all (Fig. 70a–c). This phenomenon, which was mainly observed when studying apothecia attached inside Petri dishes, is so far not understood. It is in contrast to the general situation in ascomycetes, in which LBs in ascospores are gradually disintegrated for the synthesis of cytoplasm and wall material during the process of germination. The increase in lipid happens simultaneously with the decrease of the spore body. Possibly, the absence of SBs means that such spores follow another strategy of substrate colonization than forcibly ejected spores containing SBs. Another surprising and not understood effect is that the number of small LBs in ascospores of *Orbilia* often increased rather strikingly if a preparation was kept moist for some hours, or rehydrated after being dried down.

In a few species (e.g., *O. quaestiformis*), it was repeatedly observed that submature spores contain 1–2 LBs of 0.3–1 µm diam. prior to spore body formation, which gradually disappear when SBs develop. Again, this is difficult to explain, because LBs in spores of other classes of *Ascomycota* generally increase in size until the spores attain full maturity prior to ejection.

LBs in vegetative cells. In the vegetative cells of paraphyses, ectal and medullary excipulum, and anchoring hyphae, LBs usually occur in low amounts near the lateral walls and especially near the septa. In many species LBs have a yellow to orange pigmentation due to the presence of carotenoids inside the droplets. In *O. xanthoguttulata* yellow LBs are found in a rather high abundance especially in the widened apical part of the paraphyses (Fig. 83).

LBs in the basal ectal excipulum may sometimes attain a size of 1–2(–4) µm (Fig. 85: a). However, such large LBs were repeatedly observed as being very inconsistent within a species or even a population of *Orbiliomycetes*. They were abundant in one apothecium, but in total absent in another (living state, full maturity). Therefore, the taxonomic value of LBs in the ectal excipulum is obviously very low.

In anchoring hyphae LBs have not been seen in remarkable quantities. Numerous small LBs have only been observed in the wide hyphae of *Lecophagus*, and especially in the assimilative hyphae also large LBs were among them (Pl. 45: 1i–j).

Refractive vacuolar bodies (VBs). Vacuoles are usually non-refractive and, therefore, more or less inconspicuous when studying living cells under the LM (oil immersion, bright field). They are perceptible as empty, transparent, small to large, globose or elongate areas within the likewise very slightly refractive cytoplasm (see, e.g., Figs 83, 86: e). A special type of vacuoles is characterized by a low to high refractivity and was termed 'refractive vacuolar bodies' (VBs) by Baral (1992: 363). Like non-refractive vacuoles, VBs usually occupy a major part of the internal lumen of a cell. The refractive substance occurs in two patterns inside vacuoles, either (1) homogeneously distributed (Fig. 86: a–c, g–h), or (2) as ± small, globose guttules (Fig. 86: d–f, i–j, l–m). In the homogeneous type the substance apparently occurs as a colloidal solution in the vacuolar water (similar as in spore bodies), whereas in the guttular type it forms individual droplets within the otherwise non-refractive vacuolar water. If

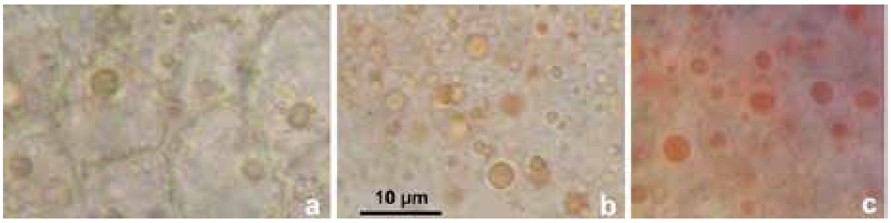


Figure 85: LBs in basal cells of ectal excipulum (*O. aristata*, H.B. 9226a). — **a**. living state (unstained); **b**. in H_2SO_4 (unstained); **c**. after H_2SO_4 stained with Réactif de Bailenger + lactic acid (same result when stained with CR_{SDS}).

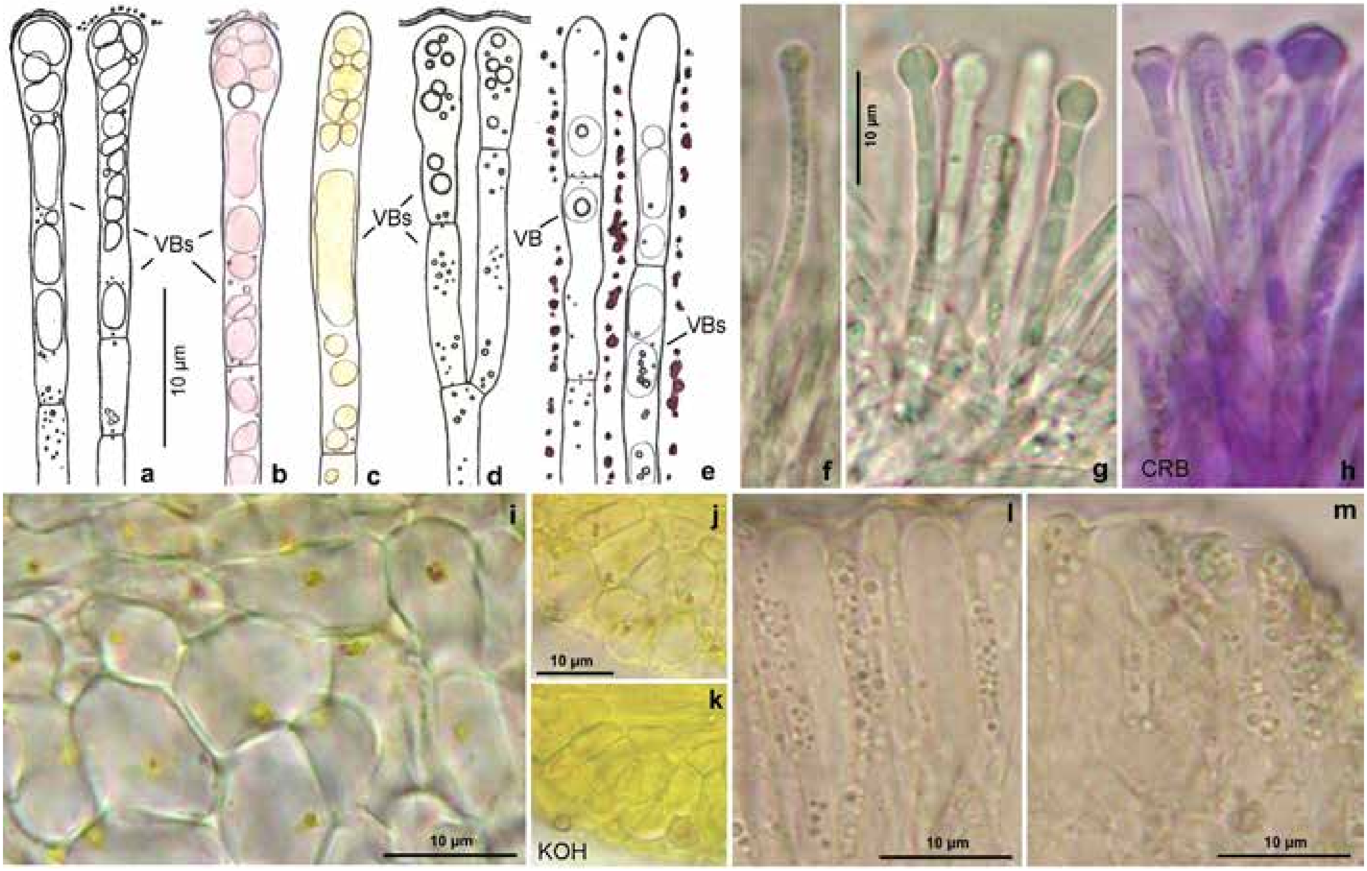


Figure 86: Refractive vacuolar bodies (VBs) in living paraphyses and excipular cells of *Orbiliomycetes*. — **a–c**, **g–h**. VBs of the homogeneous type; **d–f**, **i–m**. VBs of the guttular type; **a**, **d–g**, **l–m**. medium to high-refractive, hyaline VBs; **b–c**. low-refractive, pigmented VBs, **i–j**. high-refractive, yellow VBs. Living state (**h**: VBs stained blue-violet in CRB), except for **k** (in KOH) where VBs irreversibly disappeared. — **a**. *Orbilia sarraziniana*, **b**. *O. rubrovacuolata*, **c**. *Hyalorbilia ulicicola*, **d**. *Amphosoma atroolivaceum*, **e**. *Lilapila oculisporella,* **f**. *O. eucalypti* (H.B. 7825), **g**. *O. dryadum* (25.IX.2010), **h**. *O. sarraziniana* (H.B. 8225), **i**. *O. xanthostigma* (H.B. 7852), **j–k**. *O. xanthostigma* (H.B. 9723), **l–m**. *A. resinicola* (H.B. 9136d, 9162e).

these droplets do not completely fill the vacuole, they perform distinct Brownian motion by trembling or moving across the vacuole. The distinction between the two different types of VBs is not always clear, for instance, in Fig. 86: f each small droplet might represent a single vacuole because no Brownian motion was noted.

VBs occur mainly in the long terminal cell but also in the shorter lower cells of the paraphyses, and in the marginal cortical cells of the ectal excipulum. VBs are consistently absent in all species with a high desiccation tolerance (*Lilapila*, *Lecophagus*, *Orbilia* sections *Lentiformes*, *Habrostictis*, *Aurantiorubrae*, *Hemiorbilia*, *Ovoideae*, and *Orbilia* series *Microsomates*).

VBs of the homogeneous type are of low to medium, but sometimes also high refractivity, and were quite frequently observed in species which are sensitive or only slightly tolerant to desiccation, such as *Hyalorbilia*, *Pseudorbilia*, *Orbilia* sections *Helicoon* and *Arthrobotrys*, and series *Orbilia*, but in many species of these taxa they were only present in some of the studied populations. VBs of the guttular type are very diagnostic for the desiccation-tolerant genus *Amphosoma*. In the four recognized species the VBs occur as small (0.2–2 µm), consistently globose, strongly refractive droplets in low to high abundance, thereby often producing a multiguttulate pattern in paraphyses and cortical excipular cells (Fig. 86: d, l–m). These droplets occur inside vacuoles in which they sometimes perform vigorous (*A. macrosporum*) or only slight Brownian motion. Similar VBs were occasionally observed in *Lilapila* in the medullary excipulum, paraphyses (Fig. 86: e), and asci, where they occur scattered in the vacuoles by showing more or less distinct Brownian motion.

Only in a few species of *Orbiliomycetes* the VBs contain a conspicuous hydrophilous pigment. In this case, the pigment is usually homogeneously distributed in the vacuole. In *O. rubrovacuolata* the very low-refractive vacuoles have a rose-red colour (Fig. 86: b). VBs in *Hyalorbilia* are often very faintly or sometimes distinctly chlorinaceous-ochraceous (Fig. 86: c), and those in *O. atlantis* and *O. xanthostigma* have a yellow-chlorinaceous colour.

In a few cases, VBs of the guttular type develop from those of the homogeneous type. In populations of *Orbilia xanthostigma* the young paraphyses contain many small, globose, medium refractive, yellow-chlorinaceous vacuoles of the homogeneous type. With increasing maturity these fuse to form one or a few larger low-refractive, homogeneously yellow vacuoles. At maturity the pigmented substance in these vacuoles precipitates to form bright golden groups of droplets showing Brownian motion. These aggregations of yellow granules also occur in large vacuoles of the inflated ectal and medullary excipular cells (Figs 86: i–j; 98: e), at a time when the vacuoles of paraphyses may still be homogeneously pigmented. In *Hyalorbilia* spp., *O. rubrovacuolata*, and *O. atlantis*, however, such precipitation of vacuolar pigments was never observed.

The vacuolar nature of the golden yellow droplets in *O. xanthostigma* is easily demonstrated by their irregular movement inside large ectal excipular cells during about one minute across large vacuoles, which have a diameter of ca. 5–10 µm.

When adding KOH to the water mount, the granular droplets instantly disappear while the yellow pigment is stable and gets homogeneously dispersed (Fig. 86: j–k). However, very similar-looking yellow, minute, KOH-resistant LBs occur outside the vacuoles, particularly in the lower half of the paraphyses and in the subhymenium. In the lower paraphysis cells both yellow vacuoles and yellow LBs occur, the vacuoles in the centre and the LBs more laterally and at the septa. Interestingly, both types of pigments stain blue-green in IKI.

Besides *Orbiliomycetes*, VBs occur in many genera of *Helotiales* (here also in the hairs), and in some taxa of *Pezizales*. In the *Helotiales* the presence vs. absence of VBs in paraphyses and excipular cells, and also their shape and pigmentation provide a valuable vital character at the genus or species level (Baral 1992: figs 27–33). VBs with a yellow or rarely orange pigmentation occur, e.g., in some species of *Calycellina*, *Hymenoscyphus*, *Lachnum*, *Mollisia*, or *Trochila*. Exceptionally, VBs occur in ascospores of *Helotiales* (Fig. 73).

Recognition of vacuoles and VBs. Generally, vacuoles can be identified by staining with basic dyes. These are added to a water mount and require some patience, because entry of the dye into intact vacuoles may take some minutes, but can be accelerated by adding very diluted alkali (NH_4OH or KOH). Non-refractive vacuoles stain in CRB (or TB) either homogeneously violet (e.g., the large vacuole of mature asci), or dark blue-violet globose precipitations (MCs = metachromatic bodies) are mostly induced. Low- to medium refractive VBs yield a homogeneously blue-violet stain (Fig. 86: h), and high-refractive VBs stain bright blue to turquoise. Neutral red stains VBs light orange-red. The cytoplasm outside the vacuoles remains unstained as long as the cells are viable. Based on the different colours between non-refractive and refractive vacuoles, we assume that the blue to turquoise stain of VBs is induced by a metachromatic effect of the refractive substance rather than a deviating pH of the vacuole sap (see Baral 1992: 363f.).

When 1–5% KOH, NH_4OH, or other toxic mountants such as lactophenol, chloral hydrate, or acids (e.g., formic, acetic or lactic acid) are added to the water mount, the VBs disappear promptly and irreversibly (Figs 73, 86: j–k). The same happens if the cells die by mechanical influence or desiccation, or when heating the slide. Also the vacuolar pigment may promptly disappear thereby or become diffuse (see Huhtinen 1990a: 71, *Hamatocanthoscypha uncipila*). VBs of *Orbiliomycetes* do not give any colour reaction in KOH (in the *Helotiales* a transient yellow reaction is known for many species of *Mollisia*, Baral 1992: 373). Oxidative colour changes of VBs which are typical of many *Helotiales* have also been noted in section *Helicoon* (see p. 104, Colours of the dead cytoplasm).

The chemical origin of VB refractivity is unknown. Perhaps phenolic compounds play a role (Baral 1992: 364–5), which lose their double bindings when the pH of the vacuoles is raised. On the other hand, the two types of VBs lose their refractivity also when adding reagents which lower the pH (contrary to a statement by Baral l.c.), i.e., they optically disappear as soon as the tonoplast is damaged.

KOH-sensitive (‘soluble’) cytoplasmic bodies (SCBs). Among the cytoplasmic inclusions that can be seen under the light microscope, a further category of transient structures provides a character of rather high taxonomic importance in the *Orbiliomycetes*. These organelles occur in two different morphological types: (1) globose SCBs (Fig. 87: a–b, l–n), and (2) variously shaped, angular to rod- or ring-shaped SCBs (called ‘crystalloid’ in the present study, Figs 87: c–n; 88: a–i). For both the term ‘KOH-soluble cytoplasmic bodies’ (SCBs) was introduced by Baral (1992: 368). Yet, the first type of SCBs never shows any kind of pigmentation, and clear cases of transitional types have not been observed, which suggests a different nature of the two types of inclusions. The refractivity and contrast of both types of organelles may vary between low and high.

Like VBs, SCBs promptly and irreversibly lose their refractivity when treated by 1–5% KOH (Tab. 8). Other toxic agents such as strong acids, lactophenol, or chloral hydrate likewise make SCBs irreversibly disappear. SCBs are never stained by CRB, even if slightly alkalinized. SCBs disappear also when cells die in water mounts. Solubility is probably an incorrect term for the disappearance of SCBs. More probable is that strong deviations from the normal pH induce irreversible chemical changes that involve the loss of refractivity, whereby the organelle gets invisible although the altered chemical compounds are still there. Globose SCBs may be stained pale reddish in CR_{SDS} (Fig. 87: b). SCBs are only observable in living cells. Dead cells often contain irregular bodies when observed, e.g., in KOH. These bodies originate from distorted lipid bodies and unexperienced workers may easily confuse them with SCBs.

Crystalloid SCBs are sometimes seen attached to the tonoplast of vacuoles (Fig. 88: h–i). This peculiarity and the impossibility to stain SCBs with CRB indicate that SCBs are extravacuolar structures. It may well be that crystalloid SCBs are always tightly associated with vacuoles and, when ring-shaped, they might encompass a vacuole in their centre. Globose SCBs may also occur in the intervacuolar space of highly vacuolated cells.

SCBs may occur in all cell types of the apothecium except for asci and ascospores, but are particularly found in the ectal excipulum and paraphyses. Both globose and crystalloid SCBs often occur in a single cell, usually one globose and 1–2 crystalloid SCBs, either side by side (Fig. 87: n), or remote from each other, thereby globose SCBs occur preferably near the tip of the terminal or cortical cells at the apothecial periphery (Fig. 87: a–b, l–m). In ectal excipular cells SCBs occur particularly at the apothecial flanks and margin, where they are usually larger than in the paraphyses, but sometimes also near the base. If the paraphyses are strongly inflated at the apex, they usually contain here larger SCBs than in the lower cells. SCBs are exceptionally found in the medullary excipulum, e.g., in *Lilapila* Pls 30: 1h–i; 32: 4c–g), or in the anchoring hyphae (in *Hyalorbilia ulicicola*, Pl. 60: 2h, 3h).

Globose SCBs vary in diameter among the species from (0.3–)0.8–1.5 up to 2–3(–5) µm and are always hyaline. Large SCBs of this type inside uninflated parts of the paraphyses sometimes take on an ellipsoid shape because of the limited space between the lateral walls (Fig. 87: l). Slow migration of globose SCBs across the cytoplasm during a few minutes can sometimes be observed. This was mainly seen in excipular cells in which the SCBs migrated from one end of the cell to the other similar as the migration of VBs inside vacuoles. Globose SCBs are often of a rather low refractivity, and in some species difficult to discern in a water mount. Although our test with various dyes such as CRB and IKI failed to stain globose SCBs, their contrast can strongly be enhanced when stained with IKI.

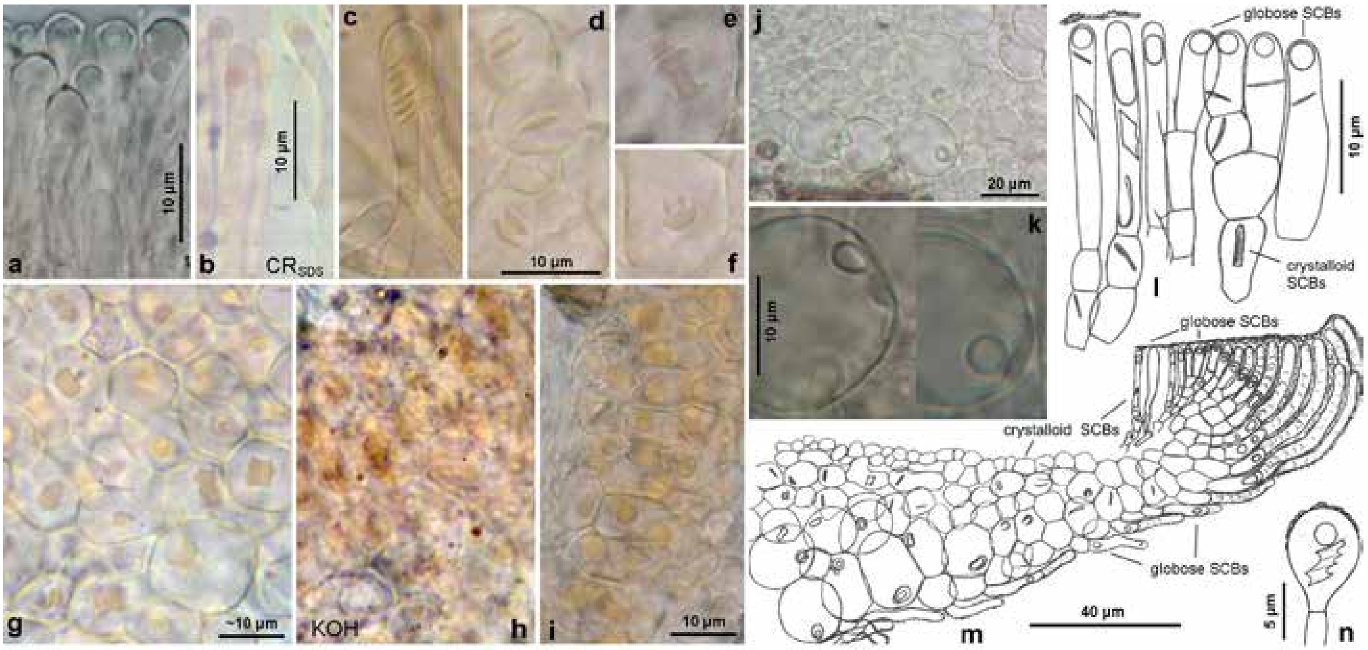


Figure 87: **a–b**. Globose SCBs in paraphyses (**a**. *O. vitalbae*, H.B. 9681, phot. R. Tena; **b**. *O. aprilis*, stained by CR_{SDS}, 15.XII.2011, phot. I. Wagner); **c**. crystalloid SCBs in paraphysis of *O.* aff. *myriella* (H.B. 8997c); **d–f**. crystalloid SCBs in excipular cells of *O. helicovinosa* (H.B. 9050b); **g–i**. crystalloid SCBs in cells of ectal excipulum at flanks (**g–h**: *O. corculispora* H.B. 7317a; **i**: *O. cercidicola*, H.B. 9151e; **h**: in KOH invisible); **j–k**: crystalloid (ring-shaped) SCBs in ectal excipulum (*O. crenatomarginata*, 27.VIII.2007, phot. P. Perz); **l–m**: crystalloid and globose SCBs in paraphyses and ectal excipulum (*O. crenatomarginata*); **n**: globose and crystalloid SCBs in terminal cell of paraphysis (*O. serpentina*).

SCBs of the globose type were observed in a majority of those species of *Orbilia* studied in the living state (84 %) and also sometimes in *Lilapila*, but could so far not be detected with certainty in *Lecophagus*, *Pseudorbilia*, and *Amphosoma*, and only exceptionally in *Hyalorbilia*. In the *Helotiales*, globose SCBs occur in several genera, being typical, e. g., of *Pyrenopeziza* (Baral 1992: 368, fig. 30).

SCBs of the crystalloid type often show a ring-, horseshoe- or keyhole-like shape, but they are also frequently rod-shaped or angular to spool-shaped, or only show an incomplete ring. Their size ranges from ~2–3 up to 5–10 µm in diam. In contrast to globose SCBs, migration of crystalloid SCBs has never been observed. Crystalloid SCBs are either hyaline or often pale to light yellowish-orange. Their pigment remains unaltered in alkali and acids.

The three-dimensional shape of crystalloid SCBs is not easy to resolve because it is impossible to turn single cells under the LM. The different aspects obviously depend on the direction of view. When viewing these bodies under an oblique angle, their spatial shape can best be resolved (Fig. 88: a, e). In top view they appear ring-like, and when viewed from the sides they look angular, reminiscent of a spool or reel with often jagged middle part (like a screw thread). The ring-like aspect varies from circular to irregularly keyhole-shaped (Fig. 88: b, g), but also incomplete rings occur or those with a strongly varying wall thickness, leading to sickle- or horseshoe-like shapes (Fig. 87: f; 88; a, b–c, f). In side view the bodies may form superimposed piles of rod-shaped structures (Fig. 87: c–e). Rings and keyholes or horseshoes on the one hand, and rod- to spool-shaped bodies on the other hand are thus mainly a matter of the viewing direction. Often one of the two types predominates in a section which suggests that the bodies tend to be oriented in one direction within an apothecium.

Like in globose SCBs, the chemical composition of crystalloid SCBs is unknown. Understanding the function of these bodies would be essential, particularly regarding the question why very closely related taxa differ in such a way that one of them has abolished formation of crystalloid SCBs. The reddish pigment suggests carotenoids, but this seems quite unlikely since IKI does not give any colour reaction to SCBs (see also p. 101–105). An osmotic test with a high-concentrated sugar solution in *Orbilia cercidicola* caused strong shrinkage of the living excipular cells but no perceptible size reduction of the crystalloid SCBs. The ontogeny of crystalloid SCBs in *Orbilia* appears to start from thin needle- or plate-like structures which are in close contact to the outer surface of the tonoplast of vacuoles.

Crystalloid SCBs occur in about 32 % of the species of *Orbilia*, and almost exclusively in desiccation-tolerant taxa. Among the desiccation-sensitive members of *Orbilia* only some species of series *Hyalinia* (*O. crenatomarginata*, *O. laevimarginata*, *O. crenatofalcata*, *O. scolecospora*) and *Xanthoguttulatae* (*O. nemaspora*, *O. crenatonemaspora*) are known to have crystalloid but always unpigmented SCBs. Very often the presence of these bodies helps in separating very closely related or otherwise similar taxa (Tab. 7). Further morphological or ecological characters are usually correlated with this feature and support the taxonomic value of crystalloid SCBs.

Although crystalloid SCBs are somewhat variable within a species regarding size, shape, and colour intensity, they must be attributed a high taxonomic value. Their remarkably consistent presence (or absence) was recorded in a lot of species, although the exceptional absence (or presence) was also sometimes noted. In only one species of *Hyalorbilia* (*H. ulicicola*) crystalloid SCBs could so far be observed, and in *Lilapila* similar ring-shaped SCBs were occasionally seen. *Lecophagus* is characterized by a special type of cubical bodies (see p. 94), whereas in *Pseudorbilia* and *Amphosoma* crystalloid SCBs never occurred. Also in *Orbilia* section *Lentiformes* they have never been observed, except for *O. cercidicola*, which has large, orange crystalloid SCBs, and which our phylogenetic analysis clearly assigns in

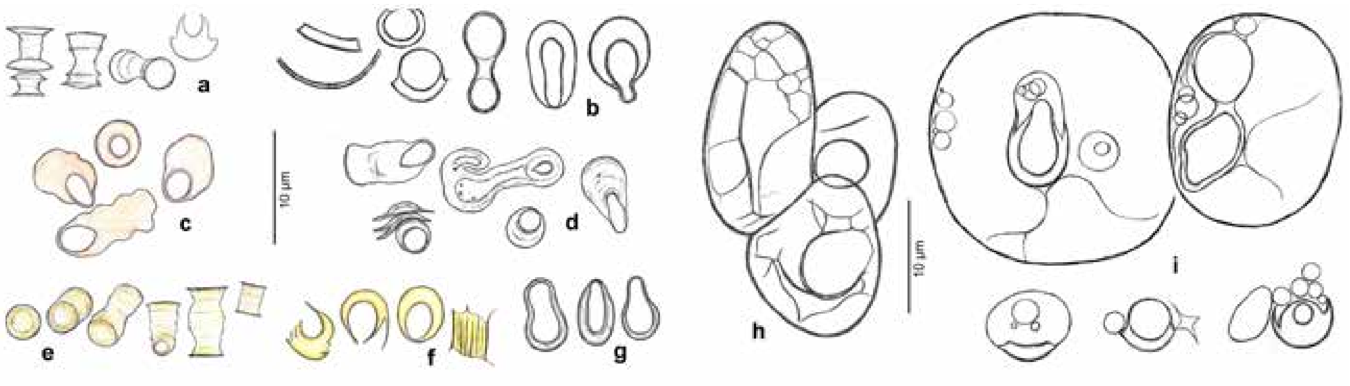


Figure 88: Different shapes of crystalloid SCBs in ectal excipular cells (cell wall only shown in **h–i**), partly seen from different viewing directions. — **a**. *O. helicovinosa*, **b**. *O. crenatomarginata*, **c**. *O. cercidicola*, **d**. *O. pleiohesperidea*, **e**. *O. pleiocoronohesperidea*, **f–g**. *O. carpoboloides*, **h**. *O. aurantiorubra*, **i**. *O. crenatomarginata*.

section *Lentiformes*. Because of this unexpected occurrence of crystalloid SCBs we place *O. cercidicola* in a series of its own.

Crystalloid SCBs resemble paracrystalline pyrenoids of algae, which likewise disappear optically in KOH and do not stain in CRB, according to our observation on an unidentified species of *Chlorophyta* associated, e.g., with *Orbilia aradi* (IVV: 25.VIII.2004, H.B. 7995). The oil bodies of liverworts (*Jungermanniidae*) are sometimes angular (e.g., in *Porella* or *Metzgeria*) and then resemble crystalloid SCBs. Contrary to SCBs of *Orbilia*, they generally do not disappear in unheated KOH, though they disappear when heating a water or KOH mount, apparently because they contain terpenoids.

Crystalloid SCBs have not been observed in any other order of *Ascomycota*. However, a similar type of SCBs usually occurs in the lanceolate paraphyses of species of *Brunnipila* and *Trichopeziza* (*Lachnaceae*, *Helotiales*): the centre of the long terminal cells typically contains unpigmented, rod-shaped or crystalloid SCBs of rather low refractivity (Baral 1992: 368, fig. 31, as 'crystalline SCBs'). Within the *Oomycota* an 'ooplast' occurs in the oospores of various genera. In *Wilsoniana bliti* (*Albuginaceae*, *Peronosporales*, Frey 2012: fig. 8–2) these ooplasts are ring-shaped with a strongly eccentric perforation, highly reminiscent of ring-shaped SCBs of *Orbilia*, apart from their larger size of ~17 µm.

Table 7. Examples of similar species differing in the SCBs.

Crystalloid SCBs present	Crystalloid SCBs absent
O. cercidicola	*O. cucumispora*
O. hesperidea	*O. montigena*
O. bicknellensis	*O. jacaensis*
O. serpentina	*O. maeandrina*
O. subvitalbae	*O. vitalbae*
O. subdelphinus	*O. delphinus*
O. nothoaprilis	*O. aprilis*

Cubical bodies. Strongly refractive bodies of a crystalloid, rectangular-isodiametric or sometimes almost globose shape are referred to as 'cubical bodies' here, which characterize the genus *Lecophagus* (Fig. 89: a–e). They might be related to Woronin bodies, but unlike those they occur more in the centre of the cell. Our tests showed that they do not take up basic dyes, although small vacuoles close to the SCBs stain deep blue (observed in *Lecophagus muscicola*). Like SCBs and WBs, also cubical bodies instantly disappear when KOH enters the cell. Abro & Dick (1990: fig. 1; Fig. 89: d) and Powell et al. (1990: figs 16, 21; Fig. 89: e) observed cubical bodies in their TEM micrographs. Obviously in error, Powell et al. identified them as large vacuoles that contain electron-dense material.

The cubical bodies in *Lecophagus* permit recognition of the genus even if only mycelial hyphae are available. These bodies also occur in the trapping organs, conidiophores, conidia,

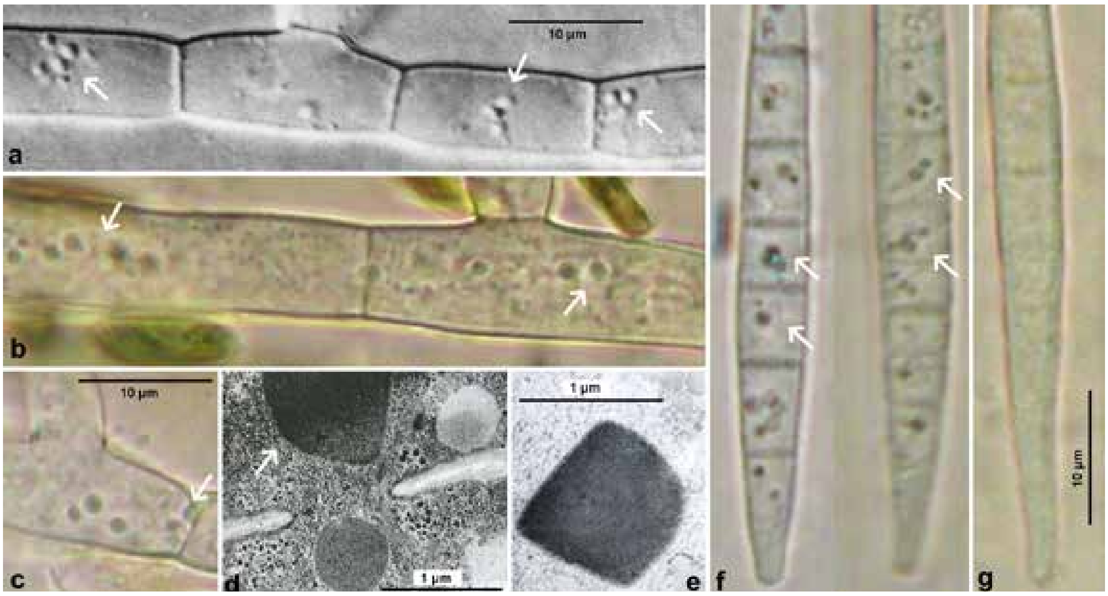


Figure 89: **a–e**. Cubical bodies in living mycelial hyphae of *Lecophagus* and conidia of *Hyalorbilia* as seen with the LM or TEM. — **a**. *L. navicularis* (from Tzean & Barron 1983: fig. 1); **b–c**. *L. muscicola* (H.B. 7771); **d–e**. *L. muscicola*, **d**. septum with WB (below) and cubical body (arrow; from Abro & Dick 1990: fig. 1, as *L. fasciculatus*), **e**. cubical body (from Powell et al. 1990: fig. 21, as *Zoophagus insidians*); **f**. conidia of *H. inflatula* (H.B. 9041a, 8173); **g**. id., in KOH, bodies disappeared (H.B. 8173).

and excipular cells. Similar bodies were observed in conidia of *Brachyphoris*, the anamorph of *Hyalorbilia* (Figs 9: a–b; 89: f–g), and also here the presence of these bodies aids identification of conidia as belonging to this genus. The bodies in *Hyalorbilia* are perhaps more globose than angular, and they were never seen in the anchoring hyphae or excipular cells, with a single exception of small ring-shaped SCBs in the centre of excipular cells in *H. fagi* (Pl. 92: 1d).

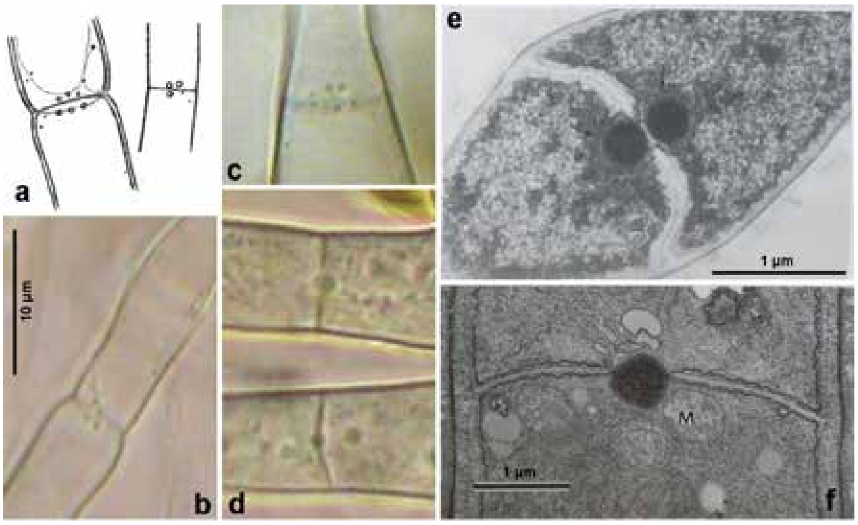


Figure 90: Woronin bodies at septa (**d–f**. while plugging the pore). — **a–c**. *O. alba* (H.B. 9051a), **a–b**. anchoring hyphae, **c**. stalk of adhesive knob; **d**. *Lecophagus muscicola* (H.B. 7771), mycelial hyphae; **e**. *Drechslerella brochopaga* (from Dowsett et al. 1977: fig. 18), mycelial hypha; f. *Lecophagus longisporus* (from Morikawa et al. 1993: fig. 10), adhesive peg.

Woronin bodies (WBs). WBs are minute, globose or crystalloid, membrane-bound structures in the cytoplasm close to the septa, and function in plugging the pore if one of the adjacent cells loses turgor (see Baral 1992: 368, also for further literature). WBs have mainly been reported in *Pezizales* and *Sordariales* (*Pezizomycotina*), but also *Neolectales* (*Taphrinomycotina*, see Landvik et al. 2003).

Under the LM, WBs are only seen in the living state, therefore, their presence usually escaped notice of those working with herbarium material. As with other sensitive organelles (SBs, VBs, SCBs), the substance which constitute WBs irreversibly loses its refractivity in KOH. This optical disappearance of WBs in alkali permits distinction from very similar looking LBs. Like LBs, WBs are found in the cytoplasm outside the vacuoles, and are not stained by vital stains.

WBs in *Orbiliomycetes* are often perceptible as very small (~0.1–0.2 µm), refractive, globose bodies that are situated very close to the septa, 1–2 on each side. They can be discerned especially in the paraphyses. In some taxa they are a bit larger, for example, in *Lecophagus* they attain ~0.3 µm diam. at the septa of anchoring hyphae. Exceptionally large WBs of 0.4–0.5(–0.8) µm diam. were observed in anchoring hyphae and adhesive knobs of *Orbilia alba* (Fig. 90: a–c). Drechsler (1937a, 1943b, 1947, 1952, 1954) frequently illustrated minute WBs at the septa of mycelial hyphae and often also conidiophores, usually two on each side, mainly in those predacious hyphomycetes that are today assigned to the *Orbiliomycetes*. However, he apparently never mentioned these bodies.

With the TEM, globose WBs were repeatedly observed at the septa of mycelial hyphae and trapping organs in *Orbilia* section *Arthrobotrys*: e. g., in *Drechslerella brochopaga* (Dowsett et al. 1977, Fig. 90: e), *D. dactyloides* (Heintz & Pramer 1972), *D. bembicodes* (Glockling & Dick 1994), *Dactylellina lysipaga* (Wimble & Young 1983), and '*D.*' *entomopaga* (Saikawa et al. 2010). Their size can be evaluated as (0.2–)0.3–0.4(–0.5) µm diam., in the latter species as 0.45–0.65 µm. WBs in *Lecophagus* show a size of 0.3–0.6 µm (*L. fasciculatus*, Abro & Dick 1990; *L. longisporus*, Morikawa et al. 1993, Fig. 90: f). Kumar et al. (2012: figs 14–17) figured WBs of 0.2–0.25(–0.35) µm diam. in cells of excipulum, paraphyses, and ascogenous hyphae in *O. tenuispora* (section *Helicoon*).

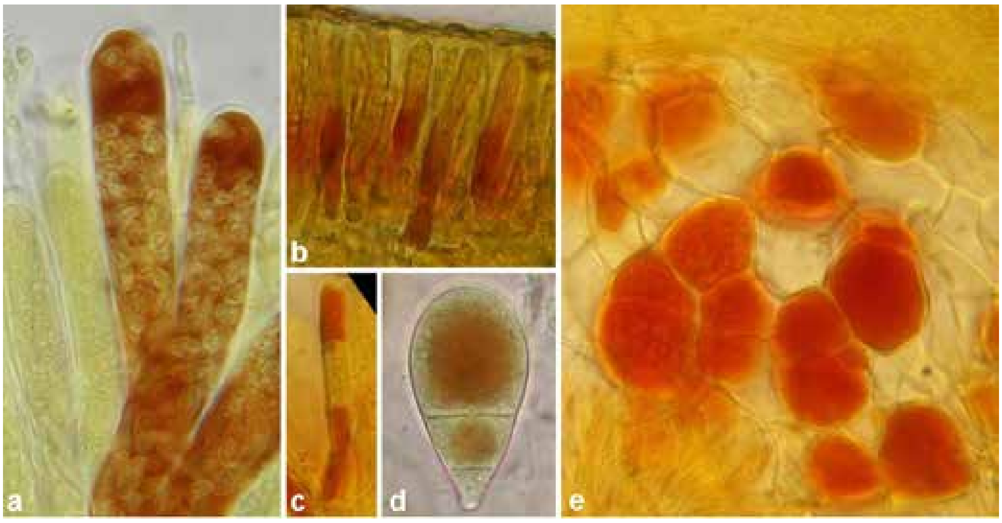


Figure 91: Glycogen in *Orbiliomycetes* stained red-brown in IKI (**e**. KOH+IKI). — **a**. mature dead asci of *Orbilia myriophanosoma* (H.B. 8865; immature asci on the left are unstained); **b–c**. mature dead asci of *Hyalorbilia polypori* (**b**. H.B. 6939a, **c**. H.B. 7965b), pars sporifera remaining unstained; **d**. living conidium of *O. elegans* (H.B. 6972a); **e**. ectal excipulum of *O. blumenaviensis*, some of the cells showing a strongly dextrinoid cytoplasm (H.B. 8029b).

Glycogen. Dextrinoid, more or less globose areas in the cytoplasm indicate the presence of glycogen depots. In many genera of the *Helotiales* they occur in ascospores with a low to medium lipid content (Baral 1992: figs 12–13), where they are usually surrounded by small LBs which form a hollow sphere around them. The reaction is light to deep red-brown and can be obtained in IKI as well as MLZ (with or without KOH-pretreatment). The dextrinoid reaction is generally attributed to the presence of glycogen as a storage carbohydrate, and

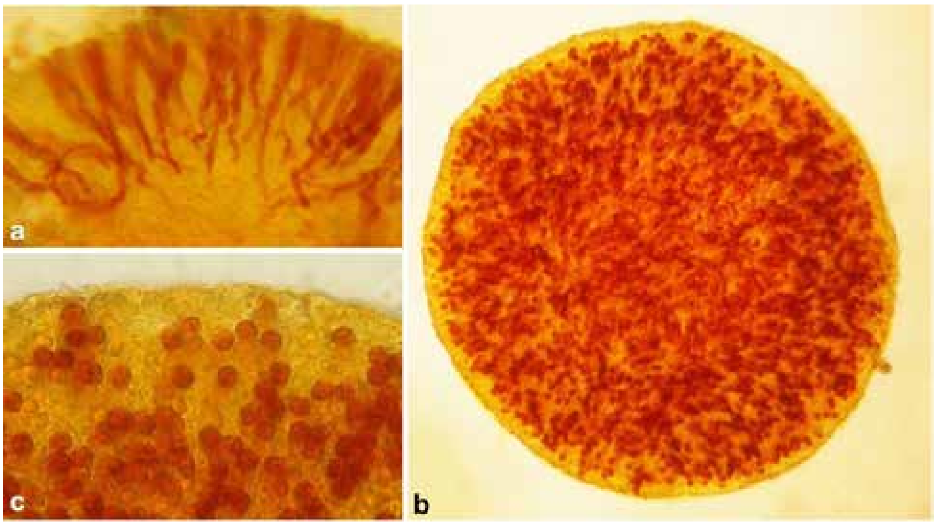


Figure 92: Asci in apothecia of *Orbilia* stained deep red-brown in IKI (KOH-pretrated) due to the presence of glycogen. — **a**. median section (*O. pleistoeuonymi*, H.B. 6494a); **b–c**. top view on apothecium (*O. sarraziniana*, H.B. 8721a).

can be observed in many classes of ascomycetes, particularly in the ascoplasm.

In the *Orbiliomycetes* such dextrinoid areas were observed in asci, ascospores, conidia, and excipular cells (Figs 91–92). Glycogen depots in ascospores were only seen in rather broad spores, e. g., in *O. lentiformis* they showed a diameter of 1–2 µm (Pl. 158: 1a). Similar dextrinoid areas occur occasionally in conidia, particularly in those species of section *Arthrobotrys* with swollen conidial cells. Such conidia contain quite large glycogen depots which attain a size of up to 5–15 µm, depending on conidial width (Fig. 91: d). Conidia without swollen cells may also sometimes contain such depots (*H. polypori*), whereas different types of branched conidia have so far never been seen to contain glycogen (see Tab. 9).

In virtually all species of *Orbiliomycetes* the whole ascoplasm stains pale to deep red-brown, while the sporoplasm remains unstained (Fig. 91: a–c). The reaction is usually strongest in mature asci, whereas young asci are non-reactive and those containing immature spores show often only a faint reaction. In living asci the reaction is less intense. Some mature, dead, unemptied asci may lack the reaction, and it seems quite obvious that these had full turgescence when still alive. Very probably, a short period of time prior to spore discharge the glycogen is degraded into osmotically active monomers which are the cause of turgor increase (see also p. 46–47, Four different states of asci).

In some species the reaction may be rather faint irrespective of ascus maturity. A pale yellowish-reddish reaction was noted in *Lilapila* and some species of sections *Aurantiorubrae* (*Orbilia kingsiana*, *O.* aff. *puyae*), *Ovoideae* (*O. cupularis*, *O. multimexicana*, *O. octosporoides*), and *Orbilia* (*O. liliputiana*).

Nuclei (N). Nuclei are sometimes discernible in young asci and in large spores when studied in the living state in water mounts under bright field optics or phase contrast (oil immersion), either unstained, or in vital stains like IKI or CRB. Nuclei form globose, non-refractive regions more or less in the centre of the cells. They always contain a nucleolus, a small, distinctly refractive, eccentric, (semi)globose body being broadly attached to the inner side of the nuclear membrane (Fig. 93: c). Nucleoli appear round in outline when seen in front or oblique view but half-moon-like in profile view (Fig. 93: a–b, see also Baral 1992: 372).

Nucleoli are selectively stained blue in CRB, whereas the remaining part of nuclei is unstained. IKI provokes a higher contrast to both nucleoli and nuclear membrane. Phase contrast may improve the visibility of nuclei in unstained preparations of living spores or young asci. In dead cells nuclei are completely invisible unless special staining techniques are applied.

The largest and most easily visible nuclei are the fusion nuclei which are found in or some distance above the centre of immature asci (Fig. 93a, see also Pls 163: 1c; 175: 2d; 375: 8b; 610: 1d). Fusion nuclei represent the short-lasting diplontic phase of an ascomycete, and can be seen with the LM in most species of ascomycetes without applying staining agents. Their diameter in *Orbilia* and *Lecophagus* was found to vary from 3.5–4.5 to 6–8 µm, and the nucleoli from 1.3 to 3 µm. Sometimes fine

Table 8. Behaviour of microstructures and pigments upon treatment with chemical reagents (KOH 2–20 %, HCl ~ 90 %, unheated, * = only visible in living state). Statement about SCBs also matches cubical bodies and Woronin bodies (WBs).

Microstructures/Pigments	IKI	MLZ	CRB	CB	CR	KOH	HCl
Spore bodies (SBs)*	–	–	turquoise-blue	–	–	disappearing	disappearing
Lipid bodies (LBs)	–	–	– / (rose)	–	–	resistant	resistant
Carotenoids	blue-green	blue-green	–	–	–	resistant	?
Vacuolar bodies (VBs)*	– / pale red	–	turquoise-blue	–	–	disappearing	disappearing
- pigment of VBs*	?	–	?	–	–	disappearing	disappearing
Globose SCBs*	–	–	–	–	(rose-red)	disappearing	disappearing
Crystalloid SCBs*	–	–	–	–	–	disappearing	disappearing
- pigment of crystalloid SCBs	–	–	–	–	–	resistant	?
Glycogen	red-brown	red-brown	–	–	–	resistant	?
Nucleoli*	–	–	pale blue	–	–	disappearing	disappearing
Gel	–	–	lilac	pale blue	–?	–	–
Exudate	red-brown	red-brown	turquoise	blue	rose-red	resistant	resistant
Pigment of exudate	–	–	–	–	–	resistant	resistant
Ascus apical dome	–	– / (reddish)	–	–	– / rose	resistant	resistant
Glassy processes	–	–	–	–	–	resistant	resistant

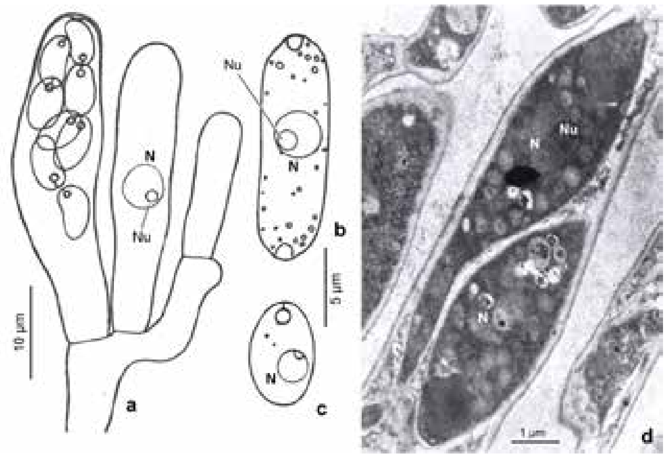


Figure 93: Nuclei. — **a**. fusion nucleus in young ascus (*Lecophagus ellipsoideus*); **b–d**. nuclei in ascospores, **b**. *Amphosoma macrosporum*; **c**. *Orbilia octosporoides*; **d**. TEM of ascospores of *O. aristata* (Müller 1998: fig. 21A, as *O. occulta*, N = nucleus, Nu = nucleolus, SB = spore body).

chromatine fibres can be seen in the non-refractive nucleoplasm of fusion nuclei.

Haplontic nuclei formed during meiotic division of the fusion nucleus are much smaller and much less conspicuous. Binucleate stages were sometimes observed, those with 4 or 8 nuclei only exceptionally, and higher stages in multispored species could never be seen.

Nuclei in the living ascospores were observed in a few desiccation-tolerant, more or less large-spored species of *Amphosoma* (*A. macrosporum*, Fig. 93: b), *Orbilia* sections *Lentiformes* (*O. patellarioides*, *O. cercidicola*, *O. cucumispora*, *O. lanternae*), *Hemiorbilia* (*O. megahesperidea*), *Habrostictis* (*O. multihamulata*, *O. barrowensis*), and *Ovoidea* (*O. octosporoides*, Fig. 93: c). In all these species the spores were uninucleate, and the size of the nuclei ranges from 1.7 to 2.8 µm, that of nucleoli from 0.7 to 1.3 µm. Uninucleate ascospores were also reported by Benny et al. (1978) in *O. sarraziniana* and by Müller (1998, Fig. 93: d) in *O. aristata*.

Weber (1992: 124) observed by means of cytofluorometry (DAPI) that the ascospores of *O. eucalypti* (as *O. coccinella*), *O. comma*, *O. ?xanthostigma* (as *O. delicatula*), *O. sarraziniana*, and *O. vinosa* are uninucleate. With this method also the cells of paraphyses were found to be uninucleate. Cultures of *Orbiliomycetes* were not available during this research, therefore, nuclear numbers in mycelia could not be observed. Berthet (1964a: 126, 1964b: 23) reported the mycelium of *O. tremulae* (as *O. xanthostigma*) to be uninucleate (stained by haematoxylin or Giemsa). Multinucleate cells were reported with the TEM for mycelia of *Lecophagus* by Dick (1990) and Morikawa et al. (1993), and in constricting rings of *Drechslerella brochopaga* by Zachariah & Insell (1979) and Nordbring-Hertz et al. (1995). Rubner (1996: 30) found mycelia, conidia, and trapping organs in most of her nematophagous species to contain more than one nucleus (stained with DAPI): depending on the species, the mycelial cells were either 1- or 2–5-nucleate, the conidial cells either (1–)2(–4)-, 6–12-, or up to 20-nucleate or more if conidial cells strongly swollen, and the cells of adhesive hyphal branches 2–4-nucleate. Nakagiri & Ito (1996) observed in *Orbilia multiformis* (as *Dactylella iridis*) (1–)2–3(–5) nuclei in each hyphal cell, and 3–14 nuclei in each conidial cell stained with Hoechst 33258. In the present study, the cells of mycelium and conidiophores in *O. menageshae* were about 4-nucleate (LM-observation, living state, in IKI).

Weber (l.c.) evaluated the relative DNA-content in various groups of ascomycetes. With eleven strains of seven species investigated, the *Orbiliomycetes* turned out to have a somewhat intermediate ploidy level in comparison with the *Helotiales*. With the assumption that the basic ploidy level is somewhat higher than in the *Helotiales*, then *O. crenatomarginata* (as *Hyalinia rosella*) has a ploidy level of 1 ×, *O. sarraziniana* and *O. vinosa* 2 ×, and *Hyalorbilia inflatula* 4 ×. *O. leucostigma*/*xanthostigma* varied in ploidy levels: some apothecia of one sample (REG 143) deviated in having 1 ×, whereas others had 2 ×; the other two samples (REG 134, 138) had consistently 2 ×. Two species were intermediate compared to these ploidy levels (*O. comma* 1.5 ×, *O. eucalypti* [as *O. coccinella*] 2.5 ×) and would thus better concur with the 2 × and 3 × ploidy levels of the *Helotiales*.

Table 9. Conidia and mycelial hyphae tested with CRB and IKI (+ = pale, ++ = medium, +++ = strong, – = unstained).

Species	Cresyl blue (CRB)		Lugol (IKI)
	lilac stain of conidial wall surface	lilac stain of hyphal wall surface	glycogen depots in conidia (staining red-brown)
H. lignatilis YMF 1.00596	–	?	–
H. inflatula H.B. 9328	(+)	?	?
H. fagi H.B. 9105a	+	–	?
H. polypori H.B. 7557a	–	–	+
O. purshiae H.B. 7462a	+	?	?
O. pleistoeuonymi H.B. 6949a	++	+	–
O. carpoboloides H.B. 6639c	–/+	–/+	?
O. cryptogena H.B. 7397a		–/+	?
O. aprilis H.B. 6715a	++	++	–
O. cocois H.B. 7647	?	?	++
O. cotoneastri H.B. 7241a, 9051b (cf.)	++	+	(+)
O. scaphoides H.B. 6972b	++	+	++
O. elegans H.B. 6972a	++	+	++
O. auricolor H.B. 6664, 7472, 9553	++	++	++/–
O. menageshae H.B. 9275	++	++	++
O. oxyspora H.B. 9390a	++	++	++

Excretions on the cell wall

Gelatinous sheaths. Gel layers that show a ± strong metachromatic reaction were observed in all groups of *Orbiliomycetes*. The gelatinous matrix is exuded from almost all types of cells of both anamorphs and teleomorph, including the asci, conidia trapping organs (Figs 94, 107: d–i), but excluding the ascospores. The gel covers the cell wall as a thin, rarely thick, usually hyaline sheath. It is either non-refractive and then invisible without staining, or more or less visible in water or KOH by a varying strength of refractivity. In those *Orbilia* species with a dark olivaceous exudate, the gel is more apparent by a somewhat olivaceous colouration.

Gelatinous excretions that are non-refractive can usually be visualized by their property to get stained in basic dyes. For example, aqueous Cresyl blue (CRB) or

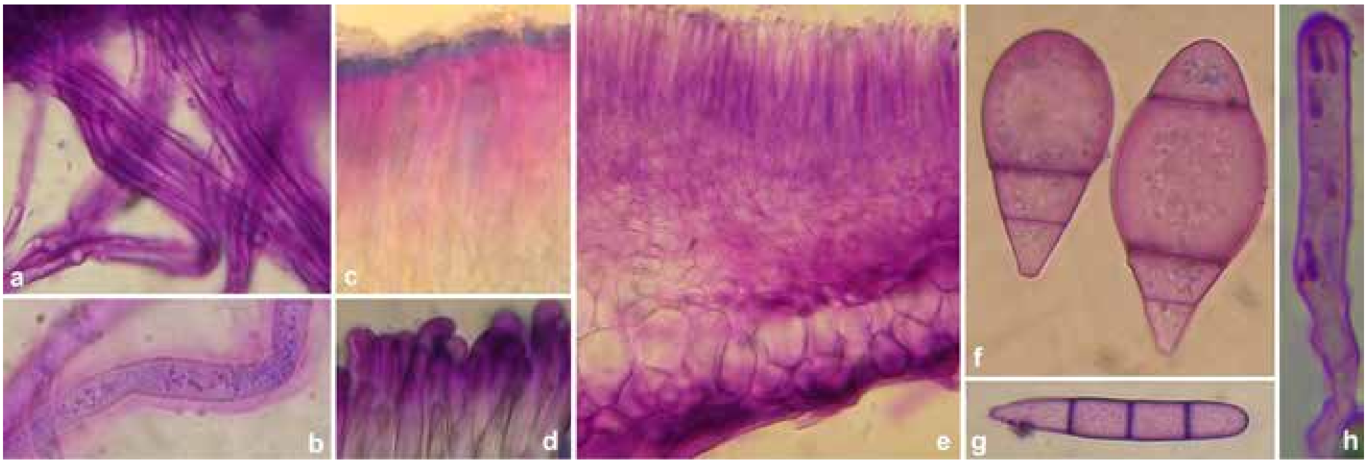


Figure 94: Gel that stains lilac in Cresyl blue (CRB) is excreted from the cell wall of most organs of *Orbilia*. — **a**. anchoring hyphae (*O. pilifera*, H.B. 8076a), **b**. hyphae in pure culture (*O. menageshae*, H.B. 9275a), **c**. hymenium (*Orbilia aristata*, H.B. 9226a, exudate over the paraphyses stained turquoise-blue), **d**. tips of glassy processes (*O. albidorosea*, H.B. 9031), **e**. hymenium, medullary and ectal excipulum (*O. alba*, H.B. 9051a), **f–g**. conidia (**f**. *O. elegans*, H.B. 6972a; **g**. *O.* cf. *cotoneastri*, H.B. 9051b), **h**. ascus (*O. vinosa*, 15.V.2010, phot. I. Wagner).

Toluidine blue (TB) provoke a metachromatic stain to the gel, i.e, the blue colour of the dye is changed to a pale or bright purplish lilac. Such metachromatic effects in the outer cell walls might be due to a more alkaline pH of the gel; yet, they are generally referred to a denser storing of the molecules (see Grube 1993). In any case, the different colour that CRB adopts in contact with exudate (Fig. 94: c) should result from a different chemistry of the stained structure. Methyl blue (CB_a) stains gel in a blue colour, and Neutral red (NR) orange-red. When ingredients such as lactophenol are added to these basic dyes (e.g., in CB_L), the staining of gel as well as the metachromatic colour change are completely suppressed. Congo red (CR) hardly gives any stain to the gel. Only when the gel is thick enough it can be visualized by adding India ink to a water mount, or by dehydrating it with alcohol (Fig. 107: d). Refractive gel is apparently more dense and contains less water, and its ability to take up stains is perhaps therefore reduced.

Gel on excipular cells and anchoring hyphae. Gel between excipular cells and on the anchoring hyphae stains generally deep lilac in CRB in the *Orbiliomycetes* (*Lecophagus*, *Hyalorbilia*, *Amphosoma*, *Orbilia*) as well as the *Helotiales* (Fig. 94: a–b, e). The cells of the ectal excipulum firmly cohere by a lower or higher amount of gel. However, even within a species the abundance of gel is rather variable. For instance, in *Hyalorbilia citrina* (Fig. 77: e–f) the gel thickness varies from 0.5–1 to 1–3(–5) µm, depending on the collection. The cells of the medullary excipulum are normally covered only by a thin gel layer and are, therefore, not firmly agglutinated. Yet, in about a third of the species of *Hyalorbilia* (*H. brevistipitata*, *H. lunata*, *H. polypori*, *H. puertoricensis*, *H. inflatula*, *H. japonica*, *H. citrina*, *H. tortuosa*, *H. fagi*, *H. arcuata*) and in a few species of *Orbilia* (e.g., *O. suberis*, *O. blumenaviensis*, *O. pilosa*), the gel was often found to be rather abundant and refractive. In *Lilapila* the gel is very abundant and provokes a rather strong gelatinous consistency of the apothecia, but it stained only faintly lilac in CRB.

As with the solid matrix of glassy processes, gelatinous sheaths can probably be interpreted as an outer layer of the cell wall. Actually, in those species of *Orbiliomycetes* with a more or less gelatinized ectal or medullary excipulum, gelatinized anchoring hyphae, or thick-walled hairs, the distinction between a thickened cell wall and refractive gel on the wall or between the cells was often quite impossible. Within the excipular texture no sharp limit is usually visible between the gel produced from two adjacent cells (Fig. 77: e), therefore, only the total thickness of both gel layers (referred to as 'common wall' in the descriptions) can be measured. At the surface of gelatinized cortical cells a sharp external limit of the gel is usually seen, which causes a thick-walled appearance of these cells (Fig. 77: f). Anchoring hyphae in *Hyalorbilia* are often thick-walled, and it seems possible that the matrix of this wall corresponds to the gel found between the excipular cells. The same could be true for the thick-walled anchoring hyphae in *O. denticulata* and the hairs in *O. pilosa* and *O. phragmotricha*.

Gel on asci and paraphyses. Agglutination of the hymenial elements is often reported as typical of the genus *Orbilia* (s.l.). However, such strong agglutination of paraphyses and asci is more or less restricted to the genus *Hyalorbilia*. Here the hymenial gel is generally abundant and more dense and tough, and stains pale to bright lilac in CRB. It holds the paraphyses and asci together by forming a coherent gelatinous matrix which often completely prohibits separation of the elements. Completely isolated, sometimes still turgescent single asci could only be seen in a few species with sparse gelatinization.

In the other genera of *Orbiliomycetes* the gel does not fill the entire intercellular space of the hymenium but forms an individual thin sheath over each paraphysis or ascus. Particularly the ascus apex is covered by a distinctly stainable gel layer which is mainly seen in species of *Orbilia* (Fig. 94: h) and *Amphosoma*, but less so in *Hyalorbilia*. The ascus gel increases in thickness towards the tips, where it seems to correspond to the 'periascus' in the sense applied by Chadefaud (1973) and Bellemère (1975, 1977). In contrast to *Hyalorbilia*, only the tips of paraphyses are more or less held together by gel, particularly in desiccation-tolerant species. If little of such material is present, the paraphyses are easily separable even by slight mechanical pressure, at least in living specimens. This feature of non-coherent hymenial elements was also stressed by Haines & Egger (1982: 112) for *O. piloboloides* (= *O. carpoboloides*) and by Spooner (1987) for those species of *Orbiliomycetes* without abundant exudate. Although the gel is quite invisible in water mounts, its presence over the tips of paraphyses and asci is evident when there is some distance between refractive exudate and cell wall (Fig. 95: b, f).

Random tests in the *Helotiales* showed that the ascus wall

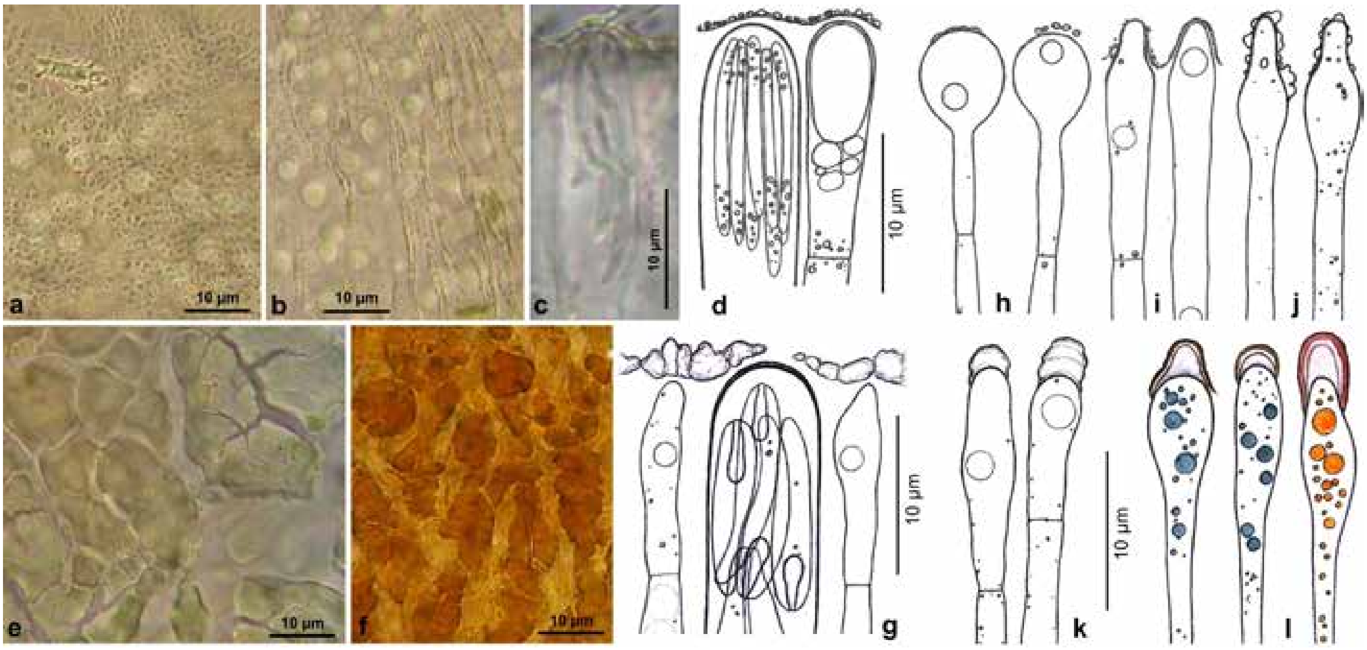


Figure 95: Exudate over paraphyses and asci in *Hyalorbilia* (**a–d**) and *Orbilia* (**e–l**). — **a–b**, **e**. top view on hymenial surface; **f**. external view on marginal excipulum; **a–d**. small angular clods on a thin, continuous, inelastic layer firmly attached to a gel matrix; **b**. after squashing, the rigid layer gets folded whereby the clods do not join; **c–d**. paraphysis and turgescent asci lifting the overlying gel and exudate; **e–g**. large irregular clods ± loosely attached to gel over paraphyses or marginal excipular cells (*Orbilia* section *Hemiorbilia*); **h–l**. exudate ± firmly attached to each paraphysis tip (but in **i** forming a thin coherent layer). Living state (in H_2O, **l** left in IKI) except for **a** (in KOH), **b**, **e** (in H_2O), **f** (in KOH+CR), **l** right (in KOH+CR). — **a**. *Hyalorbilia inflatula* (VII.1881); **b**. *H. fagi* (H.B. 7812); **c**. *H. berberidis* (H.B. 7648b); **d**. *H. juliae* (H.B. 7029); **e**. *Orbilia pleionavajoana* (H.B. 8049a); **f**. *O.* aff. *aprilis* (H.B. 9132a); **g**. *O. montigena* (H.B. 7152a); **h**. *O. cylindrosoma* (H.B. 6393); **i**. *O. rubella* (H.B. 7442); **j**. *O. euphorbiae* (S-F 41427); **k**. *O. aradi* (H.B. 7628c); **l**. *O. xanthoguttulata* (H.B. 7464).

surface does not stain in CRB, except for the periascus which gets pale lilac (e.g., in *Hymenoscyphus*). Metachromatic reactions of ascus walls (including the endotunica) and gel sheaths were reported for members of *Arthopyrenia* by Grube (1993) using mainly Toluidine blue. Also in *Deltopyxis* the ascus wall surface stains faintly to deeply lilac in CRB (Baral & Marson 2012).

Gel on ascospores and conidia. The ascospores of some helotialean genera are covered by an often invisible gel that stains pale to bright purplish-lilac in CRB (see Baral 1992: 356). No such gel layer on the walls of ascospores could be found in any of the many species of *Orbiliomycetes* tested. However, when dead spores inside dead asci are examined, the spores look seemingly ensheathed because both the asco- and sporoplasm may be detached from the spore wall, which provokes the impression of a spore sheath (see Fig. 10: d–e).

The gel layer over conidial walls is usually very thin and also here only seen when applying a stain (Fig. 94: f–g). A survey on the examined species with a CRB-lilac conidial gel is found in Tab. 9. Rubner (1996: figs 14, 46) found the large cell of the 1-septate conidium of *Drechslerella polybrocha* (as *Monacrosporium*) to be often enveloped in a layer of mucus. A ~1–2 µm thick gel layer was seen in our isolate of *O. polybrocha*.

Function. The function of gel is not clear in every case. In the ectal excipulum it undoubtedly provides mechanical stability of the tissue. In the hymenium the gel might serve as a lubricant for the growth of young asci. This is supported by the fact that the thickness of the gel layers in the hymenium decreases with maturity. In contrast to exudate, gel swells upon water uptake. In addition to serving as a gluing substance to affix the exudate clods to the wall of the paraphysis apices, gel in desiccation-tolerant apothecia of *Orbilia* should play a role in the de- and rehydration process: shrinkage and swelling of the gel might assist in closing and opening of the crevices between the exudate clods in *Orbilia*, and in folding of the continuous, inelastic exudate layer in *Hyalorbilia*.

An ecological function of gel in apothecial tissue was frequently believed to lie in retarding evaporation, but we doubt this view. When observing specimens during drying at normal room conditions, small-sized apothecia dry down within a few minutes when they adhere to rather small portions of substrate, irrespective of being gelatinized or not.

Gel also facilitates attachment of conidia to invertebrates which serve as vectors or victims (see Fig. 118).

Amorphous exudate. In many desiccation-tolerant taxa of *Orbiliomycetes* a usually strongly refractive, solid, amorphous, mostly cloddy or granular exudate covers the exterior of the apothecia (tips of paraphyses, cortical cells of ectal excipulum on margin and flanks), whereas in most desiccation-sensitive taxa the exudate is quite poorly developed or more or less absent. The exudate forms ~0.3–2 µm, rarely ~3–5(–8) µm thick granules or clods which are attached to the gel exuded by the paraphysis tips and cortical cells (Fig. 95). The outer surface of exudate is often strongly uneven by protuberances and clefts. In section *Aurantiorubrae* and series *Microsomates* (section *Orbilia*) the exudate often individually covers each paraphysis tip as ± firmly attached, thin granules or thick glassy caps (Figs 95: k–l; 96: h–k).

Usually the exudate is hyaline or shows a faint to distinct yellowish colour. In *Hyalorbilia* it is generally faintly chlorinaceous-amber. In a few species of *Orbilia* and *Amphosoma* the exudate is deeply olivaceous, and in *Lilapila* and *Liladisca* it has a deep purplish-lilac colour (see p. 102). In *Lilapila* the exudate occurs as granules between the cells of the whole excipulum, also between the paraphyses but not above their tips, and the anchoring hyphae are covered by a thin, rough, hyaline exudate; all this is quite unusual within the *Orbiliomycetes*.

The exudate neither swells by imbibition during water uptake, nor does it shrink during drying. Nevertheless, it is hydrophilous, which is obvious when spraying water on dry desiccation-tolerant apothecia: the water is immediately absorbed, and there is rarely any trapped air to be seen around the exudate in a water mount. In contrast to this, the hymenia of *Propolis* or *Mellitiosporiella* (*Rhytismatales*) are very difficult to rehydrate, and trapped air is often found among the exudate which is rather hydrophobous.

There is a noticeable difference between exudate in *Orbilia* and *Hyalorbilia*, particularly when comparing desiccation-tolerant species. In *Orbilia* the exudate is usually broken by a web of cracks into irregularly-shaped pieces of clods of varying size (about 1–10 or even 20 µm diam., best seen in surface view, Fig. 95: e–f). When the apothecia shrink during drying, the clods close their crevices by forming a continuous shield over the complete surface of the apothecium, also the underlying gel matrix contracts thereby. Upon rehydration the gel matrix and cell lumina swell by water uptake and the clefts reappear.

In *Hyalorbilia* the compact gel matrix is terminated by a ~0.2–0.3 µm thick refractive, inelastic, continuous layer of exudate which is densely covered by small roundish warts or angular clods ~0.2–1.5 µm diam. (Fig. 95: a). Although the borders of these warts seem to match together as in *Orbilia*, the thin inelastic, continuous layer beneath gets folded in squash mounts (Fig. 95: b), a phenomenon never seen in *Orbilia*. This folding of the exudate certainly happens also upon drying. Both gel and exudate cover the asci even when they attain full turgescence. Thereby the asci sometimes lift the covering layer a few micrometers above the paraphyses (Fig. 95: c). The continuous outer layer appears to burst only when the asci explode. In *Orbilia* the gel is more isolated around each paraphysis and, therefore, much less coherent, and the clods of exudate easily separate from each other, when the asci elongate at full turgescence.

Terminology. Höhnel (1907a: 132, *Hyalinia crenatomarginata*) and Boudier (1904–10: 269, pl. 465, 466, *H. rosella* and *H. crystallina*) were apparently the first to mention the exudate in *Orbilia* (= *O. crenatomarginata*), the former as a ‘cuticle-like waxy layer’, the latter as ‘epithecium’. Spooner (1987) called the exudate ‘amorphous matter forming an (encrusting) epithecium’ in which the apices of paraphyses are ‘embedded’. We have avoided the term epithecium which means ‘above the hymenium’ or ‘above the asci’, since its application in the literature is not very consistent, and since the very same exudate is also found on the surface of the excipulum. In the literature, the apices of paraphyses in various groups of ascomycetes are frequently reported to form a coherent epithecium above the asci due to the presence of some intercellular, hyaline or pigmented amorphous matrix. However, such application of the term epithecium is more or less connected to the dead state of asci: living, fully turgescent asci frequently penetrate and overtop the ‘epithecium’ prior to spore discharge. The creators of the term epithecium were obviously unaware of the much greater length of living asci, and refer to the artificial situation in dead herbarium material in which the shrunken asci are usually overtopped by the apices and the exudate of the paraphyses. A different definition of the term ‘epithecium’ is found in Cannon et al. (1995, see also Korf 1973: 250): ‘tissue at the surface of an apothecium formed by the branching of the ends of the paraphyses above the asci’. In this literature another term (‘pseudoepithecium’) appears better to apply to the exudate of the *Orbiliomycetes*: ‘an amorphous or granular layer overlying paraphyses in an apothecium and in which their tips are immersed, but not forming a separate tissue’. We feel, however, that it is very difficult to decide whether apically branched paraphyses do actually form a tissue or not, especially considering the fact that, within a species, the amount of branching varies and increases with the age of the apothecium. In *Orbilia* frequent branching near the paraphysis apices is typical of desiccation-tolerant species, but is not coupled with a higher amount of exudate over them.

Formation. The exudate is formed at an early stage of ascoma development, long before the ascogenous hyphae reach the hymenium. It is excreted from the tips of the vegetative cortical cells by passing both cell wall and gel. During growth of the young apothecium the clods increase in size and number. In *Orbilia* the exudate often detaches from the tips of the paraphyses when squashing a water mount. This is particularly the case when the apothecia are still rather young. During maturation, however, the exudate becomes more and more firmly attached, apparently because of the underlying gel becoming significantly more able

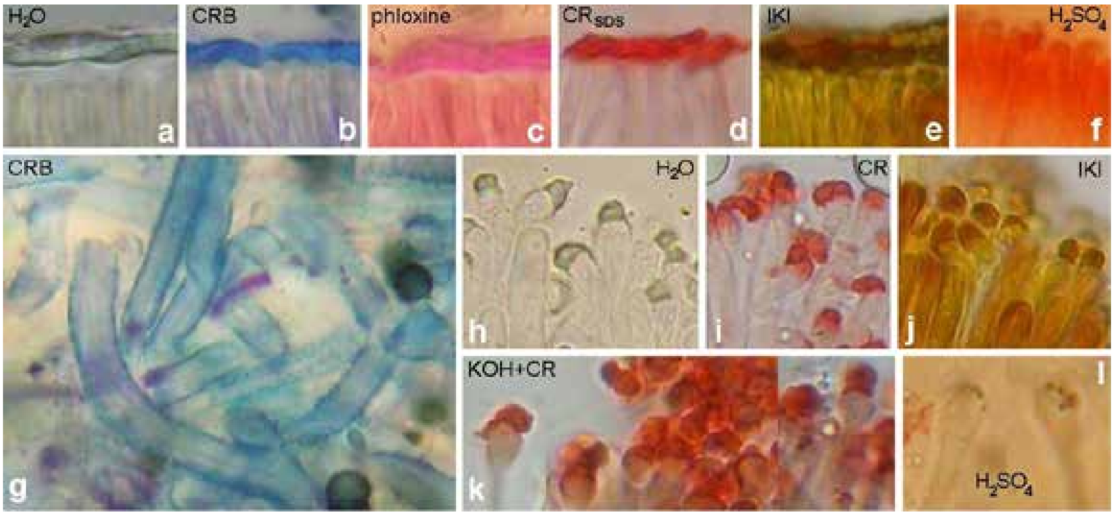


Figure 96: Hyaline exudate stained by different dyes and reagents, and dissolved by acids. — **a–f**. *Orbilia aristata* (H.B. 9226a): **a** in H_2O, **b** in CRB, **c** in phloxine, **d** in CR_{SDS}, **e** in IKI, **f**. exudate dissolved when heated in 60% H_2SO_4, neutralized with KOH, stained by CR_{SDS}; **g**. exudate on anchoring hyphae of *Lilapila oculispora* (H.B. 9162h) in CRB; **h–j**. caps of exudate over paraphyses in *O. kingsiana* (H.B. 8303b) in H_2O, CR, and IKI; **k**. caps of exudate in *O. denticulata* (H.B. 5430) in KOH+CR, **l**: id., dissolved in heated 60% H_2SO_4, neutralized with KOH.

to swell. In submature apothecia of section *Hemiorbilia* the exudate may completely detach from the whole hymenium and float in the medium as an entity or broken in several parts.

Chemistry. The chemical nature of the exudate is unknown. Höhnel (1907a) concluded from its insolubility in high-concentrated ethanol that the thin covering layer in *O. crenatomarginata* is of a waxy rather than resinous nature. Further properties were found in the present study: the exudate is insoluble in high-concentrated alkali (KOH) and in not too strong acids, and is usually strongly stained in CRB, phloxine, CR, and IKI (Tab. 8, Fig. 96, also in Vert lumière = Fast Green fide Bellemère 1968: 548). In 60 % sulphuric acid (H_2SO_4) the exudate of *Orbilia* dissolves, at least when briefly heated (Fig. 96: f, l), whereas it resists in hydrochloric acid (HCl). In *Hyalorbilia*, however, the warts and the underlying continuous exudate were not found to dissolve when briefly heated on the slide in a drop of 60 % H_2SO_4 or 10 % KOH.

A high affinity to all these above-mentioned dyes is observed in *Orbilia*: the exudate takes up the dye already at rather low concentrations (about 0.1 %) at which other parts of the apothecia are not stained. Hyaline exudate stains in a clear turquoise to blue colour in CRB (Fig. 96: b), but the stain turns more deep blue or (violet-)blue at high concentration. The exudate of *Hyalorbilia* often shows a lower affinity to these dyes, staining only light blue(-turquoise) in CRB or hardly at all, but also sometimes deep blue(-violet). Also in CR the reaction was often less intense. This might indicate a chemical composition different from *Orbilia*.

Neutral red (NR) stains the exudate of *Orbilia* bright orange-red, Methyl blue (CB_a) uniformly blue, and phloxine in a bright pink colour (Fig. 96: c); these colours correspond to the colour of the dye because they do not show a metachromatic effect.

CR stains the exudate of *Orbilia* generally light to deep rose-red (Fig. 96: d, i, k), also the thin exudate of *Hyalorbilia*. IKI stains the exudate of *Orbilia* often pale to bright dirty red-brown (dextrinoid, Fig. 96: e, j, KOH-pretreated or not), though this was mainly observed in taxa of section *Hemiorbilia* with thick exudate. In MLZ the reaction is less distinct.

In its behaviour with staining reagents, the exudate of *Orbiliomycetes* resembles hyaline to yellowish 'resinous' exudates of the *Helotiales*, e. g., in *Hyaloscypha aureliella* (see Huhtinen 1990a: 62, 110) and *Dasyscyphella*. These exudates likewise stain turquoise in CRB, but they differ in disappearing instantly in KOH (including their often yellow colour), perhaps also in being less solid.

Function. Exudate might function as a mechanical protection of the hymenial and excipular elements during periods of drought: the compact casing by exudate would serve as a barrier against mycophagous invertebrates. The rough surface of exudate could also support condensation of atmospheric humidity. Both this would explain the scantiness of exudate in desiccation-sensitive apothecia with a much shorter life span.

Autofluorescence. The yellow exudate on the exterior of the apothecia often shows a more or less striking autofluorescence under UV-illumination (365 nm). This was particularly observed in multispored members of series *Vibrioides* of the genus *Orbilia*.

Under UV in a dark room the apothecia then appear yellow to orange (Fig. 97: f). Taxa with unpigmented exudate do not show this effect. In case the surrounding substrate does not show a similar autofluorescence, the effect permits rather easy detection of scattered growing apothecia even in the dry state. The yellow colour of the exudate is best seen on macro- and microphotographs when using LEDs with a high proportion of blue (e. g., Luxeon) under reflected or transmitted illumination, while under halogen lamps the exudate may appear rather uncoloured.

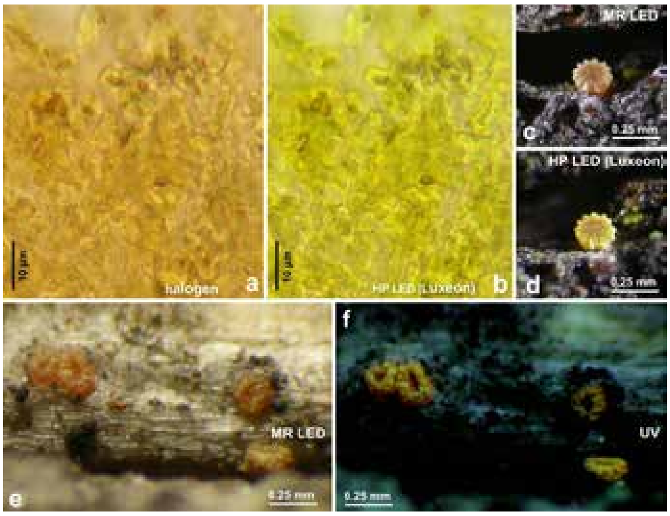


Figure 97: Autofluorescence of yellow exudate in *Orbilia myrioobliqua* and *O. angustoobliqua*. — **a**. illuminated by a halogen bulb; **b**, **d**. by HP LED (Luxeon); **c**, **e**. by MR (mid range) LED; **f**. by UV (365 nm). **a–b**. *O. angustoobliqua* H.B. 9050; **c–d**. *O. myrioobliqua* H.B. 8391a; **e–f**. *O. myrioobliqua* H.B. 7087b.

Extracellular crystals. Crystalline excretions of any kind are normally absent in the *Orbiliomycetes*. Particularly octahedral crystals, usually identified as calcium oxalate, excreted from hairs, excipular cells, or paraphyses in many genera of *Helotiales*, have never been encountered in the *Orbiliomycetes*, neither in apothecia, nor in pure culture. Rarely, small crystals were seen on the surface of gel which covers the tips of cortical excipular cells and paraphyses in *O. cucumispora* (Pl. 179: 1f, 2b–c). Crystals were infrequently observed below apothecia on the natural substrate. However, they were not formed by the fungus but originate from inside host cells.

Pigments

The apothecial colour of a species of *Orbiliomycetes* (see also p. 34, Apothecia) has generally a genetical basis, but it depends also on rather complex interactions of various parameters. What we can see under a handlens or dissecting microscope, or on a photography depends on influences such as exposition to sunlight during growth, development stage, rate of hydration, and long-term storage in herbaria, but also the spectral properties of the light source, and (in photography) white balance effects. The colour of the living apothecia results from a superposition of apparently four different types of pigments (Tab. 10). These are located in four different microstructures in- and outside the vegetative cells (paraphyses and ectal excipulum, see also Baral 1992: 370). Most of them may occur simultaneously within an apothecium. Secondary pigments which arise in some species through apparently oxidative chemical processes during senescence or when preserved as herbarium material need to be sharply separated from the original pigmentation (see p. 104, Colour of the dead cytoplasm).

Extracellular pigments are those of the exudate which is mainly found on the exterior of the apothecium, sometimes also in the intercellular space of the tissue. Intracellular pigments comprise lipophilous compounds (carotenoids deposited in LBs), hydrophilous pigments in vacuoles, and pigmentation of crystalloid SCBs.

Typical of section *Hemiorbilia* are thick yellowish exudates (Fig. 98: a). Yellowish-orange LBs characterize quite a number of species of *Orbilia* (e.g., *O. euphorbiae*, Fig. 98: b; *O. xanthoguttulata*, Figs 83, 98: c, 99) but are rarely seen in *Hyalorbilia*. Rose-red vacuoles (VBs) are so far unique to *O. rubrovacuolata* (Fig. 98: e), and a yellow vacuolar pigment is typical of *O. flavovacuolata* and *O. xanthostigma* (Fig. 98: f). Pale yellow-orange crystalloid SCBs occur in many desiccation-tolerant species (e.g., *O. cercidicola*, *O. hesperidea*, Fig. 98: d, see also Figs 87–88). A little understood diffuse pale rose-orange pigment of the whole apothecial texture is typical of many desiccation-tolerant species and could not clearly be allocated. Olive-brown and purplish-lilac pigments were so far exclusively found in the exudate. In all these types of pigments the intensity of colour may vary considerably within a species (living hydrated state, see p. 34, Pigmentation of apothecia).

The colour of apothecia in external view is usually the result of a superposition of pigments from two or three of these microstructures, though often one of them strongly prevails. For instance, bright golden-yellow to yellow-orange apothecia may originate from a combination of yellow-orange LBs and VBs (*O. xanthostigma*), or of yellow exudate and yellowish-orange SCBs (e.g., *O. hesperidea*). Likewise, the chlorinaceous colour of *Hyalorbilia* apothecia derives from chlorinaceous exudate and vacuoles. The colour of yellow-orange apothecia of *O. xanthoguttulata* is exclusively provoked by abundant yellow-orange LBs (Fig. 98: c). In multispored taxa of series *Vibrioides* the yellow dots of exudate on the surface and the diffuse pale rose-orange pigment of the excipular and hymenial texture are even macroscopically separately recognizable, provoking the appearance of a crumble cake.

1. **Extracellular pigments (exudate)**. Apothecial colours in *Orbiliomycetes* often originate from pigmentation of the **exudate** on the surface of the apothecium. Under transmitted light the exudate in bright yellow to orange apothecia appears pale yellowish, chlorinaceous, or even colourless, depending on the thickness of the sections. Only in thick sections a bright yellow exudate can be seen (Fig. 98: a).

The dark pigmented exudate of black-olivaceous apothecia in some species of *Amphosoma* and *Orbilia* (Fig. 98: j) might be due to a chemical change from yellowish to dark olivaceous, judging from the fact that very closely related taxa mainly differ herein. Moreover, in the dark-coloured *O. patellarioides* the hyaline medullary excipulum was found to be pale rose in some collections, but this pigmentation is completely masked in external view by the dark cortical pigment. The bright lilac exudate of the purplish-black apothecia of *Lilapila* occurs inside granules among the paraphyses and excipular cells, and also as a covering layer over the hairs (Fig. 98: g). Light grey-brown-olivaceous granules and clods of exudate are more or less typical of *O. polybrocha* and may not only occur on the apothecial surface but also in the marginal ectal and perihymenial medullary excipulum (Pl. 1003: 1e–f). Similarly, a yellowish-ochraceous exudate occurs in *O. pilifera* in the medulla and on the ectal excipulum (see Pl. 496: 5c).

The chemical nature of the pigments in exudate is unknown. Dissolution in strong alkali (10% KOH) has never been observed in all of these pigments, even when briefly heating the slide, while they are more or less dissolved only in very strong

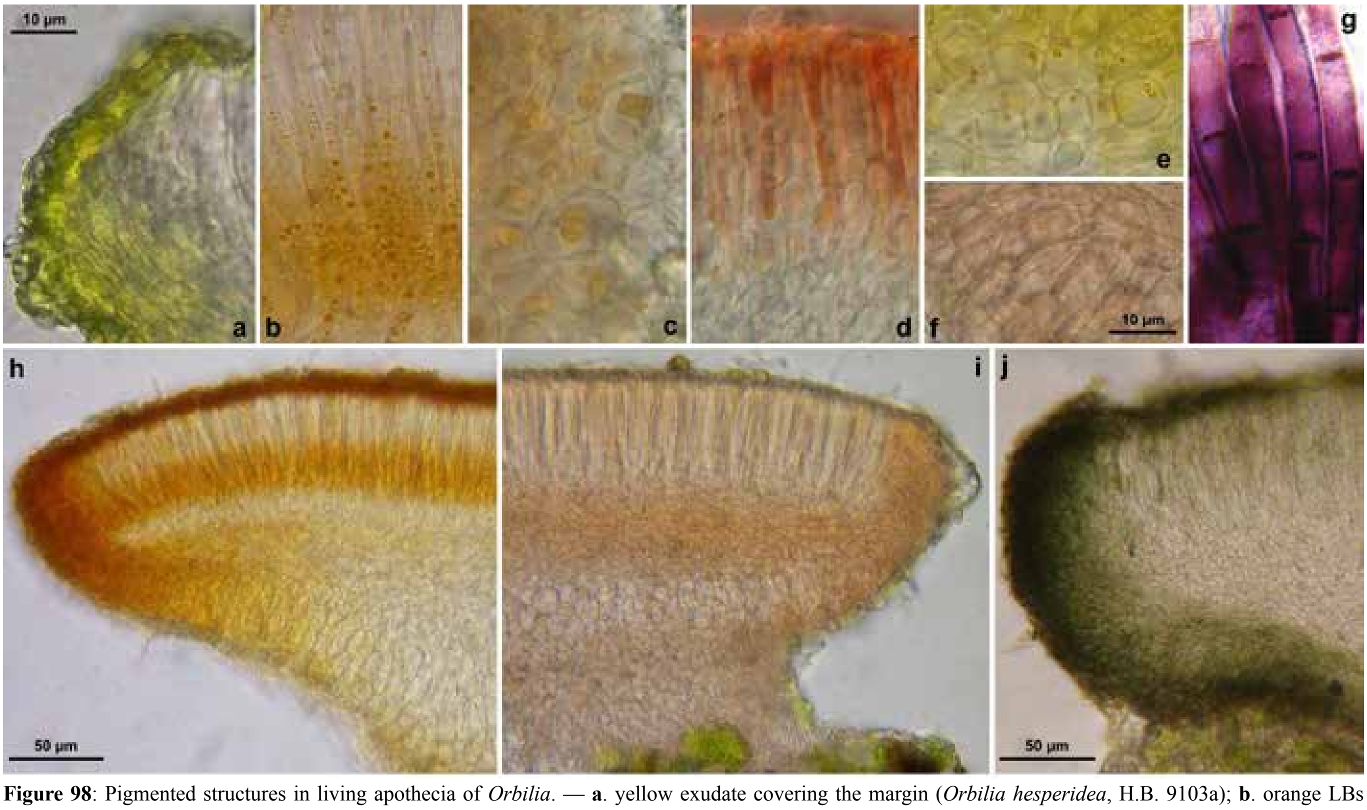


Figure 98: Pigmented structures in living apothecia of *Orbilia*. — **a**. yellow exudate covering the margin (*Orbilia hesperidea*, H.B. 9103a); **b**. orange LBs (carotenoids) in paraphyses (*O. euphorbiae*, 8777c); **c**. orange SCBs in ectal excipular cells (*O. hesperidea*, H.B. 8883b); **d**. red vacuoles (VBs) in paraphyses (*O. rubrovacuolata*, H.B. 7719a); **e**. yellow trembling VBs in inflated cells of medullary excipulum (*O. xanthostigma*, H.B. 7848a); **f**, **i**. diffuse rose pigment in *O. clavuliformis* (H.B. 8218); **g**. dark lilac hairs in *Lilapila oculisporella* (7.IX.2010); **h**. distribution of orange carotenoids in apothecium of *O. xanthoguttulata* (H.B. 8208); **j**. dark olivaceous exudate in *O. patellarioides* (H.B. 9173a).

Table 10. Four different types of pigments observed within the *Orbiliomycetes*.

Pigments		Colour	Microstructure	Organ	Affinity
Extracellular pigments		chlorinaceous, yellowish, purplish-lilac, olive	exudate	covering apothecial surface, rarely between cells	?
Intra-cellular pigments	Vacuolar pigments	chlorinaceous, yellow, rose-red	vacuoles and VBs	paraphyses, marginal cortical cells	hydrophilous
	Carotenoids	yellowish-orange	lipid bodies (LBs)	paraphyses, medullary excipulum	lipophilous
	Pigments in SCBs	yellowish-orange	crystalloid SCBs	paraphyses, excipulum	?

acids (H_2SO_4). Colour changes of the pigments may occur: hyaline and yellowish exudates remain unchanged in KOH, whereas olivaceous (blue-green) exudates turn ochraceous-olive or yellowish- to reddish-brown; yet, also purplish-lilac exudates turn yellowish- to olive- or violaceous-brown. The original colour of these dark pigments is restored in full strength when enough acid is added, or when transferring the apothecial fragment into PVA, hence the colour depends on the pH. The absence of a bluish or greenish IKI-reaction of yellowish exudate appears to exclude carotenoids.

2. **Pigments in lipid bodies (carotenoids)**. Golden-yellow to orange LBs occur in the paraphyses and marginal region of the excipulum in various groups of *Orbilia*, particularly in section *Aurantiorubrae* (e.g., *O. xanthoguttulata* Fig. 99: a, *O. aradi*, *O. euphorbiae* Fig. 98: b, *O. denticulata*), more exceptionally in sections *Hemiorbilia* (e.g., *O. arachnovinosa*, Pl. 269: 4e) and *Orbilia* (*O. xanthostigma*, *O. xanthoflexa*), and in *Hyalorbilia* (e.g., *H. erythrostigma*, Pl. 126: 1b, 6b, 7b, h). LBs with a high amount of carotenoids considerably contribute to the colour of the apothecia. Within a species the abundance of carotenoids is often rather variable, however.

That these lipophilous pigments should fall in the category of carotenoids can be concluded from the fact that they typically show a faint to distinct dirty blue-green iodine reaction (Fig. 99), in contrast to yellowish vacuolar pigments which do not react in this way. The reaction of carotenoids is obtained in both IKI and MLZ, with or without KOH-pretreatment (Baral 1987b: 428, see also Arpin 1968: 429). In *O. xanthoguttulata* and *O. xanthostigma* a change of colour from blue-green to brownish at a high IKI concentration was sometimes observed, similar as reported for *Scutellinia* by Baral (l.c.).

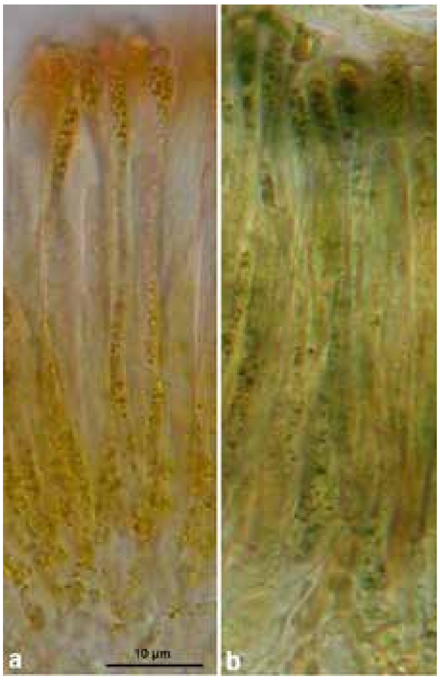


Figure 99: IKI reaction of carotenoids in paraphyses. — **a**. in water, **b**. stained blue-green in IKI (*O. xanthoguttulata*, H.B. 8698).

A faint rose pigmentation is often perceptible throughout the tissue (ectal and medullary excipulum, hymenium) in sections of living xerobiotic apothecia with a reddish external colour. The location of this pigment is unclear. It could be located in the extracellular space, perhaps in the gel, or in the cytoplasm in which a very faint homogeneous pigmentation, or a location in minute LBs, cannot be excluded with certainty.

In dead herbarium material of such reddish-coloured desiccation-tolerant apothecia, the faint rose pigmentation is enhanced and may turn more orange, but it is then clearly located in the dead granular cytoplasm. Again it is unclear whether this effect originates from a secondary pigmentation of the previously hyaline cytoplasm, or is due to carotenoids in LBs which were, in the living state, located at the periphery of the cytoplasm, but scattered throughout the cytoplasm in the dead state. IKI never gave a perceptible reaction to this faint rose pigmentation, however.

Mycelia in pure culture of xerobiotic taxa also frequently exhibit orange to pink colours (Fig. 102). Also Olivier (1978) noted pink to orange mycelia in pure culture of the two treated anamorphic species, *Retiarius superficiaris* and *R. bovicornutus*, that grew on exposed living leaves. She mentioned that this type of pigmentation was characteristic of many phyllosphere inhabitants, but also of some aquatic hyphomycetes and predacious fungi in culture. It is uncertain if these colours are due to the deposition of carotenoid-containing lipid droplets in the ageing mycelium.

3. **Pigments in VBs**. A very pale chlorinaceous colour in low-refractive VBs is typical of *Hyalorbilia*. In *Orbilia* refractive vacuoles occur only in more or less desiccation-sensitive species of sections *Helicoon*, *Orbilia*, and *Arthrobotrys*. Pigments inside these vacuoles were only found in a few species (*O. rubrovacuolata*, *O. flavovacuolata*, *O. atlantis*, *O. xanthostigma*) where they have a faint to light rose-red or yellowish-chlorinaceous colour. In *O. xanthostigma* the pale yellow vacuolar content precipitates at a later stage of development by forming groups of adhering yellow granules that tremble within the large non-refractive vacuoles (see Fig. 86: i–j).

The chemical nature of these hydrophilous pigments is unknown. The refractivity of VBs instantly disappears in both KOH and acids, while the pigment may remain recognizable. The granular VBs can easily be mistaken for yellow LBs, which also occur in apothecia of *O. xanthostigma* but which resist treatment with KOH.

4. **Pigments in crystalloid SCBs**. Pale to light yellowish-orange crystalloid SCBs occur in quite a few desiccation-tolerant species of various subgroups of *Orbilia*, but exclusively in sections *Hemiorbilia* and *Habrostictis*, and in the single species of series *Cercidicola* of section *Lentiformes* (Fig. 87). The chemical nature of this pigment is unknown. Even large, bright orange SCBs did not show a blue-green IKI reaction typical of carotenoids. Moreover, SCBs disappear in alkali or acids, whereas those types of carotenoids that form needle-shaped crystals in paraphyses of *Scutellinia* (Baral 1992: fig. 38) are KOH-resistant, i.e., they remain visible in full strength. Although SCBs op-

tically disappear concerning their shape, their pigment is still present and unchanged in these media (Fig. 87: h).

Loss of pigmentation in the dead state. In the dry state, the external colour of recently collected apothecia is generally much more intense due to concentration of the pigments. On the other hand, apothecia may completely lose their original colour in the herbarium over some 3–10 years concerning most types of pigments (Fig. 15: a–h). Only the dark pigments located in the exudate persist unaltered during longtime storage in the dry state, and also the yellowish pigment in the exudate of *Hyalorbilia* generally persists. For instance, *H. citrina* was still bright yellow ca. 100 years after it was collected.

Fading of pigmentation is also a frequent feature of, e. g., helotialean and pezizalean discomycetes which completely lose their bright original, particularly yellow and red colours. Carotenoids are known to strongly fade in colour within some decades in the herbarium (see Baral 1992: 372). For instance, Döbbeler (2004) reported a vivid orange-red colour of *Octosporella erythrostigma*, provoked by oil drops inside excipular and paraphysis cells, which gradually disappears in herbarium material. The yellowish pigmentation of the exudate in *Orbilia* appears to fade more slowly but fast enough in order to alter bright orange apothecia towards pale orange-ochraceous or whitish-cream within ~10–20 years. Different species or even different groups of apothecia of the same population may behave very different: e. g., *O. breviaristata* (H.B. 7171a) completely lost its colour after about 4 years, although *O. vitalbae* and *O. clavuliformis* which grew in the same collection were still bright orange. *O. occulta* (H.B. 7402a) lost its pigment already after 3.5 years in the herbarium. In *O. pleionavajoana* (H.B. 8049a) and *O. aviceps* (H.B. 7322a), groups of apothecia completely faded within 8 years, while others in the same population had fully retained their original orange-red colour. *O. obtusispora* (IVV: H.B. 6294) was still bright orange after 9 years, but rather strongly discoloured after 12 years, and *O. multiurosperma* (IVV: H.B. 9573c) was still bright orange after 16 years.

A phenomenon difficult to understand concerns the pigments in VBs and SCBs. These are often not further recognizable inside the dead cells in a water or KOH mount, although the apothecia still show the reddish colour several years after placing them in the herbarium. For example, the red vacuoles in the desiccation-sensitive *O. rubrovacuolata* disappear very soon in the herbarium concerning both refractivity and pigment, but the dried apothecia remain bright salmon- to blood-red over many years. The red colour was still perceptible even in material collected about 150 years ago by H.M. & P.L. Crouan (J.P. Priou pers. comm.). Instantaneous loss of colour and refractivity of VBs that contain yellowish or reddish hydrophilous pigments occurs when pressing on the slide or when adding KOH to a water mount.

Colour of the dead cytoplasm (secondary pigmentation). In addition to pigment loss, hyaline apothecia may turn yellow or reddish-brown by some oxidation process of the dead cytoplasm, either with senescence or bruising, or during drying of fresh, desiccation-sensitive apothecia. This is especially observed in taxa with refractive vacuoles (VBs) in the vegetative cells, which are actually responsible for these colour changes (see Baral 1992: 364). In *Orbiliomycetes*, changes towards a faint to distinct, mostly golden- to ochraceous-yellow pigmentation of previously hyaline VBs were recognized in water mounts, particularly in subtropical collections of *Orbilia* section *Helicoon*. Also the exudate in these species frequently turns more yellow with the age of the population. Likewise, hyaline VBs of the guttular type in *Amphosoma* turn copper-amber in dead cells. A change to reddish-brownish, typical of various *Helotiales*, has never been observed in the *Orbiliomycetes*, however.

Both colour loss and secondary pigmentation can be observed within the same taxon. When a fully viable apothecium of a *Hyalorbilia* is very gently squashed in a water mount, the numerous asci may remain intact although most of the paraphyses die and the VBs then completely disappear, including their chlorinaceous colour. However, if the paraphyses die during ageing of the apothecium in the field, the VBs do not disappear but become distorted and gain a more intense yellow-amber colour.

Huhtinen (1990a: 71) restricted the term ‘pigment’ to coloured substances inside the cells and used the word ‘resin’ for (yellowish) excretory substances. Since Huhtinen often had only herbarium material at his disposal, he could not notice that some of the treated species were white when fresh and formed a ‘yellow pigment’ only in the herbarium. For this reason, he often could not distinguish between coloured substances inside living cells and those inside dead cells. Due to his predominant herbarium studies, he considered pigments to be ‘typically persistent in most reagents’, a feature characteristic of secondary pigmentation of the dead cytoplasm. Yet, he emphasized the observation that a faint yellowish pigment is seen in fresh material of *Hamatocanthoscypha uncipila* which becomes invisible in water-mounted herbarium material.

A striking brown secondary pigment in old herbarium material was noted in a few cases. For example, the type of *Hyalinia rectispora* var. *majuscula* (= *Hyalorbilia inflatula*) showed varying degrees of a deep ochre-brown pigment in the cytoplasm of the asci, but also the excipular cells (Fig. 100: a–b). This pigmentation was not observed in other material of the same species, whether old or recent, and is thus an inconsistent feature of herbarium material with enigmatic origin.

Pigmented dead cytoplasm is a common feature of fungal genera that have a strikingly pigmented exudate or gel (e. g., *Chlorociboria*, with a blue-green dead cytoplasm). In the

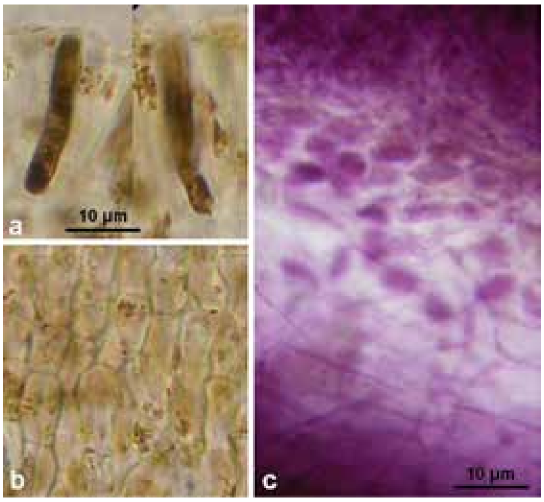


Figure 100: Secondary pigment in cytoplasm of asci (**a**), ectal (**b**) and medullary excipulum (**c**). — **a–b**. type of *Hyalinia rectispora* var. *majuscula* (= *H. inflatula*), examined ~90 years after collecting (in KOH); **c**. *Lilapila oculisporella* (in PVA, H.B. 7063a).

Orbiliomycetes, those species with a dark olivaceous exudate show a pale olivaceous pigmentation of the dead cytoplasm (ochre-brown in KOH), and in *Lilapila* dead cells may contain a bright lilaceous cytoplasm (Fig. 100: c). The effect might be explained as follows: under physiological conditions, a hyaline precursor molecule in the living hyaline cytoplasm is exuded through the cell wall and gets coloured outside. When the cells die, this precursor molecule becomes coloured also in the cytoplasm. According to Baral (1992: 372), the cytoplasm of fungal cells outside the vacuoles is generally colourless in the living state, except for lipophilous pigments and carotenoid crystals. The pigment in crystalloid SCBs of *Orbilia* represents a further exception of this rule.

Function of pigments. The function of exudate that carries a dark pigment could be seen in the longevity of dark-coloured apothecia, which usually grow at sun-exposed habitats and might need a strong protection against ultraviolet light. However, dark pigments are quite a rare feature in *Orbilia*, whereas reddish pigments are the most typical colours of desiccation-tolerant species of that genus. Dark pigments are more frequent in other genera of inoperculate discomycetes that belong to different orders and classes (e.g., *Claussenomyces* s.auct., *Durella*, *Patellaria*, *Sclerococcum*). Although all these genera form their apothecia under xeric conditions, the exposure to light varies strongly and includes also rather shaded situations. Differences in the desiccation tolerance between light- and dark-coloured species of *Orbiliomycetes* could not be found. Dark pigments are thus no prerequisite for either longevity, desiccation tolerance, or exposure to a high strength of illumination. Like the dark pigments, yellowish-reddish pigments in *Orbilia* are also often located in the exudate. Due to their frequency in desiccation-tolerant species of *Orbilia*, we assume a filter function against ultraviolet light for both dark- and light-coloured exudate, considering the fact that the life span of apothecia in semiarid areas undoubtedly lasts several years (see p. 158).

Intracellular pigments (carotenoids and pigmented SCBs), however, can hardly serve as a protection against UV, because they generally occur in the lower part of paraphyses and in the region of the marginal ectal excipulum. Their function could be to attract invertebrates which might play a role in ascospore dispersal. Particularly species with bright orange disc and white hairs might well have a function similar as showy flowers of higher plants.

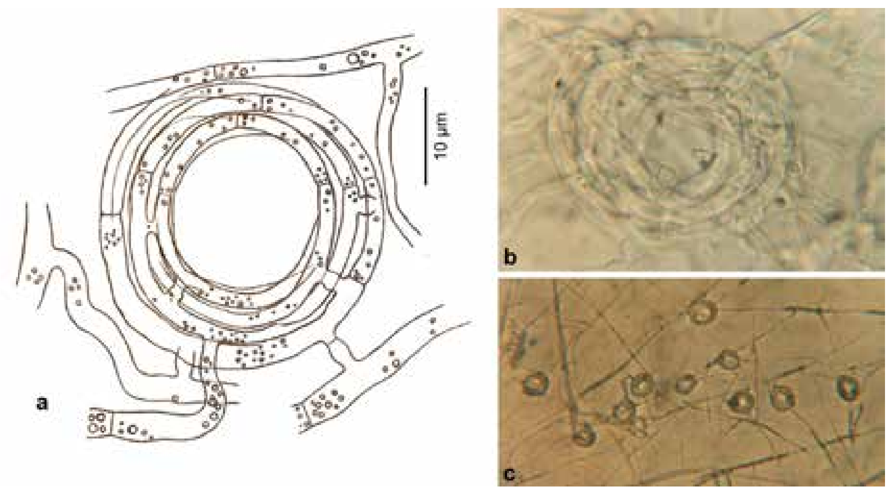


Figure 101: Coiled aerial hyphae formed in pure culture (MEA). — **a**. *O. aurantiorubra* (H.B. 5041); **b–c**. *Orbilia eucalypti* (H.B. 5023a).

CULTURAL AND ANAMORPH CHARACTERISTICS

Observations in pure culture

Isolation from ascospores. Spore discharge from fresh, desiccation-intolerant apothecia of *Orbiliomycetes* generally starts within a few minutes or hours, whereas discharge from rehydrated, desiccation-tolerant apothecia was observed within (0.5–)1–4 days. When subjected to vibration and slight heating, discharge often occurred within about 15–30 min (P. Perz pers. comm., see p. 11). Ascospores of *Orbiliomycetes* are ejected as a cluster, i.e., all spores of an ascus stick together and remain so on the agar surface (see p. 60–61). Germination takes place one or a few days later. Yet, for reasons unknown to us, the ascospores often germinated only tardily or not at all on the used media (mainly CMA:2 and CMA:4), e.g., in most of the tested species of *Hyalorbilia*, or in *Orbilia xanthostigma*, in which the spores germinated only after several trials. Also Pfister (2015) noted for *Hyalorbilia* ‘only a few reports of successful cultivation’, whereas in *Orbilia* he observed that ‘spores germinate quickly, and growth is often luxuriant on substrates containing glucose’.

Mycelial characters. Under the light microscope, mycelial hyphae are hyaline, ± sparingly septate, thin-walled, smooth, ca. *2–6(–8) µm wide, branched and anastomosing. Those hyphae being immersed in agar are often flexuous. The cells usually contain some minute guttules (LBs), sometimes also larger ones in greater abundance. Aerial mycelium was abundant in series *Arthrobotrys* but usually sparse or absent in all the other series and sections of *Orbilia* (Tab. 11; see also, e.g., Chen et al. 2007b, c), including all desiccation-tolerant taxa, and also in *Hyalorbilia*. A thin or sometimes 0.5–2.5 µm thick mucilaginous sheath that stains lilac in CRB covers the aerial or immersed hyphae (see p. 97–98).

Coiled aerial hyphae were rather frequently observed in our pure cultures of *Orbilia*, e.g., in *O. aurantiorubra*, *O. eucalypti*, or *O. menageshae*, often in great abundance (Fig. 101). The hyphae form ring-like structures lying on the agar surface, and superficially resemble ring traps. Their outer diameter lies in the range of ~(20–)25–50(–65) µm and their inner diameter ~15–30(–40) µm. The hyphae are *1.5–3(–4) µm wide and perform about 3–8 turns, being finally connected by a few to many anastomoses. Tarjan (1961: fig. 1ah, as ‘spiral mycelial ramifications’) observed them in several nematophagous fungi, such as *Dactylellina drechsleri*, and considered them as ‘purely vegetative and wholly without nematode-trapping ability’. Rubner (pers. comm.) obtained them in virtually every culture of nematophagous and also non-nematophagous orbiliaceous anamorphs.

Observations by one of us (G.M.) suggest that coiled aerial hyphae originate from long, erect hyphae growing vertically from the agar. These hyphae instantaneously coil down to the agar surface when touched or otherwise disturbed. A still air with high humidity

Table 11. Cultural characteristics in 48 investigated strains of 41 species from different series and sections of *Orbilia*, isolated mainly from ascospores [MEA 2 %, under artificial light-dark and temperature change (20/12 °C), each lasting 12 hours].

Infrageneric groups and their species	H.B. number (or coll. date)	Diameter after 1 week [mm]	Diam. after 2 weeks [mm]	Diam. after 4 weeks [mm]	Colour of colony	Aerial mycelium	Desiccation tolerance of apothecia
Section *Lentiformes*		< 1–2	11–15	15–28	pale to bright orange to salmon-coloured, sometimes brownish	none to sparse	+
O. lentiformis	6740d	< 1–2	14	25	orange-brown	(+)	+
O. pleistoeuonymi	6494a	< 1–2	~11	28	pale salmon	(+)	+
O. plurilentiformis	6740c	< 1–2	~15	22	bright salmon-orange	–	+
O. pluristomachia	6617a	< 1–2	~15	~15	orange-brown	–	+
Section *Hemiorbilia*		< 1–2	5–20	(5–)15–35	pale to bright orange, rose, reddish to salmon-coloured, rarely somewhat brownish	none to sparse	+
O. aprilis	6801	< 1–2	13	25	bright salmon-orange	(+)	+
O. aprilis	6715a	< 1–2	~15	20–25	bright orange-salmon	–	+
O. australiensis	7208b	< 1–2	13	21	bright rose-salmon	(+)	+
O. clavuliformis	6714	< 1–2	~10	15	brownish salmon	–	+
O. corculispora	6279	< 1–2	~20	~35	salmon-orange	–	+
O. hesperidea	6694	< 1–2	~5	22	bright salmon-rose	–	+
O. hesperidea	6468a	< 1–2	~7	26	salmon-orange	–	+
O. myriofusiclava	7237a	< 1–2	~15	26	pale salmon-brown	(+)	+
O.pleioaustraliensis	6277e	< 1–2	11	~26	bright salmon-red	–	+
O. subaristata	6685a	< 1–2	~1–7	~5–7	pale rose	–	+
O. vinosa	6715b	< 1–2	< 10	17	pale orange-salmon	–	+
O. cf. vinosa	6748g	< 1–2	~12	22	pale salmon-rose	(+)	+
Section *Aurantiorubra*		1–18	20–35	30–full	hyaline to (pale) cream to rose	none to sparse	+
O. comma	6639b	< 1–2	20	30	cream to pale rose	–	+
O. xanthoguttulata	6989	13–18	30–35	full	hyaline	(+)	+
O. euphorbiae	9869	18	40	full	hyaline to cream, concentric	(+)	+
Section *Helicoon*		12–30	42–50	50–full	whitish, pale rose to salmon-coloured	none	–
O. rosea	6756a	21–25	~50	full	pale salmon	–	–
O. sarraziniana	7235	~12	42	full	pale salmon	–	–
O. sarraziniana	6727a	25–30	~45	full	pale rose	–	–
Section *Habrostictis*		1–16	(10–)15–25	(12–)18–50	pale to bright cream-orange to salmon-orange-coloured, rarely pale brownish or hyaline	none to sparse	+
O. carpoboloides	6639c	~13–16	~25	45–50	hyaline	–	+
O. cylindrosoma	6711	< 1–2	15	30	bright salmon-orange	–	+
O. halimi	6472b	< 1–2	22	42	salmon	–	+
O. multimaeandrina	6737a	< 1–2	~10	12	pale salmon	(+)	+
O. serpentina	6609d	< 1–2	20	40	salmon	(+)	+
O. serpentina	6525a	< 1–2	20	36	pale ochraceous-orange	(+)	+
O. sonorensis	6721b	< 1–2	18	40	pale ochraceous salmon	–	+
O. subvitalbae	6504a	< 1–2	20–25	40	pale ochraceous-orange	(+)	+
O. vermiculati	6739b	< 1–2	~12	18	salmon-orange	–	+
Section *Ovoideae*		< 1–2	10	18	orange to salmon-coloured	none	+
O. polyspora	7243b	< 1–2	~10	18	orange-salmon	–	+
Section *Orbilia*		1–22	(10–)20–45	(12–)36–full	hyaline, (pale) cream, pale rose, rarely pale brownish	none to sparse	–/+
O. eucalypti	6662	8–11	30–33	full	cream	–	(–)/+
O. eucalypti	5023a	~12	35–40	full	pale salmon	–	(–)/+
O. eucalypti	17.XI.2002	7–22	~45	full	pale salmon	–	(–)/+
O. leucostigma	6810c	15–17	45	full	pale cream	–	–/(+)
O. xanthostigma	6749	< 1–2	~22	36	hyaline	(+)	–/(+)
O. liliputiana	6905	< 1–2	~10	12	pale cream	–	+
O. microsoma	6738a	< 1–2	< 10	15	pale brownish	–	+
O. tremulae	6963a	16–17	45	full	pale cream	(+)	–/(+)
Section *Arthrobotrys*							
Series *Neodactylella*		15–18	32–35	full	orange to salmon-coloured	sparse	–
O. cotoneastri	7241a	15–18	32–35	full	orange-salmon	(+)	–
Series *Arthrobotrys*		26–45	> 50	full	hyaline to pale salmon-coloured	abundant	–
O. auricolor	6664	~40	> 50	full	pale rose	+	–
O. auricolor	6763	~40	> 50	full	pale salmon, hyaline	+	–
O. elegans	6972a	26–40	> 50	full	pale salmon	+	–
O. scaphoides	6972b	~45	> 50	full	pale salmon	+	–
Series *Dactylellina*		~1–15	20–50	full	hyaline to pale cream-coloured	sparse	–
O. mammilata	7165c	~15	~50	full	hyaline	(+)	–
O. rubrovacuolata	6598a	< 1–2	20–22	full	pale cream	(+)	–
Series *Drechslerella*			~20	full	hyaline	sparse	–
O. bembicodes	7165b	?	~20	full	hyaline	(+)	–

appears to be a precondition for their growth. Possibly, on the natural substrate they detach when touched by animals and adhere to them, thereby contributing to the dispersal of the species. Our observations showed that such coiled hyphae may also occur in cultures of other, quite unrelated fungi. A figure of coiled hyphae in a helotialean species is found in Görke (1998: 302, fig. 125, *Phialocephala fortinii*).

Growth rates. Colonies of desiccation-tolerant species of *Orbilia* (anamorphs trinacrium-, dwayaangam-, dicranidion-, tridentaria-, descalsia-, vermispora-like) were generally slow-growing. A radial growth rate of ~0.2–0.9(–1.3) mm/day was noted on MEA 2%. Colonies of the desiccation-tolerant *Lilapila oculispora* and *L. oculisporella* showed a comparably low growth rate of ~0.37–0.43 mm/day (10–12 mm diam. after 2 weeks, 20–25 mm diam. after 4 weeks, on CMA:5). When grown on CMA:3 in a single Petri dish, the growth rate was much lower, but striking differences were observed between both species: after 2.5 months *L. oculisporella* formed a colony of 17–20 mm in diam., whereas *L. oculispora* only 8–10 mm. Possibly *L. oculispora* was inhibited by the mycelium of *L. oculisporella*.

Generally higher growth rates of ~0.6–2 mm/day on CMA, PDA, or MEA 2% at 20–25 °C were found in predominantly desiccation-sensitive species: in those of section *Orbilia* with dicranidion-like anamorphs, including the desiccation-tolerant *O. eucalypti* (see Tab. 11), in desiccation-sensitive species of *Hyalorbilia* (including *Vermispora*; Chen et al. 2007c, Harris 1985, Liu et al. 2005b, *H. polypori* in this study); in semiaquatic species of series *Helicoon* (*O. rosea* and *O. sarraziniana*, this study Tab. 11, Liu 2006, *O. yuanensis* in Qiao et al. 2015), and in series *Pseudotripoconidium* (Su et al. 2011c, Yu et al. 2011). In *Orbilia* spp. with arthrobotrys-, dactylella-, dactylellina-, drechslerella-, and gamsylella-like anamorphs, growth rates may attain the highest values observed: ~(0.7–)1.2–4(–6) mm/day, though sometimes only ~1 mm (Chen et al. 2007b, Liu 2006, Rubner 1996, this study Tab. 11). The highest growth rate was observed by us in *O. menageshae* (series *Arthrobotrys*) with 4–5.5 mm/day on MEA.

Rubner (1996: 26) found in her study on predacious hyphomycetes of the '*Dactylella-Monacrosporium* complex' that species forming adhesive networks (now placed in *Arthrobotrys*) grew faster than species with other trapping organs (at room temperature of 20–23 °C, but also at 15 or 30 °C). They showed the highest radial growth rates (up to 6.5 mm/day on CMA:2 at ~23 °C, though rarely only 2.2 mm/day (*A. eudermatus*). Those with unstalked or stalked adhesive knobs and/or adhesive hyphal branches (*Dactylellina*, *Gamsylella*) grew more slowly (1.7–3.3 mm), and those with constricting rings (*Drechslerella*) were the slowest (1.7–2 mm). At 15 °C a growth rate of only (0.8–)1.6–2.8 mm was noted in *Arthrobotrys* (*A. thaumasius*, '*A. rutgeriensis*', *A. eudermatus*), 0.7–1.4 mm in *Dactylellina* (*D. ellipsospora*, *D. lysipaga*, *D. mammillata*, *D. phymatopaga*) and *Drechslerella* (*D. effusa*). In conclusion, *Arthrobotrys* species grew distinctly faster at 30 °C compared to 15 °C, except for one strain of *A. eudermatus* which grew faster at 15 °C. *Dactylellina* species (except for *D. phymatopaga*) and *Drechslerella effusa* hardly grew at all at 30 °C but were slow-growing at 15 °C. Instead, *Dactylellina phymatopaga* grew fast at 30 °C but very slowly at 15 °C.

Colony colours. In desiccation-tolerant species of *Orbilia* with trinacrium-, dwayaangam-, dicranidion-, tridentaria-, descalsia-, or vermispora-like anamorphs and frequently reddish apothecia, colonies usually had a pale to bright cream to orange or salmon to pink colour (on MEA 2%, under artificial light, Tab. 11, Fig. 102). However, in several subgroups of *Orbilia*, the colony colour of a few species of sections *Lentiformes*, *Hemiorbilia*, *Habrostictis*, and *Orbilia* deviated in showing a pale salmon- to orange-brownish tinge. On the other hand, *O. patellarioides* with dark olivaceous apothecia produced a bright pink mycelium.

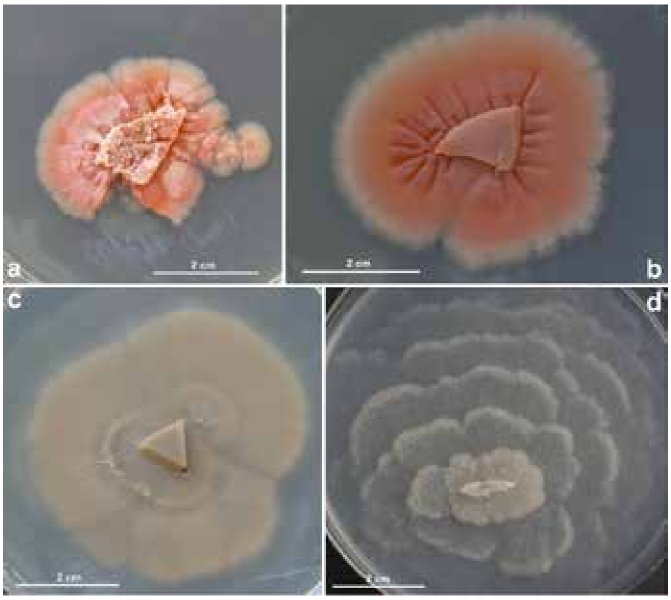


Figure 102: Colonies of desiccation-tolerant (**a–c**) and -sensitive (**d**) species of *Orbilia* in pure culture. — **a**. *O. pleistoeuonymi* (H.B. 6494a); **b**. *O.* cf. *vinosa* (H.B. 6748g); **c**. *O. carpoboloides* (H.B. 6639c); **d**. *O. sarraziniana* (18.X.2012). **a–c** on MEA, **d** on CMA:2.

The colony colour of desiccation-sensitive species of *Orbilia* was ± hyaline, (very) pale cream (series *Orbilia* with dicranidion-like anamorph), but also pale rose to salmon(-orange), or reddish-brownish. In desiccation-sensitive species of *Hyalorbilia* the colony colour was white, sometimes becoming slightly yellowish or brownish with age (MEA 2%, OA, CMA, CMA:2, PDA).

Colonies with distinct concentric zones were observed by us only in *O. sarraziniana* on CMA:2 (Fig. 102: d), but also X.Z. Jiang (pers. comm., IVV: 25.VII.2008) obtained them in the closely related *O. luteorubella* on PDA.

Chlamydospores have never been observed by us in our cultures, although they were frequently described in the literature in many desiccation-sensitive *Orbilia* species (e.g., Drechsler 1937a, 1943b, 1950a, 1952; Rubner 1996: 13; Yu et al. 2011; Chen et al. 2007b; see also Jarowaja 1970: 342).

Chlamydospores were reported as occurring either singly or in long moniliform chains, terminally or intercalarily, with individual cells more or less isodiametric or elongated (~*7–30 × 7–20 µm), multiguttulate, with hyaline, ± thickened, smooth or warted walls. They serve as resting spores which are able to survive unfavourable conditions like drought or heat (Rubner l.c.).

No chlamydospores were so far seen by us in pure culture of any desiccation-tolerant *Orbilia*. However, in one such species (*O. occulta*) Y.Y. Shao observed small, subglobose, cells with ochraceous wall formed on short side branches. Despite its unusual colour it appeared that these structures do not represent a contaminant (Shao et al. 2018).

Formation of conidial state. Conidia developed rather frequently in our ascospore cultures. CMA:2 and CMA:4 were found to be the best among the used agar media for inducing the formation of conidial states. On WA conidia formation was moderate, and rare on MEA 2 %. Conidia usually appeared within one or some weeks. Yet, in species of section *Arthrobotrys* and sometimes also in series *Orbilia* (*O. dryadum*) they appeared already within a few days. Those species which failed to produce conidia on the agar media tested, also failed on water agar with sterilized fragments of decayed branches. Yet, conidia formation was stimulated when pieces of inoculated agar were flooded with distilled water (see p. 12). This method was successful in many desiccation-tolerant species of *Orbilia*, but also in the anguillospora-like anamorph of the semiaquatic *O. rosea*.

Out of a total of ca. 160 cultured species of *Orbiliomycetes* with known teleomorph which came to our notice, connections to an anamorph have been established in ca. 140 species (sometimes by molecular methods), ca. 45 of which have already been published (see Appendix 4 & Tab. 41). Most of them were gained from ascospore isolates in pure culture, but some from hyphae growing out of apothecia on the lid of a Petri dish (Tab. 12, for literature reports see also Tab. 41). In further 90 species connections could only tentatively be suggested based on conidia observed on the natural substrate.

Since the anamorph and teleomorph of a given species may, in our experience, occur both successively as well as simultaneously on the natural substrate, conidia can be found regardless of the presence of apothecia, and very often no conidia at all could be detected around the apothecia. Indeed we have several times found quite characteristic conidia which we were able to connect to a teleomorph (species or species aggregate) by its peculiar conidial morphology, although the apothecia growing there in association belonged to very different sections of *Orbilia*. Therefore, rarely observed associations of anamorphs and teleomorphs need confirmation by pure culture studies.

Formation of apothecia in pure culture. During our study on ~ 160 cultured strains of *Orbiliomycetes*, apothecia developed in pure culture only in two strains (*Orbilia flavida*, mature apothecia on WA in the presence of sterilized wood fragments; *O. alba*, immature apothecia on CMA:4 with or without sterilized wood fragments). No anamorph was formed in the *O. flavida* strain, whereas another strain of *O. flavida* produced conidia but no teleomorph.

Literature reports of apothecial production in *Orbiliomycetes* concern *Hyalorbilia erythrostigma* (Matsushima 1995, as *O. trinacriifera*), *Orbilia* sp. (Drechsler 1937a: 458, in a culture of *Arthrobotrys superbus*, see under *O. auricolor*), *Orbilia* sp. [Zachariah 1983, in a culture of *Drechslerella* (‘*Arthrobotrys*’) *dactyloides*], *Orbilia* sp. (as *O. coccinella*, anamorph *Arthrobotrys* sp., Guo et al. 2009b), *O. auricolor* (Guo et al. 2009a/b), *O. ?cardui* (Thakur & Zachariah 1989, as *Orbilia* sp.), *O. crenatomarginata* (Guo et al. 2009b), *O. dorsalis* (Yu et al. 2007b, Guo et al. 2009a/b), *O. elegans* (Rubner 1996, as *O. auricolor*), *O. oligospora* (Guo et al. 2009a/b, Zhang et al. 2011b), *O. rosea* (Descals et al. 1999), and *O. sarraziniana* (Guo et al. 2009a/b). Guo et al. (2009a) found that certain nitrogen (L-proline, L-tyrosine) and carbon sources (D-mannose, D-cellobiose) strongly stimulate the formation of apothecia. Zachariah (1983) discussed the possibility that auxotroph strains of predatory anamorphs, which need several amino acids for growth, especially histidine and methionine, are essential for the initiation of teleomorphogenesis. (see also p. 40, Sexual reproduction).

Table 12. Number of anamorph-teleomorph connections within *Orbiliomycetes* known at present (*in pure culture or from unsterile formation on lid of Petri dish, or by DNA comparison, literature reports included; **conidia observed on natural substrate). Numbers include undescribed (aff./cf.) taxa listed in Tab. S3, see also List of anamorph-teleomorph connections.

Genus or section	Connection assured*	Connection presumed**
Liladisca	–	–
Lilapila	–	–
Amphosoma	1	2
Lecophagus	–	1
Bryorbilia	–	–
Pseudorbilia	–	–
Hyalorbilia	7	13
Orbilia section *Lentiformes*	11	7
section *Hemiorbilia*	16	17
section *Aurantiorubrae*	21	15
section *Helicoon*	13	–
section *Habrostictis*	23	13
section *Ovoideae*	–	6
section *Orbilia*	14	4
section *Arthrobotrys*	38	12
Total	**144**	**90**

Tests with nematodes, rotifers and pollen

Formation of trapping organs. Living **nematodes** were added to 30 of our cultures (Tab. 13). In nine strains belonging to eight species the formation of trapping devices could be induced. Those 21 tested strains of *Orbiliomycetes* with brachyphoris-, dactylella-, dicranidion-, trinacrium-, vermispora-, and anguillospora-like conidia did not form any trapping devices when treated with nematodes.

In one species (*O. menageshae,* H.B. 9309b) with an arthrobotrys-like anamorph, sparse adhesive networks developed without the presence of nematodes. Also in *O. alba* (H.B. 9645a) adhesive knobs were spontaneously formed.

Our tests with **rotifers** (*Macrotrachela quadricornifera* and unidentified bdelloid rotifer) failed to induce trapping organs. The rotifers often increased in size by forming eggs, but we never observed a connection between fungal hyphae and eggs or adult rotifers. One reason of this negative result might be the low number of rotifer individuals. The tests were soon stopped because of considerable difficulties to maintain the rotifer culture.

In order to find out whether parasitism on **pollen** is a common feature of *Orbiliomycetes*, we started a study with living pollen grains of *Sambucus nigra* and *Corylus avellana*, which we added to 20 strains of 19 different species of *Orbilia.* In 13 of these species we found hyphae that formed haustoria in some of the pollen grains within 1–2 weeks (Tab. 14, see also Fig. 110).

However, not only orbiliaceous fungi are capable of parasitizing pollen (see also Magyar et al. 2017a). We tested cultures of four species of *Helotiales* (*Durella atrocyanea*, H.B. 7074; ‘*Hymenoscyphus*’ *salmanovicensis*, H.B. 6977; *Ombrophila janthina*, H.B. 7044; *Gemmina gemmarum*, H.B. 6883) and one of *Dothideomycetes* (*Rhizodiscina lignyota*, 20.V.2001). In those of *R. lignyota* (Fig. 110: k–m) and ‘*H.*’ *salmanovicensis* many infected pollen grains (*Corylus avellana*) were observed, whereas the other three species were negative. Obviously, the ability to infect pollen grains is not restricted to the genus *Orbilia*, but it appears to vary between species of a given genus or family.

Table 13. Strains of *Hyalorbilia* and *Orbilia* treated with nematodes in the present study (*Acrobeloides maximus* and unidentified spp.).

Taxonomic group	Species	Anamorph	Nematode	Desiccation tolerance	Formation of trapping devices
Hyalorbilia	*Hyalorbilia polypori* (H.B. 7557a)	brachyphoris-like	unidentified	–	–
Orbilia section *Lentiformes*	*Orbilia subocellata* (H.B. 6474)	vermispora-like	*A. maximus*	+	–
section *Hemiorbilia*	*O. hesperidea* (H.B. 6468a)	trinacrium-like	*A. maximus*	+	–
	O. myriofusiclava (H.B. 7237a)	vermispora-like	unidentified	+	–
	O. vinosa (H.B. 6715b)	trinacrium-like	unidentified	+	–
	O. cf. vinosa (H.B. 6748g)	trinacrium-like	unidentified	+	–
section *Helicoon*	*O. rosea* (H.B. 6756a)	anguillospora-like	*A. maximus*	–	–
	O. sarraziniana (H.B. 7235, 8225)	~ anguillospora-like	unidentified	–	–
section *Habrostictis*	*O. bicknellensis* (H.B. 6480a)	trinacrium-like	*A. maximus*	+	–
	O. halimi (H.B. 6472b)	trinacrium-like	*A. maximus*	+	–
	O. serpentina (H.B. 6609d)	trinacrium-like	unidentified	+	–
section *Habrostictis*	*O. pilifera* (H.B. 8076)	trinacrium-like	unidentified	+	–
section *Orbilia*	*O. battenii* (H.B. 8004)	dicranidion-like	unidentified	+	–
	O. cejpii (H.B. 8201)	dicranidion-like	unidentified	+?	–
	O. dryadum (H.B. 8224a)	dactylella-like	unidentified	–	–
	O. eucalypti (H.B. 6662)	dicranidion-like	unidentified	–	–
	O. microsoma (H.B. 6738a)	trinacrium- & descalsia-like etc.	unidentified	+	–
	O. xanthostigma (H.B. 6749)	dicranidion-like	unidentified	–	–
series *Neodactylella*	*O. cf. clavispora* (H.B. 8207)	dactylella-like	unidentified	–	–
	O. cotoneastri (H.B. 7241a)	dactylella-like	unidentified	–	–
	O. epipora (H.B. 8153)	dactylella-like	unidentified	–	–
series *Arthrobotrys*	*O. auricolor* (H.B. 6664)	arthrobotrys-like	*A. maximus*	–	adhesive networks
	O. auricolor (H.B. 6763)	arthrobotrys-like	*A. maximus*	–	adhesive networks
	O. elegans (H.B. 6972a)	arthrobotrys-like	unidentified	–	adhesive networks
	O. scaphoides (H.B. 6972b)	arthrobotrys-like	unidentified	–	adhesive networks
series *Dactylellina*	*O. mammillata* (H.B. 7165c)	dactylellina-like	unidentified	–	adhesive knobs
	O. rubrovacuolata (H.B. 6598a)	dactylellina-like	*A. maximus*	–	adhesive knobs
series *Drechslerella*	*O. orientalis* (H.B. 8146a)	drechslerella-like	unidentified	–	constricting rings
	O. bembicodes (H.B. 7165b)	drechslerella-like	unidentified	–	constricting rings
	O. polybrocha (H.B. 8317a)	drechslerella-like	unidentified	–	constricting rings

Morphology of the anamorph

Conidiophores. Conidiophores in pure culture develop scattered to abundantly as hyphal outgrowths from mycelial hyphae. They are thin-walled, smooth, hyaline, one-celled or sparsely septate, morphologically similar to the mycelial hyphae, and occur solitary or in loose fascicles. On the natural substrate, conidiophores emerging from mycelial or anchoring hyphae, or from the apothecial tissue were only occasionally seen, although detached conidia were frequently encountered. Conidiomata have never been observed in pure culture by us. Exceptional records on the natural substrate include synnemata in *Dicranidion fragile* (Seifert et al. 2011, pl. 300A, see under *O. eucalypti*, p. 1364) and a few species of *Arthrobotrys* (*A. stilbaceus*, Meyer 1958, Matsushima 1995; *Roigiella lignicola*, Castañeda Ruíz 1984; *A. dendroides*, Kuthubutheen et al. 1985, Yu et al. 2014), and sporodochia in association with *O. purshiae* (H.B. 7462a, see p. 467).

Table 14. Strains of *Orbilia* species treated in pure culture with pollen grains of *Sambucus nigra* and/or *Corylus avellana*. + = pollen invaded by mycelium, – = no invasion of pollen.

Species	*Sambucus nigra*	*Corylus avellana*
O. aprilis (H.B. 6801)	+	
O. auricolor (H.B. 6664)		+
O. cisti (H.B. 6500)		+
O. cucumispora (H.B. 6762a)	–	
O. eucalypti (H.B. 6662)		–
O. eucalypti (5023a)	–	
O. hesperidea (H.B. 6694)	+?	+
O. leucostigma (H.B. 6810c)	+	
O. mesaverdiana (H.B. 6736a)	–	
O. multiurosperma (H.B. 6493a)		–
O. ocellata (6736d)	–	
O. octocercocarpi (H.B. 6609c)		+
O. octoserpentina (H.B. 6609b)		+
O. pleistoeuonymi (H.B. 6494a)		+
O. plurilentiformis (H.B. 6740c)	+	
O. pluristomachia (H.B. 6617a)		–
O. rubrovacuolata (H.B. 6598a)		+
O. serpentina (H.B. 6609d)		+
O. subaristata (H.B. 6685a)	+	+
O. cf. *vinosa* (H.B. 6748g)	+	

Depending on the group, conidiophore length encompasses a wide range of 1.5–20 up to 40–400(–600) µm. Long conidiophores (predominantly over ~50 µm) occur mainly in section *Arthrobotrys* (series *Arthrobotrys*, *Neodactylella*, *Dactylellina*, *Drechslerella*, *Gamsylella*), in series *Hyalinia* and *Xanthoguttulatae* p.p. of section *Aurantiorubrae*, and in series *Pseudotripoconidium* of section *Helicoon*, rarely in *Hyalorbilia*. Anamorphs with long conidiophores and their teleomorphs are desiccation-sensitive, i. e., they require a protected environment of still air and continually high humidity. Short conidiophores (up to ~50 µm) were observed in sections *Lentiformis*, *Hemiorbilia*, *Aurantiorubrae*, *Habrostictis*, *Orbilia*, and *Helicoon* (p.p.), exceptionally in series *Neodactylella* of section *Arthrobotrys*, also in most species of *Hyalorbilia* and all of *Lecophagus*. They are typical of desiccation-tolerant species. Anguillospora-, vermispora-, and helicoon-like anamorphs reported in series *Helicoon* vary in conidiophore length between short and medium long, although these taxa are adapted to hygric, semiaquatic habitats. Also some ± desiccation-sensitive taxa of section *Orbilia* with dactylella- and dicranidion-like anamorphs (*O. dryadum*, *O. battenii*, *O. cejpii*, *O. fissilis*, *O. tremulae*, *O. leucostigma*/*xanthostigma*) were found to have a conidiophore length of only (1.5–)7–50(–105) µm.

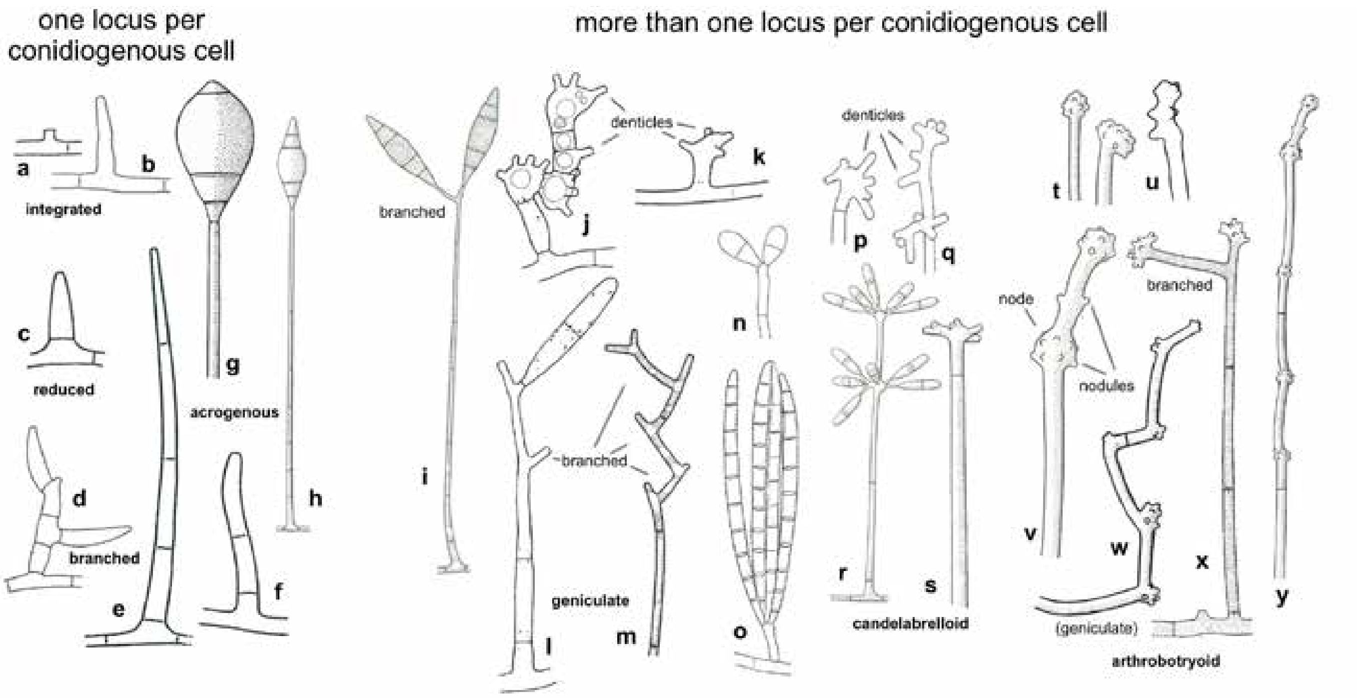


Figure 103: Conidiophore morphology: different types of conidiophore tips in regard to branching and conidiogenous loci (mainly according to Jarowaja 1970, Rubner 1996, and Seifert et al. 2011). — **a–h**. conidiogenous cells with one locus; **i–y**. conidiogenous cells with several loci (sympodial); **a–d**, **f**, **j–k**, **o**. conidiophores short; **a–c**. conidiophores one-celled, integrated (non-septate) or reduced (with one basal septum); **e**, **g–h**. conidiophores long and unbranched (acrogenous); **m**, **w**. geniculate upper part of conidiophore (knee-like branching of the conidiogenous cells); **n–o**. conidiophore tip not swollen, without nodules or denticles; **p–s**. conidiogenesis from aggregated denticles (candelabrelloid); **t–y**. conidiogenesis from aggregated nodules on ± swollen nodes (arthrobotryoid), nodes either singly at the conidiophore tip, or at intervals. **— a**. *Trinacrium incurvum* (Matsushima 1980); **b**. *Dicranidion ontariense* (Matsushima 1984); **c**. *D. gracile* (Matsushima 1971); **d**. *D. fragile* (Matsushima 1975); **e**. *D. tenue* (Matsushima 1993); **f**. *D. parapalmicola* (Matsushima 1981); **g**. *Drechslerella bembicodes* (Drechsler 1937a); **h**. *Dactylellina ellipsospora* (Drechsler 1937a); **i**. *D. haptotyla* (Drechsler 1950a); **j**. *Orbilia pleistoeuonymi* (H.B. 6494a); **k**. *Trinacrium gracile* (Matsushima 1975); **l**. *O. epipora* (H.B. 8153); **m**. *Dactylella rhopalota* (Drechsler 1943b); **n**. *Arthrobotrys flagrans* (Cooke 1969); **o**. *Lecophagus muscicola* (Barron et a. 1990); **p**, **s**. *A. musiformis* (Drechsler 1937a); **q**. *A. thaumasius* (Drechsler 1937a); **r**. '*Dactylellina*' *entomopaga* (Drechsler 1944b); **v**, **y**. *A. oligosporus* (Drechsler 1937a); **t**. *A. cladodes* (Drechsler 1937a); **u**. *O. auricolor* (H.B. 5058); **w**. *A. superbus* (Drechsler 1937a); **x**. *A. macroides* (Drechsler 1944a).

Long conidiophores are ± straight in their lower part, sparsely septate, with the septa often more aggregated near the base. Usually, conidiophores get gradually narrower from base towards apex, but may also show short to long cylindrical parts. Short, one-celled conidiophores may rarely be slightly capitate or dumbbell-shaped (*Lecophagus*, Fig. 103: o). Conidiophore width in the lower part is 1.5–9 µm, rarely up to 7–14 µm (*Lecophagus* p.p.). In some species the conidiophores are entirely reduced, consisting merely of an intercalary conidiogenous denticle inserting as a lateral protuberance on a mycelial hypha (Fig. 103: a–b).

Conidiophores may either be unbranched, or they are branched in the lower, middle, or upper part. Branching in the lower and middle part is considered to be of low taxonomic value (Rubner 1996: 9), whereas branching in the upper part, and particularly shape and arrangement of the conidiogenous loci have some taxonomic importance. Four main types of conidiophore apices can be distinguished within the nematophagous species: acrogenous, geniculate, candelabrelloid, and arthrobotryoid (Fig. 103: g–h, l–m, p–s, t–y). These types and terms were used in the past for the distinction of different anamorph-typified genera within the predatory taxa (Jarowaja 1970, Rubner l.c.). Today, these morphological types are considered to be stable only at the species level or within small groups of closely related taxa, and some variation and intergradations may even occur within a species.

Conidiogenesis. In all studied species of *Orbiliomycetes* conidiogenesis is found to be holoblastic: conidia are formed as hyphal outgrowths from the conidiogenous loci, thereby all wall layers of the conidiogenous cell contribute to the conidial cell wall (see also Rubner 1996: 11). The conidia strongly enlarge before a basal septum is formed. Conidial secession is always schizolytic, i. e., conidia separate by disintegration of the middle lamella of the septum between conidium and conidiophore, so that half of the septum remains at the conidiogenous locus. Each locus is able to produce only one conidium.

Conidial production is either monoblastic, i. e., a conidiogenous cell has a single conidiogenous locus (Fig. 103: a–h), or polyblastic when there are multiple conidiogenous loci per conidiogenous cell. Polyblastic conidiogenesis occurs more or less sympodially, i. e., conidia are successively produced from the conidiogenous cell by continued growth of the main axis. In cases of a crowded arrangement of the loci at the conidiophore tip or on more or less swollen nodes, conidiogenesis tends to be synchronously, e. g., in *Arthrobotrys* p.p. and particularly in *Lecophagus*. Each conidiogenous locus is either at the tip of a small projecting branch which is called denticle (Fig. 103: j–k, p–s), or it appears after secession of the conidium as a short protuberance which is referred to as nodule (Fig. 103: t–y). Sometimes the conidia are sessile and the conidiogenous locus more or less invisible and then named scar (Fig. 103: n–o).

Electron microscopic studies of conidiophore tips confirm the holoblastic conidiogenesis in *Orbiliomycetes* (Morikawa et al. 1993: fig. 8, TEM, *Lecophagus longisporus*; Glockling & Dick 1994: fig. 10, SEM, *Drechslerella brochopaga*). Reports

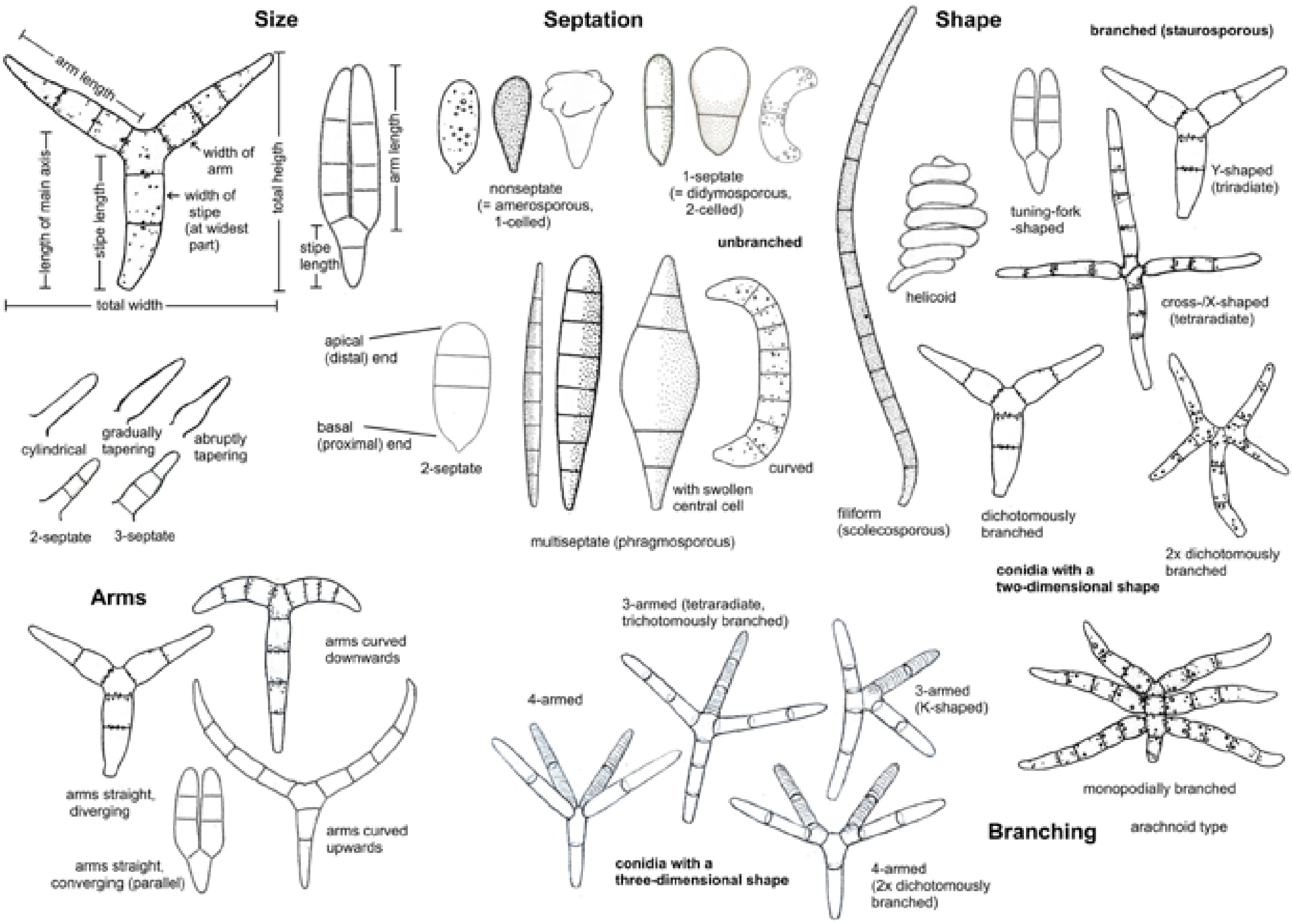


Figure 104: Morphology of conidia (see also Fig. 46 (ascospores) for further shapes).

of phialidic conidiogenesis in the class are either incorrect, e. g., in the recently described *Dactylella bolusanthi* Crous (see under *Orbilia* series *Neodactylella*, p. 1438), or originate from a contamination, as assumed by us in *Amphosoma persooniae* Crous (see under *Amphosoma*, p. 272).

Conidia. Conidia of *Orbiliomycetes* are always hyaline and thin-walled (illustrations of seemingly thick walls are due to plasma detachment in the dead state). At the base they are often somewhat truncate (place of detachment, called hilum) or possess a ± distinct small protrusion with a truncate base. A very wide range of diversity in conidial morphology is observed within the class, the different types being classified in earlier times according to their shape, branching, and curvature (Fig. 104). Similar as with the conidiophore types, different conidial types led in the past or even today to the distinction of different anamorph-typified genera. However, various studies – including ours – showed that conidial morphology is only in some cases correlated with the here presented infrageneric groups of *Orbilia*.

Unbranched conidia vary in shape between ellipsoid, (sub) cylindrical, clavate, obovoid, obpyramidal, fusiform, or top-shaped (see also Fig. 46, spore shape). They are mostly septate, either 1-septate (didymosporous) or with more septa (phragmosporous), rarely non-septate (amerosporous). Conidia which are more than 15 × longer than wide are termed scolecosporous. Branched (staurosporous) conidia are almost always multiseptate. They have usually one stipe and two, three or four (rarely more) arms, and are mainly Y- or T-shaped, more rarely ┼-, H-, K-, U-, V- or tuning fork shaped, thereby forming either 2- (flat) or 3-dimensional (spatial) structures. Conidia or conidial arms are usually straight or, more rarely, distinctly curved (Fig. 104).

Conidia with a spatial structure are frequent among those with more than two arms. The arms usually project at a maximum distance from each other (Fig. 104, 3–4-armed conidia). The natural orientation of the arms is easily overlooked when studying such conidia in a water mount because of the limited space beneath the cover slip and the motility of the arms at their hinge-like base.

The stipe has a truncate base which is formed during secession from the conidiogenous locus. Instead of the word stipe some authors prefer the term main axis which, however, in our understanding includes also the complete upper prolongation of the stipe (Fig. 104), although different authors use main axis differently. Controversy exists also concerning the question whether or not the basal septum of a branch (stipe, arm) is counted, which is complicated by the fact that the proximal septum may occur a varying distance away from the branching point, for which reason we have consistently counted all septa of a branch (see p. 10, Microscopic measurements).

A correlation between conidial branching and desiccation tolerance can be noted within *Orbiliomycetes*. Desiccation-sensitive species possess in almost every case unbranched, straight conidia (exception: *O. multiformis*). In some of these species one conidial cell is much larger than the others. Desiccation-tolerant species have often branched conidia; if unbranched, the conidia are usually more or less curved, and their shape is always ± cylindrical. In *Hyalorbilia*, however, unbranched conidia are generally straight or only slightly curved, often fusiform, irrespective of being desiccation-tolerant or not.

The size of unbranched conidia ranges from ca. 10–20 up to 100–200 µm in length and from ca. 2–3 up to 20–25 µm in width. Broad conidia may attain a maximum length of ca. 100(–130) µm, whereas longer conidia are only ca. 4–6(–10) µm wide. Branched conidia range from ca. 5–20 up to 50–100 µm in their total width.

The cytoplasmic contents of living conidia may show differences between the taxa. The cytoplasm often contains some minute, KOH-resistant lipid guttules (LBs), usually near the septa or the lateral walls, rarely large ones more in the centre of the cells (seen only in some species of *Orbilia* series *Helicoon* and all of series *Pseudotripoconidium*). Non-refractive vacuoles are commonly observed in conidial cells, either many small or a few large ones. One or a few small to large glycogen bodies occur in some taxa. These are only perceptible by their dextrinoidity (Fig. 91: d, Tab. 9), and were so far not observed in desiccation-tolerant species. Strongly refractive non-lipidic bodies (SCBs, Fig. 89: f) were observed in conidia of several *Hyalorbilia* species, which appear to be characteristic of brachyphoris-like anamorphs. They instantly disappear in KOH, and are not stained in $\mathrm{CRB_A}$. Similar bodies are typical of *Lecophagus*, where they are referred to as 'cubical bodies' because of their more or less angular shape, and where they also occur in the vegetative hyphae (Fig. 89: a–e).

In many species, conidia germinate quickly and also form anastomoses among each other, whereas in others germination was rarely observed and germ tubes soon stopped growing on agar. The direct formation of conidia from germinating conidia (microcyclic conidiation) was never observed by us with certainty (see also p. 113, Microconidia), although connections between conidia by anastomoses are sometimes interpreted in such a way.

Differences in conidial morphology between populations. Some variability in conidial size and shape was often noted between collections here referred to the same species. In some cases such variation might support separation into different species, whereas in others it is thought to represent natural variation. In extreme cases the obtained conidia strongly differed between isolates, although their teleomorphs were without any significant morphological deviation. In these cases the two conidial types never occurred mixed within a single strain. For example, in a number of collections referred to *O. ocellata* s.l. and *O. lentiformis* s.l., a group which forms an aggregate of unsharply delimited taxa, two different conidial types are formed in pure culture: some formed vermispora-like phragmoconidia while others formed trinacrium-like stauroconidia. However, these anamorphs were not clearly correlated with differences in the teleomorphs. Instead, strains of both collective species formed either only trinacrium- or only vermispora-like conidia. Our sparse molecular data indicate that about six taxa are involved (including *O. foliicola* and *O. subocellata*) which can hardly be recognized by their teleomorph alone (see Phyl. 8).

A comparable phenomenon of deviating anamorphs characterizes the very complex species aggregate around *O. auricolor*. Eight more or less distinguishable *Arthrobotrys* anamorphs have been found connected to teleomorphs with a rather invariable morphology that strongly resembles the holotype of *O. auricolor* (see p. 1530): *A. superbus* (Pfister 1994), *A. cladodes* var. *macroides* (≡ *A. macroides*) & *A. oligosporus* (Pfister & Liftik 1995), *A. cladodes* & *A. javanicus* (Liu 2006), *Monacrosporium psychrophilum* (≡ *A. oudemansii*) (Rubner 1996), *A. yunnanensis* (Mo et al. 2005a), and *O. menageshae* (present study). *A. oudemansii* (see under *O. elegans*, p. 1554) is very distinctive in acrogenously formed, broadly fusiform, 2–3-septate conidia with inflated middle cell. *A. yunnanensis* was only described from its microconidial stage but is conspecific with isolates with acrogenously formed, narrowly fusiform multiseptate macroconidia (see under *O. multiformis*, p. 1547). The unidentified *Arthrobotrys* state of *O. menageshae* is unique by its acrogenously formed, variable, obpyriform to fusoid, 0–3-septate conidia. The remaining five have similar ellipsoid to obovoid or obpyriform, (0–)1-septate conidia. Among them, *A. javanicus* (see under *O. javanica*, p. 1551) and *A. oligosporus* (see under *O. oligospora*, p. 1540) more or less sharply deviate from the remaining three in conidia with eccentrical septum and broader upper cell, the former also in candelabrelloid conidiophores. Because of the different anamorphs, Pfister & Liftik (1995) and Webster et al. (1998) concluded that *O. auricolor* is an aggregate of different species.

But even cultural results are not always convincing: we have grown cultures from three European collections and observed anamorphs also on the natural substrate of some other samples here referred to *O. auricolor*. They were at first tentatively referred to *A. superbus* (?= *O. auricolor*) or to the very similar *A. cladodes* (≡ *O. cladodes*), in one case (Pl. 948: 5) somewhat resembling *A. oligosporus* (≡ *O. oligospora*), and no sharp separation was possible between them. Due to a more or less strong similarity among these three *Arthrobotrys* species and due to our observation that a certain variation often occurs within a single strain, we concluded that in this case a morphological differentiation is not practicable, contrary to the opinion of Pfister (1994) and Pfister & Liftik (1995). However, molecular data on this group suggest that even strains with a very similar anamorph may belong to different taxa (see p. 1533), and the *O. auricolor*-complex is still far from being solved.

Different conidial types within a species (conidial dimorphism). Strong variation in conidial morphology is frequently observed within a specimen. Particularly in cultures we often recognized two, rarely three or more different conidial types which were even referable to different form genera. For example, a small number of unbranched phragmoconidia more or less regularly occurred among the abundant branched trinacrium-like conidia in a number of species: e.g., in *O. flavida* (Pl. 172: 4), *O. foliicola* (Pl. 168: 1), *O. microserpens* (Pl. 740: 4), *O. ocellata* (Pl. 164: 7), *O. pleiovitalbae* (Pl. 710), *O. spermoides* (Pl. 358: 4), *O. vermiculati* (Pl. 689: 1), and *O. vinosa* (Pls 257: 5; 258: 1). Likewise, in *O. eucalypti* (H.B. 6213), *O. xanthostigma* (H.B. 6745), and *O. tremulae* (H.B. 6963a) a more or less small number of phragmoconidia occurred among the prevailing tuning fork shaped dicranidion-like conidia, and rarely also a few 3-armed conidia of this type. Comparable observations of unbranched conidia have been reported in *Dicranidion* and *Trinacrium* by Berthet (1964a), Tubaki & Yokoyama (1971), Butterfield (1973), Matsushima (1981, 1993, 1995), Magyar & Révay (2008), and others.

Four different conidial types were obtained by us in pure culture of *O. microsoma*: unbranched phragmoconidia, 2-armed conidia (triradiate, trinacrium-like), and 3-armed conidia (tetraradiate, descalsia-like), besides a fourth type with 4-armed

¥-shaped conidia. Comparable cases were observed in series *Hemiorbilia*, e.g., in *O. subaristata* and *O. aristata*: 2- and 3-armed conidia (trinacrium- and descalsia-like) were recorded in pure culture and on the natural substrate, whereas 4-armed dwayaangam-like conidia only on the natural substrate. Similar observations on three to six different conidial types within a strain, comprising dicranidion-, trinacrium- and dwayaangam-like conidia, were made by Drechsler (1938), Ando (1992), Ando & Tubaki (1984b), Matsushima (1981), and Barron (1991c).

Microconidia. Another kind of conidial dimorphism occurs predominantly in nematode-trapping species of section *Arthrobotrys* (Tab. 15), and here especially in taxa of series *Arthrobotrys* and *Drechslerella*. Besides the normal 'macroconidia' which have one or more septa, distinctly smaller, mostly 0–1-septate conidia with often very different shape are formed, which are currently referred to as 'microconidia' (or 'secondary conidia'), sometimes also as 'spore-like bodies' or 'conidioid bodies' (Drechsler 1940). Their size in section *Arthrobotrys* lies in the range of 10–30(–40) × 3.5–10(–15) µm. Either length or width, or both, are distinctly below that of the associated macroconidia, and their volume is about 1/20–1/3 of those. Microconidia are often cylindrical but also long-ellipsoid to clavate. They are formed on similar but mostly shorter conidiophores, which sometimes emerge directly from germinating macroconidia. Microconidia may germinate to produce small trapping organs (*O. brochopaga*, Barron 1979a, as *Drechslerella*), or they produce shorter secondary microconidiophores and microconidia (*O multiformis*, series *Arthrobotrys*, Dowsett et al. 1984, as *Dactylella*). Although usually sharply delimited from macroconidia, cases of unsharp differentiation with intermediate conidial types occur (see Tab. 15).

According to Barron l.c., microconidia in predatory fungi occur 'sporadically and most frequently in association with macroconidia', and were solely obtained in the presence of nematodes. However, in the ex-type culture of *Gamsylella gephyropaga* (CBS 228.37), Rubner (l.c., as *Monacrosporium*) found only microconidia. Apparently, the ability to produce macroconidia was lost in this case. Two cases are worth mentioning here, in which two newly described anamorphs gained from ascospore isolates formed only microconidia, whilst in different strains, which are identical in the ITS region, both micro- and macroconidia were observed. *Drechslerella yunnanensis* was described by Yu et al. (2009b) gained from a teleomorph very similar to *O. orientalis*, but in another strain gained by Liu (2006) also macroconidia occurred (as *O. yunnanensis* in the present study, see Pl. 1014: 2). Likewise, *Arthrobotrys yunnanensis* was described by Mo et al. (2005) gained from a teleomorph that resembles *O. auricolor*. Only microconidia were observed, but molecular data indicates that other strains, which also form macroconidia, are conspecific (as *O. multiformis* in the present study, see p. 1549).

In *A. scaphoides* Peach (1952) obtained microconidia in addition to macroconidia, but in other isolates of the same species they were not observed (Zhang et al. 2010). Likewise, Rubner (1996) figured microconidia in *Monacrosporium*

Table 15. Species of section *Arthrobotrys* in which microconidia have been observed: 11 species of series *Arthrobotrys* (green), three of series *Dactylellina* (blue), one of series *Gamsylella* (red), and 11 of series *Drechslerella* (yellow). [1]) as *A. psychrophilus*, [2]) as *M. elegans* and *M. psychrophilum*, [3]) as *Monacrosporium ?doedycoides* (anamorph of *O. pilosa*), [4]) as *Kafiaddinia fusariispora*.

Species	Septa of microconidia	Septa of macroconidia	Differentiation from macroconidia	Reference	Figure in present study
Arthrobotrys eudermatus	0	(1–)3	sharp	Drechsler 1950a, Van Oorschot 1985, Rubner 1996	
A. gampsosporus	0	(3–)4	sharp	Drechsler 1962, Rubner 1996	
A. conoides	1	1	sharp	Jarowaja 1968 (as *A. tortor*)	
A. mangrovisporus	0(–1)	0–3	unsharp	Swe et al. 2008b	
Orbilia menageshae	(0–)1	(1–)2(–3)	unsharp	present study	Pl. 965: 1–2
O. multiformis	0–1(–2)	(2–)4–12	sharp	Watanabe 1992, Dowsett et al. 1984, Rubner 1996, Elshafie et al. 2003, Mo et al. 2005a	Pl. 958: 1–2
O. auricolor s.l.	0–1	1	unsharp	present study	Pl. 948: 2, 5; 951: 1, 3–4; 954: 7a
O. elegans	0–1	(2–)3(–4)	sharp	Drechsler 1944a[1], Rubner 1996[2], present study	Pl. 961: 1
O. latispora s.l.	0	1	unsharp	Zhang et al. ?2020	Pl. 973: 2c, 4e
O. scaphoides	0	(1–)2(–3)	sharp	Peach 1952	Pl. 974: 2
A. thaumasius	0	(2–)3	sharp	Rubner 1996, H.Y. Su pers. comm.	
Dactylellina leptospora	3–8	5–15	unsharp	Drechsler 1937	
D. leptospora	0–3	3–13	sharp	Mekhtieva 1978[4]	
O. biforma	1(–3)	((3–))4(–5)	sharp	Zhang et al. ?2020	Pl. 992
Gamsylella gephyropaga	1	(2–)3–4	sharp	Drechsler 1962, Rubner 1996	
Drechslerella anchonia	0	1(–2)	sharp	Barron 1979a	
O. bembicodes	1	(2–)3	sharp	Drechsler 1962, present study	Pl. 999: 2–3
O. brochopaga	1(–2)	(2–)3	sharp/unsharp	Barron 1979a, Ren et al. 2014a	
O. yunnanensis	(0–)1	(2–)3(–4)	sharp	Yu et al. 2009b, Liu 2006	Pls 12: a; 1014: 1–2
D. dactyloides	1	1–2	unsharp	Drechsler 1937a, Barron 1979a, Van Oorschot 1985	
D. doedycoides	0–1	2	sharp	Drechsler 1940, Pfister 1997[3]	Pl. 12: c
D. effusa (= *A. constringens*)	(0–)1(–2)	(1–)2(–3)	sharp/unsharp	Jarowaja 1968b, Dowsett et al. 1984, Van Oorschot 1985, Rubner 1996	
D. hainanensis	(0–)1	(0–)1–2	sharp	Li et al. 2013	
D. heterospora	1	2	sharp	Drechsler 1943b	
O. polybrocha	0–2	1	sharp	Pfister 1997, present study	Pls 1003: 1; 1005: 1p
O. pseudopolybrocha	1	2	sharp	Zhang et al. 2020	Pl. 1009: 2–3
O. tonghaiensis	1	(1–2–)3	sharp	Zhang et al. 2020	Pl. 1020: 1–2

elegans (≡ *A. oudemansii*) only in one out of three strains. Due to their inconsistent presence, microconidia are considered to be of limited taxonomic value (Barron l.c.). For *Vermispora cauveriana* Rajashekhar et al. (1991) reported small aseptate microconidia formed on long and thin germ tubes that emerge from the large multiseptate macroconidia. The species is, therefore, perhaps misplaced in *Vermispora* (= *Hyalorbilia*) (see Pl. 24: f).

Within section *Helicoon* of *Orbilia*, short oligoseptate microconidia were reported for the anguillospora-like anamorph of *O. rosea* by Pfister (1997), Webster & Descals (1979), and Descals et al. (1999, & Pl. 528: 1, 4–5). Yet, these microconidia were stated by Descals et al. (1999) to be not sharply differentiated from the scolecosporous macroconidia, rather they seem to form a continuum. Descals & Moralejo (2001: 16) argued that they might combine a spermatial and dispersive function. Also in *O. yuanensis* (0–)1–3-septate microconidia were seen (Qiao et al. 2015, & Pl. 546: 7). Similar but curved microconidia were observed in the present study in the helicoon-like anamorph of *O. luteorubella*, deviating from the coiled barrel-shaped macroconidia in showing max. 1–2 coils (see Pl. 536: 1).

In *O. carpoboloides* (section *Habrostictis*) we obtained small 0–1-septate, C-shaped conidia in pure culture, in concordance with Haines & Egger (1982, as *O. piloboloides*). Although no macroconidia were seen in these strains, we believe that the species is able to form phragmosporous C-shaped macroconidia, which were repeatedly seen by us on the natural substrate. *O. subocellata* (section *Lentiformes*) formed small 1(–3)-septate conidia together with large 3–6-septate ones in pure culture of a paratype, while the holotype culture produced only the large conidial type (see Pl. 166). The two types of conidia did not clearly overlap in size.

Phylogeny of anamorphs. Similar as stated for the ascospores, a logical phylogenetic system of conidial shapes would start from broadly ellipsoid to ovoid, non-septate conidia which might have evolved fusoid, or cylindrical conidia in which one or more septa are included (phragmoconidia). Cylindrical conidia may have further developed from straight to curved (vermispora-like) and/or increased their length/width ratio by forming long and slender, anguillospora-like conidia.

However, the phylogeny of conidial shape undoubtedly took also the opposite direction within *Orbiliomycetes*. This is particularly apparent in *Orbilia* section *Arthrobotrys*. Here the plesiomorphic conidial shape is unquestionably a straight phragmoconidium as represented by the non-nematophagous series *Dactylella*, because this group always formed the first branch in phylogenetic analyses, and similar conidia occur in various other groups of *Orbiliomycetes*. Conidia of the more advanced series *Arthrobotrys*, *Dactylellina*, *Drechslerella*, and *Gamsylella*, which are characterized by nematophagy and desiccation-sensitivity, appear to have evolved from cylindrical to ellipsoid-ovoid or fusiform, and from multi- to biseptate.

In various groups of non-nematophagous, desiccation-tolerant taxa, different types of branching led to a high diversity of staurosporous conidia with a varying number and length of usually multiseptate, sometimes curved arms. A single branch resulted in 2-armed conidia with the shape of a tuning fork (dicranidion-like) or a Y (trinacrium-like). Another branch (secondary dichotomy) of each of the two branches leads to dwayaangam-like conidia, if one of each secondary arm points downwards, to tree-shaped conidia if all arms point upwards, or to psammina-like conidia if the many arms lie in one plane and point in all directions.

Instead of four arms formed by two successive dichotomies, more than two arms may be formed synchronously by a single branching event at the apex of the main axis. Such conidia are always 3-dimensional and often trichotomous but also with more arms, and are referred to as tridentaria-like. A further type forms lateral pairs of 'legs' from a septate main axis reminiscent of spiders.

The evolutionary pathway may actually have started from unbranched to higher-branched. Drechsler (1937) argued in a similar direction when stating that, starting from an unbranched conidium like in *Dactylella*, a single bifurcation results in two-armed conidia like those of '*Pedilospora*' (= *Dicranidion*) *dactylopaga*, and after a second bifurcation in conidia as in '*Triposporina*' (= *Tripoconidium*) *aphanopaga*. On the other hand, tree-like conidia with the highest known (tertiary) dichotomy are characteristic of a monotypic genus with a very basal phylogenetic placement (*Mycoceros*), and also trinacrium-like conidia are found in different basal genera.

Conidiophore length shows a correlation with desiccation tolerance in that long and slender conidia are only found in desiccation-sensitive taxa, mainly in *Orbilia* section *Arthrobotrys*, therefore, they are to be considered as apomorphic. The plesiomorphic conidiophore is an integrated conidiogenous cell or a very short hyphal branch. Conidiophores with apical branches and multilocular conidiogenous cells occur in various groups, so that evolutionary lines are difficult to assess. The arthrobotryoid type of conidiophores, characterized by swollen nodular conidiogenous cells, appears to have evolved within series *Arthrobotrys* from the denticulate type, but since both types occur scattered in various clades of that series, the arthrobotryoid type appears to have emerged polyphyletically.

Differences between pure culture and natural substrate. Conidia collected from natural substrate were sometimes larger or higher-branched than those gained in pure culture. For example, in field samples we sometimes found longer arms and stipes in the trinacrium-like conidia of *O. microserpens* (Pl. 740: 4) and *O. vinosa* (Pl. 258) and in the dicranidion-like conidia of *O. leucostigma*/*xanthostigma* (Pl. 876).

In *O. aristata* we obtained in pure culture conidia with three arms (descalsia-like), whereas on the natural substrate occurred in addition conidia with two arms (trinacrium-like) and conidia with mainly four arms (dwayaangam-like) (Pls 342–343). Similarly, Butterfield (1973) and Matsushima (1975) observed larger conidia from natural substrate in *Dicranidion fragile*, and Matsushima (1987) in *D. ontariense.* However, conidia collected from the natural substrate cannot be attached with final certainty to a teleomorph growing closely adjacent, because *Orbilia* species with similar anamorphs often grow in association and do not always simultaneously form a teleomorph.

Rubner (1996: 26) observed that cultural conditions may influence conidial characters. In *Arthrobotrys oudemansii*, length/width ratio of conidia formed in pure culture depended on the temperature at which they were incubated: conidia were slightly wider and sometimes also longer at 25 °C compared to 15 °C. In four tested species, conidia were often longer and/or wider when grown on CMA:2 compared to water agar to which nematodes were added.

Table 16. Seven main types of trapping organs observed in *Orbiliomycetes*. * = *Hyalorbilia quadridens*; ** = *Dicranidion dactylopagum*, *Tridentaria glossopaga*, *T. tylota* (relationship of these three species within *Orbiliomycetes* uncertain); *** = '*Dactylella*' *passalopaga*.

Trapping organ	Adhesive	Main prey	Genus and section	Series
Adhesive pegs	+	rotifers, tardigrades	*Lecophagus*	–
Sessile adhesive knobs	+	rhizopods	*Hyalorbilia* * ?*Orbilia* **	– ?
	+	nematodes	*Lecophagus vermicola* *Orbilia* section *Arthrobotrys*	– *Dactylellina*, *Gamsylella*
Adhesive columns and arches	+	nematodes, rhizopods, arthropods	*Orbilia* section *Arthrobotrys*	*Gamsylella*
Stalked adhesive knobs	+	nematodes, arthropods	*Hyalorbilia* *** *Orbilia* section *Arthrobotrys*	 *Dactylellina, Gamsylella*
Adhesive networks	+	nematodes	*Orbilia* section *Arthrobotrys*	*Arthrobotrys*
Non-constricting rings	–	nematodes	*Orbilia* section *Arthrobotrys*	*Dactylellina*
Constricting rings	–	nematodes	*Orbilia* section *Arthrobotrys*	*Drechslerella*

Trapping organs. During our study we had the albeit rare opportunity to examine several types of trapping organs, either in axenic culture or in the natural environment. Our observations include unpublished or little-known data and a critical study in regard to living cells and their behaviour in killing agents, hence it seems justified to provide here a detailed report on trapping organs in *Orbiliomycetes*.

Several groups of *Orbiliomycetes* have developed different types of trapping organs in order to attract, catch and digest small invertebrates. Within *Orbilia*, all members of four series of section *Arthrobotrys* (*Arthrobotrys*, *Dactylellina*, *Drechslerella*, *Gamsylella*) are known to produce such organs of capture. The fifth series of this section (*Neodactylella*) is characterized by the absence of trapping organs. In all the remaining groups of *Orbiliomycetes* trapping devices are unknown, with only a few exceptions. Sporadically, trapping organs were reported in species with tridentaria-, dicranidion-, and brachyphoris-like anamorphs, and they are characteristic of members of *Lecophagus*. Two species were found to be predacious although they did not form conspicuous trapping organs (*Tripoconidium aphanopagum*, *Tridentaria carnivora*). Besides those fungi being predacious on motile prey, some taxa parasitize non-motile stages of invertebrates (eggs), or they form haustoria in spores and pollen (see p. 144–146).

Trapping organs, especially adhesive networks of series *Arthrobotrys*, are usually formed in pure culture in response to living nematodes. However, Nordbring-Hertz (1968) has shown that in *A. oligosporus* they are also formed in the presence of living earthworms, fly-larvae, or springtails. Members of the other three nematophagous series (*Drechslerella*, *Dactylellina*, *Gamsylella*) are generally capable of forming traps spontaneously (Gray 1987).

The first report of an orbiliaceous trapping organ appears to be that by Zopf (1888) who treated the adhesive nets of *Arthrobotrys oligosporus* (see Drechsler 1937a). About seven main types of orbiliaceous trapping organs can be distinguished (Tab. 16, for a survey see also Barron 1977, Rubner 1996, Scholler et al. 1999). According to molecular data, the different trap types are quite strictly diagnostic for the four nematophagous series of section *Arthrobotrys*. Usually, one species is able to produce only one type of trapping organ. However, in series *Dactylellina* about seven species simultaneously form two types, stalked adhesive knobs and non-constricting rings (Figs 174–176). In the aberrant *Dactylellina parvicollis* (a synonym of *D. phymatopaga*), stalked and sessile knobs are reported to occur with adhesive loops and columns (Figs 106: i–j; 175: d, i; Drechsler 1962; Jarowaja 1968a: figs. 1–22; Rubner 1996: fig. 44). Besides a certain variation in trap morphology and partial absence of certain types, this complicates a clear assignment to an anamorph-typified genus. Hypotheses on the evolution of these trapping organs can be found in Li et al. (2005), Yang et al. (2007, 2012a), and are discussed on p. 121 (Phylogeny of trapping organs).

All these organs of capture are generally formed as lateral, usually upward oriented outgrowths of the mycelial hyphae, but sometimes they may also arise from conidia, either directly or on short germ tubes (see Rubner 1996: 20). Except for those trapping organs that form regularly ring-shaped structures and trap the prey mechanically (constricting and non-constricting rings), apparently all exude an adhesive mucous substance being sticky to various invertebrates. This substance usually forms a thin film but in a few species a very copious sheath (Figs 106: c–e, 107: d–j). Nordbring-Hertz (1988) found that the adhesive substance contains lectins that show affinities to carbohydrates of the invertebrate cuticle with a rather high selectivity. A total of 17 adhesion-associated protein-coding genes were found in the *A. oligosporus* genome (Yang et al. 2014). The studies by Jansson & Nordbring-Hertz (1979) suggest that there may also be a substance that attracts the prey.

Regardless of their thickness, the mucous substance is invisible in water mounts under bright field illumination, therefore, even thick sheaths are easily overlooked and might exist in more species than hitherto known. The mucus can be visualized with CRB by staining lilac (Fig. 107: g–h), but hyphal surfaces of *Orbiliomycetes* generally stain so in that dye. Actually, all parts of an adhesive knob including the supporting hypha stain faintly to bright lilac, without any difference between head, stipe, and hypha. The assimilative hyphae inside the captured nematode did not stain, however, even when squashed out of the nematode.

Constricting rings are generally stated to be non-adhesive, but also here the wall surface stains pale lilac in CRB, while the supporting hyphae and stipes of these ring traps stain medium to deep lilac. Hence, the adhesiveness of a thin mucous layer is only demonstrated when an animal gets attached to it. When the adhesive substance is very abundant it can clearly be seen under the LM in water mounts, but only by using special techniques such as phase contrast, dehydration in ethanol, or staining with CRB. The thickness of such mucus strongly depends on its hydration rate: in water the mucus swells to a maximum diameter, whereas even in an atmosphere of rather high humidity it is quite contracted by showing a crumpled surface (Fig. 107: e, j).

Loop or ring traps are formed by the curved growth of side branches. In adhesive loops (arches and networks) the branch tip generally fuses with the hypha from which it emerged (Figs 106: m, u; 108: b, d), or with adjacent arches or columns (Fig. 106: o, v), rarely with its basal cell (Figs 106: t; 108: c). In contrast to loops, true ring traps are consistently formed by fusion of the branch tip with the lowermost ring cell and, in

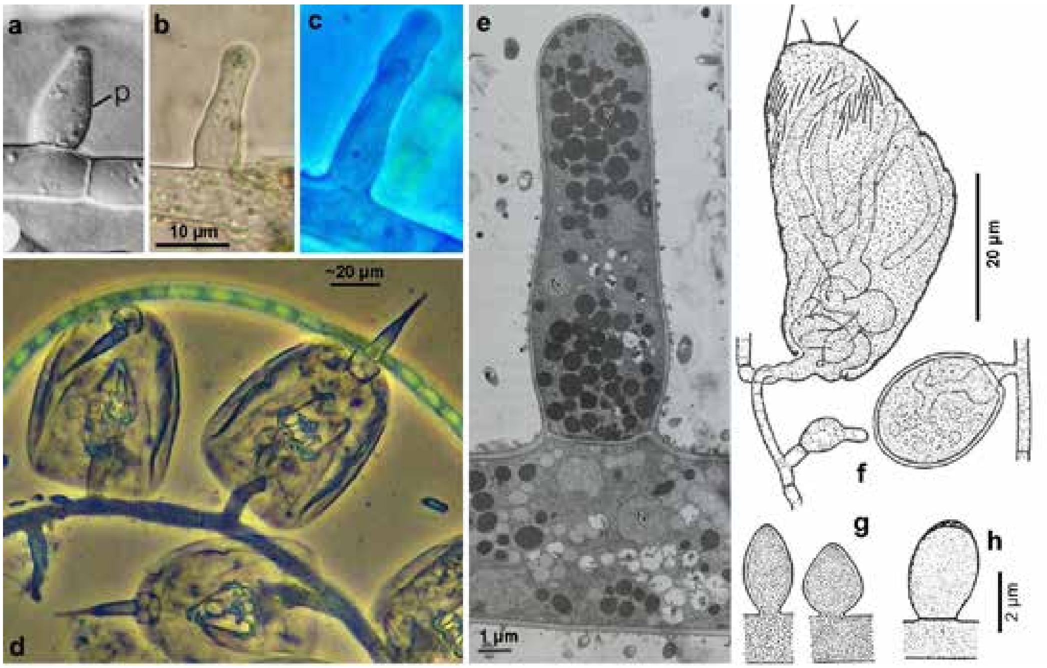


Figure 105: **a–e**. Adhesive pegs in *Lecophagus* (**d**. with captured rotifers); **f–h**. adhesive knob- to peg-like trapping organs in *Hyalorbilia* (*Brachyphoris*) and *Tridentaria*. **f**. with captured rhizopods *Euglypha laevis* and *Geococcus vulgaris*. — **a**. *L. navicularis* (from Tzean & Barron 1983), **b–e**. *L. muscicola* (**b–d**. H.B. 7771; **c–d**: phot. P. Bergmann, d phase contrast; **e**. Morikawa et al. 1993, TEM). **f**. '*Dactylella*' *passalopaga* (from Drechsler 1936), **g**. *Tridentaria tylota* (from Drechsler 1964), **h**. *T. glossopaga* (from Drechsler 1962). **a–b**, **f–h**. living state, **c–e**: dead state (**c**. in CB_L).

constricting rings, in addition also with the upper cell of the stalk (Figs 109, 110: a).

At least in two main trap types (sessile and stalked adhesive knobs, non-constricting rings), the trapping organ may more or less regularly break from the hypha as a consequence of heavy struggling of the prey. In this way the knobs and non-constricting rings do function as diaspores, and contact of the nematode to further traps may occur (Fig. 109: f, Barron 1977, Rubner 1996: 14, 17, Nordbring-Hertz et al. 2011). In series *Dactylellina* sessile or sometimes stalked adhesive knobs are formed on the tip of conidia (Pl. 7: f–g, j–k), even when still attached to the conidiophore, and are thus able to attach to passing nematodes (Barron l.c.).

Apart from adhesive pegs, the course of events after capture is the same in all types of trapping devices: penetration of the cuticle by a narrow tube, and formation of an infection bulb (haustorium) from which assimilative hyphae grow into the prey. The complete consumption of the victim will be accomplished within ~12–24 hours, which may in some cases stay viable for most of this time. In the case of adhesive pegs and knobs in *Lecophagus* and *Hyalorbilia*/*Brachyphoris*, the infection usually takes place in the region of the mouth or the shell opening. The peg apex does not swell or only slightly, when the assimilative hyphae grow out directly from the apex of the peg. However, infection bulbs are produced when adhesive peg-like appendages grow out of conidia and attach to the cuticle away from the mouth region (*Lecophagus navicularis*, Tzean & Barron 1983: fig. 6).

TEM-investigations have shown abundant electron-opaque inclusions (vesicles) ~0.1–0.3 µm diam. near the periphery of the cytoplasm close to all those surfaces which have the potential to trap animals. These vesicles cannot be seen with the LM, and are thought to contain enzymes which disintegrate the host cuticle and digest its protoplasm (Heintz & Pramer 1972, Dowsett et al. 1984, Glockling & Dick 1994).

Trapping organs observed in the present study. In a collection of *Lecophagus muscicola* the trapping of rotifers by adhesive pegs could be observed (Fig. 105: b–d & Pl. 51). Adhesive columns of *Gamsylella gephyropaga* occurred once on the natural substrate in mixture with *O. alba* (H.B. 9051c). Stalked adhesive knobs were obtained in pure culture of *Orbilia rubrovacuolata* (Fig. 106: b) and *O. mammillata* (see Pl. 981 & IVV), and on the natural substrate we saw them in a few cases, e.g., emerging from the apothecial base of *O. mammillata*. A peculiar type of large adhesive knobs with lageniform heads (Fig. 107: d–j) occurred in abundance close to apothecia of *O. alba*. These rather robust organs of capture have very strong adhesive properties, and are adapted for trapping small arthropods. Sessile adhesive knobs were repeatedly seen on conidial cells of *Lecophagus vermicola* (Pl. 52) and *Haptocara* sp. (Pl. 53).

Adhesive networks were obtained by us in *O. auricolor* (Pl. 951: 1), *O. elegans* (H.B. 6972a, not figured), *O. scaphoides* (Pl. 974: 1), and *O. menageshae* (Pl. 965: 2), but we never saw them on the natural substrate. Non-constricting rings we have never obtained in our cultures, nor did we observe them with certainty in the natural environment. Constricting rings were formed in pure culture of *O. orientalis* (H.B. 8146a, IVV) and *O. polybrocha* (Fig. 110: i–j, m–q, Pl. 1005). On other occasions we found them on the natural substrate (e.g., *Drechslerella bembicodes*, Fig. 110: a). A survey on the different types of trapping organs is shown in Tab. 16. A detailed discussion of each type with illustrations of its characteristics is given below.

Adhesive pegs (Fig. 105: a–e). This type of trapping organ is reported within the *Orbiliomycetes* mainly for the genus *Lecophagus* (see p. 238), but the term adhesive peg is also in use for similar organs in the *Zoopagales* ('*Zygomycota*'), with which *Lecophagus* has previously been confused, and small adhesive peg- or knob-like structures occur in *Hyalorbilia* (treated below under adhesive knobs). The trapping organ in *Lecophagus* consists of a single cell which is either cylindrical or often ± lageniform with a bulbous base. The apex often forms a slightly enlarged roundish head. The pegs are 10–24 µm long and in their lower part 3.5–12 µm wide. The adhesive substance is apparently restricted to the apex, but it is not even perceptible under the TEM (see Morikawa et al. 1993: figs 2, 7; Fig. 105: e). The living trap cells contain small refractive cubical bodies similar as the other cells of the fungus (Fig. 105: a–b). The peg apex may sometimes proliferate to form a new peg (Dick 1990).

Adhesive pegs of *Lecophagus* are known to trap rotifers and tardigrades. In contrast to most of the other trap types and

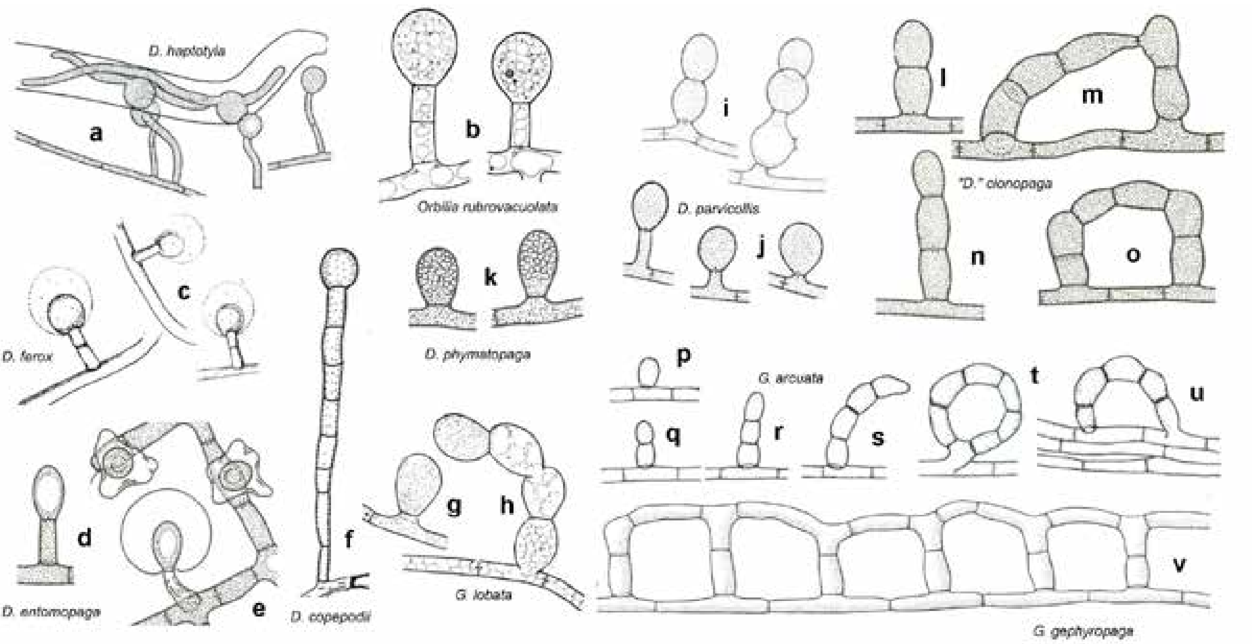


Figure 106: Adhesive knobs and branches (columns and loops) in series *Dactylellina* and *Gamsylella* of *Orbilia* section *Arthrobotrys*. — **a**. with trapped nematode; **a–f**, **j** (left). stalked adhesive knobs (**c–e**. with thick adhesive mucilage); **g**, **k**, **j** (right), **p**. sessile adhesive knobs; **h**, **i**, **l**, **n**, **q–s**. superimposed (proliferating) knobs or adhesive columns; **m**, **o**, **t**, **u–v**. adhesive loops (**v**. ladder-shaped). Note unsharp limits between stalked and sessile knobs, or between knobs, columns, and loops; (**a**. from Drechsler 1950a, **b**. present study, **c**. from Onofri & Tosi 1992, **d–e**. from Drechsler 1944b, **f**. from Barron 1990, **g–h**. from Duddington 1951b, **i–j**. from Drechsler 1962, **k**. from Drechsler 1954, **l–o**. from Drechsler 1950a, **p–u**. from Scheuer & Webster 1990, **v**. from Drechsler 1937a).

despite the aquatic habitat of our studied German collection of *L. muscicola*, the hyphae and trapping organs survived complete drying, which indicates an adaptation to periodically dry environments such as ponds or river banks. Adhesive pegs were also seen on anchoring hyphae of apothecia on xeric bark by D. Magyar (pers. comm.) and one of us (G.M.), referred to the here described desiccation-tolerant species *L. ellipsoideus*.

Sessile adhesive knobs (Figs 105: g–h, 106: g, k, j, p). This rather primitive type of trapping organ is known from a few nematophagous species of series *Dactylellina* (*D. phymatopaga* = *D. parvicollis*) and *Gamsylella* (*G. robusta* and others). Sessile knobs are broadly or narrowly attached to the supporting hypha, cylindrical to clavate-ovoid or globose, 6–10(–13) × 4–5.5 up to 6–8(–12) µm, in *G. robusta* 16–24 × 9–10 µm, and coated by a thin adhesive mucus. In *D. phymatopaga* both sessile and stalked (mainly short-stalked) adhesive knobs occur, but their stalk has never a basal septum (Fig. 106: j–k). In some species the traps may form short, ± strongly constricted chains of superimposed knobs (Fig. 106: h–i), which are referred to as proliferating knobs but cannot sharply be delimited from adhesive columns (Fig. 106: l, n, q–s).

A similar type of adhesive knob (or peg) is adapted to the capture of testaceous rhizopods. It is known from two species of *Brachyphoris* (anamorph of *Hyalorbilia*), namely *B. tenuifusaria* and '*Dactylella*' *passalopaga* (Fig. 105: f), also from *Tridentaria tylota* (Fig. 105: g), *T. glossopaga* (Fig. 105: h), and *Dicranidion dactylopagum*. In their mode of capturing the victim in the region of food intake (here the shell opening) these anamorphs are reminiscent of *Lecophagus*. However, their organs of capture either resemble sessile adhesive knobs though being distinctly smaller (2.5–4 × 1.3–2.2 µm), or closely match stalked adhesive knobs (in '*Dactylella*' *passalopaga*; in *Brachyphoris tenuifusaria* they appear to be sessile). Drechsler (1934, 1962, 1964) named those in *Tridentaria* and *Dicranidion* adhesive protuberances. In *T. glossopaga* he stressed the consistent presence of a basal septum, whereas in the other two he did not figure septa at their place of attachment. Very similar knobs as in the two *Tridentaria* species occur in the basidiomycete *Lactydina tylopaga* (Drechsler) Subram., which consumes non-testaceous amoebae (Saikawa et al. 1994).

Adhesive columns and loops (Fig. 106: l–o, q–v). This type of trapping organ is characteristic of series *Gamsylella*. It originates from sessile adhesive knobs which regularly proliferate at their tip to form further adhesive cells. The resulting ± moniliform rows are either straight (adhesive columns) or tend to get curved by forming loops, either roundish arches, or angular bridges between columns (scalariform = ladder-shaped). Rarely, single cells of such arches may proliferate laterally to form more complex structures similar to adhesive networks (*Gamsylella gephyropaga*, Drechsler 1937a: fig. 12E; Rubner 1996: fig. 31b, in *G. arcuata* the arches even proliferate regularly). All these types may occur within a single strain. The adhesive cells are ~5–8 µm wide and the loops have an outer diameter of ~24–38 µm.

Stalked adhesive knobs (Figs 106: a–f, j (left), 107). Trapping organs of this type are the key character of series *Dactylellina*. The stalks are 1.5–4.5(–5.5) µm wide and mostly have a basal septum (in contrast to sessile adhesive knobs which occasionally form a short stalk). They are usually 4–15(–40) µm long and 1–2(–4)-celled, in one species even 40–280 µm long and multiseptate (*Dactylellina copepodii*). In contrast to adhesive pegs, the swollen terminal cells of adhesive knobs are always segregated from the stalk cells by a septum.

In species which trap nematodes the adhesive cell is ± globose to obovoid, 6–10(–12) × 5–8.5(–10.5) µm, and the mucous layer is, when hydrated, usually very thin (< 1 µm). Yet, in three arthropod-capturing species referred by us to series

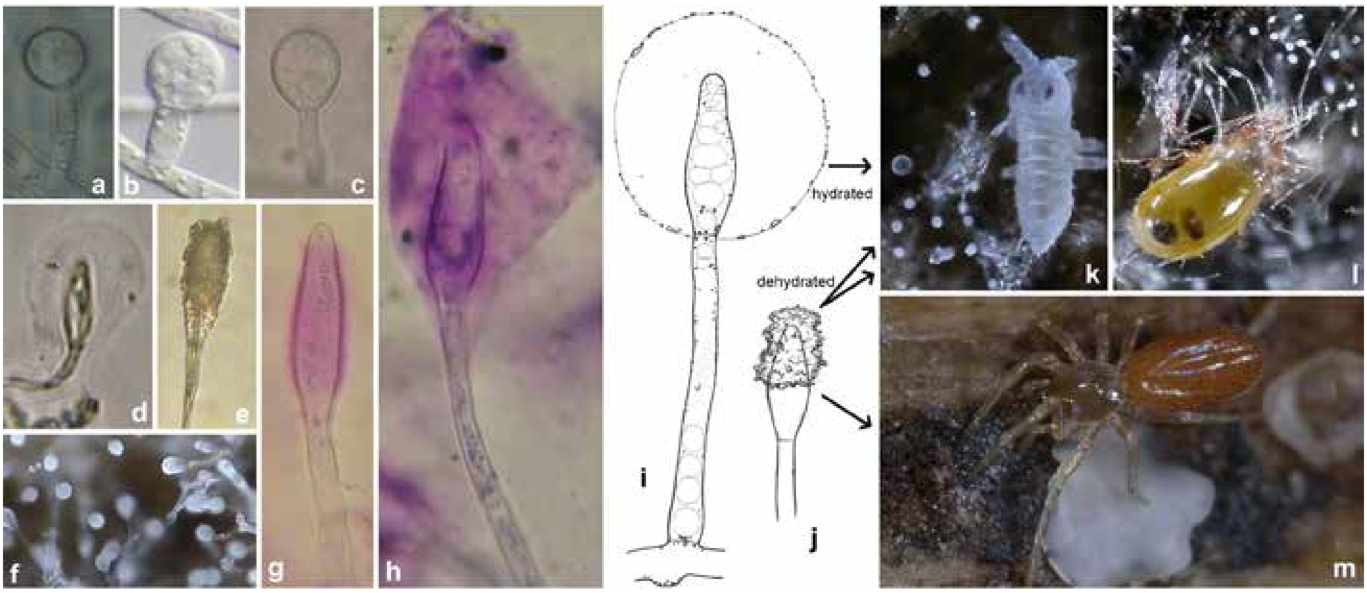


Figure 107: Stalked adhesive knobs in series *Dactylellina* and *Gamsylella* of *Orbilia* section *Arthrobotrys*. — **a–c**. with globose heads (capable to trap nematodes), **d–l**. with lageniform heads (capable to trap arthropods: **k**. springtail, **l**. mite, **m**. spider). **a**. *O. rubrovacuolata* (phot. M. Scholler), **b**. *O. ellipsospora* (from Liu 2006, as *O. quercus* var. *hainanensis*), **c**. *O. mammillata*, **d–m**. *O. alba*. The thick ball of adhesive gel in *O. alba* is invisible in water mounts but quite distinct when dehydrated in alcohol (**d**) or when stained with CRB (**g–h**). Even in a high atmospheric humidity the gel is rather dehydrated (**e**, **f**, **j**). Larger arthropods (**m**) are only temporarily trapped and thus unsuitable as prey.

Gamsylella (‘*Dactylellina*’ *ferox*, ‘*D.*’ *entomopaga*, and *Orbilia alba*) the mucus is much more abundant and strongly swells to 6–10 or even 20 µm in thickness when hydrated. The adhesive heads in these species differ clearly from each other in shape and size (‘*D.*’ *ferox*: globose, 18–31 × 16.5–24.5 µm, ‘*D.*’ *entomopaga*: ellipsoid, 8–13 × 4.5–8 µm, *O. alba*: lageniform, 27–36 × 8–11 µm). Similar balls of strongly adhesive gel characterize *Nematoctonus* (anamorph of *Hohenbuehelia*, *Basidiomycota*) with hourglass-shaped adhesive knobs.

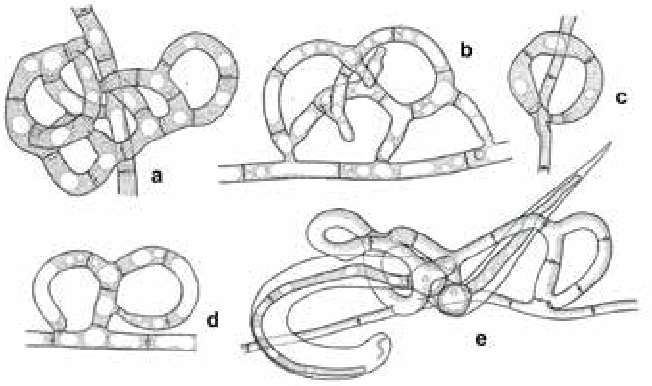


Figure 108: Adhesive networks in *Orbilia* section and series *Arthrobotrys*. — **a**, **d**. *A. eudermatus* (from Drechsler 1950a), **b**. *A. thaumasius* (from Drechsler 1937a), **c**. *A. musiformis* (from Drechsler 1937a), **e**. *A. cladodes* with captured nematode (from Drechsler 1937a); **c–d** are somewhat exceptional or initial stages (that in **c** resembles a constricting ring).

Adhesive networks (Fig. 108). This type of reticulate trapping organ is the key character of series *Arthrobotrys*. Adhesive networks are formed by lateral proliferation from adhesive loops to form a multibranched three-dimensional structure composed of a varying number of arches. Mainly nematodes are trapped, either by external contact, or by entering the perforations of the net. In rare cases only one or a few arches are formed, and the network may predominantly be two-dimensional. Rarely, incomplete arches (‘adhesive loops’) were observed (‘*Arthrobotrys oligosporus*’ CBS 289.82, Scholler et al. 1999: 94, fig. 1) or adhesive hyphae together with adhesive nets (*A. botryosporus*, Barron 1979b). The inner loop diameter ranges at ~10–40 µm, and loop cell width at ~(3–)4–7(–8) µm.

Delimitation from adhesive loops and from non-constricting rings is sometimes not very sharp. True ring traps differ in not including parts of the stalk within the ring, whereas adhesive loops differ in being more constricted at the septa and usually two-dimensional.

Non-constricting rings (Fig. 109). This ring type is known from ca. seven species of series *Dactylellina* (see Figs. 174–176), where it inconsistently occurs in culture, mostly in combination with stalked adhesive knobs. The rings are 3(–4)-celled and supported by a 12–35(–?50) µm long, slender (1.5–2.5 µm), 1–3(–4)-celled stalk. They have an outer diameter of 13–24 µm (inner diameter 7–17 µm), and their cells are 2–5 µm wide. Contrary to constricting rings, the stalk is only connected to one of the ring cells, and the ring cells are in their middle region usually not distinctly thicker than at the septa. Moreover, triangular wall thickenings at the septa typical of constricting rings have so far not been reported. Sherbakoff (1933) believed that the rings developed from stalked adhesive knobs, but this

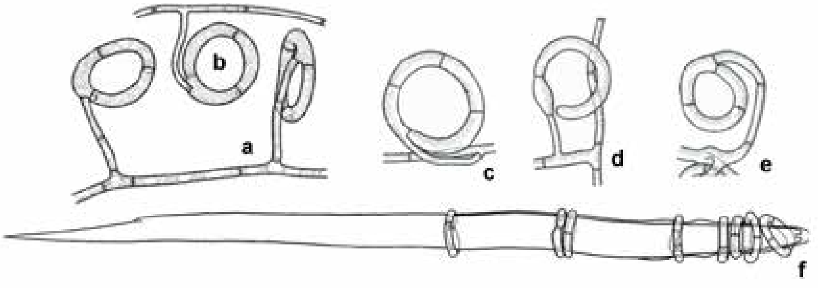


Figure 109: Non-constricting rings in *Orbilia* section *Arthrobotrys* series *Dactylellina*. — **a–b**. *Dactylellina leptospora*, **c–f**. *D. lysipaga* (both from Drechsler 1937a), **f**. a nematode accumulated 8 rings by tearing them off from the stalk.

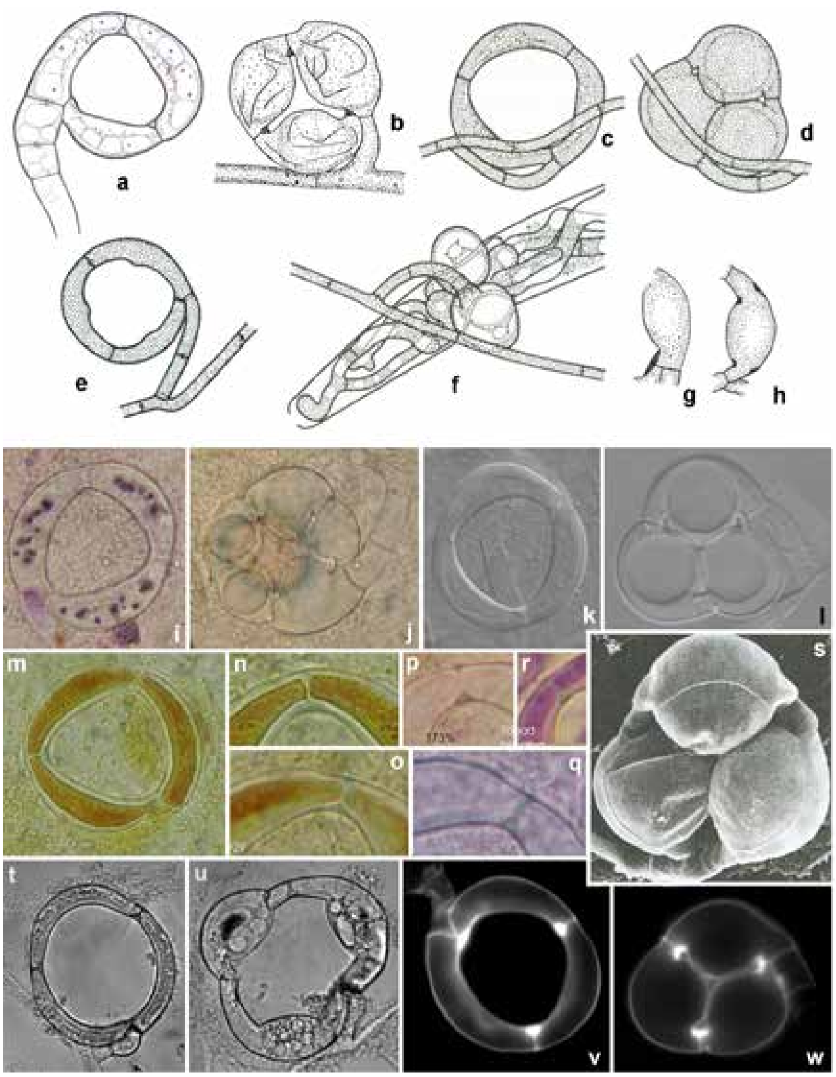


Figure 110: Constricting rings in *Orbilia* section *Arthrobotrys* series *Drechslerella* as seen under the LM (**s**. SEM); unexpanded in **a**, **c**, **e**, **i**, **k**, **m–r**, **t**, **v**; expanded in **b**, **d**, **f** (with captured nematode), **j**, **l**, **s**, **w**; partially expanded but ends of cells remaining unexpanded in **g–h**, **u**. Note triangular to lens-shaped wall thickenings at septa (**a–b**, **g**, **m–r**, **t–w**); transient annular wall thickenings during expansion (**h**); inner bulge-like projections of unexpanded ring cells (**e**); MCs formed inside intact vacuoles when stained with CRB (**i**); large vacuoles in expanded ring cells (**j**, **l**, **u**); rupture of outer wall layers at demarcation line during expansion (**s**). — **a**. *Drechslerella bembicodes* (H.B. 7165b); **b**. *D. dactyloides* (Muller 1958); **c–d**, **f**. *D. aphrobrocha* (Drechsler 1950a); **e**. *D. heterospora* (Drechsler 1943b); **g–h**. *D. doedycoides* (Muller 1958); **i–j**, **m–q**. *D. polybrocha* (H.B. 8317a); **k–l**. *D. doedycoides* (phot. H.Y. Su, H.B. 8929); **r**. *D.* cf. *bembicodes* (H.B. 9051g); **s**. *D. anchonia* (Barron 1979a); **t–u**. *D. dactyloides* (mutant with giant traps, Cui 2014); **v–w**. *D. dactyloides* (with normal traps, Cui 2014, stained with 0.2 % calcofluor White solution and viewed under dark field, Y.L. Cui pers. comm.). Living state (H_2O, **i**: CRB): **a**, **c–f**, **?g–h**, **i–l**, **q**, **u–w**; dead state: **b** (H_2O), **m–o** (KOH+IKI), **p** (KOH), **r** (CRB), **s** (REM), **t** (H_2O).

was never confirmed by later authors. The basal ring cell is actually sometimes markedly swollen (Sherbakoff, pl. 35 fig. A), a feature stressed also by Barron (1977) as characteristic, but this is only rarely clearly seen on illustrations, e.g., on Drechsler's drawings (Fig. 109: d).

This type of trapping organ is passive in its action, i.e., neither constriction nor adhesion occurs. It appears to be solely adapted to the capture of rather small nematodes which, during entering, cause the ring to wedge around their body. Following struggling, the ring easily breaks off at a point of weakness near the stalk apex (Barron 1977). Sherbakoff (l.c.) observed also trapping of larvae of minute flies by non-constricting rings.

Constricting rings (Fig. 110). Constricting rings are a consistent and exclusive characteristic of series *Drechslerella*. The main difference to the preceding type of trapping organ is the ability of a sudden expansion of the ring cells (within less than 0.1 sec, after a lag of 1–2 sec) to a 3(–4)-fold volume (Fig. 110: b, d, f). Constricting rings often capture nematodes at their tapered ends, rarely in the broad middle part, thus they can trap a prey with a body diameter much wider than the ring aperture.

Judging from Drechsler's observations, constricting ring diameters are species-specific to some extent, but vary also considerably within a strain. When micro- or macroconidia germinate to form a single trap, Barron (1979a) found that the diameter was determined by conidial size, i.e., the amount of available nutrients within the conidium. The outer diameter of constricting rings formed on mycelium usually ranges at 20–32(–40) µm, the inner at 12–20(–30) µm (Drechsler 1954). Exceptionally small rings were noted by Barron (l.c., 8–15 µm outer diam., formed from microconidia of *Drechslerella brochopaga*), and unusually large rings occurred in '*Dactylella*' *megalobrocha* (?= *D. bembicodes*, 40–48(–56) µm outer diam., Glockling & Dick 1994). Giant ring traps of 105–130 µm in outer diameter were formed together with the normal rings of 25–40 µm in an authentic strain of *D. brochopaga* incubated under conditions of poor ventilation (Turnbull & Zachariah 1978). In a Chinese strain of *O.* cf. *tonghaiensis* (YMF 1.01829), giant traps of 85 µm outer diam. regularly occurred 1–2 days after the normal rings of 30–42 µm appeared (Z.F. Yu pers. comm.). Cui (2014: fig. 2.4, see Fig. 110: t–u) saw giant traps in *D. dactyloides*, and believed them to be inefficient because their individual ring cells are not much wider than in normal rings and, therefore, do not achieve a closed aperture after full expansion. We assume that suitably large nematodes may well be captured by such giant ring traps.

Unexpanded constricting rings differ in several morphological details from non-constricting rings. The ring cells are with a width of (4–)5–7(–8) µm more swollen in their middle part, which is about twice as thick as at the septa. This usually results in a somewhat triangular shape of the ring aperture (Fig. 110: a, c, i, k, m). However, this feature is rarely also seen in adhesive networks (Fig. 108: c). In some species (*D. acrochaeta*, *D. doedycoides*, *D. heterospora*) each ring cell has an inner bulge-like protrusion (Fig. 110: e). Expanded ring cells attain a width of *10–18 µm. The stalk is (1–)2(–3)-celled and with 9–20(–32) × (2.5–)3–5(–6.5) µm usually shorter and particularly wider than in non-constricting rings. Constricting rings are always reported with three ring cells, but we saw once a ring with five cells (Fig. 110: j). Rubner (1996: 18, fig. 9) observed degenerated constricting rings in three strains of *D. doedycoides*, *D. effusa*, and *D. polybrocha*, showing a spiral shape without

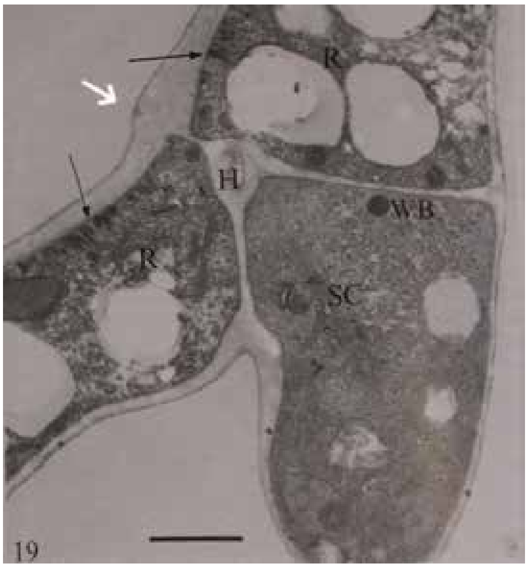


Figure 111: Junction between upper stalk cell (right below), basal ring cell (right above), and terminal ring cell (left), showing three septa surrounding a central hole (H), also a wall thickening over the septum (anastomosis) between the two ring cells (white arrow, after Glockling & Dick 1994, two black arrows pointing to tubular vesicles ('possibly lysosomes', *D. megalobrocha*, TEM). Scale bar = 2 µm.

fusion of the terminal cell. Also Cui (2014: fig. 5.2) reported in *D. brochopaga* similar 'multiple loops', but of helicoid shape.

Another characteristic of constricting rings is that during their formation the terminal ring cell fuses with the upper end of the stalk, and afterwards an anastomosis is formed between the terminal and basal ring cell (Higgins & Pramer 1967; Dowsett et al. 1977: fig. 57; Glockling & Dick 1994: fig. 19). This peculiarity results in the presence of three septa at the junction (Fig. 110: a), in contrast to two septa in non-constricting rings. The feature is often not clearly visible on illustrations, e.g., in many of Drechsler's otherwise very accurate drawings. It is, therefore, still not confirmed for all *Drechslerella* species, e.g., *D. heterospora* (Fig. 110: e).

In all constricting rings which we have studied, a remarkable microstructure is seen under the LM, which is frequently not specifically mentioned in the literature: distinct triangular or sometimes more lens-shaped wall thickenings occur especially at the two distal septa (Fig. 110: a–b, k, m–r, t–w). They are mainly seen at the internal side of the ring but sometimes also at the external side and at the proximal septum. These wall thickenings are present in both living and dead ring cells and do not change their thickness and refractivity in KOH. Undoubtedly, the wall thickenings form an annular structure around the whole margin of the septum by decreasing in thickness towards the outer side of the ring.

On several LM photographs of Zachariah & Insell (1979: figs 2–4, 7, 9), Glockling & Dick (1994), and Cui (2014: figs 2.1, 2.3–4) these triangular wall thickenings can very clearly be seen in the rather large rings of *Drechslerella brochopaga*, *D. dactyloides*, and *D. megalobrocha*. Under dark field fluorescence they appear with strong contrast (Fig. 110: v–w). The wall structure is not mentioned by these authors, however, and a TEM micrograph by Glockling & Dick (Fig. 111) shows only the proximal septum adjacent to the stalk where the wall thickening is more flattened instead of triangular. Likewise, on the TEM micrograph of Dowsett et al. (1977: fig. 16) strong wall thickenings are visible at the septa but are not sharply delimited from the cell walls away from the septa.

For *D. dactyloides* Tzean & Estey (1979: fig. 1–2) illustrated and discussed a thick inner wall layer of the ring cells which is responsible for their expansibility. At the septa the wall is not thicker, but clearly lacks a visible fibrillar structure. In the expanded state (fig. 8) the stretchable inner wall layer gets thin while it retains its thickness at the septa. This illustrates a different nature of the wall at the septa. Muller (1958) figured lens-shaped wall thickenings for the proximal septum (Fig. 110: g) and triangular ones at the three septa of an expanded ring (Fig. 110: b), but saw them only in some rings. During the expansion process, Muller sometimes saw transient wall thickenings at the edge where the cells expand (Fig. 110: h).

In a video showing ring expansion in *D. brochopaga* and *D. dactyloides*, Nordbring-Hertz et al. (1995) reported the peculiar triangular microstructure as T-shaped wall thickenings at all three septa. The authors considered that their function was to avoid interference of the three swelling cells. A more probable explanation could be that the wall thickenings provide a higher mechanical stability of the ring in order to avoid rupture when a nematode tries to escape. This hypothesis is supported by the observation that the wall thickening is usually less developed at the proximal septum, at which the two ring cells are held together also by the fusion between terminal ring cell and upper stalk cell.

Based on TEM-observations, Dowsett et al. (1977: fig. 12), Tzean & Estey (1979) and Glockling & Dick (1994: figs 20, 22) found the wall of unexpanded ring cells to consist of several layers. The mechanism of rapid expansion happens by rupture of the more rigid outer wall layers and a stretching process of the thicker inner layers (Fig. 110: s, Dowsett et al. l.c.: fig. 17; Glockling & Dick l.c.: figs 12, 15; Barron 1979a: fig. 8). The demarcation line where the outer layers ruptured is also visible under the LM (Barron l.c.: fig. 9).

The rupture and swelling of ring cells may be compared with fissitunicate asci with an inner wall layer (endotunica) that is able to swell. Similar as in ascus walls, an increase in wall thickness can be observed under the LM when the unexpanded ring cells are killed, though less significantly than in asci: from about 0.3–0.5 µm when viable (Fig. 110: a, i) to 1 µm when treated with KOH (Fig. 110: n, r). As in asci, the wall appears two-layered in the dead state, with a thin refractive outer layer and a swellable non-refractive inner layer. Our images show this swollen inner layer on both sides of each ring cell (Fig. 110: m–n), whereas Dowsett et al. (l.c.) and Glockling & Dick (l.c.) emphasized the inner side of ring cells to be much thicker-walled than the opposite side.

Like ascus explosion, ring expansion is a physiological process based on internal osmotic pressure. Contrary to asci it does not result in the death of the cells. Instead, due to a rapid conversion of reserve materials, the osmotic pressure is rebuilt after expansion in order to constrict the body of the victim (see Barron 1977: 54), and the ring cells grow out and penetrate the nematode. While still unexpanded, a number of vacuoles can be seen under the LM or TEM in the outer part of each ring cell (Figs 110: a, i,). These rapidly increase by water uptake from the environment during expansion, whereas fusion to one large vacuole (Fig. 110: j, l) is said to take place at a later stage (Muller l.c., Dowsett et al. l.c.). The inner non-vacuolar region of the unexpanded protoplast is slightly denser and more granular under the LM and contains vesicles with possibly enzymes which are only seen under the TEM (Fig. 111).

The process of sudden expansion is triggered by touch when a nematode enters the ring. Triggering is also possible with a micromanipulator, sudden increase in temperature (adding a drop of 33–75 °C warm water), or electric stimulation (Couch 1937, Muller 1958, Higgins & Pramer 1967 and others). Killing agents such as KOH, MLZ, or CB_L added to constricting rings, or temperatures above 80 °C, do not induce expansion, but rather cause a hardly noticeable or very slight shrinkage (see also Muller l.c.: 345 who added HCl, NaOH etc.). Although constricting rings appear to be solely adapted to the capture of nematodes, they are rather unspecific concerning different nematode genera, and were sometimes even seen to catch rotifers (Drechsler 1937a: fig. 18N; Glockling & Dick 1994).

Phylogeny of trapping organs. The phylogenetic origin of trapping organs of *Orbiliomycetes* is unknown. The capture of pollen by hyphal structures or conidial arms in the phylogenetically basal genera *Mycoceros* and *Retiarius* (Magyar et al. 2017a, b) may represent a precursor of these trapping devices, although the ability to invade living pollen appears to be widespread in fungi (see p. 145). The homology between the adhesive organs in the three lineages *Lecophagus*, *Hyalorbilia*, and *Orbilia* series *Arthrobotrys*, *Dactylellina*, and *Gamsylella* seems likely, whereas a polyphyletic origin would be more difficult to conceive.

According to various phylogenetic analyses, the three main trapping organs constricting rings, adhesive networks, and adhesive knobs or columns form monophyletic clades within section *Arthrobotrys* (see Phyl. 25). From a morphological point of view, constricting rings might have evolved from non-constricting rings, as was presumed and illustrated in hypothetical diagrams by Rubner (1996: fig. 13) and Li et al. (2005: fig. 4). Yet, the early analyses by Ahrén (1998) and Tanabe et al. (1999) based on SSU rDNA already showed that species with constricting rings clustered as a basal sister clade of the remaining nematophagous lineages, and various other phylogenetic results contradict the above hypothesis, with a few exceptions (see p. 1433). The two clades with adhesive organs appear to trace back to a common ancestor (Hagedorn & Scholler 1999: 34) which, in turn, descended together with taxa with constricting rings from a common nematophagous ancestor that emerged from the non-nematophagous, paraphyletic series *Neodactylella*.

Hagedorn & Scholler (1999: 36) hypothesized that also taxa with non-constricting rings might form a monophyletic group, given that the only strain of *Dactylellina leptospora*, for which a sequence was available at that time, was misidentified because it did not form non-constricting rings. However, a new unpublished strain with both adhesive knobs and non-constricting rings clustered with rather high support sister to this *D. leptospora* strain, suggesting that non-constricting rings occur in different clades and may get lost during evolution, unlike the other three trapping organs.

Tanabe et al.'s (1999) phylogenetic analysis suggests that the rotifer-capturing adhesive pegs of *Lecophagus* (as *Cephaliophora*) form a basal group within the *Orbiliomycetes*. This would make sense as their structure is more primitive than stalked adhesive knobs, nets, or rings. However, their analysis contains only two non-nematophagous orbiliaceous taxa and cannot answer the question whether trapping devices got lost during evolution or arose independently within the *Orbiliomycetes*. From the basal placement of constricting rings the authors concluded that 'complexity of infection organs is not reflected by the position of nematophagous clades'.

Li et al. (2005) considered adhesive knobs as the ancestral type of trapping organ, because their phylogenetic analyses show a basal placement of adhesive trapping organs. Also they assert a lineage from non-constricting rings to constricting rings, but for this no evidence is seen in the phylograms. Yang et al. (2007: fig. 4) illustrated three hypotheses on the evolution of orbiliaceous trapping organs. Their lower left figure is a modification of Rubner's (1996) hypothesis which also implies that sessile adhesive knobs represent the trapping device of the common ancestor of nematode trappers and have their origin in simple adhesive hyphae. In all three hypotheses the constricting rings diverge early, but only in Yang et al.'s personal hypothesis non-constricting rings developed independently of them, while constricting rings branched off before sessile adhesive knobs appeared for the first time.

MOLECULAR BIOLOGY

Ribosomal DNA (= rDNA) of eukaryotes consists of three main regions: SSU (= 18S), ITS (= ITS1-5.8S-ITS2), and LSU (= 28S). rDNA is generally accepted as the basic gene region for fungal taxonomy, because it demonstrated suitability in many fungal groups and its repetitive occurrence in the genome facilitates amplification. During transcription, rDNA is transformed to rRNA, in which the nucleotide sequence becomes reverse-complementary and T (thymine) is exchanged by its demethylated form U (uracil) while the other three bases (G = guanine, A = adenine, C = cytosine) remain unchanged. DNA sequences are currently processed in correspondence to the 'sense strand' (coding strand) of the double-stranded DNA, which concurs with the messenger RNA and the herefrom produced protein code. Because transcription takes place from the 'antisense strand' (template strand), the reverse-complementary base pair sequence of the produced rRNA is the same as that of the sense strand of DNA. As an example, Fig. 113 shows the stem-loop E23-1 of SSU rRNA, the end-loop of which in *Saccharomyces cerevisiae* is CGA**UUUUU**UCG, which corresponds to CGA**TTTTT**TCG in the rDNA sense strand. In *Orbiliomycetes* the end-loop is CGC**CUAACC**GCG and CGC**CTAACC**GCG, respectively (see Tab. 17). By convention, DNA and RNA sequences are always noted by running from their 5'-end (left) to 3'-end (right). The terms upstream and downstream refer to the direction from 5' to 3' in the sense strand but from 3' (right) to 5' (left) in the antisense strand.

rRNA is a structural biopolymer which constitutes a main part of the ribosomes. Ribosomes are roundish particles of ca. 0.02–0.03 µm diam. that are mainly found on the endoplasmic reticulum and serve as the site of protein synthesis. The two ITS regions are removed from the rRNA after transcription, so that only the three subunits 18S, 5.8S, and 28S form together with proteins the ribosome. The three subunits of rRNA show a secondary structure with numerous loops caused by hydrogen bonds (base pairing: A•T and G•C) between reverse-complementary motifs. Besides stem-loop E23-1, examples mentioned in the following include stem-loop B8 in the 5.8S and stem-loop H700 in the L4 primer of LSU. Therefore, the information in rRNA (and rDNA) contains redundant information, except that occasionally G–U base pairing occurs

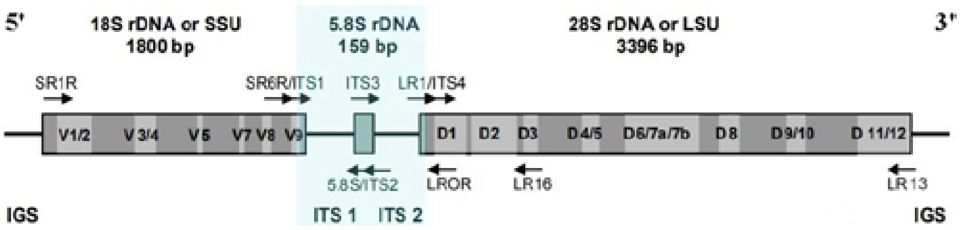


Figure 112: Map of the nuclear ribosomal DNA gene showing three main regions (SSU, ITS, LSU) and location of variable regions in SSU (V1–V9) and LSU (D1–D12) and location of some basic primers (from Meyer et al. 2011).

in these loops (Fig. 113). In addition, the folded rRNA molecule shows a tertiary, 3-dimensional structure. Also the ITS1 and ITS2 regions show a secondary structure of loops and, therefore, redundant information. Because of the limited information in rDNA, other gene regions, mainly protein-coding genes, are today included in multiple phylogenetic analyses.

Molecular data for inferring the phylogeny within the *Orbiliomycetes* have firstly been applied by Liou & Tzean (1997) and Pfister (1997), followed by Ahrén et al. (1998), Tanabe et al. (1999), and Hagedorn & Scholler (1999). Ahrén et al. and Tanabe et al. based their phylogenetic analyses on the SSU rDNA, the preferred marker gene at that time. SSU is a highly conserved gene region of about 1800 nt, showing a low resolution at the species level. Within *Orbiliomycetes* it usually permits distinction between closely related species, because molecular distances in that class are comparatively high in each of the three main subunits of rDNA. Yarza et al. (2014) divided the bacterial SSU into six segments (R1–R6) and recognized nine variable regions (V1–V9), six of which being included in three R-segments (V1 & V2 in R1, V5 & V6 in R4, V7 & V8 in R5). The V-regions occur dispersed within the more conserved core segments of SSU which include, e. g., the primers SR1–SR6, and are currently also adopted in eukaryotes. Within *Orbiliomycetes*, variation in the SSU only occurred at a few positions of these V-regions and some regions did not vary at all, especially V2 and V6 (Tab. S1), but also the conserved segments between the V regions may show some variable positions.

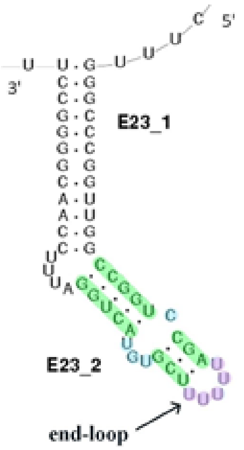


Figure 113: Stem-loop E23-1 formed by base pairing in the V4 variable region of the R3 segment of SSU rRNA of *Saccharomyces cerevisiae*, its upper half (25 nt) showing the motif CCGGTCCGATTTTTTCGTGTACTGG. In comparison, the motif of *Orbiliomycetes* is TCGGTCCGCCTAACCGCGTGCACTGA. Note that thymine (T) in DNA is replaced by uracil (U) in RNA, and that the unusual (wobble) base pair G-U occurs twice in this stem-loop. Green: paired elements of the loop, blue/lilac: unpaired elements. From http://bioinformatics.psb.ugent.be/webtools/rRNA/secmodel/Scer_SSU.html, modified.

Liou & Tzean (1997) based their analyses on the ITS region, also Pfister (1997) and Hagedorn & Scholler (1999) mainly relied on this gene region, and most later workers included it in their studies. It is the most widely used phylogenetic marker, which was proposed as the barcoding gene of fungi by Nilsson et al. (2008) and Schoch et al. (2012). The entire ITS region of *Orbiliomycetes* comprises around 490–525 nt and includes in the middle the highly conserved, 155 nt long 5.8S rDNA subunit with the 5.8S primer motif, flanked by the ITS1 and ITS2 regions which are of about equal length (Fig. 112). Because ITS1 and ITS2 are not part of the ribosome but disintegrate after their removal, they are considered to be of low functional importance and, therefore, subjected to a constant mutation rate that is little influenced by selection. Anyway, some orders of pyrenocarpous ascomycetes show extremely low rates of divergence between species in this barcoding gene region (see p. 18, Taxa concepts).

The LSU has a length of over 3300 nt and contains twelve variable domains (D1–D12) which occur dispersed among more conserved core segments that include the primers LR1–LR13 (see Ki & Han 2007). Distances in the LSU of *Orbiliomycetes* are generally slightly higher than in the SSU, except that the short D4 and D9 domains are highly conserved and also the D10 and D11 domains show little varation in the few available sequences. Li et al. (2005) analysed the LSU in combination with *TUBB* in nematode-trapping *Orbiliomycetes*. Also Liu et al. (2006a) and Smith & Jaffee (2009) used LSU in addition to ITS by including also many non-nematophagous species of the class. Generally, only the D1–D2 regions are selected for analysis (ca. 600 nt) by using the NL4 (LR3) primer, sometimes also D3 (LR4) and D4 (LR5) (see Tab. S1).

In the present study, sequences were generated from the partial or sometimes the entire nuclear rDNA. The ITS region was generally sequenced, usually with a primer (ITS1-F, SF16a) that encompasses the frequently present S1506 intron. Often also the partial SSU and LSU were obtained. The SSU included either only the V7 region (primer NS7 [G. Hagedorn]) or also V6 (NS23 [M. Weiß]). The partial LSU either comprised the D1–D2 domains [NL4, M. Weiß] or D1–D4, rarely D1–D6 [G. Hagedorn, G. Marson]). A few of our sequences include the entire LSU and often also the entire SSU region (see Tabs 27–28).

The ITS region is easily recognized in a sequence by conserved motifs at the 3'-end of SSU (ATCATTA) and 5'-end of LSU (TGACCT), between which it is located, and the conserved 5.8S subunit by AAAACTTT at its 5'-end and GAGCGTC at its 3'-end (see Tab. S1). These motifs are fairly constant in most groups of ascomycetes but show rare exceptions: within *Orbiliomycetes*: ATCATT**G** (possibly ATCATT–**G**) was exclusively observed in *Mycoceros*, GAGCGT**G** and T**C**ACCT only in *Hyalorbilia erythrostigma* and *H. orbiliicola* (and the associated but distant clone 3674), GAGC**A**TC and TGA**T**CT only in *H. hergiswiliana* s.l. (GAGC**A**TC also in KY687852/3, U2 clone from Amazonas), and GAG**A**GT**G** and T**A**AC**T**T only in two species of uncultured fungi (clones B1–B2) forming a basal clade with *Bryorbilia arenicola*. The definition of the ITS region and the included 5.8S subunit is adopted here from Kim et al. (2006) and results in 155 nucleotides for the 5.8S. Some authors define these regions differently: their 5.8S subunit starts 2 nt upstream or 1–2 or even 5 nt downstream and ends 1–4 or even 12 nt downstream compared to the above definition. For instance, in O'Donnell & Gray (1995) and Bengtsson-Palme et al. (2013) the 5.8S starts with AAACTTT and ends with GAGCGTCATTA, resulting in a length of 158 nt. The four additional nucleotides downstream of the 5.8S, which are assigned by Kim et al. to the

ITS2 region, show in *Orbiliomycetes* a lot of variants (see Tab. 20). A very wide definition of the 5.8S subunit is that of Katsu et al. (2004), who included 2 nt at the 5'-end and 12 nt at the 3'-end, resulting in 169 nt. Different definitions exist also for the LSU which starts with TTGACCT in O'Donnell & Gray (l.c.) and with NNTTGACCT in Bengtsson-Palme et al. (l.c.).

Specific nucleotides and motifs

Various examples of critical taxa illustrate the taxonomic value of specific nucleotide positions in the frequently recorded regions of the rDNA. Besides the species level, this concerns taxa at the series and section but also higher level. Specific positions may occur in variable or medium to highly conservative regions. If a position is consistent within a taxonomic unit, the character appears to trace back to a common ancestor and never changed since the ancestor evolved by speciation. If a position varies between, e. g., C and T across different taxonomic units, this must be interpreted as consecutive forth and back mutations, not as indication of a phylogenetic relationship. Such variable, rather unreliable molecular information appears to be frequent in fungal DNA.

SSU rDNA. Besides results from phylogenetic analyses, characteristic molecular motifs in the rDNA may supply additional information on phylogenetic relationships. One of them was discovered by Eriksson (in Eriksson et al. 2003) in each of the 21 sequences of *Orbiliomycetes* available at that time (mainly desiccation-sensitive members of *Orbilia* section *Arthrobotrys*): a characteristic signature of six nucleotides (CTAACC) in the end-loop of the stem-loop E23-1 in the V4 region of SSU (Fig. 113, lilac element) provides additional evidence for the rather isolated phylogenetic position of *Orbiliomycetes*. At present, about 55 orbiliaceous sequences exist in GenBank which cover this region by consistently showing this motif. They include ca. 38 species of *Orbilia*, one of *Hyalorbilia* (*H. inflatula*), two of *Lilapila*, two of *Lecophagus*, and two basal clades of uncultured clones (U5, U6).

When considering the entire upper half of this loop (marked in colour in Fig. 113), interesting further positions are informative (Tab. 17). Those parts marked in green represent paired elements, so that a change at one position usually requires a complementary change of its counterpart. One such deviation is observed at the two ends of this motif: the available sequences of *Lecophagus* (*L. longisporus*, *L. muscicola*) and *Hyalorbilia* (*H. inflatula*), including two clades of unidentified environmental samples distantly related to them, show here C•G compared to T•A as occurring in *Lilapila* and *Orbilia*. As an exception, the type strain of *Dactylellina sichuanensis* (= *O. lysipaga*) has C–G, and a strain of *Arthrobotrys thaumasius* (EU107342) the rare variants CT**C**ACC and T•G. The variant C•G is also observed in many other classes of *Ascomycota* and appears to be characteristic of this phylum, whereas *Basidiomycota* generally differ in having G•T (Tab. 17).

The paucity of available sequences is due to the fact that this gene region is outside the 562 nt long V6–V9 or 362 nt long V8–V9 region of SSU which was frequently sequenced in the present study by using the primers NS23 or NS7, respectively. Since we have rarely sequenced the V1–V5 region of SSU, most sequences which include the signature CTAACC were obtained by other workers. Within *Orbilia*, sequences of V1–V5 were available for various species from all five series of section *Arthrobotrys*, but only for a few species from other sections (see Phyl. S1): three from section *Orbilia* (*O. leucostigma*, *O. xanthostigma*, *O.* cf. xanth*ostigma* D.H.P. 111), four from section *Helicoon*, three from section *Aurantiorubrae* (*O. nemaspora*, *O. aradi*, *O. ficicola*), one from section *Habrostictis* (*O. septispora*), and one from section *Lentiformes* (*O. euonymi*), the latter four being the only species with a pronounced desiccation tolerance.

Other classes of *Ascomycota*, such as *Pezizomycetes*, *Leotiomycetes*, *Dothideomycetes*, *Sordariomycetes*, and *Lecanoromycetes*, mostly show the signature CT**C**ACC. However, as already stated by Eriksson (l.c.), a few non-orbiliaceous species from some lichenized (*Arthoniales*, *Lecanorales*, *Lecideales*, *Peltigerales*, *Rhizocarpales*, *Teloschistales*, *Umbilicariales*) but also non-lichenized orders (*Acrospermales*, *Botryosphaeriales*, *Dyfrolomycetales*, *Stigmatodiscales*, *Symbiotaphrinales*) possess the signature of *Orbiliomycetes*, as can be evaluated from BLAST searches in GenBank for the loop motif (26 nt). This reduces the taxonomic value of the signature and raises the question whether it might have independently arisen in different lineages, as was assumed by Eriksson. In *Taphrinomycotina* (*Neolecta* and *Taphrina*) the signature is CTAAC**G**, whereas in *Saccharomycotina* it is CT**TTGA** (*Dipodascus*) or **TTTTT–** (*Saccharomycetaceae*).

Some positions in the SSU V8–V9 provide characteristic motifs within *Orbiliomycetes*. A remarkable symmetric pair

Table 17. Comparison of upper half of stem-loop E23-1 in SSU V4 region (26 nt, shown in Fig. 113) between *Orbiliomycetes* (in bold) and other selected fungal groups, with paired nucleotides in green and unpaired nucleotides in blue (small side-loops) and lilac (end-loop signature). Motifs are highly consistent within *Orbiliomycetes*, but also within *Symbiotaphrinales*, *Xylonales*, *Leotiomycetes*, *Taphrinomycetes*, and *Neolectomycetes*, but more variable in other groups, where often a lot of variants occur. Nucleotides deviating from the motif of *Orbilia*/*Lilapila* are highlighted in bold. Note symmetry in deviating characters within the green parts due to predominant base pairing A•T or G•C. For further variants of the end-loop signature in *Ascomycota* see Eriksson et al. (2003).

Taxa	Stem-loop E23-1 in V4 region of SSU
Orbilia*, *Lilapila	TCGGTCCGCCTAACCGCGTGCACTGA
Lecophagus*, *Hyalorbilia*, *Orbilia* (*Dactylellina*) *lysipaga, *Stigmatodiscales, Lecanoromycetes* p.p.min., *Arthoniomycetes* p.p.	**C**CGGTCCGCCTAACCGCGTGCACTG**G**
Symbiotaphrinales, Lecanoromycetes p.p.min.	**C**CGGTCCGCCTAACCGCGTG**T**ACTG**G**
***Arthrobotrys thaumasius* (EU107342)**	TCGGTCCGCCT**C**ACCGCGTGCACTG**G**
Xylonales, *Lichinomycetes* p.p.maj., *Leotiomycetes*, *Lecanoromycetes* p.p.maj., *Dothideomycetes* p.p., *Sordariomycetes* p.p., *Arthoniomycetes* p.p., *Tuber* (*Pezizomycetes*)	**C**CGGTCCGCCT**C**ACCGCGTGCACTG**G**
Dothideomycetes p.p., *Lecanoromycetes* p.p., *Sordariomycetes* p.p.	**C**CGGTCCGCCT**C**ACCGCGTG**T**ACTG**G**
Morchella p.p. (*Pezizomycetes*)	TCGGTCC**T**CCT**C**ACCG**A**GTG**T**ACTGA
Sarcoscypha (*Pezizomycetes*), *Dothideomycetes* p.p.	**CG**GGTCCGCCT**C**ACCGCGTGCACTC**G**
Ascobolaceae p.p.maj. (*Pezizomycetes*)	**C**CGGTCCG**T**CT**C**A**T**CGCGTG**T**ACTG**G**
Taphrinomycetes & *Neolectomycetes* (*Taphrinomycotina*)	**C**CGGTCCGCCTAAC**G**G**T**GTGCACTG**G**
Saccharomycetes p.p. (*Saccharomycotina*)	**C**CGGTCCG**AT**T**TTT-T**CGTG**T**ACTG**G**
Basidiomycota p.p.	**G**CGGTCCGC**T**TAAC**G**GCGTG**T**ACTG**T**

of nucleotides is found at pos. 154 & 166 (when starting after primer N7 with CCTTAGATGTT), which belong to the loop at pos. 1360 of *Escherichia coli*. Here section *Habrostictis* (**G**AGTCATCAGCT**C**) differs from most other orbiliaceous groups (**A**AGTCATCAGCT**T**). The latter motif is also characteristic of *Helotiales* and most *Pezizales*, but **G**AGTCATCAGCT**C** also occurs, e. g., in *Thelebolales* and some *Lecanorales*. A similar pair of nucleotides occurs at pos. 109 and 126: here the genus *Hyalorbilia* and members of section *Arthrobotrys* with adhesive traps have AG**G**GC and GC**C**CT but all other *Orbiliomycetes* AG**A**GC and GC**T**CT (Tab. 60). Also pos. 141–142 is diagnostic, separating the genus *Orbilia* (AT**AT**CT) from other orbiliaceous groups (AT**TC**CT, a few *Hyalorbilia* spp. have AT**AC**CT) (Tab. 60).

5.8S and LSU rDNA. Smith & Jaffee (2009) developed '*Orbiliales*-specific' PCR primers for the 5.8S and 28S rDNA in order to directly detect nematode-trapping fungi in soil or plant substrate without culturing. The three primers (Orb5.8s1F, Orb5.8s3F, Orb28s2R) have a length of 18–21 nucleotides and differ from non-orbiliaceous ascomycetes and basidiomycetes at 1–3 positions (see Tabs 18–19). The investigated groups were mainly those of *Hyalorbilia* ('*Brachyphoris* clade') and section *Arthrobotrys* ('*Orbilia* clade'). When including all orbiliaceous sequences available at present, the primer Orb5.8s1F exactly matches almost all taxa of *Orbiliomycetes*, but only when omitting one nucleotide at its 3'-end. The other two primers match around 90 % of the available orbiliaceous sequences.

Our sequence data show that a fairly large number of orbiliaceous taxa deviate at 1–2 or sometimes 3–4 positions in a given primer region (Tabs 18–19). Even some nematode-trapping *Orbilia* species deviate from primer Orb28s2R (*Dactylellina appendiculata*, *D. lysipaga* = *D. sichuanensis*, *Gamsylella cionopaga*). However, these deviating motifs are usually still different from non-orbiliaceous fungi, with the exception of *Mycoceros* in Orb5.8s1F, and *Lecophagus* and some species of *Amphosoma*, *Retiarius*, and *Orbilia* in Orb28s2R.

Smith & Jaffee's three primer regions provide interesting character patterns which permit distinction between orbiliaceous genera. For instance, *Hyalorbilia* shows some peculiarities in which the genus differs from *Orbilia*, with the exception that *H. erythrostigma*, *H. orbiliicola*, and *H. latispora* deviate in some of these conserved regions. In the following, the main characteristics are summarized:

(1) In primer Orb5.8s1F (pos. 47–64), *Orbilia* and *Hyalorbilia* are identical (GCAGCGAAACGCGATAG**T**, see Tab. 18), with the exception of (a) *H. erythrostigma*, *H. orbiliicola*, and *H. latispora*, which deviate by one nucleotide at the 3'-end (GCAGCGAAACGCGATAG**G**) by concurring with all the remaining orbiliaceous genera, and (b) *Mycoceros*, which deviates also at two further positions (GCAGCGAAA**T**GCGATA**AG**). *Mycoceros* exactly matches many non-orbiliaceous ascomycetes as well as basidiomycetes, but variant (a) also occurs, e. g., in *Malasseziales* and *Trichosporonales* (*Basidiomycota*). As a consequence, primer Orb5.8s1F does not cover various basal taxa of *Orbiliomycetes*, but would do so (except for *Mycoceros*) if it were shortened at its 3'-end by one nucleotide.

(2) At pos. 83–85 of 5.8S ('unnamed') the most frequent signature is TCA, but some rare variants exist (see Tab. 18). CTA is characteristic of *H. erythrostigma* and *H. orbiliicola* and a clade loosely associated with them, CCA occurs in some uncultured isolates belonging to *Hyalorbilia*, TTA was observed in some strains of series *Dactylellina* and in two environmental isolates near *Bryorbilia* and *H. ulicicola*, TTC in a strain of *O. blumenaviensis*, and TCC in *Lecophagus longisporus* and the *Vermispora* clade of *Hyalorbilia*.

(3) Another region in the 5.8S represents stem-loop B8, with 2 × nine positions (117–125 with 130–138) being rather strictly complementary by base pairing (G•C or A•T, see Tab. S4). Many of the observed motifs of *Hyalorbilia* and *Orbilia* occur here in more or less distantly related taxa of *Orbiliomycetes*, suggesting a polyphyletic origin of some of these motifs. Those of the genus *Lecophagus*, however, are unique within *Orbiliomycetes*. Likewise, members of *Orbilia* differ at pos. 121•134 by A•T or G•C from the other orbiliaceous genera which have C•G (like various other fungi) or T•G, rarely T•A (the latter case also occurs in some *Orbilia* species, including all of section *Helicoon*). Series *Pseudotripoconidium* and *O. yuana* differ at pos. 117•138 from other *Orbiliomycetes* by A•T vs. G•C.

(4) In the primer Orb5.8s3F (pos. 137–157), which includes the motif GAGCGTC at the 3'-end of 5.8S, the nucleotide at its 3'-end (157) varies within orbiliaceous fungi in having T in *Orbilia* (very rarely A or C), *Lilapila*, *Mycoceros*, and *Bryorbilia*, but G in *Amphosoma*, *Lecophagus*, *Retiarius*, and *Hyalorbilia* (including the *Vermispora* clade). Non-orbiliaceous ascomycetes have T or C, and several of their variants of primer Orb5.8s3F also occur in a few orbiliaceous taxa. When including the next two positions downstream which were assigned to the 5.8S subunit by some authors, different sections and series of *Orbilia* show highly characteristic signatures (see Tab. 20).

(5) At one position in the middle of Orb28s2R (Tab. 19, pos. 616), mainly three character states are observed within orbiliaceous fungi: GC**T**TA in *Orbilia* and the *Vermispora* clade of *Hyalorbilia* p.p., **C** in *Hyalorbilia* (incl. *Vermispora* clade p.p.), and **G** in *Amphosoma*, *Lecophagus*, *Lilapila*, *Mycoceros*, *Retiarius*, and a number of species of *Orbilia* section *Habrostictis*. Exceptions are *Hyalorbilia erythrostigma*, *H. orbiliicola*, and *H. latispora* (**T**) and a few species of *Orbilia* section *Aurantiorubrae* (**A**). Non-orbiliaceous ascomycetes show the character **G**, basidiomycetes **A**. Many orbiliaceous taxa showing **G** fully concur in the Orb28s2R with non-orbiliaceous ascomycetes.

In ascomycetes associated with ectomycorrhizas, Tedersoo et al. (2009: appendix 1) listed deviations from the newly designed *Pezizomycotina*-specific (reverse) primer LR3-Asc (forward: CG**CT**TGGATTTGAGTA**R**G**T**G), which is located in the D3 domain of LSU (pos. 761–780). One such deviation was observed by these authors in a single species of *Orbiliomycetes* (CG**GA**TGGATTTGAGTA**T**G**A**G). In fact, this motif is widespread in *Orbiliomycetes* but also occurs in at least two further variants in that class (CG**GA**TGGATTTGAGTA**G**G**A**G, rarely CG**GA**TGGATTTGAGTA**A**G**A**G). All these variants also occur in helotialean and other groups, e. g., the variant with T is typical of *Chaetomellaceae* (*Helotiales* s.l.) and some other taxa with distant position, *Corticifraga* (*Graphidales*) and *Symbiotaphrina* (*Xylonomycetes*).

Introns in the rDNA

Introns are non-coding nucleotide sequences of different length which are inconsistently present at various positions in the genome, in contrast to the non-coding internal transcribed spacer DNA (ITS1, ITS2) that every fungus has. Almost all

Table 18. Variation in three semiconserved regions of the 5.8S rDNA, with indication of the species or group of species where they occur. Those variants which predominate within *Orbiliomycetes* are highlighted in bold. Two of these predominant variants (Orb5.8s1F, Orb5.8s3F) were proposed by Smith & Jaffee (2009) as '*Orbiliales*-specific' primers. Position numbers start with AAAACTTT (5.8S) by omitting rare inserts (in Orb5.8s3F: GAGCGTC**T**AC). Non-orbiliaceous taxa found with BLAST in GenBank as having the same motif are given in the middle column, indicating independent convergent mutations at the same loci. For the numbering of uncultured clones see phylogenetic analyses of respective group [B = *Bryorbilia*, H = *Hyalorbilia*, L = *Lecophagus*, M = *Mycoceros*, O = *Orbilia*, R = *Retiarius*, V = *Vermispora* (= *Hyalorbilia*), U = unknown genus].

Orbiliomycetes	**Other classes of fungi**	**Orb5.8s1F** (pos. 47–64 of 5.8S)
Bryorbilia sp. (B2)	*Camarotella* sp. (*Phyllachorales*), *Ajellomyces dermatitidis* (*Onygenales*)	GCAGCAAAACGCGATAGG
Mycoceros sp. (M1), *Amphosoma* (incl. A1–6), *Lilapila, Lecophagus* (incl. L1–5), *Retiarius* (incl. R1–4), *Bryorbilia* (incl. B1, B3–4), *Hyalorbilia erythrostigma*, *H. orbiliicola*, *H. latispora* (incl. H29–32), *H. hergiswiliana*, *Hyalorbilia* p.p.min. (*Vermispora* clade, incl. V1–13), uncult. (U2)	some *Ustilaginomycotina*, *Tremellomycetes*, *Eurotiomycetes*, *Lichinomycetes*	GCAGCGAAACGCGATAGG
Orbilia, Hyalorbilia p.p.maj. (H1–28)	*Tilletiopsis pallescens*	**GCAGCGAAACGCGATAGT**
Mycoceros antennatissimus, uncult. (U3)	various other classes of ascomycetes and basidiomycetes	GCAGCGAAATGCGATAAG
	ascomycetes, basidiomycetes	GCAGCGAAATGCGATACG
Orbiliomycetes	**Other classes of fungi**	**unnamed** (pos. 79–88 of 5.8S)
Lecophagus longisporus (incl. L2–3), *Hyalorbilia* (*Vermispora* clade, incl. V1, V3–13)		GAATTCCGTG
Hyalorbilia sp. (H4 p.p.maj.)		GAATCCAGTG
Hyalorbilia erythrostigma, *H. orbiliicola* (incl. H29–32)		GAATCTAGTG
Amphosoma (incl. A1–6)*, Bryorbilia* (incl. B1–4), *Lilapila, Lecophagus* p.p.maj. (incl. L4), *Retiarius* (incl. R1–4), *Hyalorbilia* p.p.maj. (incl. H4 Guangdong, and *Vermispora* clade, V2), *Orbilia* p.p.maj.		**GAATTCAGTG**
Bryorbilia sp. (B3), *Hyalorbilia* cf. *ulicicola* (JQ638671), *Orbilia rubrovacuolata* (TFC Mic. 23599), *O. elegans* (KT215292)		GAATTTAGTG
Orbiliomycetes	**Other classes of fungi**	**Orb5.8s3F** (pos. 137–157 of 5.8S)
H. inflatula, *H. fagi*, *H. japonica*, *H. citrina*, *H. arcuata*, *H. lunata* s.l., *H. helicospora*, H1–3		GCACGCCCGTTTGAGCGTCAG
H. berberidis, *H. polypori*, *H. ulicicola* s.l.*, H. lignatilis* s.l., H4		GCACGTCCGTTTGAGCGTCAG
Hyalorbilia sp. (H13)		GCACGTCCGTTCGAGCGTCAG
H. subfusispora (incl. H14)	uncult. (?*Ciliolarina*, KF617413; *Chalara hyalocuspica*, EU690112)	GCACGCCTGTTCGAGCGTCAG
H. hergiswiliana s.l.		GCACGCCTGTTTGAGCATCAG
H. oviparasitica-multiguttulata clade (incl. H15–16), H5–6, H13 p.p., H27–28		GCACGTCTGTTCGAGCGTCAG
H. juliae-tenuifusaria clade (incl. H17–26)		GCACGCCTGTCTGAGCGTCAG
H. fusispora (incl. H9–H10, H33)		GCACGTCTGTCTGAGCGTCAG
H. latispora, H8, H11–12, H30–31, R4 p.p.		GCACGTCTGTTTGAGCGTCAG
Hyalorbilia erythrostigma s.l. (incl. H29)		GCATGTCTGTTTGAGCGTGAG
Hyalorbilia orbiliicola		GCATGTCTATTTGAGCGTGAG
clone U2		GCATGTCTGTCTGAGCATCAG
H. spermatophaga, *H. fusarina*, *H. leguminacea* (incl. V1–2, V5–7, V12)	various *Saccharomycetales*, *Boletales*	GCATGCCTGTTTGAGCGTCAG
Amphosoma p.p.maj. (incl. A1–6)*, H. fusarioides* (incl. V11)*, Retiarius* (incl. R1–2, R4 p.p.), H32		GCATGTCTGTTTGAGCGTCAG
Hyalorbilia (V3–4)		GCATGCCTGTTCGAGCGTCAG
Hyalorbilia (V8)		GCATATCTGTTTGGGCGTCAG
Hyalorbilia (V9–10)		GCATATCTGTTTGAGCGTCAG
Lecophagus (incl. L1, L3–4), *Amphosoma resinicola*, *Hyalorbilia* (V13)	a few uncult. of unclear relationship	GCATGTCTGTCTGAGCGTCAG
Lecophagus vermicola (incl. L2)	various *Pezizales*	GCATGCCTGTCTGAGCGTCAG
Bryorbilia arenicola	some ascomycetes	GCATGTCTGTCCGAGCGTCAT
Bryorbilia sp. (B1 p.p.)		GCACGTCTGTTCGAGAGTGAT
Bryorbilia spp. (B1 p.p., B2)	uncult. *Dothideomycetes* (KF675685, KF675649)	GCATGTCTGTTCGAGAGTGAT
Bryorbilia sp. (B3)	various ascomycetes	GCATGTCTGTTCGAGCGTCAT
Hyalorbilia tortuosa, *Orbilia* series *Hemiorbilia* p.p.maj., *aprilis-crenatovinosa* clade, *O. poitevinica*, section *Orbilia* p.p.maj.		GCACGTCTGTTTGAGCGTCAT
Orbilia ovoidea, *O. polyspora*		GCATGCCTGTTTGAGCGTCAT
section *Ovoideae* p.p.maj.	various *Saccharomycetes*	GCATGCTTGTTTGAGCGTCAT
Dactylella longquanensis, uncult. (U1 p.p.)		GCATGTCTGTTTGAGCGTCAA
uncult. (U1, GU314758)		GCATGTCCGTTTGAGCGTCAA
Mycoceros antennatissimus, *Lilapila*, *Orbilia* p.p.maj.	*Candida blankii*, *Kregervanrija* spp., *Zygoascus tannicola*, *Cyphellostereum* sp.	**GCATGTCTGTTTGAGCGTCAT**
Dactylellina haptotyla		GCATGTCTGTCTGAGCGTCAT
O. dryadum, O. microsoma, Dicranidion inaequale, *O.* cf. *aureocrenulata* B.L. 6212, *Orbilia* spp. (O1, O16–17), *Mycoceros* sp. (M1)		GCACGTCTGTCTGAGCGTCAT
Orbilia guyanensis†		GCACGTCTGTCTGAGCGTCAC
	many non-orbiliaceous ascomycetes	GCATGCCTGTTCGAGCGTCAC GCATGCCTGTTCGAGCGTCAT

Table 19. Variation in Orb28s2R, a semiconserved region of LSU D2 rDNA proposed by Smith & Jaffee (2009) as '*Orbiliales*-specific' primer, with indication of the species or group of species where they occur. The predominant case within *Orbiliomycetes* is highlighted in bold and represents the variant used by Smith & Jaffee. Position numbers starting with TGACCT by omitting predominant gaps in alignment of all groups of *Orbiliomycetes*. The reverse primer Orb28s2R is given here in forward version (reverse complement) to conform with current sequence data. Non-orbiliaceous taxa found with BLAST in GenBank as showing the same motif are given in the middle column, indicating independent convergent mutations at the same loci.

Orbiliomycetes	Other classes of fungi	Orb28s2R (pos. 606–626 of LSU)
Orbilia vinosa, *O. subvinosa*	some *Eurotiomycetes*	GGACGCTGGCTTAATGGTCGT
O. caulicola, *O. aradi*, *O. denticulata*, *O. brachychitonis*, *O. ficicola*	some *Lecanoromycetes*, *Saccharomycetes*	GGATGCTGGCATAATGATTGT
	various basidiomycetes	GGATGCTGGCATAATGGCTTT
Hyalorbilia p.p.maj. (core clade, incl. U2)	*Onygenales* sp., *Teratosphaeria tinarooa*	GGATGCTGGCCTAATGGTTGT
Lilapila jurana, *L. gallica*	*Ciboria shiraiana*	GGATGCTGGCGTAATGATCGT
Lilapila oculispora, *Mycoceros*, *O. myrionamibica*, *O. caudata*	various ascomycetes	GGATGCTGGCGTAATGATTGT
Amphosoma resinicola, *Retiarius revayae*	various ascomycetes	GGATGCTGGCGTAATGGTCGT
Lilapila oculisporella, *Retiarius bovicornutus*, *R. superficiaris*, *Amphosoma* p.p.maj., *Lecophagus*, *Orbilia* section *Habrostictis* p.p.	various ascomycetes	GGATGCTGGCGTAATGGTTGT
Amphosoma aff. *resinicola*		GGATGCTGGCGTAATGGTTGC
Orbilia cryptogena, O. sarothamni		GGATGCTGGCTTAATAGTTGT
O. polyspora, uncult. *Gamsylella* sp. (KC966182)	uncult. *Dothideomycetes* (KF567610)	GGATGCTGGCTTAATGGTCGC
O. aprilis, O. cf. *dryadum, O. cejpii, O. leuco- & xanthostigma, O.* cf. *xanthoflexa* (ga026b), *Dactylellina* p.p. min., *Gamsylella cionopaga*	*Glutinoglossum australasicum*, *Ascosphaera* spp.	GGATGCTGGCTTAATGGTCGT
Bryorbilia arenicola	*Lichenotheliaceae*	GGATGCTGGCTTAATGGTGGT
Orbilia p.p.maj., *Hyalorbilia erythrostigma*, *H. orbiliicola*, U4: KF566145, KF568246; B3: KF566789; B5: KY687789, KY687788	a few *Dothideomycetes*	**GGATGCTGGCTTAATGGTTGT**
U1: KY687771; U4: KF750308, KF566233		GGATGTTGGCTTAATGGTTGT
Hyalorbilia (*Vermispora* clade: V7, V11, V12, V16, *H. fusarioides*, *H. rotifera*)		GGGTGCTGGCCTAATGGTTGT
Hyalorbilia (*Vermispora* clade: V5, V8, V14, *H. fusarina*, *H. leguminacea*, *H. spermatophaga*), *H. latispora*		GGGTGCTGGCTTAATGGTTGT

introns found in fungal rDNA appear to be self-splicing group I introns. These occur across the eukaryotes and are excised from the rDNA during RNA processing. The number of insertion sites within the rDNA is limited to about 77. Group I introns occur only in highly conserved segments of SSU and LSU, and never in the 5.8S region (Johansen & Haugen 2001). A single species may contain 0–8 introns in the SSU and 0–5 in the LSU. The majority of these introns appear to to be species-specific, but in some species a given intron was either absent or present depending on the strain.

Group I introns have a length of ~200–450 nt, exceptionally up to ~1500 nt. They can be used for phylogenetic analyses of closely related taxa because they are subjected to a similar mutation rate as ITS1 and ITS2. Group I introns are even alignable when they are excised from different positions within the rDNA, apparently because a transfer of introns from one to another position rarely occurred during evolution. Not understood seems to be the fact that an intron at a given position may either get lost or reappear during evolution, judging from the inferred phylogeny in a given taxonomic group.

Group I introns are classified by their position number in the rDNA, which is evaluated by alignment with a reference sequence of *Escherichia coli* (J01695, Gutell 1993, http://www.rna.icmb.utexas.edu/SAE/2C/rRNA_Introns/), a method of intron nomenclature being broadly accepted for all kinds of organisms. Based on this method, Johansen & Haugen (2001) introduced a system of naming a group I intron of a given species by an abbreviation code of the species name, the character S (SSU) or L (LSU), and the position left (upstream) of the intron in the *E. coli* rDNA by using another *E. coli* strain (AB035922). This system is adopted here, though by using J01695 and omitting the abbreviation code. Hereafter, the frequently sequenced intron at the 3'-end of SSU is called S1506.

Due to some infraspecific variation among the different strains of *E. coli* it is necessary to evaluate positions by a standard strain. Johansen & Haugen (l.c.) and Hafez et al. (2012) used *E. coli* AB035922 which shows the same SSU positions as Gutell's J01695 but differs in the LSU by two inserts and one gap. Because position numbers based on *E. coli* J01695 were also used, e. g., by Gargas et al. (1995), Takashima & Nakase (1997), Hambleton & Sigler (2005), Gutiérrez et al. (2007), and Xu et al. (2013), we here follow Gutell's sequence J01695 as standard.

Saccharomyces cerevisiae (J01353) was alternatively used as reference organism for fungi, e. g., by Medjedović et al. (2014), because it gives a better alignment. When aligning herewith, the S1506 intron occurs after pos. 1767 (Medjedović et al. l.c.), although with Réblová & Réblová (2013: suppl. fig. 1) it would be at pos. 1769 of the same sequence. Since group I introns occur only in conserved regions, evaluation of position numbers based on *E. coli* is rarely problematic, and also Medjedović et al. used the intron nomenclature based on *E. coli*.

The secondary structure diagram of rRNA available at the link of the Texas University (http://www.rna.icmb.utexas.edu/SAE/2C/rRNA_Introns/) includes 38 positions of group I introns in SSU and 39 in LSU. Within *Eumycota*, Gargas et al. (1995: tab. 1) observed 17 different positions in SSU at which group I introns may occur. Twelve of them were found in lichen-forming fungi (including calicioid taxa), seven in *Chlorophyta*, but only one in *Rhodophyta* (S1506). Within *Xylonomycetes* nine group I intron positions were observed in the SSU and six in the LSU (Baral et al. 2017a: tab. 3). Multiple introns may occur within a species: a maximum of seven SSU- and five LSU-introns were observed in *Symbiotaphrina microtheca* (Baral et al. l.c.) and eight SSU-introns in *Lecanora dispersa* (Gargas et al. l.c.).

Comparative phylogenetic analyses of group I introns and ITS or SSU were carried out by, e. g., Holst-Jensen et al. (1999) in *Sclerotiniaceae* (L798), Feau et al. (2007) in *Mycosphaerella* (S1199 & S1506), and Hafez et al. (2012) in some *Microascales* (S943 & S1199). Feu et al. and Hafez et al. obtained a partly different tree topology between ITS and S1199, or SSU and S1199/S943, respectively. Holst-Jensen et al. observed more

Table 20. Variation of the semiconserved 4 nucleotide motif at the 5'-end of ITS2 (downstream of GAGCGTC) within *Orbiliomycetes,* sorted alphabetically, with indication of species or group of species where they occur. The first two nt are part of Orb5.8s3F.

5'-end of ITS2	Taxa
AAGG	uncultured basal *Orbiliomycetes* (clade U1)
ACGT	*Orbilia* series *Orbilia* (*O. guyanensis*), under omission of the inserted nucleotide **T** in GAGCGTC**T**ACGT
AGCA	*Hyalorbilia fusarina*, *H. leguminacea*, *H. spermatophaga*, *H. fusarioides*, *Hyalorbilia latispora*, *H. juliae*, *H. rotifera*, *H.* aff. *hergiswiliana*, clades U2, V1–13, H5, H9, H20, H30–31
AGCG	*Hyalorbilia hergiswiliana*
AGCT	*Hyalorbilia* p.p.maj., H1, H3–4, H8, H17
AGTA	*Lecophagus* spp., L1–5, *Amphosoma* spp., A5–A6, *Retiarius* spp., R1–4, *Hyalorbilia oviparasitica* s.l., *H. multiguttulata*, *H. brevistipitata*, *H. tenuifusaria*, *H. fusispora*, *H. ulicicola*, H6, H10–11, H13–14, H18, H24, H26, H28, H33
AGTG	*Hyalorbilia erythrostigma*, *H. orbiliicola*, *H. berberidis*, *H. subfusispora*, H13, H27–28
ATAT	*Bryorbilia* spp., B3, B5, *Orbilia* series *Abutilones* (*O. milinana*, *O. aethiopica*, *O. paravitalbae*), series *Orbilia* (*O.* cf. *leucostigma* B.L. 6420)
ATCA	*Orbilia* series *Vibrioides* (*O. graminis*), section *Ovoideae* (*O. polyspora*), series *Orbilia* (O15), series *Gamsylella* (*G. gephyropaga*)
ATCG	*Orbilia* series *Orbilia* (*Tridentaria subuliphora*, *O. cylindrospora*, *O. brettii*, *O. liliputiana*, O17)
ATCT	*Orbilia* series *Hyalinia* (*O. crenatofalcata*), series *Orbilia* (*O. cunninghamii*, *O. tremulae*, *O. xiushanensis*, *Orbilia* sp. ga055b, *D. inaequale*)
ATGA	*Mycoceros antennatissimus*, M1, *Orbilia* series *Orbilia* (*Tridentaria implicans*)
ATGC	*Orbilia* series *Orbilia* (*O. aureocrenulata*)
ATGT	*Bryorbilia* (B4), *Orbilia* series *Hyalinia* (*O. scolecospora*, *O. crenatomarginata*, *O. laevimarginata*), series *Orbilia* (*O. dryadum* s.l., *O. fissilis*, *O.* cf. *aureocrenulata*, *O. renispora*, *O. leucostigma*, *O. xanthostigma* s.l., *O. xanthoflexa* s.l.)
ATTA	uncultured basal *Orbiliomycetes* (U6), *Lilapila* spp., *Hyalorbilia tortuosa*, *Orbilia* section *Hemiorbilia* (except *cryptogena-sarothamni* clade), section *Habrostictis* (except *O. carpoboloides*), series *Xanthoguttulatae*, series *Regales* p.p., series *Albovinosae*, section *Helicoon* (*O. tianmushanensis*), series *Orbilia* (*O. fabacearum*, *O.* aff. *plurivacuolata* bhi-F948), section *Arthrobotrys* p.p.maj.
ATTG	*Orbilia* series *Hemiorbilia* (*cryptogena-sarothamni* clade, except O2), section *Ovoideae* (except *O. polyspora*), series *Microsomates* (*O. mirabilis*), series *Orbilia* p.p. (most ellipsoid-spored taxa)
ATTT	*Orbilia* section *Lentiformes*, series *Aurantiorubrae*/*Rubellae*/*Commatoideae*, series *Regales* p.p., series *Abutilones* p.p., series *Piliferae*, series *Poitevinicae*, series *Habrostictis* (*O. carpoboloides* & O11), section *Helicoon* (except *O. tianmushanensis*), series *Drechslerella* p.p.

incongruent tree topologies and speculated about a transfer of introns between closely related species by viruses. In order to verify such intron transfers, Bhattacharya et al. (2005) included group I introns from 16 different positions of SSU and 10 of LSU from 84 species of *Ascomycota* in a single alignment and compared it with an analysis of the SSU+LSU+*RPB2* region of these species. In their fig. 3 they report seven putative cases of intron movement between distant positions of SSU and/or LSU, which occurred between different classes or also within a class.

Intron S1506. When obtaining sequences of the ITS1-5.8S-ITS2 region, a group I intron at the 3'-end of SSU is often included in the sequence when using forward primers such as ITS5, ITS1-F, or SF16a, whereas the intron is missed when using the forward primer ITS1. The intron always occurs at the very same gene locus between the primers ITS5 and ITS1 (Tab. 22). Strains which lack the intron show near the 3'-end of SSU the motif GGTTT, whereas strains which possess the intron show this motif much more upstreams, but instead GTT near the 3'-end. Due to the tandem repeat of TT at the 5'-end and TT at the 3'-end of the intron, the exact position of the intron is ambiguous when comparing rDNA sequences with and without intron. According to Gargas et al. (1995) and Hagedorn & Scholler (1999), the intron is positioned between GT and TT, because group I introns generally have G at their 3'-end (P. Haugen pers. comm.) and consequently TT at their 5'-end, which fixes the intron position as given in Tab. 22. The NS24 primer, which ends with its forward version as GGTTT, includes the intron position but, because of the tandem repeat of TT, it works also with sequences that possess the intron.

Various taxa of *Ascomycota*, but none of *Orbiliomycetes*, show the much less frequent variant GGTCT instead of GGTTT. In this variant the NS24 primer would possibly fail in binding to the DNA. Because of this variant, two cases can be observed in sequences which possess the S1506 intron (see Tab. 22): (1) the 3'-end of the intron ends as G|TT; (2) the 3'-end of the intron ends as G|CT. Interestingly the intron in the second variant starts with the tandem repeat CT, as GGT|CT at its 5'-end. However, a rare case was observed in which the intron

Table 21. Variation (yellow) in the primer LR4 (grey) and adjacent nucleotides between domains D3 and D4 of LSU rDNA (stem-loop H700, see Gillespie et al. 2005) in different classes of *Ascomycota* (obtained by BLAST search in GenBank and personal database). *Orbiliomycetes* are highlighted in bold. Listing of other classes incomplete.

Taxa	Primer LR4 (grey) and adjacent nucleotides of LSU D3/D4
***Orbiliomycetes* p.p.maj.**, *Pezizomycetes*, *Saccharomycetes*, *Neolectomycetes*, *Lecanoromycetes*, *Lichinomycetes*, *Leotiomycetes*, *Xylonomycetes* p.p.maj., *Eurotiomycetes*, *Dothideomycetes*, *Sordariomycetes*, *Basidiomycota*	GGGTGAAGCCAGAGGAAACTCTGGTGGAGGCTCG
Dothideomycetes, *Eurotiomycetes*, *Basidiomycota*, non-fungal groups	GGGCGAAGCCAGAGGAAACTCTGGTGGAGGCTCG
Mycoceros, *Pezizomycetes*, *Sordariomycetes*, *Basidiomycota*, *Dothideomycetes*, *Saccharomycetes*	GGGTGAAGCCAGAGGAAACTCTGGTGGAAGCTCG
Hyalorbilia latispora, ***Orbilia septispora***, ***O. quaestiformis***, ***O. multiurosperma***, ***O. octoserpentina***, ***O. mesaverdiana***, *Rhytismatales*, *Mucoromycetes*, *Lecanoromycetes*	GGGTGAAGCCAAAGGAAACTTTGGTGGAGGCTCG
Bryorbilia arenicola, **uncultured clones B2 & B5**, *Moniliella* (*Basidiomycota*)	GGATGAAGCCAGGGGAAACCCTGGTGGAGGTCCG
Leotiomycetes, *Lecanoromycetes*, *Dothideomycetes*, *Sordariomycetes*, *Basidiomycota*, *Zygomycota*	GGGTGAAGCCAGGGGAAACCCTGGTGGAGGCTCG
Symbiotaphrina kochii (*Xylonomycetes*), *Phaeodimeriella* (*Dothideomycetes*)	GAGTGAAGCCAGGGGAAACCCTGGTGGAGGCTCG
Dothideomycetes, *Sordariomycetes*, *Lecanoromycetes*, *Basidiomycota*, non-fungal groups	GGGCGAAGCCAGGGGAAACCCTGGTGGAGGCTCG

Table 22. Location of the S1506 group I intron (yellow) between two ITS primers at the 3’-end of SSU (blue), within the motif **GGT|TT** (frequent variant) or **GGT|CT** (more rare variant). Depending on the variant, the 5’-end of the intron starts with the tandem repeat TT or CT, whereas its 3’-end always ends with G, except for the very rare case of taxa with the frequent variant in which the 5’-end was CT. – Freq. = frequency within *Ascomycota*.

ITS5 primer S1506 intron ITS1 primer 3’-end of SSU	Intron	Freq.
CATTTAGAGGAAGTAAAAGTCGTAACAA**GGT**TTNNNNNNNN.....NNNNNNNNNNNG**TT**CCGTAGGTGAACCTGCGGAAGG**ATCATTA**	present	****
CATTTAGAGGAAGTAAAAGTCGTAACAA**GGT**CTNNNNNNNN.....NNNNNNNNNNNG**TT**CCGTAGGTGAACCTGCGGAAGG**ATCATTA**	present	*
CATTTAGAGGAAGTAAAAGTCGTAACAA**GGT**---------------------------**TT**CCGTAGGTGAACCTGCGGAAGG**ATCATTA**	absent	*****
CATTTAGAGGAAGTAAAAGTCGTAACAA**GGT**CTNNNNNNNN.....NNNNNNNNNNNG**CT**CCGTAGGTGAACCTGCGGAAGG**ATCATTA**	present	**
CATTTAGAGGAAGTAAAAGTCGTAACAA**GGT**---------------------------**CT**CCGTAGGTGAACCTGCGGAAGG**ATCATTA**	absent	***

starts with GGT|CT but ends with G|TT. This rare case was so far only detected in *Calycina citrina* (KY462815) and *Calycina* sp. (?= *Mollisia caespiticia*, KY965813). Other sequences of *C. citrina* agg. show the variant GGTTT by lacking the intron (e. g., AY789386), which concurs with the currently accepted intron position GGT|TT.

Liu & Tzean (1997: tab. 2) referred to this intron as ‘insert’ and observed it in 10 out of 29 orbiliaceous species by listing a length between 391 (*Geniculifera cystosporia*) and 428 (*Arthrobotrys botryosporus*), rarely 1294 nt (*A. superbus*). Hagedorn & Scholler (1999: fig. 3), who named it ‘second insert’, found it with a length of 385–416 nt in 15 species of section *Arthrobotrys* and provided a neighbour joining analysis of the alignable part of this insert for them. We have observed the S1506 intron in 150 species of *Orbiliomycetes* and in 262 its absence, including data retrieved from GenBank (Tab. 23). Within a section or series of *Orbilia* the intron may be present or absent in a similar frequency, but in some groups and particularly in other orbiliaceous genera it was rare or even absent, with the exception of *Hyalorbilia* (Tab. 23). In a number of cases we observed that closely related species consistently differed in the presence vs. absence of the intron (Tab. 25), whereas in others it showed variation within a species (Tab. 26).

Table 23. Presence of S1506 intron in the genera of *Orbiliomycetes* and subgroups of *Orbilia*. The two right columns indicate the number of species in which the intron was absent or present (data from Tab. S5).

Genus/infrageneric group	Without intron	With intron
indet. basal genera (uncult. clones U1–3)	3	0
Mycoceros (incl. uncult. clone M1)	2	0
Retiarius (uncult. clones R2–4)	3	0
Amphosoma (incl. uncult. clones A2–6)	8	0
Bryorbilia (incl. uncult. B1–5)	6	0
Lilapila	4	0
Lecophagus	4	0
Hyalorbilia p.p. (*Vermispora* clade, incl. uncult. clones V1, 3, 5–9, 11–13)	11	0
Hyalorbilia s.str. (incl. uncult. clones H2, 4, 6–8, 11, 14, 24, 26, 30–32, 37)	28	10
H. latispora	1	0
H. erythrostigma/*H. orbiliicola*	2	0
H. hergiswiliana	1	0
Orbilia series *Lentiformes*	9	0
series *Phanosomates*	2	1
series *Microspermae*	1	3
series *Cercidicola*	1	0
series *Ovales*	1	0
series *Hesperideae* (incl. uncult. clone O2)	21	11
series *Hemi*	5	5
series *Vibrioides*	2	3
section *Aurantiorubrae* (incl. uncult. O8–9)	30	17
section *Helicoon*	6	7
section *Habrostictis* (incl. uncult. O10, 12)	16	16
section *Ovoideae*	5	2
section *Orbilia* (incl. uncult. O15, 18)	17	16
series *Neodactylella* (incl. uncult. O22, 24, 26–28)	16	20
series *Arthrobotrys* (incl. uncult. O30)	25	21
series *Dactylellina*	17	7
series *Gamsylella*	7	2
series *Drechslerella*	10	9
Total	**264**	**150**

The S1506 intron may occur in two very different length variants: the long variant ranges between 1266 and 2053 nt, rarely only 547 or 701, and was observed in eight strains of eight rather distant species of *Orbilia*. In all other orbiliaceous species, in which the intron occurred, it had a length of 381–459, rarely 330–366 nt (*Hyalorbilia*) (Tab. 24). However, the two categories are not sharply separated. The frequent short variant aligns more or less well and can be used for phylogenetic analyses. When aligning the short with the long variant, it aligns to the 5’-end of the latter.

The S1506 intron was observed with varying frequency in most groups of ascomycetes, also in the exobasidiomycete *Tilletiopsis flava* and in *Rhodophyta* (*Porphyra spiralis* var. *amplifolia*, *Hildenbrandia rubra*). The two length variants chiefly contain six conserved motifs which occur with minor variation also in other classes of ascomycetes, for instance in *Leotiomycetes*. One of them is located near the 3’-end of the short variant and usually looks like this: GCTTAAGATATAGTCGGGC, but some strains showed some variation. Sometimes it starts with **A**CTTAAG or ends with GTCGGG**T** or GTCGG**T**C, or it may show some rare other variants. In *Hyalorbilia* the motif was predominantly GC**C**TAAGATATA**A**TCGG**GT**. The right, downstream part of the long variant appears to represent an intron of its own. In two species (*O. quaestiformis* of section *Habrostictis*, *O. zhongdianensis* of series *Neodactylella*) both length variants occurred in different strains (Tab. 24).

Intron S1506 in other classes. The S1506 intron also occurs in various members of *Helotiales* by usually showing exactly the motif GCTTAAGATATAGTCGGGC near its 3’-end, though also some other variants. Also various *Dothideomycetes* exactly concur with this motif, according to BLAST search for this motif in GenBank. This indicates homology of the S1506 intron region across the *Ascomycota*. Also in the *Rhodophyta* the intron occurs, with the conserved motif deviating at three positions from the current motif of *Ascomycota*: GCTTAAGA**GAC**AGTCGGT, which suggests that this intron is a very old gene region that traces back to a common ancestor of both phyla.

Gargas et al. (1995) observed intron S1506 in *Helotiales*, *Taphrinomycotina* (*Pneumocystis*), *Dothideomycetes* (*Cenococcum*), *Chaetothyriales* (*Phialophora americana*), also in *Chlorophyta* and *Rhodophyta*, but not in lichens. Gutiérrez et al. (2007), however, found intron S1506 in various *Parmeliaceae*, with three size ranges between 224 and 614 nt. Takashima & Nakase (1997) observed intron S1506 in *Tilletiopsis flava* (*Exobasidiomycetes*) and Xu et al. (2013) in *Botryosphaeria dothidea* (*Dothideomycetes*), and both classified it as group IC1 intron.

Other SSU introns in *Orbiliomycetes*. Apart from intron S1506, *Orbiliomycetes* did not show any further introns in the SSU region in most of those taxa which comprise more than the V6–V9 regions, with a few exceptions. Hagedorn & Scholler (1999) observed the S943 intron in two species of section *Arthrobotrys* (*Dactylella cylindrospora*, *Gamsylella arcuata*) and named it 'first insert' in reference to S1506 as the 'second insert' in orbiliaceous taxa. We found intron S943 also in *Lilapila oculispora*, five species of *Hyalorbilia*, and in 11 of *Orbilia* from five different sections (see Tab. 27). However, sequences that include the V6 region were at pesent predominantly available for nematode-trapping taxa. The intron S943 is located between the motives CACCAGAWGT[intron]GGAGCCTGCG.

Orbilia ovoidea (H.B. 6489a) possesses the intron S1516 with a length of only 70 nt, which is located in the region of the ITS1 primer. These two exceptional group I intron positions were also reported by Gargas et al. (1995), the former in various orders of fungi, the latter in *Cladonia chlorophaea* and *Lecanora dispersa*, though here with 210–228 nt. Because the S1516 intron of *O. ovoidea* is much shorter and ends with an A, it is probably not a group I intron; its position could also be 1517, in which case it would actually end with a G.

LSU introns in *Orbiliomycetes*. Three group I introns were observed in the LSU of *Orbiliomycetes*, one occurring in the D9 domain (L1921), one between D10 and D11 (L2449), and one in D11 (L2563) (Tab. S1). At present, sequences from 15 species of *Orbiliomycetes* comprise the complete D9 domain, from 14 species the complete D10 domain, and from 13 species the D11 domain (Tab. 28). These introns are recognized when aligning the LSU with orbiliaceous or other LSU sequences which lack the introns. Their length varied between 429 and 738 nt. The strong length difference in L2449 is due to more and longer (up to 68 nt) inserts in *O. xanthostigma*, and in L2563 it is an insert of 54 nt in *O. leucostigma*. No intron was observed in the D1–D8 domain.

BLAST searches of the L1921 intron yielded alignments with the L798 intron of *Dothideomycetes* (*Pseudorobillarda siamensis*, *Wiesneriomyces laurinus*) or *Saccharomycetes* (*Diddensiella* ['*Candida*'] spp.), but also with the S943 intron of *Dothideomycetes* (*Botryosphaeria* spp.) and even *Chlorophyceae* (*Spermatozopsis exsultans*). These alignments are very fragmentary, but they may include regions of up to 150 nt which align without gaps though with a high distance. This result, which can hardly be accidental, supports the hypothesis that group I introns in the fungal genome may have a viral origin. The general presence of 'G' at the 3'-end of group I introns has a special role in their splicing as mobile genetic elements (P. Haugen pers. comm.).

Protein-coding genes

Different gene regions of the DNA that code for proteins have been investigated by different authors regarding members of *Orbiliomycetes*, particularly nematode-trapping taxa (Tab. 29). They were used in multigene analyses in order to obtain a better backbone phylogeny with higher bootstrap support at the main branches.

The affiliation of *Orbiliomycetes* in the *Ascomycota* was explored by various authors based on two or rarely three species of *Orbilia* (*O.* aff. *sinensis* [as *O. vinosa*], *O.* aff. *elegans* [as *O. auricolor*], *O. elegans* (as *Arthrobotrys elegans*]) by using rDNA in combination with protein-coding genes: James et al. (2006), Spatafora et al. (2007), Schoch et al. (2009), and Gueidan et al. (2011) with *RPB1*, *RPB2*, and *TEF1*; Prieto & Wedin (2013) with *RPB1*, mtSSU, and *MCM7* (the latter two lacking for *Orbilia*); Gazis et al. (2012) with mtSSU, *RPB1*, and *RPB2*; and Beimforde et al. (2014) with *RPB1* and *RPB2*.

Different Asian workers have investigated protein-coding genes of larger data sets of *Orbiliomycetes*. Li et al. (2005) analysed LSU in combination with two *TUBB* genes (1A/1B, 2A/2B) in nematophagous taxa. Yang & Liu (2006) and Yang et al. (2007) combined ITS, *RPB2*, *TEF1*, and *TUBB* (2A/2B); Swe et al. (2008b) ITS and *TUBB* (2A/2B); Yang et al. (2012a) *RPB2*, *TEF1*, *TUBB* (2A/2B), *mapk*, and *sp*; and Zhang et al. (ined.) mtLSU, *RPB2*, *TEF1*, and *TUBB* (2A/2B). Li et al. (2016) found in the MAD1 gene (uncombined) a correlation with the adhesive properties of trapping organs as a support for the monophyly of the different trapping devices.

Whole-genome sequences

Up to the present, the whole genome from three nematophagous species of *Orbilia* is available in GenBank, being sequenced in the 'Gold Project' (Gp, https://gold.jgi.doe.gov/): *Orbilia oligospora* (Gp0005961, ATCC 24927, CBS 115.81, as *O. auricolor*/*Arthrobotrys oligosporus*, accession number ADOT00000000, Yang et al. 2011), *Dactylellina haptotyla* (Gp0047799, CBS 200.50, as *Monacrosporium haptotylum*, AQGS00000000, Meerupati et al. 2013), and *Drechslerella stenobrocha* (Gp0005661, strain 248, YNWS02-9-1, AS/CGMCC 3.6768, ASQI00000000, Yang et al. 2007, Liu et al. 2014). The size of the genome varied strongly among the species, ranging between 29.02 Mb (millions of basepairs, *D. stenobrocha*) up to 40.07 Mb (*A. oligosporus*) or 40.4 Mb (*D. haptotyla*).

Usually rDNA is not available in whole-genome data, since repetitive genes are hard to assemble with confidence (D. Ahrén pers. comm.), but it is often separately supplied to enable identification at the species level. Only for *Drechslerella stenobrocha* the complete SSU-ITS-LSU could be retrieved from the whole-genome data (ASQI01000343, W.W. Zhang pers. comm.). Available rDNA data are for *O. oligospora*: complete SSU (AJ001986), SSU V8–V9, ITS, and LSU D1–D2 (KY463695); for *Dactylellina haptotyla*: complete SSU (AJ001990), ITS (U51957), and LSU D2–D4 (AQGS01000586); and for *Drechslerella stenobrocha*: ITS (AY773460).

Further 18 nematode-trapping *Orbilia* species, being among those treated in Yang et al. (2007), have been investigated for the whole genome (W.W. Zhang & X.Z. Liu, pers. comm.), for instance, *O. auricolor* (Gp0004966, NCBI 53381, as *O. auricolor*/*A. cladodes*, CBS 433.81). However, uploads and a published report were not yet available.

Phylogenetic position of *Orbiliomycetes* within the *Ascomycota*

Historical review. When Nannfeldt (1932) erected the family *Orbiliaceae* as a member of *Helotiales*, he included three genera: *Orbilia*, *Hyalinia*, and *Patinella*. Benny et al. (1978) suggested to remove the family from the *Helotiales* by tentatively transferring it to the *Lecanorales* and within this order to members with iodine-negative asci. The authors based their

Table 24. Total length of S1506 intron in *Hyalorbilia* and different sections and series of *Orbilia*. Only those species are listed in which the intron was obtained in full length or when its length was approximately certain.

Group	Species	Strain	Intron length
Hyalorbilia	*H. polypori*	H.B. 7557a	336
	H. inflatula	H.B. 9915	330
	H. fagi	H.B. 9724	339
	H. helicospora	G.M. 2015-10-29.1 G.M. 2015-11-09.1 G.M. 2016-10-12.3	342 342 342
	H. juliae	G.M. 2014-12-17.1	366
Orbilia section *Lentiformes*	*O. myriosphaera*	H.B. 6679a G.M. 2018-09-12.10a	395 395
	O. euonymi	G.M. 2016-09-10.1	444
	O. pleistoeuonymi	H.B. 6494a	1555
section *Hemiorbilia*	*O. corculispora*	H.B. 6279a	433
	O. australiensis	H.B. 7208b	388
	O. pleioaustraliensis	H.B. 6277e	385
	O. paramontigena	H.B. 10013	413
	O. vinosa	H.B. 6715b G.M. 2011-04-19.1 G.M. 2014-07-12.1 G.M. 2016-05-04.1 G.M. 2017-02-09.1	413 413 413 414 414
	O. cf. *subvinosa*	H.B. 6748g	408
	O. subulivinosa	G.M. 2017-09-04.1	441
	O. velutina	H.B. 9772a	407
	O. aprilis	H.B. 6715a, H.B. 6801 G.M. 2017-07-30.1	390/391 391
	O. aff. *aprilis*	bhi-F628a	391
	O. crenatovinosa	G.M. 2014-05-10.1 G.F. 20160008	396 396
	O. spermoides	H.B. 7517	403
	O. aff. *subaristata*	G.M. 2015-02-22.1	547
	O. subclavuliformis	G.M. 2017-09-05.5	421
	O. graminis	G.M. 2017-05-20.1	489
	O. vibrioides	G.M. 2016-10-11.1	389
	O. myrioobliqua	H.B. 7204s H.B. 8391a	385 388
section *Aurantio-rubrae*	*O albidorosea*	H.B. 6615a	401
	O. cf. *paracaudata*	H.B. 8685	387
	O. ebuli	H.B. 9550	416
	O. ficicola	G.M. 2016-09-12.1a/b, GJO 88305	411 411
	O. xanthoguttulata	H.B. 6989a, 7464, 7915b, G.M. 2017-12-27.2, G.M. 2017-9-28.1	384/387/386/388/388
	O. brachychitonis	H.B. 7578a	459
	O. crenatomarginata	H.B. 9452	393
	O. phragmotricha	H.B. 7535a	401
	O. pilifera	G.F. 20110193	398
section *Helicoon*	*O. rosea*	CCM F-08983	406
	O. luteorubella	H.V. A327 H.B. 9705	1326 701
	O. sarraziniana	H.B. 6727a	442
	O. tianmushanensis	YMF 1.03563	401
section *Habrostictis*	*O. mesaverdiana*	H.B. 6736a	407
	O. octoserpentina	H.B. 6609b G.M. 2007-10-27.1	403 427
	O. cisti	H.B. 6500	419
	O. carpoboloides	H.B. 6639c, H.B. 9233	396/396
	O. trapeziformis	A.P. 18/55	403
	O. quaestiformis	H.B. 7121 G.M. 2014-07-25.4	2053 ~435
	O. septispora	G.M. 2016-09-20.1	429
	O. vermiculati	H.B. 6739b	390
	O. calyptrata	H.B._8079c	450
	O. gambelii	G.M. 2017-08-30.1	421
	O. macroserpens	H.B. 6721c	390
	O. cercocarpi	H.B. 6737b	394
	O. myrionamibica	H.B. 10119a	454
section *Ovoideae*	*O. ovoidea*	H.B. 6489a	401
section *Orbilia* series *Orbilia*	*O. paracylindrospora*	H.B. 9484	437
	O. brettii	H.B. 10130	392
	O. cf. *xanthostigma*	bhi-F037a/b	432
	O. cf. *xanthostigma*	G.M. 2018-04-28.1	584
	O. cf. *xanthoflexa*	ga026b	400
	O. leucostigma	H.B. 6810c G.M. 2015-08-15.4a	455 455
	O. renispora	ga038, bhi-F097	380
	O. frangulae	H.B. 9970a G.M. 2014-07-12.2	1266 1266
	O. tremulae	H.B. 6963a NBR C9521 G.M. 2015-07-09.1	393 393 393
	O. eucalypti	H.B. 6662 G.M. 2015-09-08.1 G.M. 2015-10-02.1, H.B. 9813b G.M. 2018-08-02.3 G.M. 2014-09-30.1 clade A1 (6 strains)	381 381 382 384 385 385 389
	O. eucalypti	G.M. 2014-10-30.2	1233
	O. plurivacuolata	H.B. 9817a G.M. 2016-02-10.2	418 419
	Dicranidion fragile	NBRC 6990	~1290 (> 1260)
	O. fissilis	H.B. 7566a	405
section *Arthrobotrys* series *Neodactylella*	*O. desertorum*	H.B. 8737 TFC Mic. 24077	389 391
	Dactylella cylindrospora	CBS 325.70	415–416
	O. epilobii	B.Ca. 080615	387
	D. longquanensis	YMF 1.01868	388
	O. zhongdianensis	H.B. 9641, H.B. 9964 YMF 1.00568	385/385 1565
	O. cotoneastri	H.B. 7241a	390
	O. rectispora	H.B. 7142 YMF 1.00582	405 ~413
	D. intermedia	BBA 69986	394
	O. aff. *oxyspora*	R.K. 4431	371
	O. clavispora	H.B. 8371a CBS 917.85	382 416
series *Dactylellina*	*Dactylellina huisuniana*	CCRC 33444	395
	D. leptospora	CBS 100579 CBS 560.92	385 385
	D. copepodii	CBS 487.90	393
series *Gamsylella*	*Gamsylella* sp.	WAC10291	416
series *Arthrobotrys*	*Arthrobotrys conoides*	SBUG-M12	405
	A. botryosporus	CBS 321.83	428
	A. reticulatus	BO4 CO4	414 414
	O. auricolor	H.B. 6664, H.B. 6763 G.M. 2014-10-11.3	393/399 399
	A. superbus	CBS 109.52	1293–1294
	O. cladodes	CBS 433.81	394
	O. elegans	H.B. 6972a	439
	A. polycephalus	CBS 175.37	395
	A. gampsosporus	CBS 127.83	399
	A. cystosporius	CCRC 32918	406
	A. xiangyunensis	DBN10-1, YXY10-1	415
	O. menageshae	H.B. 9275a	405
series *Drechslerella*	*O. bembicodes*	H.B. 7165b CCRC 33278	382 386
	Drechslerella dactyloides	CBS 334.94	390
	O. polybrocha	CBS 319.56	407
	O. brochopaga	CBS 218.61	391

Table 25. Examples of closely related species or genotypes which differ in the presence vs. absence of S1506 intron (number of strains and partly their origin indicated in brackets).

Without S1506 intron	With S1506 intron
O. succulenticola (11: Macaronesia), *O. xanthoguttulata* (1: USA)	*O. xanthoguttulata* (8: Europe)
O. subvinosa (4), *O. angiosubvinosa* (1)	*O. vinosa* (8), *O. arachnovinosa* (3)
O. hesperidea (2), *O. australiensis* s.l. (1)	*O. australiensis* s.l. (4)
O. aristata (5), *O. subaristata* (5), *O. breviaristata* (1)	*O. flagellispora* (1), *O.* aff. *subaristata* (1)
O. rubella (2: Norway, Portugal)	*O. phragmotricha* (2: Luxembourg)
O. flavidorosella (2)	*O. carpoboloides* (2)
O. xanthostigma s.l. (9: Europe, 3: New Zealand)	*O. leucostigma* (3: Europe), *O. xanthostigma* s.l. (15: New Zealand, USA, Luxemb.)
O. orientalis s.l. (8: Europe, China)	*O. naumburgensis* (2: Germany)

Table 26. Examples in which a species varies among the strains in the presence of the S1506 intron (number of strains and their origin indicated in brackets).

Without S1506 intron	With S1506 intron
O. myriosphaera (1: France, *Cercis*)	*O. myriosphaera* (2: France, *Cercis*; Croatia, *Olea*)
O. euonymi (1: Luxembourg, *Pseudotsuga*)	*O. euonymi* (4: Lux., *Pseudotsuga*; Turkey, *Cedrus*; France, *Buxus*)
O. corculispora (2: France)	*O. corculispora* (1: Australia)
O. vibrioides (1: France, *Arbutus*)	*O. vibrioides* (1: France, *Picea*)
O. crenatomarginata (1: Merseburg, *Tilia*)	*O. crenatomarginata* (1: Tübingen, *Fagus*)
O. gambelii (1: France, Gard, *Quercus ilex*)	*O. gambelii* (1: France, Hautes-Alpes, *Clematis*)
O. rosea (7: Europe & China)	*O. rosea* (1: UK, type of *Anguillospora rosea*)
O. sarraziniana (6: Germany & China)	*O. sarraziniana* (2: Germany & Luxembourg)
O. luteorubella (1: China)	*O. luteorubella* (2: Germany & Austria)
O. cejpii (4: Europe)	*O.* aff. *cejpii* (2: Europe)
O. cladodes (= *O. auricolor* s.auct.) clade C1 (2: USA, China)	*O. cladodes* (= *O. auricolor* s.auct.) clade C1 (2: Belgium, Finland)

conclusion on the study of two species, *Orbilia sarraziniana* (as *O. luteorubella*) and *O.* cf. *pulviscula* (the latter species in its original sense represents a *Calycellina*, see p. 1682). Their criteria were (1) the exceptional ultrastructure of the ascus apex being truncate and thin-walled, without an amyloid apical ring structure, and (2) the basal anchoring hyphae forming haustoria in blue-green algae. This tempted the authors to speculate 'that many, if not all, species of *Orbilia* are lichenized'. However, a connection of any member of *Orbiliomycetes* to algae by haustoria could never be demonstrated in the present study (see also p. 148–150).

Although Hawksworth et al. (1996) retained the *Orbiliaceae* in the '*Leotiales*' (*Helotiales*), the authors mentioned Sherwood's opinion who asserted (in litt.) that the family is better included in the *Gyalectales* (*Ostropomycetidae*, *Lecanoromycetes*). This opinion was one of the stimuli for a comparative study of these two groups by Müller (1998). However, Müller's observations on ascus structure and spore morphology did not reveal convincing similarities between *Orbiliaceae* and *Gyalectaceae*, a result which is supported by later molecular analyses which identified a great distance between these families

In Eriksson et al. (2003) the new order *Orbiliales* and class *Orbiliomycetes* were proposed to accomodate the only family *Orbiliaceae*. Morphological data and a specific molecular signature in the SSU rDNA supported removal from the *Helotiales*. The *Orbiliomycetes* were thought to represent a class separate from the other two classes of non-lichenized discomycetes, roughly represented by the operculate (*Pezizomycetes*) and inoperculate discomycetes (*Leotiomycetes*). Later, Eriksson (2005) presented arguments for a primitive, lichenized, fruitbody forming common ancestor of all main groups of *Ascomycota*, with the exception of *Saccharomycotina* and *Taphrinomycotina*. This so-called 'Protolichenes Hypothesis' implies that classes like *Orbiliomycetes* or *Pezizomycetes* lost their photosynthesising symbiont and became saprobionts, parasites, or symbionts on various substrates, including animals. Eriksson also compared the truncate thin-walled ascus apex of *Orbilia*, *Taphrina*, and *Neolecta* with Chadefaud's hypothetical, primitive 'préarchaeascé' type with uniformly thickened ascus wall, from which the lecanoralean ascus type was said to have evolved.

Molecular phylogenetic analyses. According to Spatafora et al. (2007) and Thorn et al. (2008), the classes *Orbiliomycetes* and *Pezizomycetes* are among the oldest of the phylum *Ascomycota* and the 'two most basal or early diverging branches of *Pezizomycotina*', by far the largest subphylum of *Ascomycota*. The node separating the two classes is generally weakly supported, therefore, it is uncertain which of the two were the first to separate from the large rest of *Pezizomycotina*. In Winka & Eriksson's (2000) analysis of the entire nuclear SSU rDNA region, the *Orbiliomycetes*, represented by a single sequence (*O. fimicola* s. Pfister, D.H.P. 60, = *O. auricolor*), clustered near the base of the tree that comprised a broad scope of *Ascomycota.* Apart from some even more basal taxa now recognized in *Taphrinomycotina* and *Saccharomycotina*, the class formed a sister group to all remaining clades of the phylum, including the *Pezizales* which separated next, and the *Helotiales* to which they are only very distantly related. In two further analyses of the entire SSU (Berbee 2001, Tehler et al. 2003), the *Orbiliomycetes*, represented by 10–16 sequences, clustered within the paraphyletic *Pezizomycetes* clade in an unsupported sister group of *Helvellaceae*, *Morchellaceae*, and *Tuberaceae*, whereas members with amyloid operculate asci (*Ascobolaceae* and *Pezizaceae*) branched off earlier and next to *Saccharomycotina*.

Later molecular studies included further rDNA gene regions and verified the basal placement of *Orbiliomycetes*, but varied in the relationship to *Pezizomycetes*. In analyses of nuSSU+5.8S+LSU by Wang et al. (2006: figs 1–4), based on two chimeric sequences under the names *Orbilia delicatula* and *O. auricolor* which belong to at least three species from six different strains representing series *Orbilia* and *Arthrobotrys* [*O. leuco-* & *xanthostigma* s.l. (D.H.P. 108, 111, YNUCC 6028), *O. oligospora* (*Arthrobotrys oligosporus*, CBS 115.81, YNUCC 2829), *O. auricolor* (*A. cladodes*, CBS 433.81)], the genus *Orbilia* branched off either after (parsimonious trees) or before (Bayesian trees) the *Pezizomycetes*. A similar set of *Orbilia* species from three different strains [*O. xanthostigma* s.l. (D.H.P. 111, YNUCC 6028), *A.* cf. *pyriformis* (as *O. auricolor*/*A. psychrophilus*: AFTOL-ID 906, CBS 547.63)] diverged after the *Pezizomycetes* in Zhuang & Liu's (2012) maximum likelihood or parsimony analysis of SSU+LSU, whereby this result was not altered when the secondary structure of rRNA was included in the analysis. In Liu & Zhuang's (2013) Bayesian analysis of SSU, however, which included the secondary structure, *Pezizomycetes*

Table 27. Occurrence and length of S943 intron in *Orbiliomycetes*.

Group	Species	Strain	Intron length	Species without S943 intron
Lilapila	*L. oculispora*	G.M. 2017-08-31.1, G.M. 2017-08-31.2, H.B. 10122	380	*L. oculisporella* (G.M. 2015-09-15.1, G.M. 2016-08-11.1, G.M. 2016-08-14.1, G.M. 2016-09-08.1), *L. jurana* H.B. 10123
Lecophagus				*L. ellipsoideus* H.B. 9902a, *L. longisporus* CBS 845.91, *L. muscicola* AFTOL-ID 183, IAM 14638, aff. *Lecophagus* (clades U9–11)
indet. basal genus				indet. uncult. clone GL29325 176 G2660 (clade U1)
Hyalorbilia	*H. inflatula*	H.B. 9915	329	*H. erythrostigma* G.M. 2017-11-23.1
	H. tortuosa	S.H. 868	min. 416	indet. uncult. clones Elev 18S 1286, Elev 18S 977
	H. helicospora	G.M. 2016-10-12.3	min. 315	
	H. lunata	N.A. 342	min. 317	
	H. oviparasitica	ATCC 38908	400	*Hyalorbilia* aff. *multiguttulata* DoUCR50 (13 strains)
Orbilia section *Lentiformes*				*O. euonymi* G.M. 2016-09-10.1
section *Hemiorbilia*	*O. vibrioides*	G.M. 2016-10-11.1	min. 363	*O. vibrioides* G.M. 2017-09-04.2
	O. subulivinosa	G.M. 2017-09-04.1	min. 374	*O. subclavuliformis* G.M. 2017-09-04.5
	O. aprilis	G.M. 2017-07-30.1	min. 351	
section *Habrostictis*	*O. gambelii*	G.M. 2017-08-30.1	min. 297	
	O. septispora	G.M. 2016-09-20.1	371	
	O. subvitalbae	G.M. 2017-09-05.1	min. 358	
section *Aurantiorubrae*	*O. ficicola*	G.M. 2016-09-12.1	356	*O. aradi* G.M. 2014-02-23.2
	O. navicularis	H.B. 10113a	min. 345	
section *Helicoon*				*O. luteorubella* gz-08, *O. rosea* CCM F-18983, *O. sarraziniana* B.L. 6574, *O.* aff. *sinensis* CBS 917.72
section *Ovoideae*	*O. canadensis*	S.H. 727	min. 284	
section *Orbilia*				*O. xanthostigma* s.l. D.H.P. 111 & G.M. 2015-08-15.4b, *O. leucostigma* G.M. 2015-08-15.4a, *O. eucalypti* G.M. 2017-08-30.2
section *Arthrobotrys* series *Neodactylella*	*D. cylindrospora*	CBS 325.70	376	*O. rhopalota* CBS 493.67, *O. oxyspora* CBS 497.92
series *Arthrobotrys*				*A. amerosporus* SBUG-M1257, *A. cladodes* D.H.P. 60, *A. cladodes* CBS 289.82, *A. cladodes* CBS 107.81, *O. auricolor* CBS 340.94, *O. elegans* L9203 & CBS 397.93, *A. musiformis* CBS 266.83, *A. flagrans* CBS 565.50 & 583.91, *A. oligosporus* CBS 115.81 & XAo1, *A.* cf. *pyriformis* CBS 547.63
series *Dactylellina*				*D. haptotyla* CBS 200.50
series *Gamsylella*	*G. arcuata*	CBS 174.89	416	*G. gephyropaga* CBS 178.37
series *Drechslerella*				*D. dactyloides* CBS 264.83, *D. doedycoides* CBS 223.54

and *Orbiliomycetes*, based on *O. auricolor* s.l. (as *O. auricolor* and *O. fimicola*, probably D.H.P. 55 and 60), formed a supported clade of their own, with the remaining *Pezizomycotina* as sister clade. In the Bayesian analysis by Ekanayaka et al. (2017: fig. 25) based on nuSSU, nuLSU, and *RPB2*, the *Orbiliomycetes* diverged shortly before the *Pezizomycetes*. As representative taxa the authors used *Orbilia sinensis* (type, YMF 1.01843, as *O. luteorubella*) and *O. tenuispora* (B.L. 691, HMAS 139703, as *O. rectispora*) for which, however, only LSU data was available. In our ML analysis based on 5.8S+LSU (D1–D6), the orbiliaceous group branched off after the *Pezizomycetes*, but without support at the branches (Phyl. 1), and this was also the case in Magyar et al.'s (2017b) Bayesian analysis of ITS+LSU which included many orbiliaceous taxa.

In two multigene analyses by James et al. (2006) and Spatafora et al. (2007) (see Fig. 114), the *Orbiliomycetes* diverged shortly

Table 28. Presence/absence of three LSU group I introns (yellow) in the few available sequences of *Orbiliomycetes* which include the D9–D11 domain. The length of the intron is given in parenthesis. ? = number of nt uncertain or unknown.

Domain	D9	D10/D11 (within primer LR11)	D11
	TAACTATGACT**L1921**CTCTTAAGGTAG	ACCACAGGGAT**L2449**AACTGGCTTGTG	TGTTCACCCACT**L2563**AATAGGGAACGT
Taxa with intron	*Hyalorbilia helicospora* G.M. 2016-10-12.3 (351) *Orbilia crenatovinosa* G.F. 20160008 (406) *O. vinosa* G.M. 2016-05-04.1, G.M. 2017-02-09.1 (428) *O. xanthostigma* G.M. 2015-08-15.4b (457) *O. leucostigma* G.M. 2015-08-15.4a (?) *O. ficicola* G.M. 2016-09-12.1a (348) *D. stenobrocha* 248 (1259)	*Lilapila oculispora* H.B. 10122 (414) *H. helicospora* G.M. 2016-10-12.3 (?) *O. xanthostigma* G.M. 2015-08-15.4b (738) *O. leucostigma* G.M. 2015-08-15.4a (576) *O. euonymi* G.M. 2016-09-10.1 (472)	*Lilapila oculispora* H.B. 10122 (338) *O. vinosa* G.M. 2017-02-09.1 (378?), *O. xanthostigma* G.M. 2015-08-15.4b (478) *O. leucostigma* G.M. 2015-08-15.4a (533)
Taxa without intron	*Lecophagus muscicola* ATCC 56071 *Lilapila oculispora* H.B. 10122 *L. jurana* H.B. 10123 *L. gallica* G.M. 2019-07-07.3 *Hyalorbilia latispora* G.M. 2013-11-16.3 *Orbilia ovalis* G.F. 20150009, G.M. 2015-09-13.1 *O. aradi* G.M. 2014-02-23.2 *O. euonymi* G.M. 2016-09-10.1 *O. septispora* G.M. 2016-09-20.1	*Lecophagus ellipsoideus* H.B. 9902a *L. muscicola* ATCC 56071 *Lilapila jurana* H.B. 10123 *H. latispora* G.M. 2013-11-16.3 *O. ovalis* G.F. 20150009, G.M. 2015-09-13.1 *O. aradi* G.M. 2014-02-23.2 *O. ficicola* G.M. 2016-09-12.1a *O. vinosa* G.M. 2017-02-09.1 *Drechslerella stenobrocha* 248	*Lecophagus ellipsoideus* H.B. 9902a *L. muscicola* ATCC 56071 *Lilapila jurana* H.B. 10123 *H. latispora* G.M. 2013-11-16.3 *O. ovalis* G.F. 20150009, G.M. 2015-09-13.1 *O. aradi* G.M. 2014-02-23.2 *O. euonymi* G.M. 2016-09-10.1 *O. ficicola* G.M. 2016-09-12.1a *D. stenobrocha* 248

Table 29. Protein-coding genes and mitochondrial SSU and LSU for which sequences of *Orbiliomycetes* exist in GenBank until 2018.

Gene region	Abbreviation	Existing sequences in *Orbiliomycetes*
largest subunit of nuclear RNA polymerase II	*RPB1*	*Arthrobotrys oligosporus*, *Dactylellina haptotyla*, *Orbilia* aff. *sinensis* (Benedict's strain)
second largest subunit of nuclear RNA polymerase II	*RPB2*	various nematode-trapping spp. of section *Arthrobotrys*, section *Helicoon* (*O. tianmushanensis*), section *Orbilia* (*O. xiushanensis*), section *Aurantiorubrae* (*O. laevimarginata*)
translation elongation factor	*TEF1*	various nematode-trapping spp. of section *Arthrobotrys*, section *Helicoon* (*Orbilia* aff. *sinensis*, *O. tianmushanensis*)
β-tubulin (*TUBB*)	*TUBB1A/1B*	various spp. of section *Arthrobotrys* including *Neodactylella*
	TUBB2A/2B	various spp. of section *Arthrobotrys* including *Neodactylella*
cuticle-degrading serine protease gene		some spp. of series *Arthrobotrys*
calmodulin		*Arthrobotrys flagrans*, *A. oligosporus*, *Dactylellina haptotyla*
mitogen-activated protein kinase	*mapk*	some nematode-trapping spp. of section *Arthrobotrys*
subtilisin-like serine protease	*sp*	some nematode-trapping spp. of section *Arthrobotrys*
mini-chromosome maintenance proteins	*MCM7*	none found
cell wall adhesin protein MAD1 mRNA	*MAD1*	various spp. of section *Arthrobotrys* including *Neodactylella*
small subunit of mitochondrial rDNA	mtSSU	none found
large subunit of mitochondrial rDNA	mtLSU	many spp. of section *Arthrobotrys*, some of series *Pseudotripoconidium*, *O. laevimarginata*, *O. xiushanensis*

before the *Pezizomycetes*, but the bootstrap support for this was not high. The analyses were based on nuSSU+(5.8S+) LSU, *RPB1*, *RPB2*, and *TEF1*, and the two included *Orbilia* species were *Arthrobotrys* cf. *pyriformis* (CBS 547.63) and *O.* aff. *sinensis* (as *O. vinosa*: AFTOL-ID 905, CBS 917.72). Also in three more recent multigene analyses by Gueidan et al. (2011, nuSSU+LSU, *RPB1*, *RPB2*, *TEF1*), Prieto & Wedin (2013, nuSSU+5.8S+LSU, mtSSU, *RPB1*, *MCM7*), and Gazis et al. (2012, nuSSU+LSU, mtSSU, *RPB1*, *RPB2*), the same two *Orbilia* species diverged with high support distinctly before the *Pezizomycetes*. However, in Gazis et al. the genus *Peziza* clustered in a clade separate from the remaining *Pezizomycetes* which diverged before *Orbilia*, whereas in James et al. and Spatafora et al. also *Peziza* diverged after *Orbilia*. In contrast to this, *Orbiliomycetes* diverged shortly after *Pezizomycetes* in the analyses of Schoch et al. (2009, based on *RPB1*+*RPB2*+*TEF1*) and Beimforde et al. (2014, based on nuSSU, nuLSU, *RPB1*, *RPB2*). The authors used again the same two *Orbilia* species, but Schoch et al. included also *O. elegans* (as *Arthrobotrys elegans*, AFTOL-ID 1252, CBS 397.93).

In a whole-genome sequencing study by Gazis et al. (2016: fig. 1), which included two species of *Pezizomycetes* (*Pyronema confluens*, *Tuber melanosporum*) and one of *Orbiliomycetes* (*Orbilia oligospora*, ATCC 24927), 174 single-copy-orthologs were aligned. The resulting phylogram with 25809 amino acid positions of well-aligned regions trimmed with gBlocks (R. Gazis pers. comm.) shows high support at all main branches. As in Liu & Zhuang's (2013) SSU analysis, *Pezizomycetes* and *Orbiliomycetes* clustered in a monophyletic clade, representing the first segregate within the *Pezizomycotina* superclade. The same result has been obtained in a Bayesian analysis of 14 mitochondrial protein-coding genes, which included 8 mainly nematophagous *Orbilia* spp. (Zhang et al. 2020b).

In a morphological phylogenetic analysis based on four characters of ascus apex and septal pore, Kumar et al. (2012: tabs I–II) confirmed that the *Orbiliomycetes* and *Pezizomycetes* are among the earliest diverging branches of *Pezizomycotina*. The authors also interpreted the closed nuclear division (retention of an intact nuclear envelope throughout mitosis) and the two-layered disk-shaped spindle pole body as ancestral state characters for *Ascomycota*.

Molecular clock. Segregation of *Orbiliomycetes* must have occurred much earlier than in the Cretaceous era, which dates 145–66 myr before present. According to phylogenetic analyses, calibrated mainly by pyrenocarpous, lichenized, and calicioid (mazaediate) ascomycetous fossils from amber and chert dating between around 460 and 15 myr ago, the earliest diversification of *Pezizomycotina*, which resulted in the *Orbiliomycetes* and *Pezizomycetes*, took place about 550–350 myr ago (see following references).

In three diversification studies on the major lineages of fungi and particularly ascomycetes, the *Orbiliomycetes*, represented by *O.* '*auricolor*' (= *Arthrobotrys* cf. *pyriformis*) and *O.* '*vinosa*' (= *O.* aff. *sinensis*), diverged either during late Ordovician (~455 myr, Gueidan et al. 2011, Prieto & Wedin 2013, calibrated using 5–8 fossils) or during middle Silurian (~430 myr, Beimforde et al. 2014, using 13 fossils). However, the variance of these results regarding the first diversification of *Pezizomycotina* spread between middle Cambrian (516 myr) and early Devonian (396 myr) in the first two studies and between late Neoproterozoic (554 myr) and early Carboniferous (353 myr) in the third study.

The divergence time, during which the lineages of these two *Orbilia* species had separated from their common ancestor, was estimated as 225 myr (Gueidan et al. 2011), 150 myr (Beimforde et al. 2014), or 106 myr (Prieto & Wedin 2013) before present. In our taxonomic concept, these two *Orbilia* species represent the lineages of sections *Arthrobotrys* and *Aurantiorubrae*, respectively.

In the analysis of Ekanayaka et al. (2017: fig. 25, tab. 4), which was calibrated based on four ascomycetous fossils, the *Orbiliomycetes* diverged ~443 (410–523) myr ago, in concordance with Gueidan et al. (2011) and Prieto & Wedin (2013). Within the class a divergence time of only 30 myr was determined by Ekanayaka et al., who incorrectly concluded that all members of the class are so young by representing 'recently evolved taxa'. Instead, Ekanayaka et al.'s result only says that the two very closely related taxa *O. sinensis* (YMF 1.01843) and *O. tenuispora* (B.L. 691), which are both members of series *Pseudotripoconidium*, trace back to a common ancestor of about that age.

Yang et al. (2012a), in their phylogenetic analysis of five protein-coding genes, used two fossils of carnivorous ascomycetes as calibration points for their evaluation of divergence times

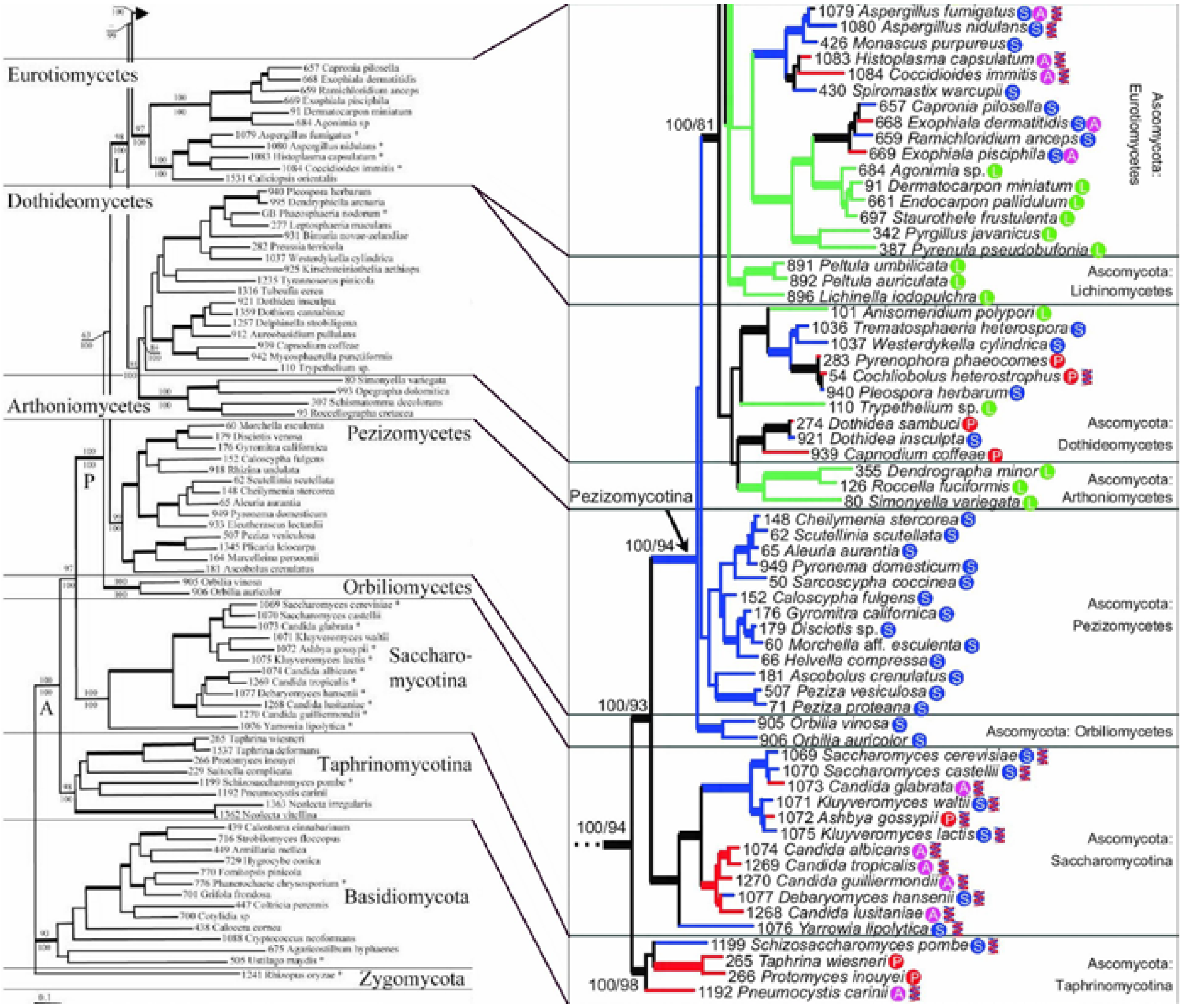


Figure 114: Phylogenetic placement of *Orbiliomycetes* within the fungi; **left**: lower part of the phylogram in Spatafora et al. (2007: fig. 2, five-gene dataset); **right**: upper part of the phylogram in James et al. (2006: fig. 1. six-gene dataset). The used gene regions were nuclear rDNA (SSU, 5.8S, LSU), *RPB1*, *RPB2*, and *TEF1*; in Spatafora et al. no 5.8S was included.

of the major lineages of predacious *Orbiliomycetes*. One of them, *Palaeoanellus dimorphus* Schmidt et al., represents a hyphomycete with unicellular, non-constricting, apparently nematophagous rings and a blastosporous, yeast-like anamorph, reported from fossil amber by Schmidt et al. (2007, 2008) and dated to 100 myr (middle Cretaceous). The other fossil concerns a member of series *Dactylellina* with conidia and adhesive, apparently stalked knobs capturing nematodes, which was dated to ~22.5–26 myr (Oligocene) (Jansson & Poinar 1986). Yang et al. interpreted the former fossil as the last common ancestor of species with septate adhesive networks (series *Arthrobotrys*) and three-celled non-constricting rings (series *Dactylellina*), and the latter fossil as the last common ancestor of two species with stalked adhesive knobs, *Dactylellina drechsleri* (CBS 549.63, as '546.63') and *D. ellipsospora* (YNWS02-8-1), included in their phylogenetic analysis.

However, there are some doubts about the correct calibration in this analysis. Regarding the first fossil, the conidial state does not resemble known anamorphs of *Orbiliomycetes*. Instead, Thorn et al. (2008) compared it with *Debaryomyces*, a member of *Saccharomycetales*, and doubted whether it belongs to the fungus that produced the rings. The authors were also sceptical about the rings being homologous to non-constricting rings of *Orbiliomycetes*. Schmidt et al. (2009), in their replica, assumed that the fossil represents an unknown, perhaps extinct type of adhesive ring trap, whereas Thorn et al. (2009) even doubted that the rings were nematophagous. The second fossil appears to be trustworthy, but the two *Dactylellina* taxa used by Yang et al. (2012a) are undoubtedly conspecific, based on a 1.7% ITS distance between them. CBS 549.63 is an authentic, probably ex-type strain of *D. drechsleri* (Rubner 1996: 58), and its sequence appears to be erroneous at the 5'-end of ITS1, which would mean an even lower distance (?1%) to YNWS02-8-1. In contrast, the neotype strain of *D. ellipsospora* (CBS 302.94, Rubner 1996) deviates hereof by ~10%. Moreover, it seems risky to assume that the fossil was a species that does not form non-constricting rings. Besides, taxa with and without non-constricting rings did not cluster in different clades in our analyses, contrary to the assumption of Yang et al. (2012a). In conclusion, the affiliation of this fossil with the *Dactylellina* clade seems to be unquestionable, but its identity and position within this series remains unknown.

When comparing rDNA phylogenetic analyses of a larger number of species of *Orbiliomycetes* (Magyar et al. 2017b, Baral et al. 2017b), it appears that the different types of nematode traps of section *Arthrobotrys* diverged fairly late in the evolutionary history of the class, and also their first appearance within that section would have happened only a few myr earlier, judging from the fact that its basal taxa represented by the paraphyletic series *Neodactylella* are found to be invariably non-predacious. According to Yang et al. (2012a), nematodes and other major invertebrate clades were proposed to have appeared during the Cambrian Explosion 600–550 myr ago, long before the first *Orbiliomycetes* emerged 419 myr ago. Under the latter premise we conclude that section *Arthrobotrys* separated into adhesive trap and constricting ring formers after the Triassic/Jurassic mass extinction 201 myr ago, not shortly after the Permian/Triassic mass extinction 252 myr ago as suggested by Yang et al. (2012a) and Liu et al. (2014). Ahrén et al. (2004) even gave for this event 77 myr (late Cretaceous), based on analysis of SSU rDNA. The predacious genera *Lecophagus* and *Hyalorbilia* diverged distinctly earlier than section *Arthrobotrys* but perhaps also less than 250 myr ago. However, it might be disputable whether rDNA is a suitable gene region for estimating divergence times.

The striking preference of the genera *Lilapila*, *Amphosoma*, *Retiarius*, and *Mycoceros* for gymnospermous substrates (resin or pollen) could be interpreted as an ecological relict of the Carboniferous and Permian 350–250 myr ago when the first conifers appeared. In the above-mentioned phylogenetic analyses, *Lilapila* and *Mycoceros* diverged earlier than any of the invertebrate-capturing genera. Possibly, carnivorism emerged independently in three different lineages of *Orbiliomycetes* from ancestors that parasitized pollen. Liu et al. (2014) hypothesized that nematode trapping fungi originated from efficient cellulolytic fungi and lost this saprotrophic capacity to a varying degree when developing into predatory fungi, the constricting ring formers more and the adhesive trap formers less.

At the present state of knowledge, the origin of *Orbiliomycetes* could therefore be sought in the Carboniferous era. Interesting in this respect is the soil-inhabiting *Bryorbilia arenicola* which appears to be connected to a bryophyte. Considering its basal affiliation in the class, this fungus might represent an old group adapted to an ecological niche in which *Orbiliomycetes* could have emerged.

Did *Orbiliomycetes* evolve from *Taphrinomycotina*? Similarities in the truncate, bilateral-symmetrical ascus apex prompted authors to assume a relationship between *Orbilia* and *Neolecta* or *Taphrina* (see p. 54). However, further similarities are largely absent.

Neolecta was referred to the *Taphrinomycotina* on account of sequence data (Eriksson & Winka 1997), and constitutes the only genus in this subphylum which is able to form ascomata. Apart from the orbiliaceous ascus apex, *Neolecta* strongly differs from *Orbiliomycetes* in a number of characteristics such as (1) club-shaped (geoglossoid) apothecia, (2) the complete ascus wall reacting faintly hemiamyloid, (3) the absence of paraphyses, (4) curious semiglobose refractive caps ~2–4 µm diam. on both sides of the septa of tissue hyphae, being KOH-insoluble and strongly dextrinoid. The caps are unknown in any other group of ascomycetes, and were observed by Landvik et al. in *N. flavovirescens* and by the first author in *N. vitellina* (IVV: H.B. 7428). The 'plasmalemmasome-like body' at the septum of the ascus base described by Landvik et al. (2003, fig. 24) perhaps refers to the same structure. A further difference to *Orbiliomycetes* might lie in the multinucleate ascogenous hyphae of *Neolecta*.

Taphrina differs from *Orbilia* in the asci having short and thick, unbranched stalks arising from simple septa. According to Martin (1940) there is an intermediate nuclear division between the ascus mother cell containing the fusion nucleus and the young ascus in which meiosis takes place. This intermediate nuclear division results in the formation of a basal cell below the ascus stipe, which is unknown in both *Neolectomycetes* and *Orbiliomycetes*.

The truncate ascus apex of *Taphrina* and *Orbilia* p.p. lacking an endoascal thickening is reminiscent of the *Pezizomycetes*, near which *Orbiliomycetes* cluster, but *Pezizomycetes* asci are never bilateral-symmetrical (see p. 54).

In both *Neolecta* and *Taphrina* yeast-like budding from the ascospores and also from the produced conidia occurs, whereas this ability is completely absent in the *Orbiliomycetes* and *Pezizomycetes*. Polyspory of asci in the latter two classes consistently originates from multiple nuclear divisions that take place inside living asci (see p. 56). True polyspory is also observed in *Saccharomycetes*. In contrast, polyspory in *Taphrinomycetes* is artificial as it occurs only inside dead asci, or on ejected ascospores. This indicates that the asci discharge only ascospores, not conidia.

BIOLOGY AND ECOLOGY

The *Orbiliomycetes* exhibit a broad ecological amplitude that comprises subarctic to tropical vegetation types. Included are more or less humid boreal, nemoral, and evergreen forests as well as cold to hot semideserts or arctic-alpine dwarf shrubs. Many species inhabit such harsh environments as the latter, which require a high tolerance against dryness and/or extreme temperatures. The species composition that is established on a given piece of substrate at a given sampling site is determined by the macroclimate on the one hand, which includes temperature (thermotype) and precipitation (ombrotype), but also by the microclimate, i. e., exposure of the substrate to desiccation and insolation, the degree of substrate decay by other fungi, and biochemical properties of the host organism.

Orbiliaceous fungi generally grow as saprobionts on a wide range of phanerogamic, rarely cryptogamic plants. However, for various species a parasitic or endophytic phase in living tissue of plants, fungi, or animals is known. Apart from pollen invasion by orbiliaceous mycelia (Magyar et al. 2017a, b; this study p. 108, Tab. 14), some rDNA isolates of *Orbiliomycetes* have been reported recently from living and necrotic pine needles, either surface sterilized (Bowman & Arnold 2018) or not (Lazarević & Menkis 2020, Lynikienė et al. 2020). Mycorrhizal associations did not come to our notice, but isolates from partly surface sterilized roots were reported for some orbiliaceous clones in GenBank, e.g., for the grass *Bouteloua* by Herrera et al. (2010, GenBank GQ924028). Some saprobic or parasitic *Orbiliomycetes* are known to be fungicolous and, last not least, many species of *Orbilia* section *Arthrobotrys* trap living invertebrates as additional, and several species of *Lecophagus* as more or less exclusive food source.

Reversely, apothecia of *Orbiliomycetes* serve as nutrient source for invertebrates, but also provide a niche for some parasitic fungi, including two *Hyalorbilia* spp. that grow on apothecia of *Orbilia* spp. The role that the ascospores and conidia play in the colonization of new substrate is little understood. They are transported by wind, water, and animals, but the circumstances where they germinate under natural condition is unknown, as is the biological function of the spore body in the ascospores.

Substrate specificity

A large number of substrates on which *Orbiliomycetes*, mainly teleomorphs, were found are reported in this monograph (see Appendix 1). They comprise various kinds of woody and herbaceous land plants, though apparently never annual herbs, exceptionally also ferns (*Polypodiopsida*) and bryophytes (*Marchantiophyta* and *Bryophyta*). A wide range of fungal substrates is observed, including aphyllophoralean or tremellalean *Basidiomycota* and pyrenocarpous or discocarpous *Ascomycota*. An overview of the plant orders and families known as hosts of *Orbiliomycetes* is shown in Tab. 30.

Particularly because of the frequent neglect of semiarid to arid regions by mycological expeditions, a lot of plant taxa are reported here for the first time as substrate of *Orbiliomycetes*. For instance, the North American *Juniperus osteosperma*, a widespread shrub in the Rocky Mountains and Colorado Plateau, was found to carry at least 14 species of *Orbilia* and 8 further non-lichenized ascomycetes, but in the fungus-host database of the United States Department of Agriculture (Farr & Rossman 2006) it is only mentioned as host of basidiomycetes. This applies also to a lot of other plants which are adapted to regions of comparatively low annual precipitation. For instance, also for *Quercus gambelii* (8 *Orbilia* spp.), *Larrea tridentata* (21 *Orbilia* spp.), and *Carnegiea gigantea* (3 *Orbilia* spp.) no discomycetes are listed in this database.

The great majority of *Orbiliomycetes* with at least about 4–8 known collections are plurivorous species growing on various phylogenetically distant hosts. Many of them can be expected to occur on all kinds of either woody or herbaceous plants that grow within a given climate region. They were often recorded on both angio- and gymnosperms, and some even on both woody and herbaceous, or even fungal substrates and dung (see Tab. 31). This results in the common experience that the list of recorded host plants increases with the collecting activities. Instead of a substrate specificity, these species merely exhibit a more or less significant climatic preference. As a result, different ecoregions are characterized by different species compositions. The substrate index given in this study is, therefore, to be considered as tentative and accidental to a certain degree, and the host spectrum known at present can only be considered as more or less final for a comparatively small minority of host-specific taxa.

Many species of *Orbilia* and also *Hyalorbilia* were named according to a host genus or sometimes a host species, and some of the names might have been given in the assumption of a certain host specificity. However, too much taxonomic weight has often been put on the inhabited substrate. Based on later research, most of these species turned out to be plurivorous by showing no limits to a host genus or family, thus having a much wider ecological amplitude than previously believed. For instance, *Orbilia euonymi* was for a long time only known from the type specimen. In the present study this species was observed on a total of 43 different genera of woody gymno- (14) and angiosperms (29), but was never recollected on *Euonymus europaeus*. On the other hand, 9 further species of *Orbiliomycetes* are reported for this host plant here. Similarly, *O. ebuli* was described from herbaceous stems of *Sambucus ebulus*, and *O. vitalbae* from bark of *Clematis vitalba*. However, they occur in fact on a wide variety of substrates (*O. ebuli*: 5 plant genera, including petioles of *Acer*; *O. vitalbae* s.l.: 24 plant genera, including woody angiosperm and herbaceous mono- and dicot substrate). Reversely, *Sambucus ebulus* and *Clematis vitalba* were found to carry at least 9 and 24 orbiliaceous species, respectively. Mainly because of the difficulty to contrive appropriate names for new species, we also followed this tradition in naming many of them after the substrate, although evidence for a host specificity was lacking (see Etymology/taxa concepts, p. 19–20).

In some cases, very closely related *Orbilia* spp. inhabit more or less closely related host plants. This is mainly observed in taxa restricted to conifers, but also, for instance, in *O. comma* and *O. neocomma* (see below). Frequently, however, more or less host-specific sibling taxa occur on very distant hosts, e.g., *O. spermoides* on bark (rarely wood) of different conifers and the very similar *O. occulta* and *O. austroocculta* on angiosperm bark (rarely wood). Likewise, the strictly conifericolous *O. sphaerospora*, here reported from 11 collections on wood (rarely bark) of different conifers is a sibling taxon of *O. subsphaerospora*, which is so far known from 16 samples on wood and bark of various angiosperm hosts. Difficult to understand is the pronounced restriction of *Orbilia carpoboloides* and *O. aurantiorubra* to the same three rather distant host families (*Ulmaceae*, *Salicaceae*, *Fabaceae*, see below).

Can fungal species richness be estimated from species richness of host plants? According to Hawksworth (1997), 'we know perhaps as few as 5% of the fungi on the planet'. This hypothesis of species richness of fungi was based on the observation that plants have on average 5–6 fungal species more or less confined to them, and results in a total number of 1,500,000 species worldwide. Others estimate up to 5,000,000 or 12,000,000 fungal species, although only around 100,000 are described and accepted (see Dayarathne et al. 2016, Wu et al. 2019). Hawksworth enumerated some unexpected habitats serving as 'untapped sources of novel fungi', like marine fungi or those growing on insects in the tropics. However, no mention is made of arid regions and air-exposed, xeric substrates, their fungi being highly underrepresented in most taxonomic and floristic treatments.

In our experience, Hawksworth's theory appears inapplicable to every climatic zone. In tropical rainforests which are known to harbour the richest species diversity in higher plants, we have so far recognized a comparatively low number of *Orbiliomycetes*, perhaps due to a paucity of collections. Available samples, particularly from southern China, northeastern Australia, and Antilles comprised predominantly hygrobiotic taxa collected, sometimes also xerobiotic ones collected either on the ground or in 1–2 m above the ground. As a possibility, dead branches in the rainforest canopy provide an important, so far completely unexplored niche of *Orbiliomycetes*.

We are also in doubt about Hawksworth's method of estimating species numbers, because many members of ascomycetes inhabit a considerably wide range of hosts, and some are not even restricted to woody versus herbaceous, or gymno- versus angiosperm substrates. This contradicts a current believe in a narrow ecological adaptation of a taxon at a time when only a few collections are available. Various new species appear to have been described mainly because they occurred on

Table 30. Total numbers of records and accepted species of *Orbiliomycetes* observed on the different lineages of plant taxa, based on data of the taxonomic part and host list (Appendix 1). Species numbers include also the mentioned undescribed taxa with or without a provisional name. Uncertain identifications of plants or *Orbiliomycetes* are counted as if certain. High record and species numbers in this table are to be considered as approximate.

Host genus or higher entity	Records	Species
BRYOPHYTA (*Ceratodon*, *Frullania*, *Hypnum*, *Radula*)	4	4
POLYPODIOPSIDA (*Angiopteris*, *Equisetum*)	2	2
GYMNOSPERMS	723	147
Pinales	683	139
Pinaceae (*Abies*, *Cedrus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*)	622	115
Cupressaceae (*Cupressus*, *Cryptomeria*, *Juniperus*, *Sequoiadendron*, *Taxodium*, *Thuja*)	80	49
Taxaceae (*Taxus*)	8	7
Araucariales (*Araucaria*, *Podocarpus*)	2	2
Cycadidae (*Macrozamia*)	3	3
Ginkgoidae (*Ginkgo*)	1	1
Gnetidae (*Ephedra*)	7	7
ANGIOSPERMS	5832	462
MONOCOTYLEDONS	222	85
Alismatales (*Elodea*, *Epipremnum*, *Aroideae*)	3	3
Asparagales, ***Pandanales*** (*Agave*, *Asparagus*, *Iris*, *Pandanus*, *Vanilla*, *Xanthorrhoea*, *Yucca*)	52	24
Arecales (*Calamus*, *Cocos*, *Licuala*, *Livistona*, *Oenocarpus*, *Phoenix*)	28	23
Commelinales (*Anigozanthos*)	4	3
Poales (*Ammophila, Arundo, Bambusa, Phragmites, Scirpus*, *Typha*, *Yushania*, ...)	137	44
DICOTYLEDONS	5610	437
Magnoliidae (*Apollonias*, *Laurus*, *Liriodendron*, *Magnolia*, *Ocotea*)	42	14
Buxales	9	5
Proteales	46	23
Proteaceae (*Adenanthos*, *Banksia*, *Brabejum*, *Hakea*)	28	14
Platanaceae (*Platanus*)	18	10
Ranunculales	91	39
Berberidaceae (*Berberis*, *Mahonia*)	17	14
Ranunculaceae (*Clematis*, *Helleborus*, *Ranunculus*, *Thalictrum*)	74	30
Dilleniales (*Hibbertia*)	1	1
Saxifragales (*Aeonium*, *Liquidambar, Ribes*)	16	14
Vitales (*Vitis*)	12	9
Celastrales (*Canotia*, *Euonymus*)	19	15
Fabales	720	174
Mimosoideae (*Acacia*, *Albizia*, *Inga*, *Prosopis*, *Vachellia*)	211	94
Caesalpinioideae (*Ceratonia*, *Gleditsia*, *Parkinsonia*), *Cercidoideae* (*Cercis*), *Detarioideae* (*Hymenaea*)	67	36
Faboideae (*Chamaecyparis*, *Cytisus*, *Dalbergia*, *Genista*, *Jacksonia*, *Melilotus*, *Olneya*, *Robinia*, *Spartium*, *Ulex*, ...)	442	90
Fagales	1429	151
Betulaceae (*Alnus*, *Betula*, *Carpinus*, *Corylus*)	448	65
Casuarinaceae (*Allocasuarina*, *Casuarina*)	16	15
Fagaceae (*Fagus*, *Quercus*, *Castanea*, *Castanopsis*)	909	115
Juglandaceae (*Juglans, Carya*)	38	21
Myricaceae (*Myrica*)	14	5
Nothofagaceae (*Nothofagus*)	5	1
Malpighiales	925	121
Achariaceae (*Xylotheca*), *Passifloraceae* (*Passiflora*)	6	4
Euphorbiaceae (*Euphorbia*, *Hevea*)	96	24
Salicaceae (*Populus*, *Salix*)	825	101
Rosales	900	138
Cannabaceae (*Humulus*), *Urticaceae* (*Cecropia*, *Urtica*)	12	8
Moraceae (*Ficus*, *Morus*, *Broussonetia*)	34	20
Ulmaceae (*Ulmus*, *Zelkova*)	283	46
Rosaceae (*Amelanchier*, *Cercocarpus*, *Crataegus*, *Malus*, *Prunus*, *Purshia*, *Rosa*, *Rubus*, ...)	510	104
Elaeagnaceae (*Elaeagnus*, *Hippophae*, *Shepherdia*)	10	10
Rhamnaceae (*Frangula*, *Rhamnus*)	52	26
Oxalidales (*Weinmannia*)	2	2
Zygophyllales (*Larrea*)	39	21
Brassicales (*Koeberlinia*)	3	3
Crossosomatales (*Glossopetalon*)	4	4
Malvales (*Adansonia*, *Abutilon*, *Brachychiton*, *Cistus, Daphne*, *Hibiscus*, *Tilia*, ...)	154	57
Sapindales	182	82
Anacardiaceae (*Cotinus, Mangifera, Pistacia, Rhus*)	22	17
Meliaceae (*Swietenia*), *Simaroubaceae* (*Ailanthus*)	2	2
Rutaceae (*Citrus, Geijera*)	7	7
Sapindaceae (*Acer*, *Aesculus*, *Dodonaea*, *Koelreuteria*)	151	67
Myrtales (*Epilobium*, *Eremaea*, *Eucalyptus*, *Lamarchea*, *Melaleuca*, *Myrtus*, ...)	132	79
Caryophyllales	101	56
Sarcobataceae (*Sarcobatus*)	15	8
Cactaceae (*Carnegiea, Cylindropuntia*, *Myrtillocactus*, *Opuntia*, *Stenocereus*, ...)	16	11
Amaranthaceae (*Atriplex*, *Beta*, *Krascheninnikovia*, *Suaeda*, ...)	43	31
Caryophyllaceae (*Saponaria*)	1	1
Polygonaceae (*Polygonum*, *Reynoutria*, *Rumex*)	17	11
Tamaricaceae (*Tamarix*)	9	5
Santalales (*Nuytsia*)	4	4
Cornales (*Cornus*, *Hydrangea*)	92	29
Ericales (*Barringtonia*, *Arbutus*, *Arctostaphylos*, *Erica*, *Fouquieria*, *Impatiens*, *Rhododendron*, ...)	73	33
Gentianales (*Nerium*, *Periploca*, *Psydrax*, *Rubia*, *Vincetoxicum*, ...)	23	16
Solanales (*Atropa*, *Ipomoea*, *Nicotiana*, *Solanum*, ...)	15	12
Lamiales	198	76
Boraginaceae (*Symphytum*, *Echium*, ...), *Lamiaceae* (*Lavandula*, *Rosmarinus*, ...), *Scrophulariaceae* (*Buddleja*, *Verbascum*), *Plantaginaceae* (*Digitalis*)	34	21
Bignoniaceae (*Campsis* ...), *Oleaceae* (*Fraxinus*, *Ligustrum*, *Olea*, *Picconia*, *Syringa*, ...), *Paulowniaceae* (*Paulownia*)	166	65
Apiales (*Angelica*, *Bupleurum*, *Foeniculum*, *Hedera*, *Heracleum*, *Oenanthe*, *Pittosporum*, ...)	78	29
Aquifoliales (*Ilex*)	32	18
Asterales (*Artemisia*, *Baccharis*, *Chrysothamnus*, *Ericameria*, *Solanecio*, *Solidago*, *Verreauxia*, ...)	133	58
Dipsacales (*Knautia*, *Lonicera*, *Sambucus*, *Viburnum*, ...)	119	47

an exceptional host. In fact, only a few *Orbiliomycetes* are more or less host-specific, such as *O. comma* and *O. pilifera* to *Ulmus*, *O. aradi* to *Fagus*, and *O. sarcobati* to *Sarcobatus*.

Gymnosperms comprise *Pinales* (conifers), *Ginkgoales*, *Gnetales*, and *Cycadales*. They are generally less rich in *Orbiliomycetes* compared to angiosperms. So far, about 147 orbiliaceous species were recorded on gymnosperm substrate. At least 18 of them are apparently confined to gymnosperms, while a majority also occur on angiosperms. Those *Orbiliomycetes* which seem to be restricted to gymnosperms are all xerobiotic, whereas plurivorous species are either xero- or hygrobiotic.

For the following species a restriction to coniferous substrate is very probable: *Orbilia alpigena* (14×, mainly *Picea*), *O. clavipisca* (4×, *Abies*, *Juniperus*, *Pinus*), *O. coniferarum* (7×, *Abies*, *Juniperus*, *Picea*, *Pinus*, *Pseudotsuga*), *O. crenatovinosa* (5×, mainly *Pinus*), *O. cucumispora* (5×, *Juniperus*, *Pinus*), *O. cylindrospora* (16×, *Juniperus*, *Larix*, *Picea*, *Pinus*), *O. magnifica* (5×, *Abies*, *Picea*), *O. ophiosoma* (6×, *Abies*, *Juniperus*), *O. patellarioides* (17×, mainly *Pinus*), *O. spermoides* (8×, *Cedrus*, *Pinus*, *Pseudotsuga*), *O. sphaerospora* (11×, mainly *Pinus*), *O. subvinosa* (24×, mainly *Pinus*). Except for *O. cucumispora*, *O. spermoides*, and *O. magnifica*, which strongly prefer bark, these species inhabit predominantly decorticated wood. Some other species being restricted to conifers were mainly found in close association with cankers and resin flow: *Lilapila* spp. (46 ×, *Picea*, *Pinus*), *Amphosoma resinicola* (9 ×, *Abies*, *Picea*, *Pinus*, *Pseudotsuga*), *A. atroolivaceum* (40 ×, *Larix*, *Picea*, *Pinus*), *Hyalorbilia resinae* (4 ×, *Larix*), and *Orbilia olivacea* (3 ×, *Pinus*). Their apothecia usually grew on old resin covered by a ± dense layer of black hyphomycetes in which the often dark-coloured apothecia are difficult to discern. In the small genus *Amphosoma*, three species known from the northern hemisphere are strictly conifericolous, and it was a surprise when a fourth species was detected on bark of an indet. *Fabaceae* in South Africa. Different non-orbiliaceous ascomycetes belonging to *Leotiomycetes, Dothideomycetes*, and *Lecanoromycetes* (*Sarea*) show the same restriction to blackened resin of conifers. Various further, possibly conifer-restricted *Orbiliomycetes* are only known from one or two collections (*Amphosoma macrosporum*, *Lecophagus pini*, *Hyalorbilia sibirica*, *Orbilia acuum*, *O. atrolentiformis*, *O. battenii*, *O. cupressi*, *O. dalmatica*, *O. edulis*, *O. liliputiana*, *O. macroasca*, *O. microlentiformis*, *O. osteospermae*, *O. pileosoma*, *O. ponderosae*, *O. subdelphinus*).

A few xerobiotic *Orbilia* species have been collected on members of *Cycadales*, *Gnetales*, and *Ginkgoales*, but all are plurivorous and inhabit predominantly angiosperms. Three of them were found on *Macrozamia riedlei* (*Cycadales*) in Australia (*O. eucalypti*, *O. myrioobliqua*, *O. nothovinosa*), 1 on *Ginkgo* (*O. euonymi*), and 7 on *Ephedra* (*Gnetales*, 6 of section *Habrostictis* and 1 of section *Hemiorbilia*).

Dicotyledonous angiosperms. The majority of *Orbiliomycetes* (ca. 437 species) have been collected on dicotyledonous angiosperms. Most of them are plurivorous, and many were even occasionally observed on gymnosperms or fungal substrates, rarely on dung (Tabs 30, 31). Only a few species appear to be restricted to dicots. Most of these dicot-specific taxa are more or less specific to one or a few host genera. Others are specific to woody dicots, e. g., *O. epipora* (40 ×) and *O. montigena* (16 ×).

The European *O. comma* is almost strictly confined to xeric bark of different species of *Ulmus* (*U. minor* and *U. glabra*, 65 ×), with two exceptions: *Broussonetia* (from central France) and *Robinia* (from southern France). An extra-European sibling, *O. neocomma*, was recorded once on *Ficus* (*Moraceae*) and three times on an unidentified climber. In this species pair the host families *Ulmaceae* and *Moraceae* belong with *Urticaceae* in a close relationship within the *Rosales*. Likewise, the atlantic *O. pilifera* seems to be restricted to bark (rarely wood) of *Ulmus* (36 records, one exception on ?*Populus*) in western and southern Europe. *O. aradi* was exclusively detected on bark of *Fagus* (18 ×), and *O. fraxini* on bark of *Fraxinus* (7 ×). *O. fraxini* deserves further attention to clarify its host spectrum, because two not included samples on *Populus* are possibly not conspecific.

Interestingly, these 5 host-specific taxa more or less exclusively inhabit xeric bark. Likewise, *O. aurantiorubra* and *O. carpoboloides* inhabit xeric bark and they share a preference for the very same group of host genera. *O. aurantiorubra* is frequently found on *Salix* (*Malpighiales*, 70 ×) and *Ulmus* (*Rosales*, 30 ×), but slightly shorter-spored records were mainly on woody *Fabales* (25 ×, especially *Cytisus*). *O. carpoboloides* prefers *Ulmus* (43 ×), but also occurs on different *Fabales* (17 ×), *Salix* (8 ×), and some other angiosperm genera. Similarly, *O. cercidicola* is so far only known from bark of *Fabales* (3 × *Cercis*), from which the first collections derive, and from *Ulmus* (3 ×).

The following two here described taxa suggest host specificity from their names but turned out to be plurivorous on bark and wood of various woody plants. *O. fabacearum* (section *Orbilia*) was at first believed to be restricted to *Fabaceae* (5 ×, on *Laburnum*, *Lupinus*, *Ulex*) but was later also found on *Clematis*, *Pinus*, *Quercus*, *Ulmus*, and *Salix*. *Hyalorbilia ulicicola* was mainly found on *Ulex* (21 ×), but later also on various other angiosperms, and even on *Pinus*, large polypores, and pyrenomycetes (see Tab. 31). Seemingly narrow host ranges may be due to the paucity of collections, and will be extended when records, especially from other geographic regions, become available.

Some xerobiotic species appear to be restricted to succulent plants. Host-specific to *Euphorbiaceae* appear to be, e. g., *O. pseudeuphorbiae* (23 ×), *O. pisciformis* (11 ×, mainly *E. canariensis*), *O. succulenticola* (10 ×), and *O. asomatica* (7 ×, mainly *E. canariensis*). However, these observations were so far made on a single Macaronesian island (Tenerife), and *O. succulenticola* occurred there once also on *Opuntia* (*Cactaceae*). Regarding *Cactaceae* in North America at least *O. cactacearum* (4 ×) seems to be specific.

The very different number of species recorded for each host genus suggests preferences but reflects to some extent also unbalanced collecting. Among the predominantly European substrates, worldwide 89 species were found on *Quercus*, 81 on *Salix*, 60 on *Fagus* (mainly *F. sylvatica*), 46 on *Ulmus*, 54 on *Populus*, 36 on *Ulex* (mainly *U. europaeus*), 31 on *Rosa*, 29 on *Cornus*, 28 on *Rubus*, 28 on *Cytisus* (mainly *C. scoparius*), and 26 on *Sambucus*. Among the predominantly Australian collections, worldwide 84 species were recorded on *Acacia*, 45 on *Eucalyptus*, 13 on *Vachellia*, 11 on *Melaleuca*, 11 on *Livistona* (*nitida*), and 11 on *Banksia*. In the semiarid to arid southwestern part of Northern America, 21 species were found on *Larrea* (*tridentata*), 16 on *Purshia*, 15 on *Cercocarpus*, 13 on *Ericameria* (*nauseosa*), 10 on woody *Artemisia*, 11 on *Cactaceae*, 9 on *Chrysothamnus*, 8 on *Sarcobatus* (*vermiculatus*), 6 on *Krascheninnikovia* (*lanata*), and 5 on woody *Atriplex*.

All of the more frequently collected herbicolous species have rarely or even frequently also been found on woody substrates (e. g., *O. atlantis*, *O. auricolor*, *O. caulicola*, *O. cylindrosoma*, *O. flavidorosella*, *O. cardui*, *O. quaestiformis*, *O. septispora*). Among the 5 xerobiotic species so far recorded on *Reynoutria*, one appears to be predominantly herbicolous (*O. caulicola*), 2 occur at a similar frequency on herbs and woody substrates (*O. quaestiformis*, *O. ungulata*), and 2 were otherwise nearly exclusively found on woody substrates (*O. cotoneastri* s.l., *O. gambelii*).

Monocotyledonous angiosperms. About 85 orbiliaceous species have been collected on monocots. Many of them were only once recorded, therefore, their actual ecological amplitude is unknown. Among the repeatedly encountered species only a few appear to be restricted to monocots. *O. junci* was so far only found on leaves of *Juncus roemerianus* (6 ×). *O. rectispora* on large, more or less aquatic monocots (25 ×, mainly *Typha* and *Scirpus*, also *Glyceria*, *Iris*, and *Sparganium*), but one was on hare dung which contained grass remnants. *O. graminis* and *O. septispora* were at first believed to grow predominantly on *Phragmites* (8 × and 27 ×, respectively). However, this seems to be a result of unbalanced collecting, as they were once also found on another monocot (*O. graminis* on *Ammophila*, *O. septispora* on *Typha*). In addition, *O. septispora* was 3× found on woody plants (*Juglans*, *Lonicera*, *Rosa*), and the type collection was on *Melilotus*, a herbaceous dicot.

Large monocots of the subtropics and tropics, such as palms (*Arecales*), bamboo (*Bambusoideae*), *Zingiberales* (*Elettaria*), *Asparagales* (*Agave*, *Yucca*, *Xanthorrhoea*), or *Bromeliaceae* (*Puya*), were found to carry some rather unique species but, due to the paucity of collections, nothing is known about their host specificity. For instance, the large and bright-coloured apothecia of *O. anigozanthi* grew on herbaceous stems of *Anigozanthos* (*Haemodoraceae*), but this *Orbilia* is only known from two abundant collections in the Kings Park of Perth in southwestern Australia.

Introduced hosts. The fact that many species exhibit little host specificity is illustrated by the observation that they also colonize introduced plants. For example, six species of *Orbiliomycetes* were detected on the large perennial herbs *Reynoutria japonica* and *R. sachalinensis* (*Polygonaceae*) being introduced from northeastern Asia to Europe (Host list). None of them are confined to this host genus, but all occur on various indigenous, often woody hosts and appear to have colonized *Reynoutria* from there. Likewise, woody plants introduced to Europe exclusively carry indigenous species that are more or less frequent in Europe, e.g., *Sequoiadendron giganteum* (*O. aprilis*, *O. euonymi*), *Cryptomeria japonica* (*Hyalorbilia subfusispora*, *O.* cf. *aristata*, *O. euonymi*), *Pseudotsuga menziesii* (*H. berberidis*, *H. polypori*, *O. aprilis*, *O. euonymi*, *O. rubrovacuolata*), or *Thuja plicata* (*O. aprilis*, *O. aristata*, *O. euonymi*). On the North American *Robinia pseudoacacia* no less than 25 different plurivorous and native species of *Hyalorbilia* and *Orbilia* were detected in Europe. Similarly, on two native European hosts planted in the mediterranean Kings Park in Perth (southwestern Australia), *Quercus robur* and *Arbutus andrachne*, three species otherwise only known from Australian hosts adapted to semihumid to arid regions were collected: *O. octoserpentina*, *O. curvativitalbae*, and *O. serpentina*.

It is obviously a characteristic feature of species with a very wide host range to colonize introduced plants. For instance, the frequent central European *Orbilia aristata* was found on various genera of gymno- and angiosperms, almost all of them being indigenous to that region, but a few times on genera introduced from southern Europe or North America (*Cotinus*, *Rhus*, *Robinia*, *Thuja*, *Syringa*). Likewise, *O. euonymi* was mainly found on indigenous woody plants, but also on some from southern Europe, eastern Asia, and North America (*Aesculus*, *Cryptomeria*, *Ginkgo*, *Juglans*, *Pseudotsuga*, *Robinia*, *Sequoiadendron*, *Syringa*, *Taxodium*, *Thuja*, *Tsuga*).

Table 31. Number of records of 17 frequently collected plurivorous species of *Hyalorbilia* and *Orbilia* regarding five main types of substrates.

Species	Angio-sperms	Mono-cots	Gymno-sperms	Basidio-mycetes	Asco-mycetes	Dung
Hyalorbilia inflatula	184	1	7	12	16	–
H. ulicicola	49	–	1	8	3	–
H. polypori	27	–	7	4	1	–
H. berberidis	27	–	3	11	1	–
Orbilia aristata	176		21	–	1	–
O. auricolor	107		5	–	6	6
O. carpoboloides	89	–	–	1	6	–
O. epipora	39	–	–	3		–
O. eucalypti	369	–	22	12	13	–
O. euonymi	68	–	54	2	–	–
O. leucostigma s.l.	68	–	9	–	–	–
O. oxyspora	26	1	–	–	–	4
O. trapeziformis	75	–	4	6	–	–
O. tremulae	81	–	4	3	2	–
O. vinosa	333	–	34	14	–	–
O. vitalbae	44	10	–	–	–	–
O. xanthostigma s.l.	> 300	–	51	5	1	–

Table 32. Preferences in frequently collected *Hyalorbilia* and *Orbilia* spp. to form apothecia on bark or wood, sorted after the percentage of collections on wood (numbers of collections indicated, collections in which both bark and wood were simultaneously inhabited appear in both columns). Right column: desiccation tolerance of apothecia, showing a slight preference of desiccation-tolerant species for bark.

Species	Section	Bark	Wood	% wood	Desiccation
Orbilia comma	*Aurantiorubrae*	77	0	0	tolerant
O. aradi	*Aurantiorubrae*	18	0	0	tolerant
O. pilifera	*Aurantiorubrae*	36	2	5.3	tolerant
O. phragmotricha	*Aurantiorubrae*	55	4	6.8	tolerant
O. carpoboloides	*Habrostictis*	71	6	7.8	tolerant
O. aurantiorubra	*Aurantiorubrae*	120	11	8.4	tolerant
O. subaristata	*Hemiorbilia*	48	9	15.8	tolerant
O. auricolor	*Arthrobotrys*	62	13	17.3	sensitive
O. clavuliformis	*Hemiorbilia*	37	9	19.6	tolerant
O. aristata	*Hemiorbilia*	146	40	21.5	tolerant
Hyalorbilia subfusispora		72	28	28.0	tolerant
O. myrioobliqua	*Hemiorbilia*	13	6	31.6	tolerant
Hyalorbilia juliae		61	28	31.5	tolerant
Hyalorbilia ulicicola		23	14	37.8	sensitive
O. australiensis	*Hemiorbilia*	15	10	40	tolerant
O. rubrovacuolata	*Arthrobotrys*	24	24	50.0	sensitive
O. eucalypti	*Orbilia*	180	187	51	tolerant
Hyalorbilia inflatula		95	100	51.3	sensitive
O. microserpens	*Habrostictis*	10	13	56.5	tolerant
O. ocellata	*Lentiformes*	12	22	64.7	tolerant
O. crenatomarginata	*Aurantiorubrae*	27	55	67.1	sensitive
O. vitalbae	*Habrostictis*	11	25	69.4	tolerant
O. polyspora	*Ovoideae*	10	24	70.1	tolerant
O. hesperidea	*Hemiorbilia*	10	26	72.2	tolerant
O. cejpii	*Orbilia*	10	27	72.3	(tolerant)
O. trapeziformis	*Habrostictis*	20	58	74.4	tolerant
O. lentiformis	*Lentiformes*	6	19	76	tolerant
O. tremulae	*Orbilia*	12	39	76.5	sensitive
O. sarraziniana	*Helicoon*	29	108	78.8	sensitive
O. epipora	*Orbilia*	6	34	85.0	sensitive
O. quaestiformis	*Habrostictis*	5	29	85.3	tolerant
O. vinosa	*Hemiorbilia*	49	326	86.9	tolerant
O. aprilis	*Hemiorbilia*	30	202	87.1	tolerant
O. euonymi	*Lentiformes*	16	109	87.2	tolerant
O. rosea	*Helicoon*	7	57	89.1	sensitive
O. luteorubella	*Helicoon*	2	27	93.1	sensitive
O. leucostigma	*Orbilia*	3	73	96.1	sensitive
O. xanthostigma	*Orbilia*	9	271	96.8	sensitive
O. dryadum	*Orbilia*	0	46	100	sensitive
O. ovoidea	*Ovoideae*	0	10	100	tolerant

Specificity to plant organs. Many species of *Orbiliomycetes* that occur on woody substrates are able to grow on both wood and bark, but some are more or less specific to either wood or bark (Tab. 32). Such preferences possibly avoid competition and might originate from different enzymatic abilities. As a rule, bark-inhabiting species are more often restricted to one or a few host genera in comparison with those growing on wood. However, within a given collection that includes different *Orbilia* species, it is often the case that one species is exclusively found on bark and the other on wood, although in other collections the preferences of the very same species may be different.

Whether the apothecia occur on bark or wood is not always easy to determine, unless the bark is very distinctly coloured or ± detached from the wood. When growing on bark, apothecia usually insert on bast (phloem), i. e., the inner and often much thicker layer of the bark. They may either occur on the inner surface of detached bark (Fig. 115: d) or at its broken edges, e. g., in emergence holes (Fig. 115: g–h), or they may grow on the outer bast surface at places where the covering periderm got ruptured (Fig. 115: e–f). In many genera of woody plants the periderm forms a thin paper-like layer which tends to roll outwards when it detaches from the bast (Fig. 115: c, f). When also the bast more or less disappeared by decay, its remnants are often found attached to the wood surface. Apothecia growing on such remnants are assumed to use both bark and wood as nutrient source (Fig. 115: a, c). Likewise, apothecia growing on boring dust (Fig. 115: l), might use nutrients from this mixture of wood and bark secreted by the bark beetle larvae. Apothecia may also occur on the outer or inner surface of the periderm, but often their insertion on the outer surface is only seemingly so as their stipe base inserts on the bast below by smaller or larger holes in the periderm.

Also the thickness of a branch may determine to some extent its species composition. Apothecia of xerobiotic taxa, e. g. many of sections *Lentiformes* or *Hemiorbilia*, often occurred on thin twigs of 1–5 mm diam., but also on much thicker branches, whereas others were never seen on twigs, e. g. *O. aradi* grows on 4–70 cm thick branches and trunks though always on the detaching bark that easily dries out. Hygrobiotic species were usually not found on twigs, e. g. *O. leucostigma* and *O. xanthostigma* occurred on (1–)3–35 cm thick branches, logs and stumps, and *O. epipora* on 3.5–30 cm thick branches and logs, though once in China on a 3–4 mm thin twig.

In a few collections the apothecia grew on leaves of different woody plants, and some of the involved species might be specific to them. This mainly concerns two species on coriaceous leaves of *Quercus ilex*/*Q. rotundifolia*, *O. quercus-ilicis* and *O. foliicola*, which are possibly host-specific to such leaves. *O. flagellispora* was described on leaves of *Rhus laurina*, but in the present circumscription it is a plurivorous species on bark (and wood) of gymno- and angiosperms. Two records on non-coriaceous leaves of angiosperms are known (*O.* cf. *mammillata* on lamina of *Quercus* leaves, *O. ebuli* on petiole of *Acer*) and two *Orbilia* species of unclear identity on *Dryas* leaves (*O.* cf. *angustoaristata*, *O. inconspicua*). Leaves of conifers were only rarely observed as substrate: *Liladisca acicola* and *O. acuum* might be restricted to needles (and bark) of *Pinus*, but the species are only known from their type collections. The plurivorous *O. aristata* and *O. auricolor* were exceptionally found on pine needles.

Beetle and ant galleries. Xerobiotic species of *Orbilia* are frequently found in and around galleries of bark beetles. Apothecia are formed in empty galleries, either on the wood surface (e. g., *O. patellarioides*, *O. microsoma*, *O. sphaerospora*, Fig. 115: i, m–n), or on the underside of detached pieces of bark of standing trunks (e. g., *O. aradi*, *O. pilifera* Fig. 115: d). Dead, decorticated, still-attached branches of gymno- and angiosperms rich in galleries are frequently associated with *Orbiliomycetes*. Some beetle species build galleries deep into the wood core, and the apothecia then occur inside the holes close to the surface (Fig. 115: j–k). Old galleries often contain boring dust on which apothecia may also grow (Fig. 115: d, l).

Whether there exists an interconnection between *Orbilia* and bark beetles is not clear. None of the more frequently collected species showed a constant association with such galleries. For example, in a collection of *O. pseudobrevistipitata* from the Philippines on xeric branch of unidentified angiosperm, the apothecia grew with striking consistency in small groups in galleries just below the scattered emergence holes through the slightly detached bark (Pls 453: 1d; 154: 1c, e). A similar situation was seen in a collection of *O. cejpii* on a dead standing young tree of *Sorbus aucuparia* in Germany: the apothecia occurred only on slightly detached bark below and in the emergence holes (Fig. 115: g–h). Yet, other collections of this plurivorous species did not show an association with bark beetles.

Kerrigan & Rogers (2003) isolated *Arthrobotrys oligosporus*, *A. superbus*, and *Drechslerella* (‘*Arthrobotrys*’) *brochopaga* from xeric branches of *Populus* and *Salix* in association with wood-boring beetles, although the teleomorphs of these species probably show little desiccation tolerance. We repeatedly observed ants colonizing tunnelled wood in dead stubs, where xerobiotic species of *Orbilia* grew on decorticated areas and exposed old galleries above the ant colony, therefore, it seems imaginable that also ants play a role in the life cycle of *Orbiliomycetes*.

Bryophytes, **lycopods**, **and ferns as hosts**. Within the large group of lycopods and ferns only two records of *Orbiliomycetes* came to our notice: Wu (1998) reported *Orbilia auricolor* on *Angiopteris lygodiifolia* (*Marattiidae*), and E. Rubio (pers. comm.) *O. auricolor* on *Equisetum* sp. (*Equisetidae*). Very few records were on bryophytes. Apothecia of the single known collection of *O. frullaniae* grew on leaves of *Frullania dilatata* (*Marchantiophyta*, Fig. 116: d) in western Europe, but this species is only tentatively separated from similar lignicolous species, therefore, the occurrence on a bryophyte might be accidental. Likewise, a collection from western France referred to *Pseudorbilia bipolaris* grew on ?*Hypnum* (*Bryophyta*), whereas the Chinese type collection was on coniferous wood and a sample from Norway on dung. In a similar case, the lignicolous *O. eucalypti* once grew on *Frullania* (J.P. Priou pers. comm.). The inhabited leaves of these bryophytes either showed signs of necrosis or entirely lost their green pigment.

Textile. Sixteen species of *Orbilia* were so far found growing on textile (see Appendix 1 & Fig. 116: e–h). This artificial substrate either consisted solely of plant fibres like cotton (*Gossypium*) or hemp (*Cannabis*) or was mixed with synthetics. Like natural substrates, textile requires constant or periodical moisture for fungal growth. Under xeric conditions in central Europe, textile must be subjected to rainfalls for several years in order to carry apothecia, whereas under hygric conditions less than a year might be sufficient.

Figure 115: Desiccation-tolerant *Orbilia* species growing on bast in clefts of bark or on the inner surface of bark (**a–f**), or in cavities of bark and wood caused by bark beetles or on their boring dust (**g–n**). — **a**. *O. lentiformis* (H.B. 9578a) on bast of *Abies* in transversal clefts of periderm; **b**. *O. magnifica* (H.B. 9578b), id., with *Melanohalea* on periderm; **c**. *O. obtusispora* (H.B. 8691), on decayed remnants of bast, partly on wood of *Quercus*; **d**. *O. pilifera* (H.B. 8362a), on inner surface of *Ulmus* bark, with cocoons of larvae; **e–f**. *O. carpoboloides* (H.B. 9233), on outer surface of bast of *Ulmus*; **g–h**. *O. cejpii* (H.B. 9135) in emergence hole in detached bark of *Sorbus* (**g**. outside view, **h**. from below); **i**. *O. microsoma* (H.B. 7518), growing in bark beetle galleries shaped in wood of *Pinus*; **j–k**. *O. vinosa* (19.VIII.2010), growing around emergence hole in wood of *Cornus*; **l**. *O. poitevinica* (H.B. 8131), growing on bark beetle boring dust of *Fraxinus* covered by algae; **m–n**. *O. patellarioides* (H.B. 9173a), growing in galleries shaped in wood of *Pinus*.

All species detected so far on textile are typically lignicolous or herbicolous and do not show a distinct restriction to a host genus. Plurivorous *Helotiales*, pyrenomycetes, and mitotic fungi are also able to grow on textile (e.g., *Neodasyscypha cerina* and *Patellaria atrata*, Baral ined.). Undoubtedly, many more species of *Orbilia* will be found on textile when more thoroughly investigated. Similarly as on natural xeric substrate, apothecia on xeric textile often occurred in sparse small groups only and were then difficult to detect. Ropes and twines or woven fabric of different natural fibres are famous substrates for xerobiotic species of *Orbilia*. They provided the substrate in the old type collections of *O. carpoboloides*, *O. chordicola* (named after the substrate), *O. decipiens*, and *O. brasiliensis*, which all belong to the *O. carpoboloides* aggregate. In association with *O. brasiliensis* grew also hundreds of rather large (0.5–1.5 mm), gregarious apothecia of *O. neocomma*.

Fungi (mycoparasitism). Some species of *Orbiliomycetes*, especially *Hyalorbilia*, were found to grow occasionally on perennial basidiocarps of either resupinate species or bracket-forming ones (Fig. 116: c, Tab. 31). With exception of *Orbilia cardui* these are all predominantly lignicolous species which are sometimes found on basidiocarps, either on the pores and lamellae, or more rarely on top of the pileus. For instance, *H. polypori* was named by Velenovský after the inhabited *Ganoderma lucidum* (as *Polyporus lucidus*), but he only knew this taxon from a single apothecium. In recent times the species was mainly discovered on woody substrates besides polypores (*Fomes*, *Ischnoderma*, *Phellinus*). Also the lignicolous *H. berberidis*, *H. inflatula*, *H. ulicicola*, and *O. epipora* (named after its growth on a polypore), may exceptionally occur on bracket fungi.

Species confined to basidiocarps are not known with certainty. The two collections of *H. fomentarii* were on *Fomes fomentarius*, but this here newly described species is only tentatively separated by ascospore size from long-spored populations of the lignicolous *H. juliae*, therefore, more collections and DNA-data are needed to clarify whether *H. fomentarii* is a separate species restricted to polypores. Many xerobiotic species of *Orbilia* (e.g., *O. trapeziformis, O. obtusispora, O. vinosa*, *O. eucalypti*) sometimes occurred on old, almost completely decayed fructifications of *Vuilleminia*, mainly in temperate Europe and often together with dark ascomycetes such as *Capronia*, *Deltopyxis*, and *Sclerococcum*, but a restriction to this ecological niche could not be verified in any of them.

Occurrence of *Orbiliomycetes* on ascomata or stromata of ascomycetes, mainly pyrenomycetes, was likewise occasionally observed. As with basidiomycetous hosts, a strong preference for pyrenomycetes cannot with certainty be seen in most of the species. *H. inflatula* infrequently forms some or all of its apothecia on pyrenomycetes, mainly when they are in a final stage of decay. When growing on old, very decayed stromata of erumpent pyrenomycetes or *Rhytismatales*, the apothecia seemingly break through the raised bark (e.g., *O. carpoboloides*, *O. eucalypti*). Lichenicolous collections of *Orbiliomycetes* were not encountered during the present study, with a single exception: one of the collections reported by Pfister & Liftik (1995) as *O. auricolor* and reidentified in the present study as *O. oligospora* (Pl. 955: 1) was on a black crustose thallus of an unidentified lichen (*Lecanorales*) growing on a rock.

H. erythrostigma and *H. orbiliicola* are the only known species of *Orbiliomycetes* for which an obligate connection to a fungal host is obvious. The former species forms its apothecia on or close to various living or ± senescent *Sordariomycetes*, but also *Auriculariales* and *Tremellales*, and the latter on living apothecia of different species of *Orbilia* (Fig. 116: b). Some collections here assigned to *H. erythrostigma* on bark and wood without a clear connection to a fungus might deserve separation based on deviating DNA data.

Drechsler (1938, 1943a, 1952, 1962, 1963, 1964) reported several orbiliaceous anamorphic species currently included in *Brachyphoris*, *Dactylella, Vermispora*, *Tridentaria*, and *Trinacrium*, which parasitize spores of oomycetes (mainly *Pythium*) or rarely zygomycetes (see Tabs 43, 45, 53–55, Fig. 118). The mode of invasion closely resembles that of pollen (Fig. 117). Mycoparasitism was also observed in species of section *Arthrobotrys*. Li et al. (2003) described the nematode-trapping *Monacrosporium janus* (≡ *Arthrobotrys janus*) as parasitizing sclerotia and hyphae of *Sclerotinia sclerotiorum* and other fungi in soybean fields. Hyphae of various nematode-trapping species may coil around hyphae of other fungi, such as *Rhizoctonia solani* (Rubner 1996: 21, fig. 11; Li et al. 2003). Such hyphal coiling is explained in terms of competition for nutrients rather than representing a true mycoparasitic relationship (see Park et al. 2002).

Dung and bones. About 12 species of *Orbiliomycetes* are known at present to form their apothecia on dung (Host list). None of them appear to be strictly coprophilous, although names such as *Orbilia fimicola* (= *O.* ?*oxyspora*), *O. fimicoloides* (= *O. oxyspora*), and *O. leporina* suggest such preference. Our morphological taxa concepts indicate that a few plurivorous species of *Orbilia* and *Hyalorbilia* occasionally colonize dung. Molecular results confirmed this view for *O. auricolor* s.l. (= *O. fimicola* s. Pfister 1994, see p. 1527).

In her study of coprophilous ascomycetes in Australia, Bell (2005: 19, pers. comm.) reported *Hyalorbilia inflatula* (as *O. inflatula*) and *O.* ?*tremulae* (as *O. alnea*) on marsupial dung (kangaroo and wallaby). She obtained apothecia generally only after incubation for 2–3 months. Within section *Arthrobotrys*, five species are known at present to occur on dung: *O. auricolor* s.l. (*Equus*, *Capreolus*, *Oryctolagus*, H.B. 4835, 5441, 6544, 6722), *O. leporina* (*Lepus*, type), *O. oxyspora* s.l. (*Equus*, type of *O. fimicola*; ?mouse, type of *O. fimicoloides*), *O. rectispora* (*Lepus*, H.B. 10049), and *Orbilia* sp. (*Ovis*, H.B. 8749).

Apothecia of two species, *O. auricolor* (Poland, Fig. 116: a) and *O. sarraziniana* (Germany, 24.X.2017, IVV), were found growing in abundance on bones of wild boar (*Sus scrofa*) lying on the moist forest floor, which is surprising because they usually grow on woody or herbaceous substrates.

Soil. The only known collection of *Orbilia terrestris* (see p. 1583) derives from the bottom of a gorge where apothecia grew on fine sandy soil containing a few organic particles. Whether this species may also occur on wood or other plant parts is unknown. The lignicolous *O. sarraziniana* was once collected in association of acrocarpous mosses on a sand bank of an artificial small lake, where the small population was occasionally flooded (IVV: H.B. 9728). In the soil below the apothecia some remains of rotten leaves occurred, but no wood debris which would be expected for this species. On the other hand, nematophagous and other orbiliaceous anamorphs have frequently been isolated from soil all over the world, but possibly all these species do not generally form apothecia on soil.

Figure 116: Extraordinary substrates of *Orbiliomycetes*. — **a**. *Orbilia auricolor* on a bone of wild boar (P.P. 20070827-1, phot. P. Perz); **b**. *Hyalorbilia orbiliicola* (pale cream) on apothecial margin of *Orbilia subaristata* (greyish-rose-orange), 28.III.07; **c**: *H. ulicicola*, on hymenophore of a polypore (*Ganoderma australe*, H.B. 8656); **d**. *O. frullaniae* on a liverwort (*Frullania dilatata*, H.B. 8760); **e**. *O. auricolor* on textile (H.B. 7912); **f**. *O. aristata* on a rope (H.B. 9226a); **g–h**. *O. auricolor* on a tennis ball (L.R. 02-206, phot. L. Rommelaars).

Nutrition

Degradation of plant substrate. Apothecia of *Orbiliomycetes* are usually formed on dead parts of plants being in an advanced stage of decomposition and, therefore, probably poor in nutrients. When growing on decorticated wood, a 0.1–0.5 or sometimes 1–2 mm thick outer layer is usually medium to strongly decayed while the wood beneath is quite undecayed. This is especially true for xeric wood which shows a permanently low internal water content, whereas hygric, internally moist wood tends to be more deeply decayed. The strong decay of the outermost region appears to be caused by earlier colonizers of the wood.

Only a few orbiliaceous species were found to form apothecia preferably or exclusively on undecayed substrate. For example, *Orbilia aradi* grows on the inner surface of detached bark of living or recently dead *Fagus* trunks, but rapidly disappears in an advanced stage of decay. There is no evidence that the fungus obtains its nutrients from other sources than the bark. Likewise, resinicolous *Orbiliomycetes* occur on living or recently dead wounds of conifers, but disappear when the substrate is too rotten. Whether these early colonizers have an endophytic phase inside the living plant tissue is unknown. In any case, plant parasitic *Orbiliomycetes* appear not to exist.

Basically, it is not clear which substrate component and how much of it is used for mycelial growth and apothecial production. When apothecia are found on substrates such as wood and bark, or basidiocarps, the mycelium appears to be able to degrade cellulose, lignin, or chitin, but might also gain nutrients from a biofilm of green algae and brown fungal cells, which often covers the substrate in a varying thickness, or it invades and degrades living pollen or microscopic animals which occur in the biofilm. About xeric woody substrate Sherwood (1981: 19) speculated that ‘many lignicolous discomycetes appear to scarcely alter the structure or appearance of the wood on which they grow, indeed the possibility that the wood itself is not the main source of nutrients for all cannot be excluded’. As a possible source of fixed carbon and especially nitrogen she suggested populations of algae, insect exudates and bird droppings, leachates from foliage and epiphytic lichens, and resin.

Observations of apothecia growing on decayed bones lying on the forest floor for some years suggest that orbiliaceous fungi may alternatively use animal proteins or fats. However, these might well have been decomposed before the *Orbilia* colonized the bone, and nematodes, bacteria, algae, or pollen could instead have been the main food source. One reason for the capture of invertebrates is seen in the supply of nitrogen, which is probably poorly present in strongly decayed plant substrate (see Barron 2003, Yang et al. 2012a). On the other hand, Scholler & Rubner (1994) found a very low predatory activity of *Arthrobotrys oligosporus* when grown in nitrogen-poor agar media, whereas predatory activity was high when the carbon source was in short supply.

It appears beyond doubt, however, that cellulose is used by the mycelium: for instance, various non-lichenized ascomycetes, including *Orbiliomycetes*, are able to form apothecia on decaying textile composed of natural plant fibres (Fig. 116), whereas such fungi have never been seen on completely synthetic fabric, or on rock, even if covered by a biofilm. Rubner (1996) observed a pronounced cellulolytic activity in most of the 44 strains of 28 orbiliaceous, mainly predacious species tested, most of them belonging to section *Arthrobotrys*. Yet, in the five *Drechslerella* species of that section the degradation of cellulose was less evident. A distinct lignolytic activity (decay of lignin) was only obtained in two of the 30 strains tested (*Brachyphoris oviparasitica*, *Drechslerella effusa*). Genes coding for cellulolytic enzymes have been found, e. g., in *A. oligosporus* (Yang et al. 2011) and *Drechslerella stenobrocha* (Li et al. 2014). A different result was obtained by Park et al. (2002) who observed in various orbiliaceous nematode-trapping species high protease and low ligninase, but no cellulase and chitinase activity.

Parasitism on animals (invertebrates) and pollen

Capture of invertebrates. A minority of *Orbiliomycetes* are known as predators of different microscopic animals such as nematodes, rhizopods, rotifers, and tardigrades, but also arthropods like copepods and springtails (see Tab. 16). The animals are captured by different types of trapping organs, and the predatory fungi have currently been classified into different anamorph-typified genera according to these organs (see p. 115 ff.)

Among the ca. 470 orbiliaceous species with a known teleomorph reported in this monograph, only about 30 are known to be predacious. However, for many further predacious species a teleomorph is so far unknown: Yu et al. (2014) list a total of 95 species within section *Arthrobotrys* being predacious. The absence of predacious activity in other groups might be due to the current routine tests with nematodes as prey. On the other hand, Nordbring-Hertz (1968) has shown that in *A. oligosporus* adhesive nets are also formed in the presence of living earthworms, fly-larvae, or springtails. It is, therefore, well possible that the majority of *Orbiliomycetes* are unable to catch animals by means of trapping organs. The trapping activities in the distant genus *Lecophagus* could even mean that predacious capabilities of orbiliaceous fungi developed independently by parallel evolution. Yet, a more conceivable scenario considers trapping organs as a plesiomorphic character within the class, being later abandoned in many taxa, or reawakened from a latent state (see p. 121).

Nematophagous orbiliaceous fungi seem to show little host specificity to certain genera of nematodes (Rosenzweig et al. 1985, Gray 1987, Scholler & Rubner 1999). Therefore, various nematode genera can be used to induce traps (for the isolation and cultivation of nematodes see Li et al. 2014). As an exception, *Dactylellina hertziana* exhibits a rather limited host range in trapping only one of the tested nematode species (Scholler & Rubner 1999). As a further example, the rhizopod-capturing '*Dactylella*' *passalopaga*, a possible synonym of *Hyalorbilia inflatula*, captures different genera of testaceous rhizopods (*Geococcus*, *Euglypha*, Drechsler 1936, see Fig. 105: f). *Lecophagus muscicola* and *L. longisporus* are known to capture both rotifers and tardigrades (Barron et al. 1990), and *Drechslerella bembicodes* nematodes but occasionally also rotifers (Drechsler 1937a: 487). Within the mainly nematophagous genus *Dactylellina*, Scholler et al. (1999: 96) emphasized that some species abandoned consumption of nematodes by switching to other hosts like copepods and springtails (fungi preying on springtails now assigned to *Gamsylella*)

Among the predatory nematophagous fungi, two main categories can be distinguished (Jansson 1982, Gray 1987): the net-formers (*Arthrobotrys*) with high saprotrophic ability, capturing nematodes not primarily for food but perhaps as a defense against mycophagous nematodes, and the constricting ring-, adhesive branch- and knob-formers (*Drechslerella*, *Gamsylella*, *Dactylellina*) which regularly capture nematodes as a main food source. The latter are more slow-growing but predaciously more efficient than the former. Despite this predacious ability, nematode-trapping fungi have been shown to effectively use plant material as saprobionts.

A few *Orbiliomycetes* are able to use animals as the main food source for apothecial production. An apothecium of the small-sized *Lecophagus ellipsoideus* (0.08–0.35 mm diam.) appears to obtain most of its nutrients from a single contracted rotifer body (0.13–0.2 mm diam.), the complete interior of which it replaced by broad hyphae (Pl. 45: 2e). It seems that the broad hyphae of *Lecophagus* spp. appear unsuitable for invading plant tissue. However, a clear evidence for this cannot be provided without experiments under controlled condition. The much larger invertebrates (insects, mites) captured by *Orbilia alba* correlate with the comparatively large apothecia (1–5 mm) in this species, but its anchoring hyphae are much narrower than in *Lecophagus*, though wider than in non-predacious groups of *Orbilia*.

Infection by ingestion. Although many species of *Orbilia* section *Arthrobotrys* possess trapping devices for a percutan infection of the captured animal (i.e., via the cuticle), their falcate ascospores with acute bases indicate a further possible strategy: infection by ingestion. Also in the four series *Hyalinia*, *Xanthoguttulatae*, *Aurantiorubrae*, and *Abutilones* (section *Aurantiorubrae*), in which organs of capture are unknown, the frequently helicoid and/or geniculate, apically acute ascospores suggest such a strategy. Also the spore base is here often acute and/or characteristically bent or nearly reflexed. In their shape and size such ascospores resemble falcate or helicoid conidia of certain species of *Harposporium* Lohde (teleomorph: *Podocrella* Seaver, *Clavicipitaceae*, Chaverri et al. 2005) which thrive as endoparasites in nematodes (Barron 1977: 73 ff.). This similarity prompted us to speculate that *Orbiliomycetes* might infect small invertebrates through peroral ingestion of ascospores (see p. 69 and 78). However, there is still no experimental evidence for this hypothesis. In *Harposporium* the peculiar shape of the conidia enables them to lodge in the oesophagus of the nematode and to penetrate with their acute and often reflexed and hooked ends between the muscle fibres during the process of swallowing.

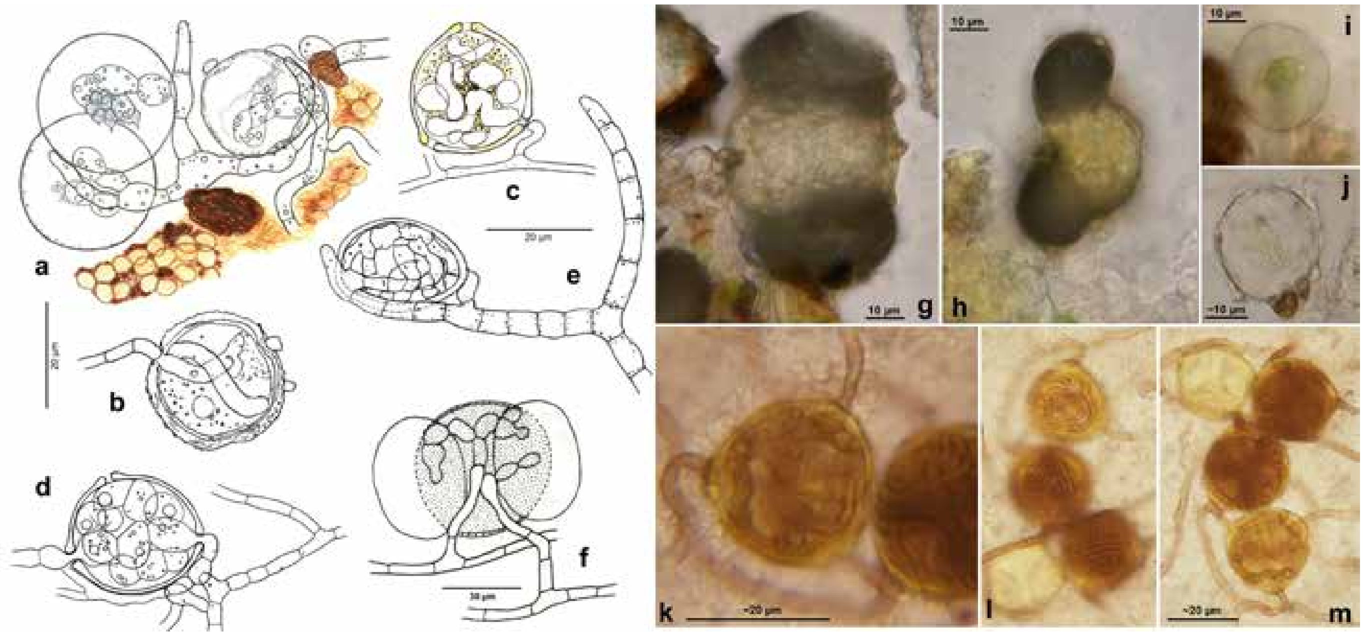


Figure 117: Parasitism on pollen grains. — **a**, **i–j**. Unidentified globose cells with very thick swollen inner wall (?pollen): **a**. invaded by mycelium, **i–j**. uninfected, **a**, **i**. close to apothecia of *O. palmicola* (H.B. 6424a), **j**. below apothecium of *O. helicovinosa* (H.B. 9050b); **b–c**. mycelium grown on water agar, invading living pollen grains: **b**. *O.* cf. *vinosa* (H.B. 6748g, pollen of *Sambucus nigra*), **c**. *O. rubrovacuolata* (H.B. 6598a, pollen of *Corylus avellana*); **d**. pollen of *Corylus* on natural substrate, invaded by *O. aristata* (H.B. 6453); **e**. ellipsoid pollen of ?*Salix* invaded by *Retiarius* cf. *bovicornutus* (11.III.2001); **f**. mycelium of *Retiarius superficiaris* invading pollen of *Pinus radiata* (from Olivier 1978); **g–h**. infected *Pinus* pollen: **g**. near *Amphosoma resinicola* (H.B. 9162e), **h**. near *O. montigena* (H.B. 7874a); **k–m**. pollen of *Corylus* added to agar culture of *Rhizodiscina lignyota* (20.V.2001). – In any of these examples the cytoplasm of the invaded host cells was always dead when the living hyphae had fully occupied it.

Up to five conidia were seen stuck in a single oesophagus. Similarly, T- to Y-shaped conidia of *Haptospora* G.L. Barron (*Hypocreales*) lodge with their hooked basal end in the mastax of rotifers (Barron 1991b).

Similar to curved ascospores, those with long and straight tails, mainly of series *Albovinosae* (section *Aurantiorubrae*) and *Hemiorbilia* (section *Hemiorbilia*), might lodge in an abruptly geniculate gullet or intestine. Also a warted spore surface might permit lodging in the narrow elastic tube of animal oesophagi during ingestion (cashew-shaped spores of the *xanthostigma-leucostigma* complex). In this context it can be speculated that spore bodies might function as some kind of poison vial (see p. 77–78). The peculiarity that ascospores of some *Orbiliomycetes* are curved or hooked, or sometimes have warts on their dorsal side, must have a functional background in the life cycle of these fungi, as it can hardly support the efficiency of spore discharge (see p. 60).

Another strategy occurs, in members of *Lecophagus* and *Hyalorbilia* (= *Brachyphoris*) which capture invertebrates in the mouth region by means of adhesive pegs or knobs. Their ellipsoid to rod-shaped ascospores appear to lack properties for lodging in the ingestion tractus. However, it is known that rotifers feed on ellipsoidal ascospores of lichens, and only some of the spores excreted by these animals are still viable (Pyatt 1968). Possibly, *Lecophagus* imitates the shape of lichen spores, but how would the fungus then be able to infect the rotifer? The function which the spore body plays in *Lecophagus* and in many other species of *Orbiliomycetes* thus remains a mystery.

Parasitism on pollen. Comparable to parasitism on fungal spores, our tests with pollen indicate, together with observations on natural substrate, that *Orbiliomycetes* may use pollen grains as food source (Fig. 117, Tab. 14). This confirms a study by Olivier (1978, see also Fig. 117: f) from South Africa on two orbiliaceous hyphomycetes growing on living leaves, where they capture wind-borne pollen grains ‘by means of short spike-shaped hyphae projecting vertically from the mycelium’, and parasitize on them. Olivier placed the two species in the new genus *Retiarius* (see Pl. 20). Magyar et al. (2017a, b) described two further species in *Retiarius* that prey on living pollen and erected the new genus *Mycoceros* for *M. antennatissimus* capturing pollen grains by means of their multibranched conidia (Pl. 18).

However, the ability to prey on pollen is not a unique feature of *Orbiliomycetes*. We found infected pollen grains also in cultures of other fungal groups, for instance, in *Rhizodiscina lignyota* (Fr.) Hafellner (*Dothideomycetes*, Fig. 117: k–m). The invasion of pollen was here very conspicuous because of the brown mycelial colour of this species. Parasitism on pollen seems to be a widespread feature. Hutchison & Barron (1997) observed this kind of nutrition mainly in basidiomycetes and considered it as a supplementary seasonal source of nutrients, particularly nitrogen. These findings are confirmed by Czeczuga & Orlowska (2001) who observed 82 species of hyphomycetes, four of which being apparently orbiliaceous, to colonize floating plant spores and pollen in stagnant and running water in Poland. Classen et al. (2000) gave an ultrastructural description of the infection of *Malva* pollen by a *Cercospora malvicola* Ellis & G. Martin (*Dothideomycetes*).

In addition to cultural studies, our field observations show that various *Orbilia* species are capable of using pollen as food source. Pollen grains launched on dead plant substrate are commonly observed on xeric branches when viewed under the dissecting microscope, most easily the large pollen of *Pinaceae* with their two air sacs (Fig. 117: f–h; Pls 264: 3c–d; 690: 2a–e). Pollen is often detected very close to apothecia of *Orbilia*, and sometimes it was found to be infected. The hyphae thereby penetrate the apertures and consume the cytoplasm by entirely colonizing the lumen of the pollen grain. It is not always clear whether the mycelium infecting the pollen belongs to the associated apothecia of *Orbilia*. Yet, the connection could often be demonstrated, not only by the close vicinity of anchoring hyphae of the apothecia, but also by the property of the hyphal surface to stain deep lilac in Cresyl blue, whereas associated mycelia of other fungal groups often remained unstained.

In two Australian samples, unidentified globose, hyaline, dead cells of ca. 22–27 µm diam., with a smooth outer and a strongly thickened (imbibed) inner wall, occur rather scattered in close proximity to apothecia of *Orbilia*. They could be pollen, oospores, or something else. In *O. palmicola* growing on petioles of *Livistona* most of these cells were found to be infected by haustoria (Fig. 117: a). The haustoria and the mycelium outside these cells were still viable when the dry sample was rehydrated 9 months after being collected. The wall surface of the emerging hyphae stains deep lilac in CRB. Particularly this feature suggests that they are anchoring hyphae of an *Orbilia*. *O. palmicola* occurs in abundance on the petioles, whereas the other associated *Orbilia* species were only rather sparsely found more remote from these cells, so we think that the haustoria-forming hyphae belong to *O. palmicola*.

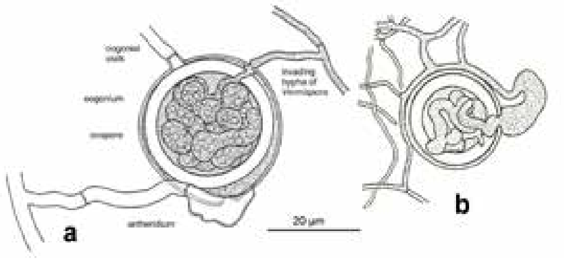


Figure 118: Parasitism on spores of oomycetes. — **a**. *Pythium oedochilum* oospore inside oogonium fertilized by antheridium, invaded by *Hyalorbilia spermatophaga* (from Drechsler 1938); **b**. oospore of *Pythium graminicola* penetrated by *Dactylella arrhenopa* (from Drechsler 1943a).

Communities with other fungi, lichens, algae, bryophytes

When collecting *Orbiliomycetes* on their natural substrate, species of other classes of fungi, besides algae and bryophytes, are often observed in more or less close association. Moreover, different orbiliaceous species frequently occur mixed on the same piece of substrate (Fig. 119). Data on such associations may help in future research to clarify the possible predominance of mycosynusia on different host plants or in different ecoregions. Due to the often intimate growth, mycelial competition can be expected to occur, either between different species of *Orbiliomycetes* or with other fungi, and symbiotic to parasitic connections, e.g. with algae, cannot be excluded.

Because of the frequency of plurivorous species, associations of fungal species on a given host are to a considerable degree accidental, and the number of species associated with a given orbiliomycete increases with the number of collections. Nevertheless, a certain correlation in the species composition on a given host is apparent, which is also determined by the climatic region. Therefore, some orbiliaceous species have considerably often been observed to grow in association with each other or with some non-orbiliaceous taxa.

A methodological problem with associations of lignicolous or herbicolous fungi is the distance between the populations, either on a given organ of the plant (branch, stem, leaf) or between different organs of the same or adjacent plants. Often, several plant parts are collected from a single plant individual, or from different individuals at the same site. If two fungal species are detected on two different branches emerging from the same tree individual, they are clearly not closely associated although they obviously prefer the same habitat, given that the branches are in a comparable exposure and state of decay. Sometimes, a third fungus grows on both of these branches, which supports the ecological similarity of the habitat. Another problem is that xeric branches were usually cut into ~10–30 cm long pieces when taken from a tree in greater quantities to facilitate transport in bags and later screening in the laboratory. During examination it is then quite impossible to say which pieces belonged to a single branch, or to determine the ends that belonged together.

A special case of association is when *Orbiliomycetes* grow as parasites or saprobionts on sporocarps of other fungi, or when parasitic fungi grow on or in apothecia of *Orbiliomycetes*. Sometimes, an orbiliomycete simultaneously forms apothecia on a fungus and also nearby on the plant substrate, which can be explained either by a low substrate specificity or by assuming that nutrient sources are not always located just below the apothecium.

Lichenized ascomycetes are very frequent companions of xerobiotic *Orbiliomycetes* on xeric woody substrates. Lichens predominantly inhabit the outer layer of bark (periderm) whereas non-lichenized ascomycetes prefer areas where the periderm or the complete bark is removed by growing on bast or wood (Fig. 115: a–b). Lichen communities start colonization of the dead outer bark layer long before the branches and trunks die off. Lichens found in association with *Orbiliomycetes* represent the remains of these communities. The occurrence of orbiliaceous taxa frequently marks the final phase of decomposition of dead xeric substrate, whereas the lichen community gradually disappears during bark decay.

Intermixed growth of orbiliaceous species. Particularly desiccation-tolerant species of *Orbiliomycetes* very often grow in mixed populations. 2–5, in rare cases even 10–15 orbiliaceous species were found on plant parts collected from one or several individuals of a given host plant at a given site. The frequent occurrence of such mixed populations is a consequence of the low host specificity of the majority of *Orbiliomycetes*. Each species thereby forms its apothecia in a more or less recognizable population. However, these populations are often very close to each other and may show a more or less strongly pronounced mosaic-like pattern (Fig. 119). Frequently, the involved species look macroscopically very similar (Fig. 119: a, c–d), which makes taxonomic work highly problematic and inevitably results in herbarium specimens containing a mixture of species (see also p. 17, Taxa concepts).

Three out of many examples illustrate the situation of species diversity within a collection. (1) About 30 petioles of a palm (*Livistona nitida*) endemic to eastern Australia (near Taroom) have been collected from 3–4 plant individuals. On these petioles 11 different species of *Orbilia* were discovered together with two other ascomycetes (*Gloniopsis* sp. and *Mellitiosporiella* sp.), all of them being preserved under the number H.B. 6424 (a–m). We assume that some further species escaped our notice and others were left uncollected at the site. (2) On branches of *Acacia* sp. collected in western Australia (near Mt. Gibson), 15 different species of *Orbilia* and 5 other ascomycetes were detected (preserved as H.B. 7204a–t). (3) On branches of

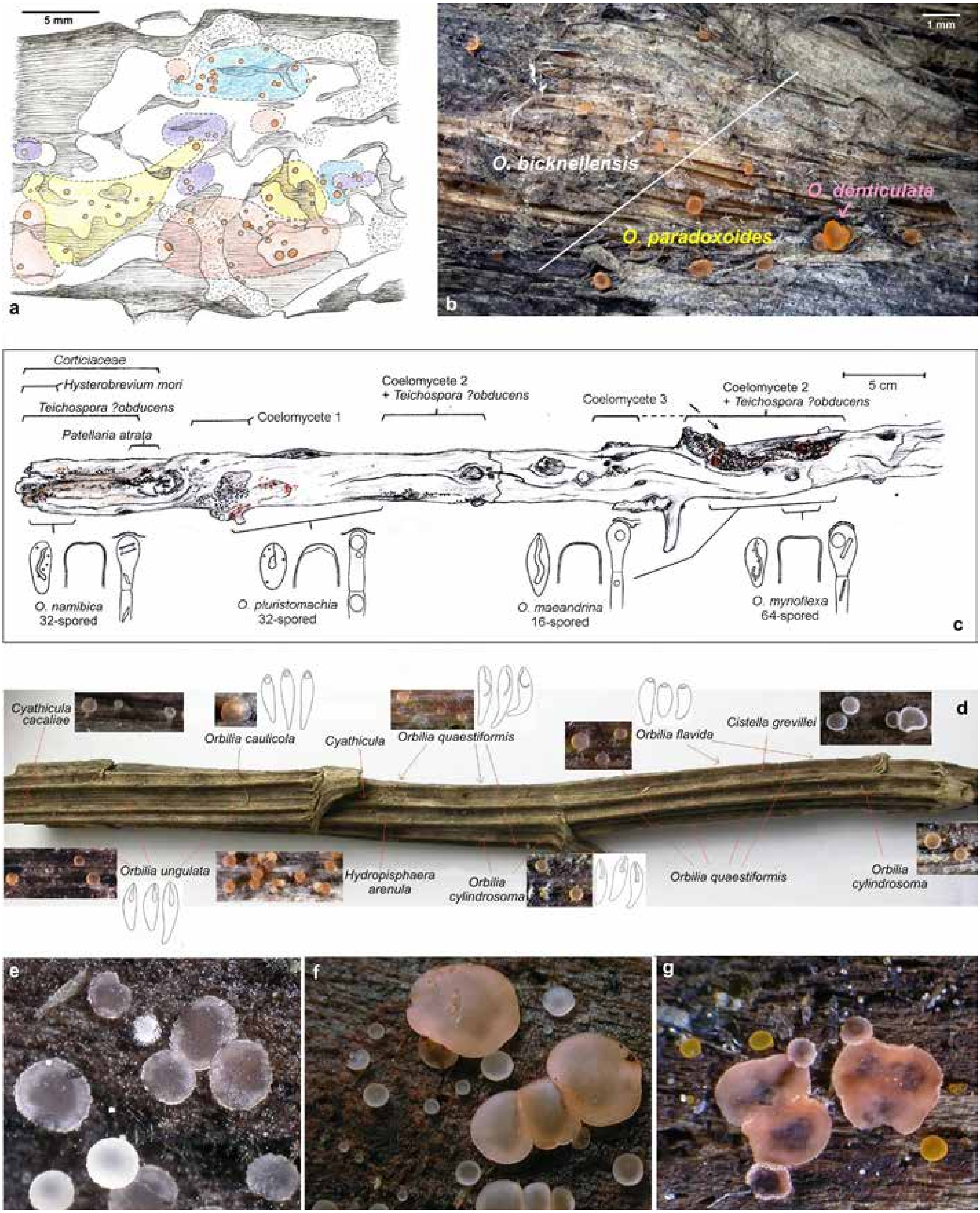


Figure 119: Intermingled growth of *Orbilia* species. — **a**. Four species growing in beetle galleries (partly filled with boring dust) of a decorticated xeric branch of *Pinus sylvestris* (yellow = *O. aprilis*, blue = *O. eucalypti*, red = *O. vinosa*, violet = *O. cylindrospora* (France, Drôme, H.B. 5626); **b**. xeric inflorescence stem of *Yucca elata* with 3 *Orbilia* spp. (Arizona, Chihuahuan Desert, H.B. 7880); **c**. decorticated xeric branch of ?*Vachellia* with 4 *Orbilia* spp. and some other fungi (Namibia, Auas Mts., H.B. 5388a–d, 5390a–c, 5398a–b); **d**. xeric stem of *Heracleum sphondylium* with five *Orbilia* spp. and 5 other ascomycetes (Luxembourg, H.B. 7869a–j, 3 spp. not shown); **e**. hygric decorticated *Carpinus betulus* branch with *O. crenatomarginata* (rosaceous-violaceous) and *O. orientalis* (white) (France, Charente-Maritime, H.B. 8146a–b); **f**. hygric decorticated angiosperm branch with *O. nemaspora* (pale rose-orange) and *O. ?brochopaga* (white) (Antilles, Martinique, H.B. 8034a–b); **g**. inner side of detached xeric *Salix* branch with *O. phragmotricha* (rose) and *O. xanthoguttulata* (yellow) (France, Savoie, H.B. 7915a–b).

Acacia cyperophylla in western Australia (Gascoyne River) 9 different species of *Orbilia* and 4 other ascomycetes were detected (preserved as H.B. 9695a–k), whereas at the same site on branches of *Eucalyptus* 5 different species of *Orbilia* occurred (preserved as H.B. 9772a–e), and only one of them (*O. pleioaustraliensis*) was found on both hosts.

In principle, every apothecium of such collections should be examined in order to avoid overlooking of a species. Since apothecia of *Orbiliomycetes* are often smaller than 0.5 mm, this would in the worst case result in a total consumption of the collection. However, small groups of apothecia looking quite homogeneous usually belong to a single species, and we recommend to examine only one out of each group. Generally about 4 to 5 microscopic spot checks on each larger piece of substrate appear to be necessary as a minimum. In other words, we found that testing 20–30 % of the apothecia of a collection consisting of couple of xeric branches is unavoidable when they occur more or less scattered over the substrate and lack characteristic macroscopic features.

In many of these interesting cases of intermingled growth, a larger proportion of apothecia was examined and the spatial distribution of the different taxa documented. Survey photographs of the populations need to be taken in advance and later cautiously marked and labelled by the resulting identifications. Preliminary spot checks are advisable in order to get a first idea of the complexity of a collection, but their spots need to be documented from the beginning.

Accidental discovery of a species plays a significant role in the study of xeric branches. When working on a given collection, the firstly examined apothecium may belong to a species that later does not show up again within this sample or turn out to occur only sporadically. As an example, the firstly examined apothecium in a collection on *Sambucus nigra* from Luxembourg was *Hyalorbilia erythrostigma* (H.B. 6908a, with subglobose ascospores), but all later tested apothecia, which superficially looked identical, turned out to be *H. rotifera* (H.B. 6908b, with fusoid ascospores). Therefore, we recommend workers to gather as many data as possible from the first preparation because, in the worst case, no further apothecium of the species in question will later be discovered.

The frequency of mixed populations is a severe problem in terms of preservation of type material, pure cultures, and molecular research. When describing a new species, the question is how many apothecia should be examined in order to recognize all occurring taxa, but without completely destroying the material? When restudying a type specimen that represents a mixed population, workers may easily doubt the correctness of the protologue. In the worst case, they overlook the presence of a mixture because the involved taxa differ mainly in vital characters, while looking virtually identical in the dead state. Reports of anamorph-teleomorph connections as well as molecular studies likewise require careful examination of the apothecium from which the isolate or extract was gained.

Associated black yeasts and other dematiaceous hyphomycetes. Light to dark brown mycelia are very frequently present among the hyaline anchoring hyphae of *Orbiliomycetes* growing on xeric substrate (Fig. 120). In median sections of apothecia they are often very conspicuous on photographs, especially if dark-coloured. Occasionally, the apothecia are more or less immersed in the brown layer, therefore, brown mycelium can be found up to the apothecial margin. Due to their intermingled growth and close contact, an interaction between the hyaline anchoring hyphae of *Orbiliomycetes* and the brown hyphae cannot be excluded.

The fungi in question are known as black yeasts, black fungi, meristematic fungi, or microcolonial fungi (= MCF) (De Hoog & Hermanides-Nijhof 1977; Butin 1991; Sterflinger et al. 1999; Selbmann et al. 2005; Sterflinger 2006; Ertz et al. 2014), and show relationships with *Dothideomycetes* but also *Eurotiomycetes* (*Herpotrichiellaceae*) or *Arthoniomycetes* (*Lichenostigmatales*). They occur on exposed, initially undecayed wood and bark, and on rock or other mineral substrate, where they form a thin surface layer, called 'biofilm'. Their presence indicates that the substrate was periodically desiccated and rehydrated, i. e., subjected to periodical rainfalls and direct insolation (ultraviolet radiation) over a period of a few years, during which these fungi provoke a distinct greyish to blackish stain to the substrate surface. Their hyphae grow only in the decayed outermost layer of plant substrate (< 1 mm deep), and here inside the lumina of the empty plant cells. Greying is also observed on exposed dead stems of perennial herbs and on dead attached coriaceous leaves. Also the black mould on coniferous resin is caused by dark brown mycelia of dematiaceous hyphomycetes.

The brown mycelia frequently form moniliform chains of rounded, smooth or sometimes encrusted cells of varying size, but cylindrical hyphae and cell aggregates also occur. Butin (1991) has shown by culture studies that at least 12 different species belonging to 11 genera occur on coniferous wood at altitudes of 1000–2000 m in the Alps, the most frequent being *Phaeosclera dematioides* Sigler et al. (*Dothideomycetes*). In pure culture the different species showed clear morphological characteristics, but when growing on natural substrate they formed very similar, scarcely differentiated structures. Within the tracheids they form a more hyphoid mycelium but above the wood surface more isolated, spherical, encrusted yeast-like cells which probably serve as dispersal elements.

Very similar black yeasts occur on stones (lithobiotic, saxicolous) and survive under the harsh conditions of long-lasting insolation and dryness, but without significant organic admixtures (Sterflinger et al. 1999, Sterflinger 2006). Repeated trials to detect apothecia of *Orbilia* on such blackened mineral substrate were unsuccessful. However, in rare cases apothecia were collected on bare soil (see p. 142), and DNA of a *Lecophagus* sp. was extracted from the microbial biofilm covering sandstone (GenBank FJ028718).

Black yeasts and other dematiaceous hyphomycetes usually grow in more or less intimate association with green algae (Fig. 120). Sometimes they form hollow spheres that include algae, so-called goniocysts. Apparently due to a higher desiccation tolerance, black yeasts also occur in arid regions where free-living algae are usually unable to survive. As with the associated algae (see below), we never observed haustoria of hyaline anchoring hyphae in these brown cells. Possibly, the brown hyphae protect the hyaline *Orbilia* mycelium to a certain degree from ultraviolet radiation.

On hygric substrates with constantly high local atmospheric humidity, black yeasts are replaced by dematiaceous hyphomycetes that produce dark brown, projecting setae or synnemata with terminal conidiogenesis. They belong to genera such as *Brachysporium*, *Haplographium*, *Cacumisporium*, *Graphium* etc., and are often found in association with desiccation-sensitive species of *Orbilia*.

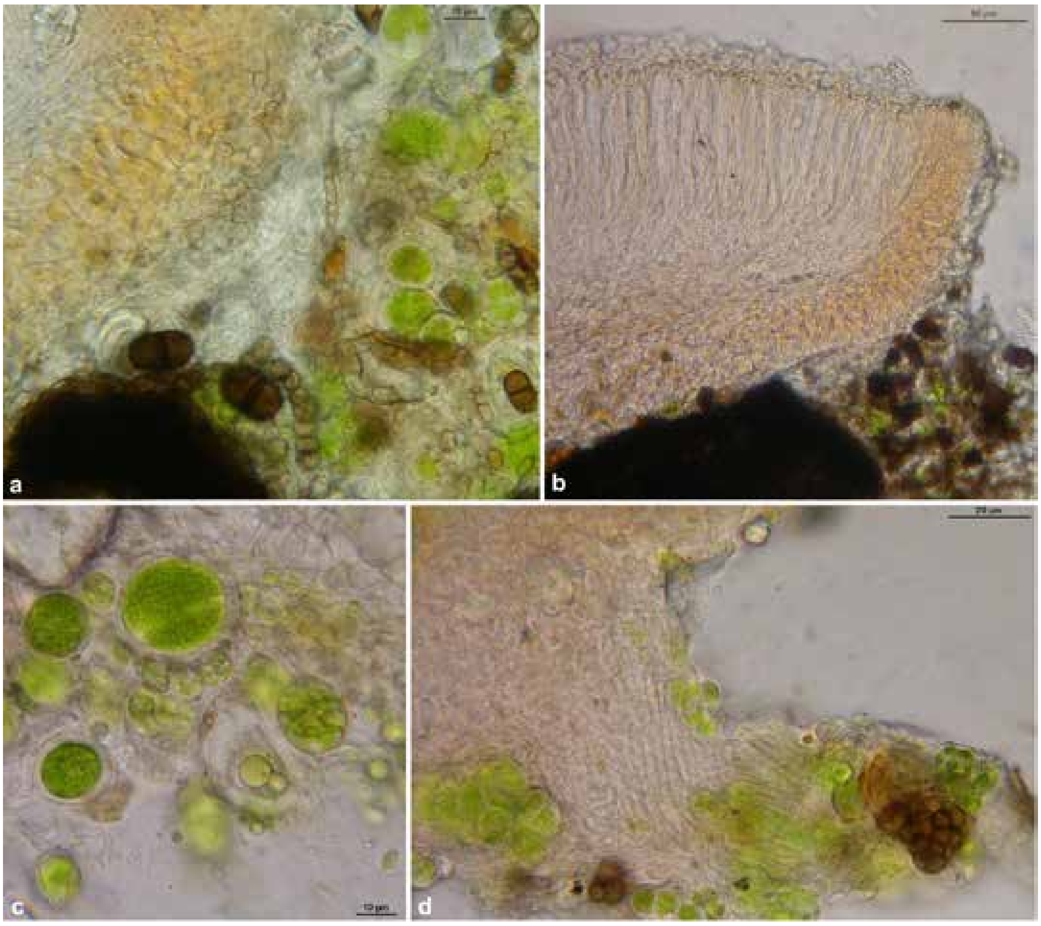


Figure 120: Median sections of apothecia formed on a biofilm composed of hyaline anchoring hyphae, coccoid green algae, brown cells of black yeasts forming chains or aggregates, brown conidia of *Diplodia*, and dark unidentified sporocarps. Note absence of brown cells on hygric substrate in **c**. — **a–b**. *Orbilia cercidicola* on xeric bark of *Cercis* (H.B. 9151e); **c**. *O. rosea* on hygric wood of *Quercus* (H.B. 9356); **d**. *O. clavuliformis* on xeric bark of *Malus* (H.B. 8212).

Associated algae. Biofilms on xeric, weather-exposed woody or herbaceous substrates often include a mixture of black yeasts and aerophytic algae, mainly *Chlorophyta* (Fig. 120), causing a characteristic, in external view greyish-olivaceous colour. Such a biofilm often covers large areas of a decorticated branch, while apothecia of *Orbiliomycetes* often occur only sparsely or in local groups on it. Also hygric branches and logs in not too shaded position are often covered by a thin to thick algal layer which may be inhabited by hygrobiotic *Orbiliomycetes* and usually lacks black yeasts. Here both coccoid and filamentous green or sometimes blue-green algae (*Cyanobacteria*) occur. If the substrate experienced occasional flooding, diatoms were also observed.

Aerophytic algae have mostly globose or ellipsoid cells which occur either singly or in small aggregates. Some are ensheathed by a thick gel layer. Others form multicellular filamentous elements. Characteristic genera are *Chlorella* (single globose cells), *Coccomyxa* (single ellipsoid cells), *Desmococcus* (aggregates of globose cells), and *Gloeocapsa* (aggregates in gel sheath). Algae with single ellipsoid cells have sometimes been misinterpreted by authors as ascospores of *Orbilia*.

The algae need a minimum intensity of light, but also a minimum amount of annual precipitation. Green algae are more or less absent in arid climates as well as on substrate lying on very shaded ground, and are sparse on those parts which are not easily wetted by rain. Algae were also not seen on substrate from tropical regions, even if collected at exposed position in open vegetation. For instance, algae could not or only very sparsely be observed in tropical northeastern Australia on standing dead stems of *Phragmites* (H.B. 8501) and *Bambusa* (H.B. 8497).

Because of the frequent presence of algae, *Orbiliomycetes* have sometimes been thought to be lichenized (Velenovský 1947: 102, *O. microclava*; Benny et al. 1978, *O. sarraziniana*). Also Haines & Egger (1982) observed algal cells in the basal apothecial tissue of several not further quoted species of *Orbilia*, but did not find any algae in their xerobiotic *O. piloboloides* (= *O. carpoboloides*), and also Kumar et al. (2012) did not observe presence of algae in *O. tenuispora*.

In our study, *O. carpoboloides* grew in some collections among abundant algal cells, while in others more or less completely without them. Quite a few species studied in this monograph were found to lack an association with algae, because they grew under extreme conditions of water supply, either in very arid or very humid habitats. Branches from arid deserts were often almost in total devoid of any algal cells, nevertheless a large number of *Orbilia* species occurred on them. On the other hand, areas with very thick layers of aerophytic algae in temperate climates are often devoid of *Orbilia* apothecia. Xerobiotic discomycetes from other relationships, such as *Durella connivens*, *Mollisia ligni*, or *Patellaria atrata*, may likewise form their apothecia in close association with abundant algae, therefore, they could as well be considered as optional lichens, but more probably they all simply share their habitat with aerophytic algae.

With the TEM, Benny et al. (1978: fig.s 21–23) observed haustoria in cells of a blue-green alga of the order *Chroococcales*. The haustoria were said to have emerged from the anchoring hyphae of *Orbilia sarraziniana* (as *O. luteorubella*). The observed alga was tentatively referred to the genus *Anacystis*, and the authors stressed the fact that a similar phycobiont is known from the lichen genus *Gonohymenia* (*Lichinales*). Besides the observation of a similar alga associated with another *Orbilia* identified as ‘probably *O. pulviscula* (Cooke) Seaver’, the authors saw some indication ‘that many, if not all, species of *Orbilia* are lichenized’.

Based on this report, an at least occasional connection of some species to algae has been considered in some books (Cannon et al. 1985, Hawksworth et al. 1996). Müller (1998) reported haustorial cells in *O. vinosa* and identified them based on their thick wall and included ellipsoidal bodies. However, his observation remains unclear as he did not observe fungal hyphae in contact with algal cells.

We have been so far unable to see haustoria with the LM in these and any other species of *Orbiliomycetes*. Pfister (1994) doubted the interpretation of Benny et al.'s TEM micrographs as penetration of an algal cell. There seems to be also an error in the scale of Benny et al.'s fig. 19, giving much wider anchoring hyphae than the treated species actually has (see under *O. sarraziniana*, p. 980).

In conclusion, we see no clear evidence for a lichenization of any of the many studied members of *Orbiliomycetes*. We confirm that most species may occasionally have at least some algal cells among their anchoring hyphae, but obviously none has evolved to a level comparable to lichens. We cannot, however, explain Benny et al.'s findings with the TEM. The mycelia obtained from ascospores of *Orbiliomycetes* are able to grow well on agar media, and they generally produce an anamorph and sometimes apothecia in pure culture without the presence of algae. The absence of *Orbiliomycetes* on purely mineral substrate supports the hypothesis that they are generally unable to obtain all their carbohydrates in symbiosis with algae as lichens do. Nevertheless, under the frequent natural condition of a rather final stage of substrate decay, it seems imaginable that *Orbiliomycetes* utilize some fixed carbon from the algae. In a much more obvious way they use pollen grains and invertebrates as a source of carbon and nitrogen (see p. 143 ff.).

Sherwood & Coppins (1980) drew attention to the apparent frequency of casual associations between lignicolous discomycetes and algae on weathered, scarcely decayed wood. The associated discomycetes thereby do not form a definite lichen thallus. The authors termed these associations 'potentially biotrophic', considering the possibility that the fungus obtains some of the fixed carbon from the algae if the fungal hyphae and algae come in contact. Wedin et al. (2004) observed optional lichenization in several species: a given species was currently placed in *Stictis* when the apothecia were non-lichenized, but in *Conotrema* when they were associated with a lichen thallus. Wedin et al.'s DNA-based study showed that such a species may have different nutritional modes: the fungus may start as a pure saprobiont on dead decorticated branches, but when the trunks become thicker it changes to a lichenized lifestyle on bark of the living trunks.

Associated mosses and liverworts. Various groups of bryophytes were noted as growing in close or remote association with *Orbiliomycetes* in the present study, and in very few cases the apothecia even grew on them (see p. 140). In central Europe, genera such as *Orthotrichum*, *Frullania*, or *Metzgeria* were often observed on xeric branches and trunks, mainly on bark, whereas on hygric wood or polypores the typical companions of *Orbiliomycetes* are genera such as *Hypnum* and *Lophocolea*.

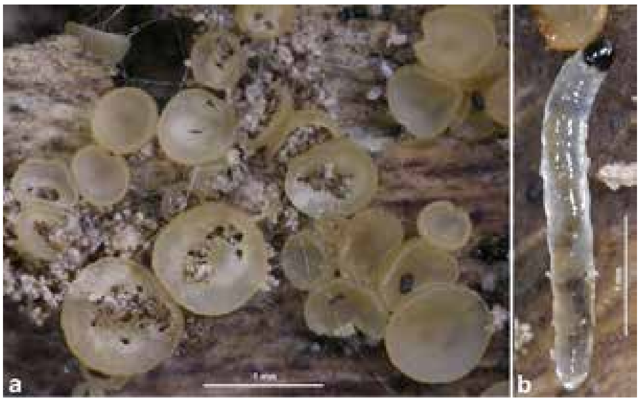


Figure 121: *Hyalorbilia inflatula* (H.B. 9041), apothecia (**a**) consumed by the fly larva in **b**.

Orbiliomycetes as a food source

Invertebrates that feed on apothecia. *Orbiliomycetes* are used as food source by various groups of invertebrate animals. On hygric substrates complete populations are consumed by snails and slugs. Also *Helotiales* are a preferred food source, whereas pyrenomycetes are protected by their thick-walled, often carbonaceous ascomata. Discomycetes on xeric substrate may be grazed especially by snails when the fungi are rehydrated during moist periods.

Among insects, damage to apothecia of *Orbiliomycetes* was noted by springtails, mites, millipedes, centipedes, and fly larvae. Such invertebrates consume apothecia even during dry periods and, therefore, also in the herbarium. In a moist chamber with *Hyalorbilia inflatula* a fly larva was observed eating cavities by starting at the apothecial base (Fig. 121).

Nematophagous *Orbiliomycetes* are thought to form trapping devices as a defense against nematodes which are adapted to fungal hyphae as food source (see p. 144–145). On the other hand, the consumption of apothecia by invertebrates might play a role in spore dispersal (endozoochory).

Fungal parasites of *Orbiliomycetes*. In 41 out of ~7200 here reported records of *Orbiliomycetes* the phenomenon of intrahymenial parasitism by the genus *Helicogonium* was observed (Figs 122–123). 35 of them were from European collections, three from North America, and three from China. In most cases the parasite was *H. orbiliarum* Baral & G. Marson. Members of *Helicogonium* produce only ascogenous hyphae and asci, rarely also phialidic anamorphs (Baral 1999). The asci are formed between the paraphyses and asci of their host species by suppressing more or less thoroughly the formation of host asci. Since the parasite often occupies the entire hymenium of the host, this kind of parasitism is easily misinterpreted as a single organism. However, if only some of the host asci are suppressed, two different types of asci occur intermingled (Figs 122: g; 123: a). Usually the wider and more projecting asci are those which belong to the parasite. Problematic is that asci of *Helicogonium* are always inamyloid like those of *Orbiliomycetes*, therefore, recognition of the parasitic relationship is easier with helotialean hosts which often have amyloid asci.

Three species of *Helicogonium* are so far known to occur in *Orbilia*: *H. orbiliarum* (from Europe, North America, China, Baral 1999: 47, Figs 122: a–e; 123), *H. hyphodisci* Baral & G. Marson (from China, Fig. 122: f), and *H. fusisporum* Baral & Kutorga (from Lithuania, Baral & Kutorga 2010, Fig. 122: g). A fourth could not be identified (from China, IVV: jgs-21). The eight ascospores of *H. orbiliarum* are globose to broadly ovoid and contain a few rather small LBs. They produce smaller ellipsoid ascoconidia which aggregate in clusters around the ascospores in the mature living asci prior to ejection and can easily be misinterpreted as warted ascospores (Fig. 122: b–c). In dead asci in which spore ejection was unsuccessful, the clusters got disintegrated (Fig. 122: e–f). The ascospores of *H. hyphodisci* are more elongate ellipsoid-clavate and produce allantoid (cashew-shaped) ascoconidia (Fig. 122: f). The unidentified species has elongate septate ascospores with two

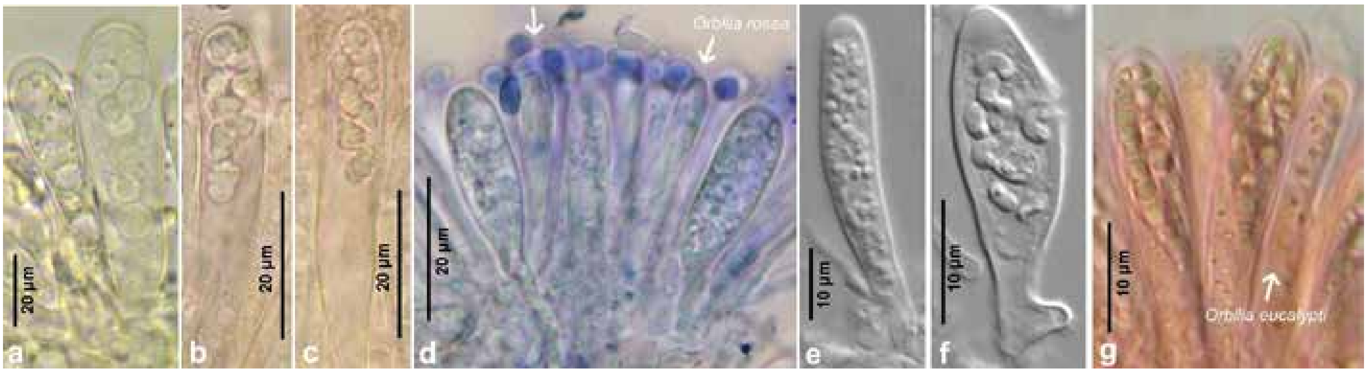


Figure 122. *Helicogonium* parasitic in hymenia of *Orbilia* spp. — **a–e**. *H. orbiliarum*, **a**. immature asci with eight subglobose ascospores (left ascus dead), **b–c**. mature living asci with dense clusters of small ellipsoid ascoconidia around ascospore, **d**. two immature living asci together with asci and paraphyses of *O. rosea* (in CRB), **e**. mature dead ascus with ascoconidia (ascospores almost invisible); **f**. *H. hyphodisci*, dead ascus with globose ascospores and allantoid ascoconidia; **g**. *H. fusisporum*, two mature asci and a host ascus of *O. eucalypti* (in KOH+CR). – **a**. P.P. 20080713-007-1 (phot. P. Perz), **b–c**. H.B. 8615a, **d**. E.R.D. 5925 (phot. E. Rubio), **e**. HMAS 75874 (phot. B. Liu 2006, as *O. euonymi*); **f**. H.B. 8978a (phot. H.Y. Su); **g**. H.B. 8533.

large LBs and elongate straight ascoconidia. The ascospores of *H. fusisporum* are comparatively large, fusoid, and also contain large LBs (Fig. 122: g), but no ascoconidia are formed on them within the asci. Only when studying dead asci with disintegrated clusters (Fig. 122: e–f), the ascoconidia may easily be confused with ascospores of multispored asci of *Orbilia*.

At least 14 species of *Orbilia* have so far been observed as host of *Helicogonium orbiliarum*: *Orbilia aristata* {1}, *O. aprilis* {1}, *O. aurantiorubra* {1}, *O. eucalypti* {14}, *O. euonymi* {2}, *O. frangulae* {1}, *O. luteorubella* {1}, *O. magnifica* {1}, *O. phragmotricha* {1}, *O. rosea* {1}, *O. sarraziniana* {3}, *O. tremulae* {1}, *O. vinosa* {7/2}, *O. xanthoguttulata* {1}. No other genus of *Orbiliomycetes* was so far found to have this intrahymenial parasite. *Helicogonium hyphodisci* in *O. laevimarginata* and *H. fusisporum* in *O. eucalypti* were each recorded only once. *H. orbiliarum* was at first thought to be adapted to the genus *Orbilia*, but we have seen it also in hymenia of different *Helotiales* (IVV: *Cyathicula* ?*tomentosa*, H.B. 5759; *Durella* ?*compressa*, H.B. 7077e; *Hyaloscypha minuta*/*intacta*, H.B. 6087; ?*Calloria* sp., H.B. 5482h). *Helicogonium hyphodisci* is otherwise only known from hymenia of *Hyphodiscus*.

No deformations to the host apothecia are provoked by any of these parasitic species. Therefore, infected apothecia cannot be recognized under the dissecting microscope. Very similar as in *Orbilia*, the asci of *Helicogonium* have long undulating stalks, which, however, vary in arising in some species from croziers and in very closely related species from simple septa. Croziers and simple septa occur even within *H. orbiliarum* in the present concept, when comparing different collections. The ascus apex is hemispherical to conical and always provided with a thin to thick apical thickening. SBs never occur in the living ascospores or conidia of *Helicogonium*.

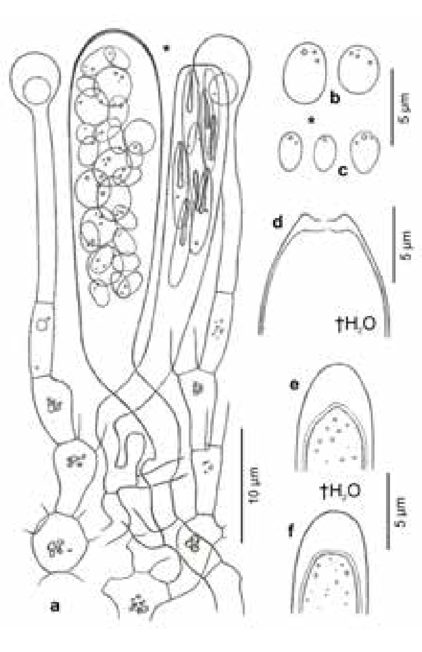


Figure 123. *Helicogonium orbiliarum* in hymenium of *Orbilia rosea* (H.B. 6366). — **a**. ascus of *H. orbiliarum* with eight subglobose ascospores and many smaller ellipsoid ascoconidia along with ascus and paraphyses of *O. rosea*, **b**. ascospores, **c**. ascoconidia, **d**. emptied ascus of *H. orbiliarum*, **e**: immature dead asci of *H. orbiliarum*.

In two Australian collections a ?chytridiomycete was found in hymenia of *Orbilia* sp. and *O. aviceps* (Fig. 124: a–e). The apparently same fungus was observed in *O. mali* in Europe (Montenegro, B. Perić pers. comm., Fig. 124: f). A similar species parasitic in hymenia of *Mollisia* was treated as a possible member of *Chytridiomycota* in Baral (1999: 11). The parasite in *Orbilia* deviates from that in *Mollisia* by sporangia with a glassy apical outgrowth with terminal globose inflation, and a subapical opening close to this outgrowth (but the outgrowth was not seen in the sample from Montenegro). The species might belong to the genus *Karlingiomyces* Sparrow, which is, however, reported to be saprotrophic (Blackwell et al. 2004). A flagellum was not observed on the sporangiospores, which could only indistinctly be seen inside the sporangia Fig. 124: a).

A few members of *Orbiliomycetes* may thrive as parasites on apothecia of *Orbilia*: *Hyalorbilia orbiliicola* forms apothecia on the apothecial margin of different desiccation-tolerant *Orbilia* species (Fig. 116: b). The hymenia of the host apothecia remain more or less immature, but the excipular and paraphysis cells are usually still viable when the apothecia of the *Hyalorbilia* develop. Frequently also the anamorph of *H. orbiliicola* (trinacrium angamosense-like) forms its conidia on the host apothecia, usually together with the teleomorph (see p. 425). A similar anamorph that deviates in more asymmetrical conidia (see p. 427) was repeatedly found to grow out of hymenia of different xerobiotic Australian species of *Orbilia*, but its presumed teleomorph was only seen in one of these records. Some other observations of parasitism by orbiliaceous anamorphs were made, for instance, asymmetrical dicranidion-like conidia formed on apothecia of *O. vinosa*, which were considered by us to belong to the closely associated apothecia of *H. hergiswiliana* (see p. 435).

A hyphomycetous intrahymenial mycoparasite, *Acremonium limoniforme* Baral, was observed in two distantly related desiccation-tolerant species of *Orbilia* (*O. cactacearum*, *O. macroasca*) in the semiarid southwest of Northern America (Baral 2019). The fungus is characterized

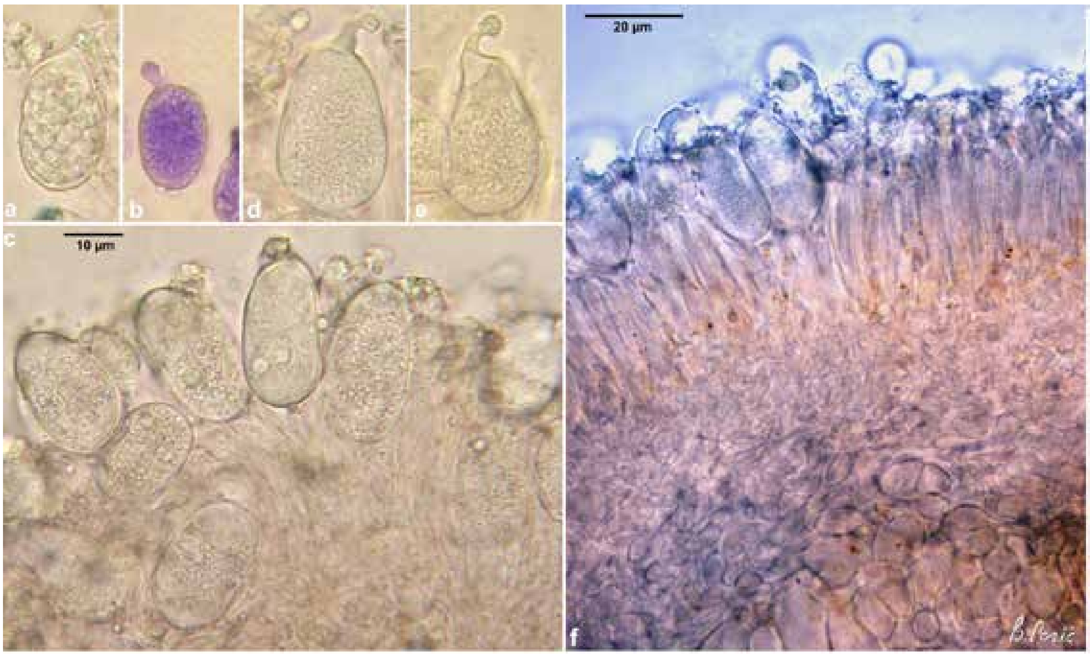


Figure 124: Sporangia of a ?chytridiomycete develop in hymenia of xerobiotic *Orbiliomycetes*: *Orbilia* sp. (**a–c**. on *Acacia*, H.B. 7204p, in CRB), *O. aviceps* (**d–e**. on *Banksia*, H.B. 8659b), *O. mali* (**f**. on *Punica*, B.P. Dgf/C7D-01-05-16b, phot. B. Perić).

by short hyaline conidiophores and non-septate, hyaline, medium-sized, limoniform conidia formed in hyaline, deeply invaginated sporodochia immersed in the hymenium of the host. Conidiogenesis seemed to be holoblastic in one of the two collections when viewed in the living state, but in the other collection the dead conidiophores showed a clearly enteroblastic (phialidic) conidiogenesis. Its phylogenetic relationship is unclear because no DNA data were available.

An unidentified species of *Niesslia* (*Niessliaceae*, *Hypocreales*) with minute dark superficial perithecia with short brown setae was 3 × found between 2009–2018 in North America growing abundantly on the hymenium of what appears to be *Hyalorbilia inflatula* (J. Karakehian, B. Liu, E. Crenson, J. Mack pers. comm., IVV: VIII.2009, VIII.2017, 23.VI.2018).

Dispersal and colonization of new substrate

Different strategies of substrate colonization can be observed within the *Orbiliomycetes*. They comprise dispersal by wind and water, but also by adherence to animals, and apparently by ingestion. Thereby, dispersal is mainly accomplished via conidia and ascospores, in some species also by detachable trapping organs, perhaps also by hyphal fragments and by chlamydospores.

Dispersal by wind and water. Dispersal by air currents is more efficient at high levels above the ground. Apothecia growing close to the ground are faced with problems of still air surrounding the substrate, whereas apothecia at higher levels are exposed to turbulent air. Sherwood (1981: 32) hypothesized that ascomycetes on exposed weathered woody substrate do not need highly developed discharge mechanisms such as amyloid apical rings, which are typical of those species adapted to the moist ground. In contrast to the *Helotiales*, we cannot see any difference in ascus morphology and spore discharge mechanisms in the *Orbiliomycetes* between these two ecological types, with the exception that asci with thick-walled apices occur exclusively in xerobiotic taxa, though only in about a third of them. It can, therefore, be assumed that asci of xerobiotic *Orbiliomycetes* are able to shoot their spore clusters as far as hygrobiotic ones, or perhaps even further when the ascus apices are thick-walled.

The frequent and exclusive occurrence of polyspory in xerobiotic species of *Orbilia* could be interpreted as an adaptation to wind dispersal, in order to increase the probability of colonization by a high number of spores. Yet, in the often small apothecia of these species the total number of spores is probably lower than in a desiccation-sensitive species with large apothecia. Another aspect could be that polyspory helps in establishing a heterocaryotic mycelium, since all spores of the spore cluster are still held together when splashing on the substrate. Especially if some of the spores do not survive long drought, polyspory might avoid single spore mycelia during substrate infection, but this would require homothally. Heterokaryosis as an advantage in xeric environment was considered by Sherwood (1981: 25). Although *Orbilia* spores often survive several years in the herbarium, they might not stay alive for such a long time when exposed to strong insolation. The consistent absence of a brown pigmentation in the spore wall in *Orbiliomycetes* suggests that the spores cannot compete in survival with brown-spored ascomycetes.

Unlike our results, Sherwood (1981: 26) found anamorphs to be absent in most xerobiotic discomycetes, and supposed that the xeric environment is characterized by low competition on substrates that are stable over a long timespan. She concluded that desiccation-tolerant fungi do not require rapid dispersal and colonization by means of asexual propagules. However, Sherwood was unaware of the predominant presence of *Orbiliomycetes* as well as their anamorphs on xeric substrate, and she might have overlooked the high competition that undoubtedly takes place during the rare events of humidity in xeric environments.

A large number of orbiliaceous anamorphs have staurosporous conidia*,* frequently with long and narrow, hyphoid extremities (curucispora/descalsia-like, dicranidion-like, dwayaangam-like, tridentaria-like, trinacrium-like). Others have unbranched multiseptate, vermispora- or anguillospora-like conidia. Almost all of them live in xeric habitats on dead exposed, mainly woody substrates and are dry during most of their lifetime. One of the advantages of such branched or C-shaped conidia might be a longer stay in the air during dispersal. Yet, stauro- and scolecoconidia have originally been reported mainly from aquatic habitats like foam or submerged leaves in streams (Ingold 1942, 1958; Miura 1974; Descals & Webster 1982; Sinclair et al. 1983). As a matter of fact, D. Magyar (pers. comm.) rarely found such conidia in air samples.

Experiments by Webster (1959) with variously shaped conidia of a number of rather distant species in a water-tunnel tested under five different water speeds showed strong differences in adhesion to an inserted collodion-coated glass rod that acted as a trap. Accordingly, tetraradiate conidia with long branches get attached with considerably greater efficiency than conidia with short branches, or unbranched conidia of various lengths. Tests on conidial sedimentation rates in motionless water yielded no correlation with conidial shape. Ingold (1966: 54) concluded that tetraradiate conidia represent an adaptation to transport in running water, their shape acting as a little anchor to get attached to submerged substrate. Therefore, later authors referred to such conidia as 'Ingoldian'.

A further property, mainly of staurosporous conidia, is that they easily get trapped by air bubbles and accumulate in foam or swim on the water surface. We have used this effect in order to collect conidia from xeric substrate in close vicinity of apothecia (see p. 6). A very similar effect was detected in ascospores of a few desiccation-tolerant *Orbilia* species which adhere solely with their apex to the surface of water drops or films (see Fig. 72) where they are transported by water currents.

Some of the filamentous (anguillospora-like) or staurosporous (curucispora-, descalsia-, trinacrium- or dwayaangam-like) conidia found in running water and currently referred to as Ingoldian more ore less strikingly resemble conidia of *Orbiliomycetes*. Yet, orbiliaceous conidia are usually not formed inside or close to waterbodies. For example, *O. junci* grows on dead dry parts of standing culms of *Juncus roemerianus* at the Atlantic sea shore in the east of Northern America. The normal tides thereby reach only the lower part of the culms, not the upper part where *O. junci* lives (Kohlmeyer et al. 1998). Because of the staurosporous, dwayaangam-like conidia of its anamorph, the habitat directly at the sea shore, and the occurrence of other *Dwayaangam* species in freshwater, the authors concluded that the anamorph of *O. junci* is an Ingoldian fungus adapted to water dispersal. However, at that time the conidia were only known from pure culture and their natural habitat unknown. Later, Kohlmeyer & Volkmann-Kohlmeyer (2001) detected conidia on the dead tips of the standing culms, and concluded that they can be wind- or water-dispersed to other senescent leaves. This is supported by our observation that the conidia of this species survive desiccation for at least a week.

Only a few species of *Orbiliomycetes* (e.g., *Lecophagus muscicola*, *Orbilia luteorubella*, *O. rectispora*, *O. rosea*, *O. sarraziniana*) actually live in wet, semiaquatic habitats. Two of them differ mainly in their anamorph, that of *O. luteorubella* being helicoon-like and that of *O. rosea anguillospora-like*. Apothecia of these two species are found at the banks of rivulets and lakes and are for most of the time exposed to dry air, into which the asci discharge their spores. The scolecosporous, worm-like conidia of *O. rosea* might show a slower sedimentation rate when floating in running water, whereas the likewise scolecosporous but strongly coiled, barrel-shaped conidia of *O. luteorubella* enable floating at the surface of stagnant water because of trapped air in their interior. Apparently, such conidia are adapted to water dispersal during high water levels.

But water comes temporarily also to dry substrates. During rainfalls, xeric substrate is covered by a water film and represents a short-time aquatic habitat with water running or dropping down from trees (Bandoni 1972, 1974). According to this author, conidia were held up on the surface tension film of the water. Several studies on stemflow from living trunks showed a rich amount of conidia of 'terrestrial Ingoldian' or 'terrestrial aquatic' fungi (see Descals & Moralejo 2001: 22), some of which are undoubtedly anamorphs of *Orbiliomycetes.* Ando & Tubaki (1984a, b) reported stauroconidia of *Curucispora ombrogena*, *Dicranidion fissile*, and *Dwayaangam yakuensis* from rainwater samples collected from aerial leaf-surfaces. Gönczöl & Révay (2003) found hyphomycetes communities with conidia of various *Trinacrium* and *Dwayaangam* species in water-filled treeholes of living broad-leaved trees. They also isolated eight different *Trinacrium* species and many other orbiliaceous anamorphs from rainwater stemflow from living trees (Gönczöl & Révay 2004, 2006 etc.). Using pressure-sensitive acrylic strips, Magyar (2008) observed various types of conidia, some of which being orbiliaceous (dwayaangam-, trinacrium-, vermispora-like), trapped by the surface of stem bark fissures during stemflow.

The origin of terrestrial conidia found in stemflow has been a matter of speculation, and especially their life cycle and desiccation tolerance was unknown. Descals & Moralejo (2001: 32) thought that the conditions on terrestrial plants may be generally too dry for the growth of Ingoldian hyphomycetes. Those taxa which spend most of their time under water may actually be sensitive to water loss. However, conidia of 'terrestrial aquatic' fungi observed in stemflow are undoubtedly formed on aerial parts of the trees, where also their mycelia and conidiophores are tolerant to desiccation.

Based on our observations of various orbiliaceous anamorphs on xeric substrate, frequently observed in association with apothecial populations, the conidia found in stemflow of living trees were formed on dead bark or wood of twigs and branches in the canopy of these trees. During rainfalls the conidia are transported downwards where they may attach to the rough, fissured bark surface or get trapped in treeholes, whereas others reach the soil, or drop directly into smaller or larger water courses, or get washed into floodings and temporary lakes. The seemingly unidirectional dispersal by dripping and running water appears at first disadvantageous, but it can be assumed that additional vectors such as arthropods and birds (see below) support a multidirectional distribution to the conidia. Magyar (2008) imagined the enormously large surface of fissured bark to act as a reservoir or 'spore bank' for further infections, allowing storage of a vast number of spores. Although some of the conidia might be transported there by air currents, Magyar concluded that 'the majority of free spores trapped inside the bark fissures was delivered by the rainwater from their colonies growing elsewhere on the host tree. Stauro- and scolecosporous taxa, especially, common in bark and stemflow rainwater but rare in the air samples, are thought to be bark-inhabiting hydrochorous species.'

Dispersal by animals. Hence, a further strategy implies the dispersal mediated by animals, either by invertebrates such as arthropods (copepods, beetles, mites, spiders, springtails) or smaller ones (nematodes, rotifers, tardigrades), or by vertebrates such as birds or mammals. Presence of *Orbiliomycetes* on the skin mucosome of larvae and adults of amphibia (*Salamandra*) in Massachusetts was demonstrated by Barnhart (2018) by molecular methods.

We suppose that spore clusters shot from asci are sticky and adhere to insects which transport them to other places (ectozoochory). Especially shortly after rainfalls when the asci are turgescent, animal activity is often high. We also assume that particularly those species with showy apothecia (e.g., *Orbilia*

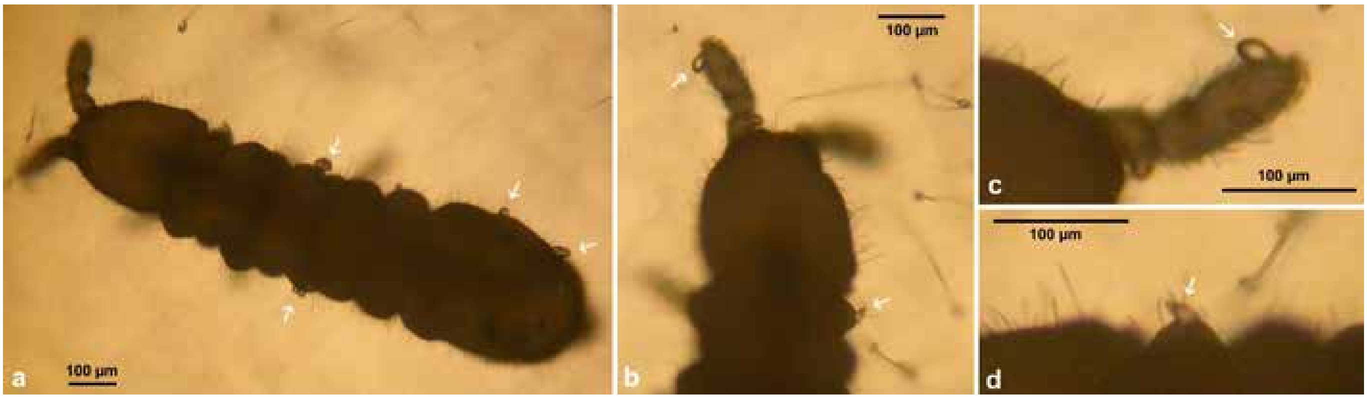


Figure 125: Springtail (*Collembola*) added to a pure culture of *O. menageshae*, with adhering conidia (H.B. 9275a).

fimbriata) attract flies and other insects (see p. 105, Function of pigments). For adherence to animal bodies, polyspory in *Orbilia* cannot be explained by a higher chance to hit the insect body, because the spores are ejected as a single entity.

Ectozoochory of conidia was, e. g., suggested by Pfister (1997: 16). It can easily be proved by adding small invertebrates to an agar culture. Conidia of many orbiliaceous species are covered by a thin gel sheath that stains lilac with CRB (Fig. 94: f–g). Only rarely the gel sheath is thick and visible without staining as in *D. polybrocha* (Pl. 12: i). The gel is adhesive to passing animals which undoubtedly serve as a vector for conidial transport. Particularly species with long, erect conidiophores, which are typical of moist habitats, possess conidia with a stainable gel film (Tab. 9). When adding a springtail to a culture of *O. menageshae*, the conidia adhered to the antennae, extremities, and the main body (Fig. 125). Then the springtail either detached the conidium from the conidiophore or, if the conidium is not mature enough, the animal escaped only with high effort. The stickiness of conidial gel seems to be comparable to that of adhesive trapping organs. Conidia formed on ± short conidiophores are likewise sometimes covered by gel. In addition, conidial shape might help in lodging to animals, especially to their legs, either by bending of phragmoconidia which are often hook-like towards the ends, or by different types of branching in the case of stauroconidia. However, in some species of *Hyalorbilia* the straight unbranched conidia seem to be devoid of such a gel as their surface did not stain in CRB (Tab. 9).

Also some trapping organs are detachable, particularly non-constricting rings (see Fig. 109: f), or they are directly formed on conidia. In both cases they are carried away by the prey. Also those aerial hyphae which coil upon touch might adhere to small invertebrates and get detached (see p. 105). Chlamydospores remain viable over a long timespan during which they are possibly translocated.

Ingestion of apothecia by snails without damage to the ascospores (endozoochory) was demonstrated in a single test with a door snail (*Cochlodina laminata* fide C. Allgaier): spores of *Orbilia aurantiorubra* looked vital in faeces of this snail which was kept in a moist chamber together with apothecia for some days. Also bdelloid rotifers were once seen under the microscope to engulf ascospores of an *Orbilia* of series *Hesperideae*, but with their trophi they were able to crush them, so in this case the animal did not contribute to the dispersal of the fungus. Our hypothesis that ascospores infect certain microscopic animals via ingestion (infection by ingestion) implies in the successful case also dispersal of the fungus.

Also larger animals such as arthropods, reptils, birds, and mammals might play a role in conidia and ascospore dispersal, either by adherence or by ingestion. Dispersal of *Orbilia arachnovinosa* and *O. pseudoaristata* (as Unidentified sp. 2170_1175 & 2170_622) by insects was shown in a study of Menkis et al. (2016) who obtained DNA from adults of the European elm bark beetle, *Scolytus multistriatus*, the vector of the Dutch elm disease, which were trapped by sticky inserts in delta traps. The beetles were not surface-sterilized prior to DNA extraction, so that it is unknown whether the propagules were out- or inside the insect body.

Desiccation tolerance

Fungi are generally devoid of structures that efficiently reduce evaporation of their internal cellular water when exposed to a low atmospheric humidity. However, they have other mechanisms to permit growth and survival in a periodically dry environment. Instead of retarding water loss, the protoplast of fungal cells of certain species is able to repeatedly withstand complete desiccation. This is often the case with propagules (meiospores and conidia), but in many fungal taxa also regarding the complete hyphal system and sporocarps of both anamorph and teleomorph.

Two main ecological groups can, therefore, be distinguished in fungi: those with **desiccation-tolerant** (= drought-tolerant) sporocarps, and those with **desiccation-sensitive** (= drought-intolerant) sporocarps. In the latter group usually only the propagules survive complete drying. Desiccation-sensitive taxa, which are also termed **hygrobionts**, grow on **hygric** substrate in continuously moist microhabitats which dry out only after prolonged periods of drought. In the worst case, this causes the death of the population, unless the mycelium shows a certain tolerance to desiccation. Desiccation-tolerant taxa, which are also termed **xerobionts**, live on **xeric** substrate which periodically dries out, therefore, their entire sporocarps survive drying. Cases in which the sporocarps are hygrobiotic but the mycelia xerobiotic are perhaps not uncommon: such fungi colonize wood of dead attached branches by their mycelia, but sporocarps are only formed on them after they fell down to the ground. For instance, *Chlorociboria aeruginascens* (*Helotiales*) causes a blue-green stain to xeric wood whereas apothecia are formed only on hygric wood on the ground. Conversely, mycelium of endophytes in living plant tissue might be intolerant to drying until the colonized plant parts die and desiccation-tolerant sporocarps are formed.

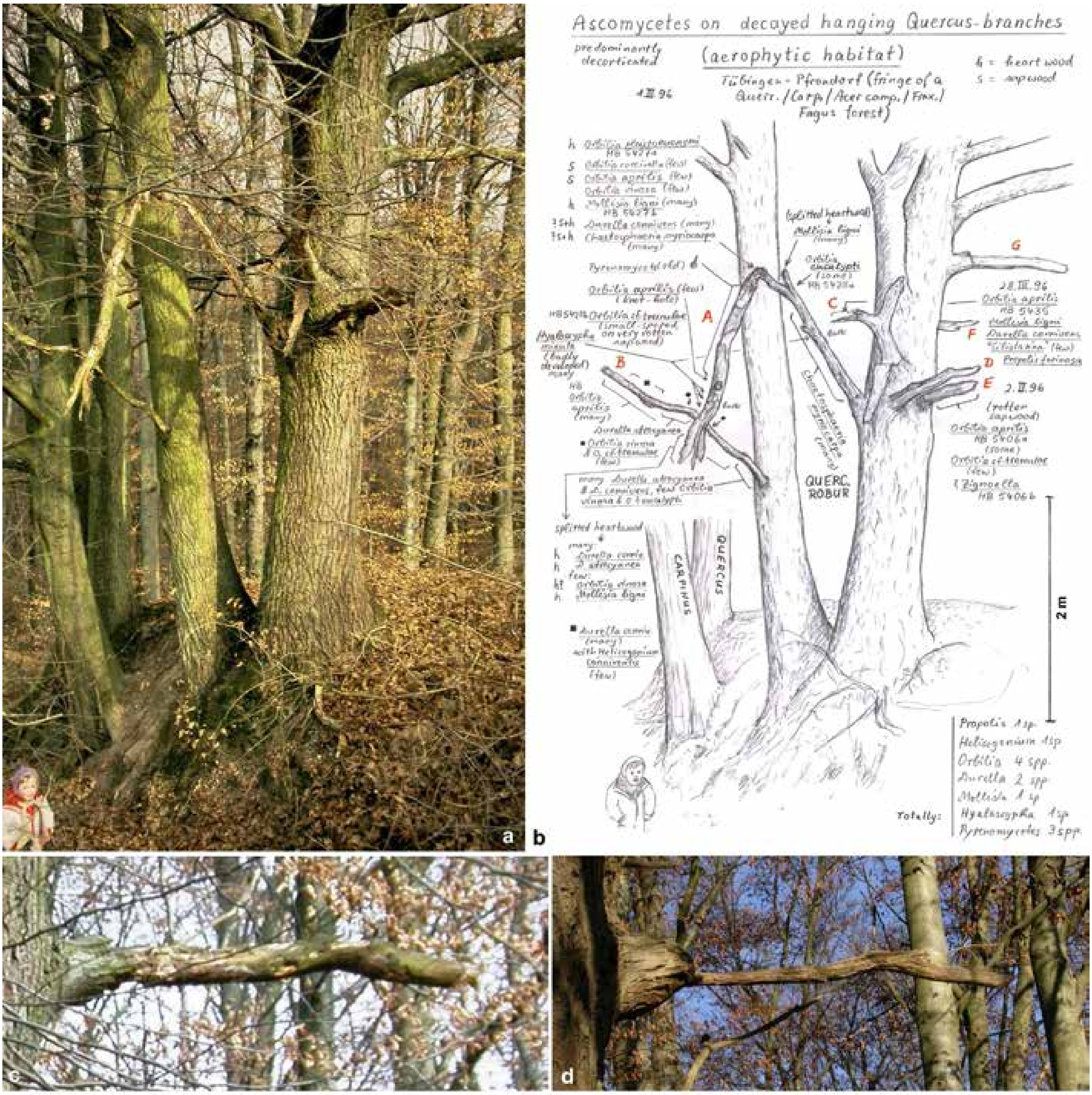


Figure 126. **a–b**: *Quercus robur* and *Carpinus betulus* at border of deciduous forest in Tübingen-Pfrondorf (southern Germany), 2.II. (H.B. 5406, **a** & **c**), 1.III. (H.B. 5423, 5427–28, **b**) & 28.III.1996 (H.B. 5435). A total of 12 species of ascomycetes (four orbiliaceous) were recorded on the attached, decayed and eroded, decorticated branches ~ 2–3 m above the ground. Branches D, F & G were not examined but monitored for their decay during the next years. **c–d**: Branch G was observed to persist for the following 14–18 years (until X.2013), during which the thickness of its decorticated part decreased from ca. 10–12 (**c**, 2.II.1996) to 3–4 cm (**d**, 14.XI.2010). During a control in X.2014 the branch had disappeared.

However, there is no sharp limit between the two groups. The strength of desiccation tolerance, i. e., the period of time the sporocarps survive complete dehydration in all their parts, strongly differs among the taxa. Some species, particularly members of *Hyalorbilia*, tolerate desiccation only for a few days or weeks, but others for several years. Moreover, considerable differences occur within a given species. For example, apothecia of *Orbilia tremulae* or *O. cejpii* usually did not noticeably withstand drying when growing on the moist ground, but they survived some weeks or months when occurring on attached xeric branches, although in such cases no differences could be observed in their ITS rDNA. Therefore, data given here on the proportion between xero- and hygrobionts are to be considered as approximate. Apothecia colonizing xeric substrate probably cover some of their water requirement from the plant tissue below. However, such water sources certainly play a subordinate role, since apothecia usually rapidly dry out during dry weather.

Parameters which determine the water relations in the substrate are the exposure against direct sunlight and rain and the humidity of the atmosphere. Three main habitat categories can tentatively be distinguished in this regard: **xeric** (periodically dry for a shorter or longer time), **mesic** (moist for a longer time but with dry intervals), **hygric** (continually moist while rarely drying out), and **semiaquatic** (continually moist but periodically flooded). Desiccation-sensitive species are unable to produce sporocarps on xeric, air-exposed substrate because the available water rather rapidly decreases after a moist period, depending on the thickness and absorptive capacity of the substrate. Vice versa, desiccation-tolerant species do not usually occur on continually moist substrate since they are unable to compete with fungi that are better adapted to hygric habitats, apparently because of a slower growth rate of their mycelia. A large amount of dead plant substrate on earth is subjected to repeated and in some areas very long-lasting dryness, and desiccation-tolerant species are adapted to colonize these enormous nutrient resources. The disadvantage of a delayed life cyle of each generation due to long periods of dormancy stands in opposition to the advantage of being protected from grazing by hygrobiotic animals, particularly from slugs, and from competition with fast-growing hygrobiotic fungi.

In the introduction to the biology of lichens, Nash (2008: 1.4) gave an excellent characterization of desiccation-tolerant, poikilohydric organisms, which widely applies also to non-lichenized ascomycetes. The unabridged paragraph seems worth reproducing here:

‘Most flowering plants and conifers have developed the capacity to maintain the water status of their leaves or needles at fairly constant levels and hence are referred to as homoiohydric organisms. In contrast, lichens are prominent members of poikilohydric organisms, whose water status varies passively with surrounding environmental conditions. Other poikilohydric organisms include mosses, some ferns and other primitive vascular plants. All of these organisms become desiccated relatively rapidly and, as a consequence, water availability is of prime importance for their survival and in explaining their patterns of occurrence.

One might assume that poikilohydric organisms are highly dependent on precipitation, primarily in the form of rain. Certainly this is true for many lichens, as can be seen for the lichen biomass relationship among interior desert sites. On the other hand, lichen biomass near the Pacific Ocean in the western part of the Sonoran Desert vastly exceeds values that would be predicted based on precipitation alone. This illustrates the ability of lichens to utilize other water sources, such as fog and dew. In addition, lichens have the remarkable ability to extract some moisture from unsaturated air under conditions of low temperatures and high humidities. This is essentially the reverse of transpirational water flow occurring through vascular plants and is due to the low osmotic values of lichen thalli. However, under intermediate to high temperatures and intermediate to low humidities, the water potential gradient from the lichen to the atmosphere is reversed and evaporation occurs.’

Hygrobiotic (desiccation-sensitive) fungi occur in zones of either medium to high annual precipitation (around 500–2000 mm), frequent fog, or low evaporation due to low temperatures. Rainfalls may occur either more or less equally distributed over the year (humid), or show a pluviseasonal change with long-lasting periods of drought either during winter (monsoon climate) or summer (mediterranean). Besides the amount and seasonality of precipitation and the microclimate, substrate humidity also depends on the average temperature of the region. Therefore, boreal zones need much less rain than subtropical zones. Particularly in the pluviseasonal zones, hygrobiotic species are usually only found during and shortly after the rainy season, whereas xerobiotic species can be collected all over the year.

Hygric substrate. Continually moist substrate enables hygrobiotic species to complete their whole life cycle without interruption provoked by dryness. When cultured on the natural substrate at room temperature in a moist chamber, the formation of fully mature apothecia of *Orbiliomycetes* was found to last about 2–5 weeks, as extrapolated by a hypothetical start from very small apothecial initials (see p. 40–41, Growth rate). The observed growth rate was distinctly lower in xerobiotic species, but due to their usually smaller size the full timespan to form mature apothecia is similar as in hygrobionts. However, this situation is artificial for a xerobiotic fungus which, under natural condition, periodically experiences dry periods and, therefore, much longer growth rates. Similarly, cold weather periods during winter interrupt or retard growth of cryotolerant hygrobionts. One of many examples for this is the genus *Sarcoscypha*, a lignicolous member of *Pezizales*, apothecia of which are formed during late autumn but become mature only in early spring.

Desiccation-sensitive species colonize rotten wood and bark, herbaceous plant parts or decayed sporocarps that lie more or less close to the moist forest floor, often at wet places or water courses, usually in shaded situation and protected from drying winds. Drying is often prevented by a cover of litter or by growing on the underside of branches and logs with close contact to the ground. Only rarely, hygrobiotic apothecia are found exposed to a dry atmosphere ~1–2 m above the ground, but then usually on deeply strongly rotten wood being soaked with water like a sponge (observed, e.g., in *Orbilia xanthostigma* and *O. orientalis*).

Xerobiotic (desiccation-tolerant) fungi occur in all climatic regions of the world where dead decayed plant substrate is exposed to alternate wetting and drying. Their highest diversity is in the subtropical to tropical, semihumid to arid zones, with occasional or seasonal precipitation ranging between around 100–800 mm per year. A distinctly lower number of xerobiotic species was found in temperate to subtropical humid to subhumid regions with continuous or seasonal rainfalls of ~800–1500 mm per year, and only a few such species were so far collected in tropical humid regions with rainfalls around 1500–2000 mm per year and only short-lasting periods of drought, or in arctic-alpine dwarf-shrub communities with a similar long-lasting humidity (see Tab. 33).

Xeric substrate. Desiccation-tolerant species live on all kinds of dead air-exposed plant parts up to the canopy of large trees. Xeric substrate comprises wood and bark of still-attached, or broken and hanging, usually dead twigs and branches, adhering dead leaves and fruits, also the dead outer bark of living trunks. It also includes more or less standing or hanging dead parts of herbaceous plants. Woody and herbaceous xeric substrate persists for a much longer time than hygric substrate. In humid areas, recently dead herbaceous substrate requires a minimum of two years until *Orbiliomycetes* develop. Woody substrate usually attains its optimum stage only when the bark starts to detach; the minimum timespan to attain optimum decay for colonization by *Orbiliomycetes* in humid regions might range at 3–5 years and in semiarid regions presumably at 10 years or more.

Typically, xeric substrate is exposed to direct sunlight for several hours on a sunny day. An old decorticated branch is poor in water content, and its surface dries out rapidly after a rainfall, at least in the course of a sunny day, in contrast to more shaded substrate in a dense forest. Due to the different degrees of tolerance to dryness, fungal communities also differ in their composition between xeric and mesic substrate.

Decorticated xeric wood usually looks more or less weathered and eroded when carrying ascomycetes. The rotten wood surface is typically covered by a biofilm of black yeasts which provoke a greyed surface (e. g., Figs 115: m, 119: b). Often free-living aerophytic algae are present in this biofilm (Fig. 120). Decorticated areas in an advanced decay, or detached hanging bark, also the presence of beetle galleries provide promising preconditions for desiccation-tolerant *Orbiliomycetes*. Only a few species were preferably or exclusively found at an initial stage of decay (e. g., *O. aradi* and resinicolous taxa).

Small ascomata on xeric substrate are unable to retard water loss from their cells for more than a few minutes or hours, depending on the size of the ascomata, the water-holding capacity of the substrate, i. e., the thickness of the substrate, the depth of its decay, and its hydrophily, and weather parameters such as temperature and wind. Therefore, the active growth period of small xerobiotic ascomycetes is usually restricted to periods of atmospheric moisture. The interruption of growth concerns all stages of the life cycle, including mycelial growth.

The natural hydration of xeric substrate is accomplished mainly by rain- and snowfalls, during the colder season or higher altitudes also by fog, or by dew during cold nights. Unpublished experiments in cold-temperate humid, colline central Europe (Tübingen, see Baral & Marson 2005) during the end of September 2010 showed that even an atmospheric humidity of almost saturated air (99 %) during the night rehydrates apothecia of *Orbilia aristata* and *Sclerencoelia fraxinicola* only to about half their full size, which is certainly not enough to enable spore discharge. Temperatures below +6–8 °C were necessary to attain a 95–100 % atmospheric humidity. In mountain ranges with oceanic influence, rehydration of xerobiotic fungi by fog and dew is probably more important than in lowland regions.

In subtropical semiarid areas the total lifetime of an apothecium can be estimated to last perhaps 5–10 years, showing active growth only during a few days or weeks per year. In temperate humid areas mature apothecia were found during summer to increase considerably in size within a period of 3–4 months, whereas during the entire winter time they showed hardly any growth (see p. 40–41). An experiment that demonstrates colonization of xeric substrate was done with a rope of plant fibres which, after exposure for about 3–4 years, carried various *Orbilia* spp. and other ascomycetes (see Baral & Marson 2005).

Desiccation tolerance within taxonomic groups, particularly discomycetes. Xerobiotic sporocarps occur in many groups of fungi, though in a strongly varying frequency. Many genera or higher taxonomic groups comprise both ecological types, whereas others are either more or less purely xero- or hygrobiotic. Within the discomycetes, these ecotypes may characterize groups at the ordinal or higher level. To the present knowledge, members of *Ostropomycetidae* and *Rhytismatales* are apparently exclusively desiccation-tolerant. Members of *Pezizales* are desiccation-sensitive in almost every case, including the genus *Octospora*, which occurs on mineral soil in a parasitic or symbiotic relationship with predominantly xerobiotic bryophytes, preferably during the cold and moist winter months. At least one species of the genus, *Octospora affinis*, is clearly xerobiotic: it grows on the rhizoids of *Orthotrichum* on bark of attached branches at ~ 0.5–3.5 m above the ground (Krieglsteiner 2006), and our tests showed that mature asci survive at least two weeks in the dry state. Another exception within the hygrobiotic *Pezizales* concerns the xerobiotic genus *Octosporella* with perithecioid ascomata occurring on bryophytes on xeric bark.

In *Leotiomycetes* both ecological types occur in rather equal frequency. Typical hygrobiotic genera comprise, for instance, *Sclerotinia*, *Ciboria*, *Hymenoscyphus*, *Ombrophila*, *Lachnum*, *Mollisia*, *Pyrenopeziza*, *Hyaloscypha*, *Calycina*, and *Calycellina*. However, some of these genera include also xerobiotic species (e. g., *Hymenoscyphus infarciens*, *Mollisia ligni*, *Hyaloscypha quercicola*). On the other hand, the heterogeneous genus *Claussenomyces* s.l. comprises mainly xero- (e. g., *C. jahnianus*, *C. atrovirens*) but also hygrobiotic species (e. g., *C. prasinulus*). Likewise, *Lachnellula* and *Capitotricha* mainly include xerobiotic taxa. Purely xerobiotic genera appear to be *Unguiculariopsis*, *Encoelia* in its old polyphyletic sense, *Tympanis*, and many others.

Desiccation tolerance within the *Orbiliomycetes*. Desiccation tolerance plays an extraordinary role within the *Orbiliomycetes* (see Tab. 5). In the present monograph, about 430 species (82 %) show a more or less pronounced desiccation tolerance of their entire apothecia, lasting about 1 month up to 4 years, ca. 94 species (18 %) were found to be more or less desiccation-sensitive, their tolerance lasting max. 1–2 weeks, and for about 10 % the available data were unsufficient.

Hygrobiotic (desiccation-sensitive) species are represented by about 65 % of *Hyalorbilia* spp., but only by ~ 18 % of *Orbilia* spp. Also the small genera *Pseudorbilia* and *Bryorbilia* belong in this group. Within *Orbilia* hygrobiotic taxa are almost exclusively found in section *Helicoon*, series *Orbilia*, series *Hyalinia*, series *Xanthoguttulatae*, and section *Arthrobotrys*. However, all these groups comprise also a number of xerobiotic taxa, e. g., *O. eucalypti*, *O. fabacearum*, *O. liliputiana* (series *Orbilia*); *O. pseudobrevistipitata*, *O. spirillospora* (series *Hyalinia*); *O. fusiformis*, *O. limoniformis* (section *Helicoon*); *O. anigozanthi*, *O. desertorum*, *O. fraxini*, *O. menageshae*, *O. rhamni* (section *Arthrobotrys*).

The cosmopolitan *O. xanthostigma* represents the most often collected hygrobiotic species of *Orbilia*. It grows on the upper and lateral side of old, mostly decorticated, water-soaked branches and logs lying on the forest floor, whereas its less frequent sibling *O. leucostigma* prefers the lower side. Further examples of frequently collected hygrobiotic species in the temperate humid northern hemisphere are *Hyalorbilia fagi*, *H. inflatula*, *H. polypori*, *Orbilia auricolor* (p.p.), *O. crenatomarginata*, *O. dryadum*, *O. epipora*, and *O. tremulae*. In the humid subtropics and tropics *H. arcuata*, *H. citrina*, and *H. japonica* are frequent along with *H. inflatula* and *O. xanthostigma*. All these species usually occur in shady forests away from surface water. Four further common hygrobiotic species of the temperate humid northern hemisphere (section *Helicoon*: *O. luteorubella*, *O. rosea*, *O. sarraziniana*; section *Arthrobotrys*: *O. rectispora*) occur on substrate close to the water level, being periodically flooded during abundant rainfalls or snowmelt by running (lentic) or stagnant (lotic) water of rivulets, ditches and marshes, or lakes. Mature apothecia are usually not found submerged by water, but a test showed that those of *O. luteorubella* completely survive several days underwater. The incidence of flooding is often recognizable on the collected substrate by aquatic organisms such as duckweed (*Lemna*), diatoms, eggs of *Cladocera*, filamentous green algae etc.

Hygrobiotic species of *Orbiliomycetes* have often comparatively large apothecia and, in contrast, small asci and ascospores. The apothecial colour is usually whitish to cream, pale yellowish or pale rosaceous-lilaceous. Only in a few species is it bright yellow, orange, or red. Also their mycelia in pure culture are generally more or less colourless. The exudate on the apothecia is often sparse, and only in slightly desiccation-tolerant species more abundant and sometimes distinctly yellowish (subtropical members of section *Helicoon*). The presence of VBs in the paraphyses is typical of many of them, and a few species are characterized by vacuolar pigments (e.g., *O. rubrovacuolata*).

Anamorphs of hygrobiotic species of section *Arthrobotrys* are characterized by long conidiophores, whereas in *Hyalorbilia* and in section *Helicoon* and series *Orbilia* they are comparatively short. The conidia are almost always unbranched (*Hyalorbilia*, sections *Arthrobotrys* and *Helicoon*), but in some species of series *Orbilia* they are branched. Many species of section *Arthrobotrys* are able to trap nematodes and other invertebrates, and since nematodes are rarely found on xeric substrate, it is logical that almost exclusively hygrobiotic species use them as prey.

Xerobiotic (desiccation-tolerant) species constitute with ~82% the majority of the large genus *Orbilia*, and with ~35% a smaller part of *Hyalorbilia*. They are also represented by the small, purely xerobiotic genera *Lilapila*, *Lecophagus*, and *Amphosoma* (see Tab. 56). Within *Orbilia*, many of the small to large subgroups are purely xerobiotic: sections *Lentiformes*, *Habrostictis*, *Aurantiorubrae* (with exception of series *Hyalinia* and *Xanthoguttulatae* p.p.), *Hemiorbilia*, and *Ovoideae*, and series *Microsomates* of section *Orbilia*.

There exists a distinct tendency of xerobiotic *Orbiliomycetes* and also other groups of discomycetes to have small apothecia and small excipular cells, but exceptions confirm the rule. In any case, xerobiotic species frequently possess rather large ascospores and/or larger asci which are often multispored, a phenomenon which seems to be related to spore dispersal in xeric habitats (see p. 152). The smaller-sized excipular cells might be a result of smaller apothecia, but certainly not a precondition for the ability to withstand desiccation. This is demonstrated by some desiccation-tolerant species with large apothecia and excipular cells, such as *O. anigozanthi* and *O. carpoboloides*. The fact that large asci are exclusively found in xerobiotic species further indicates that small cells are not required for a long-lasting desiccation tolerance.

Apothecial colour in xerobiotic species of *Orbiliomycetes* is very often orange or rose-red, rarely whitish, yellow, lilaceous, olivaceous-, or purplish-black (see Tab. 3), and also their mycelia in pure culture are usually pale orange to salmon-pink, exceptionally somewhat brownish. These pigments are thought to protect from ultraviolet radiation, but might also serve in attracting insects (see p. 105).

Anamorphs of desiccation-tolerant species possess more or less short conidiophores and often branched conidia (mainly trinacrium-, also dicranidion- and dwayaangam-like etc.), though many others produce unbranched conidia (vermispora-, brachyphoris-, and lecophagus-like). To the present knowledge, none of these anamorph-typified genera produce organs for trapping nematodes, with exception of *Lecophagus* which mainly preys on rotifers and tardigrades, i.e., invertebrates that are well-known for their high desiccation tolerance (see p. 238, 288).

High species diversity in semideserts. Although fungal growth depends on the presence of water, it was highly surprising to experience that there exist also a high number of different *Orbilia* species in dry regions. About 77 species are known at present to exclusively or occasionally occur in desertic, semiarid to arid areas of North America, and 94 species in those of Australia (Tab. 33). Almost all of them are newly described in the present study. The genus *Orbilia* is remarkable among the non-lichenized discomycetes in showing an adaptation to very long periods of drought similar as in lichenized fungi. This high number of xerobiotic species along with the total absence of hygrobionts in semiarid to arid regions indicates that the genus *Orbilia* is very successful under conditions of water shortage. Various other groups of non-lichenized discoid ascomycetes, mainly *Helotiales*, *Ostropomycetidae*, *Sordariomycetes*, and *Dothideomycetes*, occur in these areas of low humidity, though with a seemingly lower species diversity.

Neglect of xeric substrates. A current belief is that non-lichenized ascomycetes are unable to survive during long periods of drought and, therefore, predominantly occur on or close to the forest floor. A similar misjudgement regarding aquatic hyphomycetes occurring solely in streams and lakes was mentioned before. The resulting unbalanced collecting activities are responsible for an overrepresentation of hygrobiotic species in official herbaria, such as *Hyalorbilia inflatula*, *Orbilia auricolor*, *O. luteorubella*, *O. rosea*, *O. sarraziniana*, *O. tremulae*, and *O. xanthostigma*, whereas similarly common xerobiotic species are often only sparsely present (e.g., *O. vinosa*, *O. eucalypti*) or almost entirely absent (e.g., *O. aprilis*, *O. euonymi*).

Collecting xeric substrate was practised by some authors of the 19th and first half of 20th century, e.g., by Fuckel, Rehm, and Velenovský, who frequently reported desiccation-tolerant discomycetes on dry branches. Nevertheless, xeric substrate was and still is strongly neglected by many workers all over the world. As a result, most of the taxa, particularly inoperculate discomycetes, recognized until now have been collected on hygric substrate, and many ecological assessments almost completely neglect xerobiotic discomycetes.

The following examples illustrate this situation concerning orbiliaceous fungi. The five species of *Orbilia* described by Dennis's (1978) British Ascomycetes are all desiccation-intolerant. In Arnolds et al.'s (1984) checklist of the Netherlands macrofungi only two out of eight species are xerobionts. Spooner's (1987) work on Australasia (including Melanesia) presents six hygrobiotic orbiliaceous species (tentatively included is the type of *O. flexispora*) and two which are xerobiotic, viz. *Orbilia vinosa* and *O. ?carpoboloides* (type of *Habrostictis decipiens*). Korf (1992) listed in his preliminary treatment on Macaronesia besides eight ± hygrobiotic taxa only one (as *O. occulta*), which represents a mixture of two species which are clearly xerobiotic, *O. euphorbiae* and *O. pisciformis*. Only a few recent reports (Karasch et al. 2005, Priou 2005) draw attention to desiccation-tolerant *Orbiliomycetes*.

One of the reasons why the ecological group of xerobiotic discomycetes has so frequently been overlooked, even in temperate regions, is that collectors are usually not on expedition during rainy weather and, therefore, do not recognize dry shrunken apothecia on dead attached branches. Mycological forays are often in want of enough rain, so collectors are focused on fungi occurring at sparse localities where the substrate on the soil remained moist. The aesthetic appearance of fresh discomycetes in contrast to the less attractive dry apothecia is surely another reason to search mainly on the forest floor. Desiccation-tolerant fungi are indeed better recognized in the field after a rain, or during fog and dew in the morning, and it is another little-known fact that dry apothecia of some helotialean or ostropalean discomycetes on xeric substrate sometimes need to be submerged in water for quite a long time (about 5 min) in order to become completely hydrated and exposed.

A main reason for the lack of xerobiotic *Orbiliomycetes* in herbaria is that many species form scattered, minute apothecia ranging often only between 0.1 and 0.5 mm in the hydrated state. Often, they are strongly retracted or closed when dry and then almost invisible, even under a 20× hand lens. Therefore, promising substrate needs to be cautiously scanned in the laboratory under a dissecting microscope, preferably in the rehydrated state at a magnification of 10–20×, illuminated by a strong daylight lamp. In addition to the loss of essential characters in old herbarium material, all this explains why the great bulk of species diversity in *Orbiliomycetes* has so far been missed worldwide.

How long do cells remain viable in the dry state? The period of time a population remains viable in all of its parts, either when kept in the herbarium or during drought outside, depends on the aridity to which the species is adapted. In collections of xerobiotic species from temperate or montane-boreal regions, living asci can still be found some weeks or months after being sampled, and in species from deserts even after 1–3 or rarely 4 years. After 5 years deposit in the herbarium we have never found living asci, paraphyses or conidia of *Orbiliomycetes*. However, in *Orbilia austroobtusispora* and *O. pilifera* many cells of the ectal excipulum were still viable after 7.5 years. Ascospores often show the highest tolerance, the maximum observed in the present study being again *O. pilifera* with 7.5 years.

High desiccation tolerance of asci was also noted in the present study in some other classes of *Ascomycota*, e. g., in *Patellaria* '*andina*' (20–34 months), *Nitschkia broomeana* (17 months), or *Schizoxylon argentinum* (14 months). Members of *Lecanoromycetes*, however, were dead after about 9–12 months, either in all parts or at least regarding their asci, whenever examined during this study. Baral (1992: 378) gave a few examples of desiccation tolerance of asci and paraphyses, with a maximum of eight months in *Lecanora conizaeoides*, but at that time the high tolerance of many *Orbiliomycetes* was as yet unknown to him.

Ascospores of many ascomycetes are able to survive very long periods of drought, irrespective of being hyaline or brown. An extraordinary tolerance of hyaline ascospores was observed in *Patellaria atrata* and *P. andina*, being viable after 6–7.5 years, and also in *Sarcoscypha* spp. they survived 4–8 years (Baral ined.). Long time survival of spores was also addressed by Nguyen (2013), but his concern was to test basidiospores of ectomycorrhizal species deposited under moist condition in soil, resulting in viable spores after min. 6 years.

Ascospores and basal cells of the ectal and medullary excipulum are usually the most desiccation-tolerant parts of the teleomorph. But also the mycelium and the anamorph including their conidia may show a considerable desiccation tolerance. This is astonishing especially in those orbiliaceous species with staurosporous conidia which are currently brought in relationship with aquatic habitats. Such 'terrestrial Ingoldian' conidia are adapted to water transport on xeric substrate during rain and, therefore, need to be able to survive periods of drought. Likewise, conidia of *Lecophagus* exhibit a rather high desiccation tolerance because they are formed in habitats (e. g., periodically dry ponds, mossy soil, air-exposed bark) that are subjected to alternate drying and wetting. Trinacrium-like conidia in samples from mediterranean Europe were viable after 36 months (*O. hesperidea* H.B. 6468a, *O. pleiogambelii* H.B. 6482) or 32 months (*O. vinosa*, H.B. 9084a). Likewise, vermispora-like conidia from subtropical semiarid North America survived 30–32 months (*O. carnegieae*, H.B. 7764f), from tropical subhumid Australia 15 months (*O. euphorbiae*, H.B. 7295), and from mesomediterranean Europe 32 months (*O. aurantiorubra*, H.B. 9087a). As a rule, ascospores and conidia in specimens from ± temperate humid zones are less desiccation-tolerant. For example, ascospores and vermispora- or trinacrium-like conidia collected in Luxembourg were still viable after two (*O. aurantiorubra*, H.B. 6251) or three months (*O. vinosa*, H.B. 6201b), but possibly not after much longer periods.

In hygrobiotic species the propagules may often withstand desiccation for several weeks and even years although their apothecia usually die off within less than a day. Conidia survived 7–10 days (*O. xanthostigma*, *O. atlantis*), rarely 2–2.5 months (*O. auricolor*, *O. crenatomarginata*), ascospores about 2 (*O. xanthostigma*) or 3–4 weeks (*O. epipora*, *O. dryadum*), rarely 27 months (*O. crenatomarginata*) or over 3 years (*O. tremulae*). Also in semiaquatic species some ascospores were still viable after 2 weeks (*O. luteorubella*) or up to 10–21 months (*O. sarraziniana*).

Can viability of cells be maintained over a longer period of time? A few experiments were undertaken to maintain viability by periodical rehydration of pieces of xeric substrate with desiccation-tolerant apothecia. Two effects were observed: (1) immature apothecia may attain maturity when kept moist over a period of 1–2 weeks, and (2) vitality is maintained for a longer timespan compared to the continuous storage in the herbarium. In *O. velutina* and further ~10 associated *Orbilia* spp. from subtropical (semi)arid Australia we were thus able to study fully viable mature ascomata more than 4.5 years after sampling of the dry *Eucalyptus* branches (H.B. 9772). However, their ascertained tolerance without intermediate hydration was also in the range of 3.5 years. Under natural condition of rare periodical hydration one may assume that such highly desiccation-tolerant apothecia persist periods of more than 5 years from initial stages up to mature apothecia.

Ultrastructural or chemical basis of desiccation tolerance. When viewed under the light microscope, no morphological traits characterizing desiccation-tolerant cells can be recognized (Baral 1992: 379). Strong variance in cell wall thickness or vacuole size is observed in both tolerant and sensitive taxa. At an ultrastructural level, concentric bodies, which are globose structures of ~0.1–0.3 µm diam. with an electron-translucent core, were merely found in fungi being tolerant to periodical drying (mainly mycobionts of lichens, rarely non-lichenized fungi), and were thought to function against drought stress (Classen et al. 2000: 317).

Desiccation tolerance appears to originate from the chemical composition of the cytoplasm. The presence of polyols (polymeric alcohols) that serve in protecting macromolecules during desiccation might be important for the survival of cells. If the pool of polyols is depleted below a critical level, then recovery from desiccation is not possible (Bewley 1979: 203).

Terminology around dry fungal habitats. There is some controversy in terminology about the adaptation of fungi to water stress or the availability of water, which led to confusion in the past. Two very different adaptations occur. (1) As discussed above, a majority of fungi form their sporocarps in periodically dry microhabitats, involving complete desiccation of the protoplast of all its cells. This means that the fungus dries out when the conditions become dry and resumes growth when it gets rehydrated. The habitat of such fungi is characterized by an extreme variance in water supply, with the periods of drought often much longer than those of full hydration. (2) Various members of *Saccharomycetales* and *Eurotiales* show an osmotic adaptation, i. e., the fungus is able to grow on substrates (e. g., preserved food) with a high concentration of osmotically active solutes such as salts or sugars. In such habitats the water is constantly available over the time, but a higher concentration of solutes within the cells is necessary to facilitate absorption of water by the fungus.

We here adopt the term **desiccation-tolerant** (= poikilohydric or poikilohydrous, = poikiloxerophytic, = drought-tolerant, = xerobiotic) for case (1). It was introduced by Bewley (1979: 196) and is in current use for both fungi (especially lichens, see Kranner et al. 2008) and plants (especially bryophytes, see Oliver et al. 2005, Proctor et al. 2007, but also higher plants, see Alpert & Oliver 2002). For case (2) the term **xerotolerant** is in use for fungi being able to grow at a water activity below 0.94, which corresponds to an NaCl solution above 10 % (in comparison: seawater has 3–5 % NaCl) or a glycerol/saccharose solution above 30 %/45 %. The lowermost value at which such xerotolerant fungi can grow lies around 0.65–0.7 = ~ 30–40 % NaCl or ~ 60–65 % glycerol. The term **xerophilic** refers to species showing their optimum growth under such a high osmotic pressure (Brown 1978, Pitt 1975). These fungi are economically important as some of them cause huge risk of product loss. The term **drought-resistant** (drought-avoiding) is used for desiccation-sensitive perennial plants such as succulents, which are adapted to arid conditions by strong reduction of transpiration (evaporation) by a thick cuticle and a reduction of the assimilative surface, often coupled with water storage organs. Water storage is also a strategy of jelly fungi, but since they have no cuticle they can only somewhat postpone complete desiccation and will die off during long-lasting drought.

The term xerotolerant was misapplied by Baral & Marson (2001), Baral et al. (2009), and Unterseher et al. (2012) in the sense of desiccation tolerance. In the present study the term **xerobiotic** is used as an equivalent to desiccation-tolerant, although it has a wider meaning which includes drought-resistant plants (xerophytes). Desiccation tolerance is also circumscribed with the term **anhydrobiosis**, which is a subcategory of **cryptobiosis**. Cryptobiosis is defined as hidden life (suspended animation) caused by cessation of metabolism (see Clegg 2001), and also includes cryobiosis (frost), osmobiosis (high solute concentration), and anoxybiosis (lack of oxygen).

Phylogeny of desiccation tolerance. The formation of apothecia on attached, periodically dry substrate and the prerequisite for such an adaptation, the desiccation tolerance of the entire fungus, is probably an ancient, plesiomorphic characteristic within the *Orbiliomycetes* and has been retained in a vast number of taxa. This assumption results from another hyphothesis: ascus apical thickenings, which are exclusively found in desiccation-tolerant taxa, are probably plesiomorphic within the class (see p. 55).

Hygrobiotic species of *Helotiales* typically possess spores consistently oriented with their broader end towards the amyloid ascus apex, whereas many but not all xerobiotic *Helotiales* have lost the amyloid apical ring and sometimes show inverse orientation of the lowermost spores. The reason for this regression seems to be that spore discharge needs not be as efficient at levels of stronger air currents (see p. 63). Within the *Orbiliomycetes* the asci are inamyloid across the class, and inverse spore orientation occurs in most of the species, irrespective of their apothecia being desiccation-tolerant or not. It seems imaginable that those orbiliaceous species, which have switched to permanently moist habitats on the ground, were unable to newly invent amyloid wall structures. Perhaps therefore, they have maintained the peculiarity to form a compact spore cluster in which inverse orientation is not a disadvantage regarding effective ejection.

Geographic distribution

Considering the ambiguous taxa concepts in earlier times and the frequency of detecting novelties during our research, the knowledge about geographic distribution and climatic preferences of *Orbiliomycetes* is still highly fragmentary. The class as a whole is undoubtedly ubiquitary, being omnipresent in almost every climatic region of the world. *Orbiliomycetes* obviously play a dominant role on xeric substrate, with about 430 xerobiotic species known at present, but is also well represented on mesic and hygric substrate, especially when including the many nematode-destroying species without a known teleomorph. Truly aquatic members are unknown, however, while a few taxa are semiaquatic, i. e., temporarily flooded.

We have supplied distribution maps of most of those species with at least about 5–10 records. A high number of species were only rarely recorded, which might suggest that they are threatened or almost extinct. However, their seemingly rare occurrence is to the most part due to lack of exploration. The high number of existing species, the difficulty in detecting them, and their manifold taxonomic problems make research on distribution very time-consuming. Hence, most of the rarely reported taxa undoubtedly display a much wider occurrence and higher frequency than the present data suggests. Although suitable biotopes are being destroyed wherever humans settle or industry is established, it appears difficult with such minute organisms to demonstrate a real threat for any of the species.

Among the larger deserts of the world, only those of Australia and North America were systematically explored in the present study. In addition, detailed research was done by L. Quijada on semi- to hyperarid low- and highlands of the Canary Islands and by R. Tena and J.P. Priou and others on semiarid low- and highlands of Spain. Collections from desertic regions of Middle and South America, Asia, and mainland Africa were only occasionally available, but their similar vegetation types strongly suggest that they house a comparably high species diversity of *Orbiliomycetes*. Comprehensive studies have been done by us and others on the semihumid, (sub)mediterranean belt of southern Europe and southwestern Australia. Among the (sub)tropical ± humid regions mainly those from southern China and to a lesser extent those from Middle America have been explored by different workers.

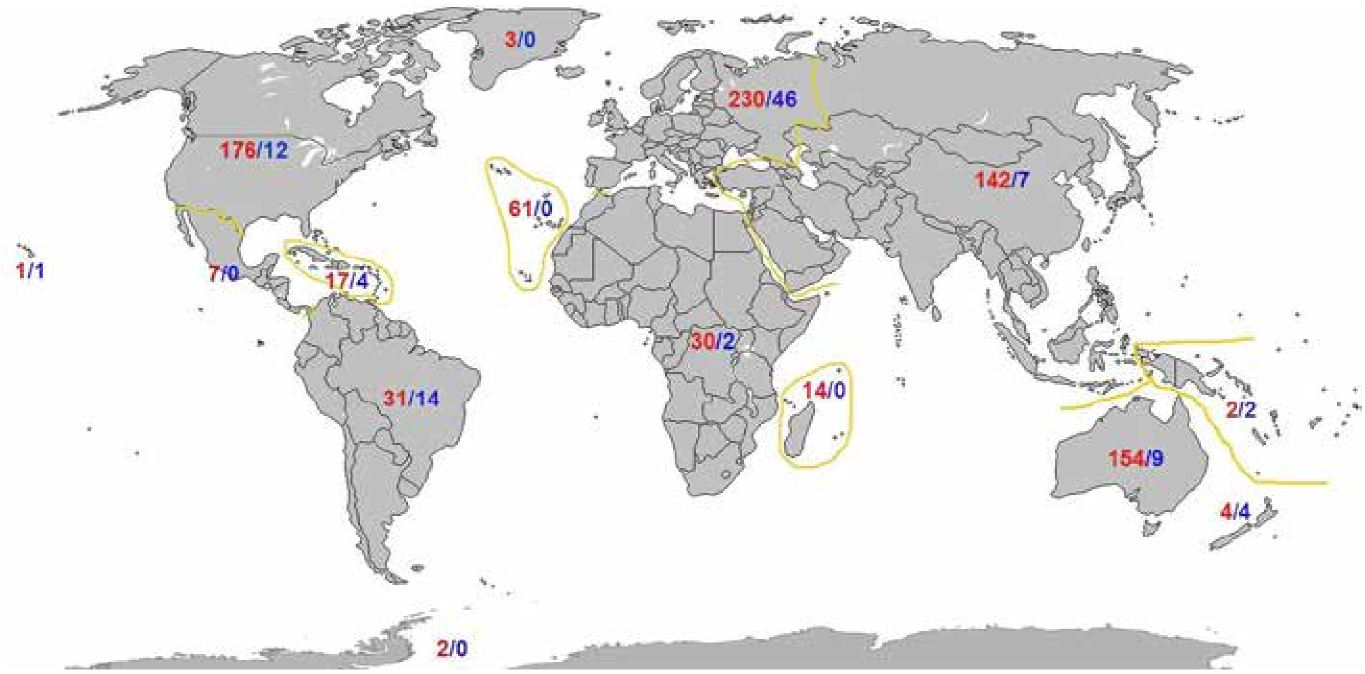


Figure 127: Approximate number of species with a known teleomorph accepted in this monograph (in red), in comparison to species recognized prior to 1989 (in blue), recorded in the different continents and archipelagos. Included are those species for which an apothecial state is known, but also a few so far purely anamorphic taxa which are treated with collection data in this study (see also p. 3, Fungal material and Appendix 2). The red numbers include also our provisional and unnamed taxa. See also Fig. 1.

Distribution and diversity in different continents and climatic regions. – **Local species diversity**. Most local treatments which include members of *Orbiliomycetes* contain rather low numbers of orbiliaceous species with known teleomorph. These numbers are generally far below of what can be expected to occur in any region with a minimum diversity of phanerogams. Vital characters have often not been used for identification in these works, therefore, some of the older reports include species which do not even belong to the class. Besides paucity of collecting, the main reason for the seemingly low species diversity is the neglect of semihumid to arid plant communities but also of xeric substrate in more or less humid regions.

In the following, the general distribution of *Orbiliomycetes* and the investigation rate of the different continents and countries is briefly treated. These considerations almost exclusively refer to collections of the teleomorph. Orbiliaceous anamorphs have variously been isolated and comprise numerous species without a know teleomorph, mainly from North America (e. g., Drechsler 1934–1950; Barron 1979–1991), Poland (Jarowaja 1968–1971), Russia (e. g., Mekhtieva 1967–1979; Soprunov 1951–1958), Japan (e. g., Matsushima 1975–2005), China (Yu et al. 2014), and Australia (e. g., Park et al. 2002).

Distribution patterns. A number of species were found to be cosmopolitan, i. e., they are known from all continents of the world. Examples are *Hyalorbilia inflatula* s.l., *Orbilia carpoboloides*, *O. corculispora*, *O. delphinus*, *O. eucalypti* s.l., *O. euonymi*, *O. lentiformis* s.l., *O. luteorubella*, *O. multiserpens*, or the *xanthostigma-leucostigma* complex. Many species are so far exclusively known from one continent, for instance, the European *O. aprilis*, *O. quaestiformis*, and *O. polyspora*. However, very similar taxa of these three species occur in Australia: *O. nothoaprilis*, *O. pleioquaestiformis* and *O. plurililacina*, respectively. But this situation may change when new collections become available. The very common *O. aprilis* was recently discovered in Northern America, but molecular data gained from one of the two samples indicates a cryptic sibling. *O. corculispora* was first detected by us in Australia, but later it was found to be rather widespread in mediterranean and atlantic Europe and to occur also in southern Africa and eastern Asia. However, their rDNA shows pronounced deviations among Australia, Asia, and Europe.

To the present knowledge, about 100 species have exclusively been recorded in Australia. However, to speak here of endemism would be premature, because many of them were rarely found and some have unclarified siblings in other continents. Among the six known species with black apothecia, three (*Amphosoma atroolivaceum*, *Orbilia patellarioides*, *O. olivacea*) were so far only recorded in Europe and the other three (*O. pileosoma*, *O. atrolentiformis*, *O. purshiae*) only in the Rocky Mountains and Colorado Plateau of North America, so one may assume that they are restricted to a continent. The genus *Lilapila* seems to be endemic to mountainous regions of central and southern Europe, but might well also occur in similar conifer forests of Northern America and Asia, being easily overlooked due to its dark apothecia growing on blackened resin.

Species diversity in different climatic zones. The total number of orbiliaceous species recorded during our research as well as the approximate proportion between xero- and hygrobionts differ among the different climatic zones. Tab. 33 provides an overview of the species diversity in four more intensely investigated regions of the world and also indicates the lack of collections in some of their climatic zones.

Apart from the European nemoral to boreal humid zone with around 170 species recognized at present, a surprisingly high species number was observed in desertic, semiarid to arid wood- and shrublands of the world, e. g., about 94 in Australia and 77 in North America. Due to the low annual precipitation and short periods of moisture, almost all species from desertic areas belong in the category xerobionts. However, the relatively low number of collections, ranging in comparison with the species numbers at 2.5 : 1 in North America and at 2.2 : 1 in Australia,

Table 33. Approximate number of xerobiotic and hygrobiotic species of *Orbiliomycetes* (before and after slash) and total number of records in 4 thoroughly explored regions in relation to 7 main climatic zones, * = zone requiring much more sampling, – = region lacking this climatic zone. Remarkable is the low number of known species in the (sub)tropical humid zone. Note the absence of hygrobiotic species in (semi)arid zones. Species numbers for North America and Australia are most likely far too low, particularly in semihumid to arid zones, when considering the roughly 10-fold higher record numbers in Europe.

Climatic zone	Europe		Macaronesia		North America		Australia	
	xerobiotic / hygrobiotic	records	xerobiotic / hygrobiotic	records	xerobiotic / hygrobiotic	records	xerobiotic / hygrobiotic	records
temperate to boreal humid	113/58	4546	–	–	68/25	246	6/8	15*
temperate subhumid	7/0	9*	–	–	59/0	132	–	–
(sub)mediterranean ± semihumid	70/15	663	25/2	47	1/0	2*	55/0	145
temperate semiarid to arid	–	–	–	–	53/0	125	–	–
(sub)tropical semiarid to arid	18/0	30*	23/0	88	41/0	94	94/0	208
(sub)tropical subhumid (savannah)	–	–	2/8	23	3/2	5*	37/0	55*
(sub)tropical humid	–	–	3/11	25	9/9	27*	15/8	28*
Total	**~173/57**	**5248**	**40/12**	**183**	**153/29**	**628**	**139/15**	**451**

illustrate our experience that about every second or third collected population belongs to new species. In comparison to the much more intensely investigated European continent with a relation of over 26 : 1 for the nemoral to boreal humid zone, the actual diversity in desertic areas of North America and Australia is most likely much higher.

Also in semihumid (summer-dry), (sub)mediterranean, more or less subtropical sclerophyllous wood- and shrublands the number of xerobiotic taxa by far exceeds that of the hygrobionts which can only be found during the rainy winter season. In southern Europe about 70 xero- and 15 hygrobiotic species were recorded, and in southwestern Australia 55 xero- but no hygrobiotic species, no doubt because hygric substrate was neglected. The relation between collected populations and species lies in semihumid southern Europe at 7.8 : 1, in Australia at 2.5 : 1, and in Macaronesia at 1.8 : 1.

In savannah-like (winter-dry), monsoon-influenced, (sub) tropical subhumid regions the xerobionts play a considerable role. Hygrobionts have rarely been encountered because substrate on the ground was ignored in this field work. The species number in northern Australia was with 37 xeriobionts and no hygrobionts comparatively low, perhaps due to activity of termites, but the only 1.5× higher number of collected populations suggests a higher diversity in these zones.

Humid (winter-dry), monsoon-influenced evergreen broad-leaved forests in the subtropics display a high diversity of hygrobionts, but xeric substrate was largely neglected by collectors. Such forests have been intensely explored in the southeast of Asia (~65 hygrobionts and ~15 xerobionts), and to a much lesser extent in a regional area in northeastern Africa (subtropical afromontane Ethiopian highlands, nine spp., probably all slightly xerobiotic). Species diversity seems thus rather high in the humid subtropics. The actually existing species number is probably much above the current level, especially regarding xerobionts which were only occasionally encountered. It appears also that drought tolerance in this environment is comparatively low, often lasting only a few weeks.

In tropical rainforests the worldwide number of orbiliaceous species known at present ranges around 60, about 18 of which being xerobionts. The relation between collected populations and species lies here at 1.2–2.7 : 1. Most of the records come from regions with a wet and dry season. Yet, it seems probable that rainforests with their high plant diversity house many more species. Tropical humid areas are not easy to explore, especially with respect to vital taxonomy, therefore, many of the species from there are only known in the dead state. Because of the paucity of collectors in the humid tropics, only 23 species are so far known from northeastern Australia (~15 xerobiotic), 20 from America (~3 xerobiotic), and 14 from Africa (12 from Comoros, 2 from Senegal; ~5 xerobiotic). Orbiliaceous xerobionts might occur in the uppermost, periodically dry canopy, which is so far completely unexplored in regard to these fungi. Xerobiotic perennial basidiomycetes are frequent in the humid tropics on hanging branches and climbers, especially on open sites being exposed to sudden changes of humidity and temperature (Nunez 1996).

The very low species diversity observed in other ± humid, temperate to alpine-subarctic regions of the world is undoubtedly due to insufficient sampling. Up to now, only 6 xero- and 8 hygrobionts are known from cold- to warm-temperate southeastern Australia, 13 xerobionts from continental highlands of western Mongolia, 3 xerobionts from the subarctic tundra of Greenland (*O. canadensis*, *O. eucalypti*, *O. flagellispora*), and 11 xero- and 2 hygrobionts from (hemi) boreal Canada and Alaska. Much better explored is the humid zone of the Rocky Mountains and Colorado Plateau in the United States with 25 xerobionts, and that of Scandinavia and European Russia with about 22 xero- and 12 hygrobionts. Particularly rich is the knowledge about the orotemperate to orosubmediterranean Alps with at present about 56 xero- and 12 hygrobionts. The lack of hygrobionts in some of these regions is due to the neglect of hygric substrate.

Restriction to a climatic zone. Each climatic zone of a continent or geographical area exhibits its own species composition, because a majority of species show a more or less strong adaptation to climatic conditions, and because of the geographical isolation. For instance, more or less humid, cold-temperate to boreal forests in the region of the Rocky Mountains and Colorado Plateau strongly differ in their species diversity not only from semiarid shrublands at lower altitude in the same region, but also from cold-temperate to subtropical humid forests of eastern North America. As an example, *Orbilia spermoides* was so far only found in montane to subalpine conifer forests in mountain ranges of the Colorado Plateau and Chihuahuan Desert and in an orosubmediterranean conifer forest of the Southern French Alps, whereas the closely related *O. occulta* is only known at present from the Appalachian Mountains and its lowlands. Likewise, a number of species were only found in atlantic or sometimes also mediterranean areas of Europe (e.g., *Orbilia atlantis*, *O. rubrovacuolata*, *O. corculispora*, *Hyalorbilia ulicicola*), though some of them also occur in Macaronesia, Asia, and/or Australia.

Some species exhibit a rather wide ecological amplitude by occurring across very different climatic zones. For example, the distribution area of *O. vinosa* covers within Europe (oro) temperate, planar to subalpine and boreal, humid, continental to atlantic but also sub- and eumediterranean climates, and also *O. euonymi* shows a comparable lack of climatic preferences. A similar ubiquitous distribution is shown by *O. aprilis*, but this species appears to avoid both subalpine and boreal zones. Many further species appear to be similarly cosmopolitan, e. g., *O. flavida*, *O. trapeziformis*, and *O. obtusispora*.

Some species are more or less adapted to orotemperate or orosubmediterranean zones of the Alps, Carpathians, and mountain ranges of southern Europe. Most of them are confined to xeric coniferous wood and bark or particularly to resinous wounds, e. g., *Lilapila* spp. were observed at an altitude of 800–1820 m (45 ×), *O. patellarioides* at 860–1830 m (17 ×), *O. sphaerospora* at 890–1615 m (11 ×), and *Amphosoma resinicola* at 925–1780 m (10 ×). The latter was also observed in the boreal Rocky Mountains, whereas the distribution area of the closely related *A. atroolivaceum* extends down to submontane regions of central Europe (350–1780 m, 43 ×). A high amplitude similar to the latter species is observed in *O. flagellispora* (40 ×) which was found at colline up to subalpine, preferably orotemperate and orosubmediterranean, but also boreal areas of Europe, but single collections in arctic Greenland (250 m), boreal Canadian Rocky Mountains (1165 m), and subtropical semiarid Mexico (350 m, type) indicate a very wide distribution. *O. alpigena* (16 ×) on gymnosperm wood is so far only known from montane to subalpine central and southern Europe at 870–1760 m, whereas *O. montigena* (14 ×) on angiosperm wood shows a wider amplitude which ranges from colline to subalpine central and southern Europe (130–1585 m) but also hemiboreal northeastern Europe (150 m).

Semihumid, (sub)mediterranean areas with mild humid winters and hot and dry summers house a number of species which are more or less adapted to this climate. Some of them were so far only detected within Europe, e. g., *O. polyspora* and *O. myriosphaera*. Others were also recorded from northern Africa, Macaronesia, North America, or Australia (e. g., *O. bicknellensis*, *O. gambelii*, *O. pleiogambelii*, *O. hesperidea*, *O. microserpens*, *O. multiurosperma*, *O. pleiogambelii*, *O. serpentina*). A disjunct occurrence was noted for the rare *O. cercidicola*, which was repeatedly collected on *Cercis* at the type locality in the submediterranean maquis of southern France, but later also on *Ulmus* in the warm-continental subhumid Volga floodplain forests in southwestern Russia.

Three cosmopolitan species merit special attention. *O eucalypti* s.l. occurs in all ecozones of Europe, from thermomediterranean to subalpine and oroboreal, and from atlantic to subcontinental (the rareness in continental temperate zones is probably due to lack of data). Also in Macaronesia it occurs across all climatic zones. In Australia the species was frequently recorded by us in the subtropical semihumid southwest, whereas in North America it came to our attention only by a few samples from the cold-temperate humid Rocky Mountains and from the mild-maritime semihumid (types of *Dicranidion fragile* and *O. eucalypti*) and subtropical semiarid pacific west of California and Mexico. Also *O. corculispora* was found all around the globe, being recorded in western and eastern Australia, southeastern Asia, southeastern Africa, Macaronesia, and also in southern and western Europe. However, it shows a preference for an oceanic climate and extends from subtropical semiarid and semihumid (mediterranean) to mesotemperate humid. Likewise, the cosmopolitan *xanthostigma-leucostigma* complex occurs from tropical to subalpine-boreal zones all over the world, and its absence in semiarid to arid areas is due to a low tolerance of its apothecia to drought.

Rareness and endangerment, **suitable biotopes**. Natural plant communities with a high diversity of phanerogams and a low amount of human impact provide the basis for a rich diversity of *Orbiliomycetes* and other ascomycetes. Profitable biotopes lack severe forestry intervention during 20–30 years as a minimum, in order to preserve trees and shrubs at all age classes and with plenty of dead branches in all stages of decay, either attached or on the ground. Usually, fungal diversity is highest when a tract of forest land in a humid region remained untouched over some decades. In more arid regions this minimum period of time probably lasts longer. Such natural wilderness, even if small-sized, may be uncomfortable to enter because of thorn thickets requiring protective clothes.

Artificial plant communities in parks, hedgerows, botanical and private gardens etc. may also provide interesting collection sites. However, the current practice of gardeners and arborists to remove all dead parts of a plant is fatal to all saprobic fungi on both xeric and hygric substrate. Current nature protection activities preserve the agricultural landscape by regularly removing bushes and shrubs or cutting reed marshes, thereby completely eliminating the natural circuit of these plants that involves the formation of dead plant substrate. These activities aim at the protection of flowering herbs which represent the basis for insects and birds. Although open vegetation provides a biotope for many organisms, species diversity in a wilderness must not be lower but consists of a very different community of usually less spectacular species with a more hidden lifestyle.

Orbiliomycetes are threatened especially in poor countries with a dry climate, in which inhabitants depend on the sparsely occurring fire wood. A strongly predominant agriculture in humid lowlands often leaves only small remnants of forest as refugia for the native flora and funga and, therefore, threatens many of the more rare and adapted species. But also natural fires often destroy large areas of xeric vegetation in subhumid to arid regions, and the recolonization of such areas may take many decades until enough dead plant parts become available. Man-made fires, the conversion to farmland, and the increase of industry, human population, and tourism reduce the number of high quality biotopes.

Out of about 470 species treated in this monograph (by disregarding provisional species without a valid name), 118 were recorded only once, 63 twice, 48 three times, and only 126 more than ten times. It appears, therefore, that a high proportion of these 470 taxa are comparatively rare. However, a majority of the rarely collected taxa are newly described here based on recent collections, and their rareness might be due to a geographical restriction to a rarely visited area rather than a true rareness. Some old taxa reported about 80–200 years ago might be extinct, as they have never been recollected, but any conclusion about species extinction of such minute fungi remains hypothetical.

The following 15 species published before 1989 are only known with certainty from the type collection (year of collection in brackets): *Hyalorbilia anonyma* (1892), *H. andina* (1892), *Liladisca acicola* (~ 1866), *Orbilia acuum* (1927), *O.*

coccinella (~1825), *O. cookei* (1873), *O. cyparissias* (1933), *O. disseminata* (1892), *O. flexispora* (1964), *O. minutispora* (1924), *O. neglecta* (1897), *O. regalis* (~1878), *O. rubella* var. *minor* ≡ *O. rehmii* (1877–78), *O. saccharifera* (~1875), and *O. terrestris* (1978). *O. coccinella* might be restricted to the north of Scandinavia and, possibly therefore, it has been overlooked in later years. *O. terrestris* occurred in the Pamir Mountains and *O. neglecta* in Java, regions which are rarely visited by collectors. Five species derive from cold-temperate humid central Europe and three from warm-temperate humid eastern North America, therefore, they should not have escaped notice in recent years. But collectors of small ascomycetes are few, particularly regarding xeric substrate, on which at least four of them grew.

Geographic and climatic preferences, examples of plant communities

In the following, a historical review is given for each continent on the collecting activities in *Orbiliomycetes*, often with a discussion of the different climates and vegetation types in which they were found. Best explored are Europe and Macaronesia, in which emphasis has equally been placed on hygro- and xerobionts, followed by North America and Australia, where hygrobionts appear to be undercollected. Intensely explored is also eastern Asia, though mainly for hygrobionts. The mentioned species numbers for each country or region neglect most of the unillustrated or otherwise unverified literature reports as well as unexamined collections in official herbaria. These numbers include only a few of the purely anamorphic or DNA isolates because these were not the subject of the present study and would have been difficult to estimate for each region (see also Fig. 127 & Appendix 2).

1. Europe

By far the highest number of around 5300 collections were obtained in Europe, which can be considered as the best explored continent. This high number permits us to analyse the species diversity in the different climatic zones of the phytogeographically very diverse continent. Despite an approximately 3-fold overrepresentation of collections on xeric substrates, it can be assumed that the many diversely focused collectors provided a more or less balanced spectrum on species richness for each climatic zone.

In any case, species diversity was best explored in regions with a humid climate. Here the relation between collected populations and species ranges at 26.5 : 1, which illustrates the high rate of investigation in this continent. Apparently therefore, the number of recorded species of presently 171 is much higher than in the European mediterranean belt with 85 spp. and a relation of 7.8 : 1. As a consequence of the higher humidity, the number of xero- and hygrobiotic species lies in the humid areas in the relation of 2 : 1, compared to 4.7 : 1 in the mediterranean belt (Tab. 33).

A total of about 230 species have been recorded within Europe up to now (Fig. 127). To the most frequently recorded species (min. ~70 collections) belong the hygrobionts *H. inflatula*, *O. auricolor*, *O. crenatomarginata*, *O. rosea*, *O. sarraziniana*, and *O. xanthostigma* and the xerobionts *H. subfusispora*, *O. aprilis*, *O. aristata*, *O. aurantiorubra*, *O. carpoboloides*, *O. comma*, *O. eucalypti*, *O. euonymi*, *O. quaestiformis*, *O. trapeziformis*, *O. xanthoguttulata*, and *O. vinosa*.

When comparing the four main thermotypes (eumediterranean, submediterranean, temperate, boreal) and their subzones, the observed species numbers are rather similar in the four well-explored regions of Scandinavia, Germany/Switzerland/Austria, France, and Spain/Portugal, which all show a high variance of climatic zones. Differences between these four regions regarding a given thermotype might originate from insufficient sampling. In any case, the present data suggest that species numbers in the Iberian peninsula decrease from eumediterranean to temperate, but tend to higher numbers at higher altitudes, whereas orotemperate regions in central Europe showed less species than temperate regions, perhaps due to unbalanced sampling.

Most of the frequently collected species were found across more or less all thermotypes of Europe and that from atlantic to continental regions. Others showed a more or less pronounced restriction to a climatic zone. Three species are adapted to the mild, oceanic western part of Europe: *O. rubrovacuolata* is a (sub)atlantic species that occurs within Europe across four different thermotypes (St, Mt, Tt, Msm, see p. 15, Abbreviations). It is so far missing in the European eumediterranean belt, but was found in the mesomediterranean (Mt) zone of Macaronesia. Similarly, *O. atlantis* and *H. ulicicola* occur in three different thermotypes (St, Mt, Msm) in atlantic western Europe, but whereas *O. atlantis* is so far known from England and France, *H. ulicicola* was found in France and Spain and also occurs in the thermomediterranean (Tt) north and eumediterranean (Tm) southeast of Spain.

Some species showed a more or less strong adaptation to a thermotype. E. g., the meso- (Mt) to supratemperate (St) zone was preferred by *O. fraxini*, *O. luteorubella* (also Hb and Tb), and *O. orientalis* the orotemperate (Ot) and orosubmediterranean (Osm) zone by *O. arachnovinosa*, *O. subtrapeziformis*, and *O. delphinus* (the former two also oroboreal), and the eumediterranean zone by *O. desertorum* (Tm), *O. bicknellensis* (Tm, Mm), *O. rhamni* (Mm), whereas other also occur in more or less cooler regions: *O. microserpens* (Tm to Sm, also Ssm), *O. polyspora* (Mm, Sm, Msm, Ssm, rarely Osm), *O. pilifera* (Mm, Sm, Msm, also Ssm, Mt and St).

1a. Scandinavia, Balticum and northwestern Russia: Previous orbiliaceous reports from Scandinavia include those of Fries (1822: 146, 1849: 357) for southern Sweden, Sommerfelt (1826) for northern Norway, and Karsten (1861: 36–39, 1869: 106, 173–176) and Nylander (1869: 54–58) for southern Finland and northwestern Russia, with 6 hygrobiotic (*H. inflatula*, *O. epipora*, *O. leucostigma*, *O. luteorubella*, *O. tremulae*, *O. xanthostigma*) and 3 xerobiotic species (*O. coccinella*, *O. eucalypti*, *O. vinosa*) (names according to present reidentification). They mainly derive from the boreal zone, but probably also from the hemiboreal zone where Fries lived. Huhtinen (1992) described for a hemiboreal site in Finland *O. phragmotricha* (as *Orbiliaster paradoxus*).

This low number of ten species stands in contrast to unpublished sampling: particularly during three excursions to supratemperate Denmark and southern Sweden (2005–2007) and one to boreal Lapland (2010), various collectors (H.B., T. Læssøe, J.G.B. Nielsen, B. Spooner, W. Jaklitsch, P. Perz and others) strongly increased this number. Further recordings were made by O.E. Eriksson (Umeå, 2007, 2014), T. Dahl (Arendal,

Figure 128: **left**: Oroboreal humid *Betula pubescens* woodland with *Juniperus communis* and *Cornus suecica* at timberline, 870 m, Satsfjället, Saxnäs, Lapland, Sweden, 24.VII.2010, phot. H.O. Baral; attached branches of *B. pubescens* (*Orbilia eucalypti*, *O. arachnovinosa*, H.B. 9360) and *J. communis* (*O. cylindrospora*, H.B. 9398), fallen branches of *B. pubescens* (*Hyalorbilia polypori*, *H. inflatula*, *O. rosea*, H.B. 9361, 9362, 9410); **right**: ibid., *Picea abies* and *Betula pubescens* forest, 475–500 m, Lillälven waterfall, Bjurälven, 27.VII.2010, phot. H.O. Baral; attached branch of *B. pubescens* (*O. arachnovinosa*, H.B. 9375), fallen branches of *B. pubescens* (*Hyalorbilia inflatula*, *O. tremulae*, H.B. 9379).

2008–2012), S. Helleman (Norway, 2011–2012), T. Læssøe (Denmark, 2001, 2008–2020), G. Marson (Oslo, 2002), M. Pennanen (North Karelia, 2010–2013), K. Põldmaa (Finland, 1995), U. Söderholm (Tampere, 1994–1998) and others. From the Balticum, K. Põldmaa collected mainly on polypores between 1993–1997 (6 *Hyalorbilia* spp.). Samples from western Russia are especially those collected and studied by E. Popov between 2002–2012 (4 *Hyalorbilia* spp., 14 *Orbilia* spp.). A few older samples of hygrobionts from the Ural mountain range were reexamined here: from the oroboreal Ob river delta region east of the northern Ural (M. Saar and M. Murdvee, 1977, *O. cardui*, *O. sarraziniana*, *O. rosea*, *H. ?japonica*), the supraboreal middle Ural (A. Raitviir, 1973, *O. tremulae*, *O. leuco-/xanthostigma* s.l.), and the hemiboreal southern Ural (A. Raitviir, 1974, *O. crenatomarginata*, *O. sarraziniana*, *O. xanthostigma*).

A total of 48 species are now known from Scandinavia, about 60% of them being xerobiotic. The current number for Sweden is 29 (see Appendix 2). Because many of the taxa were undescribed, Eriksson's (2009: 117, 209) checklist contains only 12 species. When including, besides Scandinavia, the hemiboreal Balticum and boreal to supratemperate regions of northwestern Russia, the current species number is about 63. This high number is mainly due to numerous Russian collections of predominantly xerobiotic taxa, particularly by E. Popov. In Estonia only 6 *Hyalorbilia* spp. and 3 *Orbilia* spp. are known, almost all of them hygrobionts. The 7 *Orbilia* spp. from Latvia and Lithuania known to us are all but one molecular isolates from soil or coniferous wood (Menkis et al. 2006, 2012, 2015).

Within the boreal zone of Europe including the Ural mountain region, 12 hygro- and 22 xerobiotic taxa are known up to now. Among the four subdivisions of the boreal zone, only one species from the cryoroboreal subzone in Lapland came to our attention, the doubtful *O. inconspicua* on *Dryas* leaves, which also occurs in the cryorotemperate Alps and represents a mixture of two distantly related species. From the oroboreal subzone 15 species have been collected, all on woody substrates, mainly of *Betula* and *Salix*, with 9 hygrobionts (*H. inflatula*, *H. ?japonica*, *H. polypori*, *O. cardui*, *O. crenatomarginata*, *O. rosea*, *O. sarraziniana*, *O. tremulae*, *O. xanthostigma*) and 7 xerobionts (*O. arachnovinosa*, *O. aristata*, *O. canadensis*, *O. coccinella*, *O. cylindrospora*, *O. eucalypti*, *O. subtrapeziformis*). In the warmer supraboreal subzone only 3 hygro- and 3 xerobionts were found (including *O. flagellispora*, *O. tremulae*, and *O. vinosa*), which is probably a result of unbalanced collecting. In the thermoboreal subzone several species appeared that were absent in the cooler regions: a total of 7 hygro- (including *H. berberidis*, *O. auricolor*, *O. epipora*, and *O. luteorubella*) and 15 xerobionts were recorded (including *H. fusispora*, *H. juliae*, *O. aprilis*, *O. breviaristata*, *O. carpoboloides*, *O. comma*, *O. ebuli*, *O. filiformis*, *O. phragmotricha*, *O. plurivacuolata*, *O. quaestiformis*, *O. vitalbae*, and *O. xanthoguttulata*.).

In the hemiboreal zone, in comparison, 18 hygrobionts and 23 xerobionts are known at present. Some of these 41 species were absent in the boreal zone: among the hygrobionts these are, e.g. *H. fagi*, *H. polypori*, *H. tortuosa*, *O. crenatomarginata*, *O. mammillata*, and *O. oxyspora*, and among the xerobionts, e.g., *O. aurantiorubra*, *O. montigena*, *O. rubella*, and *O. siculispora*.

O. coccinella can be considered as a rarity of the boreal zone, being only known from the type collection in oroboreal Nordland. A restriction to the boreal zone can be assumed for *O. canadensis*, which was found in oroboreal Norway, subarctic Greenland, and boreal Canada. Various European species appear to prefer an orotemperate (altimontane to subalpine) and particularly orosubmediterranean climate, but only three

Figure 129: **left**: Supratemperate (cold-temperate) humid, colline *Aceri-Fraxinetum* with *Fagus*, *Alnus*, *Fraxinus*, *Acer*, *Allium ursinum*, *Anemone nemorosa* etc. on Knollenmergel, 410 m, Tiefenbach, Tübingen-Pfrondorf, Germany, collected between 1988–2012, phot. 27.V.2006, H.O. Baral; fallen branches and logs of *Acer pseudoplatanus* (*Orbilia leucostigma* H.B. 3543), *Alnus glutinosa* (*O. xanthostigma* H.B. 6745), *Tilia cordata* (*Hyalorbilia inflatula*, *O. eucalypti*, *O. crenatomarginata*, *O. dryadum*, H.B. 4726, 4727, 4738, 4894) and *Fagus sylvatica* (*O. sarraziniana*, H.B. 7000, 9707); **right**: orotemperate humid, subalpine spruce forest, 1550 m, Glaubenbielen, view to Alpoglerberg, Obwalden, Switzerland, 17.VIII.2006, phot. H.O. Baral; attached branches of *Picea abies* (*O. alpigena*, *O. flagellispora*, H.B. 8272).

of them were so far encountered in the boreal zone as well: *O. arachnovinosa*, *O. cylindrospora*, and *O. subtrapeziformis*.

1b. **Great Britain and Ireland**: Berkeley (1860: 370), Berkeley & Broome (1865, 1866, 1873), and Cooke (1871) recognized for Great Britain a total of 6 orbiliaceous species (all as *Peziza*): *H. erythrostigma*, *O. auricolor*, *O. carpoboloides* (as *P. lasia*), *O. leucostigma*, *O. vinosa*, and *O. xanthostigma*. Phillips (1887: 327–335, as *Calloria*) and Massee (1895: 143–149) raised the number to 10 by adding *H. inflatula*, *O. coccinella*, *O. luteorubella*, and *O. rubella*. Yet, the identity of some of them remains doubtful.

Nine orbiliaceous species were reported by Dennis (1978: 187, 196), 16 by Clark (1980b), 14 by Ellis & Ellis (1985: 11, 248, 267), and 21 in the checklist of British ascomycetes (Cannon et al. 1985: 97, 104, 168) when counting those taxa which we consider orbiliaceous. Included are *O. comma* described by Graddon (1977) and *O. dryadum* (as *O.* cf. *acuum*) reported by Kirk & Spooner (1984: 573). Webster et al. (1998) added a further species, *O. oxyspora* (as *O. fimicoloides*). Descals isolated *Anguillospora rosea* (= *O. rosea*) between 1974–1981 in England, Wales and Scotland.

At present (2019), 48 orbiliaceous species are known from the Britannic islands, 11 in *Hyalorbilia* and 37 in *Orbilia*. About 30 of them grew on ± xeric substrate. A majority were recorded in England, but only 4 species in Scotland and 3 in Ireland. Seven species of *Hyalorbilia* and 18 of *Orbilia* were gathered by E. Batten and S. Francis between 2001–2006 in the coastal lowlands of Suffolk or rarely Norfolk in eastern England, a region with an oceanic humid climate which ranges at the border between supra- and mesotemperate. Rarities or unique collections from there were *H. rotifera*, *H. ulmi*, and *O. battenii*. Remarkable was the repeated detection of the mediterranean *O. corculispora* at supratemperate sites, though often with ± subglobose spores and only rarely with the typical curved ones. Further records from England were made between 2011–2019 by N. Aplin (South East England), J.P. Priou (Wales), B. Thompson (mainly West Midlands), C. Yeates (Yorkshire) and many others, and by one of us (H.B.) during two forays in South Yorkshire (2011) and Cambridgeshire (2017). The mild climate of England supports occurrence of atlantic species such as *O. atlantis* and *O. rubrovacuolata*. The most frequently recorded species were *O. eucalypti* and the previously overlooked *O. aprilis*. One of the rare records was *H. lunata* from meso- and supratemperate sites, though its core area appears to lie in the mediterranean laurel forest of Macaronesia.

1c. **Germany**: Fuckel (1870, 1871, 1874) reported 5 orbiliaceous species for Hessen: *Liladisca acicola* (as *Pezicula*), *O. carpoboloides* (as *Habrostictis rubra*), *O. sarraziniana* (as *Calloria vinosa*), *O. xanthostigma* (as *C. chrysocoma*), and *Orbilia* sp. (as *Pezizella rubella*). Rehm (1891: 453–460) reported about 10 orbiliaceous taxa for Germany (see p. 194). For Brandenburg Rehm (1894: 1224) added *O. flavidorosella* and Kirschstein (1938) *O. auricolor* (as *Orbiliella armeniaca*). About 8 of Rehm's 11 taxa are xerobionts. From Baden-Württemberg Ade (1924) described *O. ?flavida* (as *O. paradoxa*) and Baral (1989) *O. septispora*, from Bayern Svrček (1987) *O. ebuli*, and from Oberfranken (Bayern) Beyer (1994, 1997, 1998) *O. aristata* (as *O. occulta*), *O. auricolor*, *O. septispora*, *O. rectispora* (as *O. luzularum*), *O. vinosa*, and *O.* aff. *cardui* (as *O.* [cf.] *rubella*). Krieglsteiner (1999: 268–272, 2004: 654–657, 2007) reported a total of 17 *Orbilia* spp. (*O. clavuliformis* as *Orbilia* sp. 1, *O. aprilis* as *Orbilia* sp. 2), 2 *Hyalorbilia* spp. (*H. inflatula* and *H. subfusispora*, the latter as *O. vitalbae*), and *Lecophagus ellipsoideus* (as *Orbiliaceae* sp.) from Mainfränkische Platten (northwestern Bayern) and Rhön mt. (border to Hessen and Thüringen), representing 11 xero- and 9 hygrobionts.

During the present study, almost 100 species have been recorded within Germany (see Appendix 2): *Amphosoma atroolivaceum*, *Hyalorbilia* (18 spp.), *Lecophagus* (2 spp.), *Liladisca acicola*, *Orbilia* (75 spp.), and *Retiarius bovicornutus* (anamorphic). However, the 13 larger administrative units have very unequally been explored. Most collections were made in Baden-Württemberg (648, 74 spp.), followed by Bayern (252, 55 spp.), Sachsen (83, 23 spp.), and Thüringen (62, 25 spp.). The other nine federal states lie in the range of 7–38 collections and 6–17 species, the poorest explored being Schleswig-Holstein and Saarland. The paucity of collections

Figure 130: **left**: Temperate humid shrubland (*Salicetum*) on moist ground (Lower Jurassic, Terres rouges) with *Salix cinerea*, *S. aurita* × *caprea*, *Corylus avellana*, *Urtica dioica*, *Rosa canina*, *Rubus* etc., 305 m, Haus der Natur, Kockelscheier, Luxembourg, collected 1994–2010, phot. 13.X.2010, G. Marson; attached branches of *C. avellana* (with *Hyalorbilia helicospora*), *R. canina* (*O. vinosa*), *Salix* (*H. orbiliicola* on *O. aurantiorubra*, *O. eucalypti*, *O. ?tremulae*, H.B. 5964, 6244, 6281), *Ulmus* (*O. aristata*, *O. carpoboloides*, H.B. 6385), *Picea abies* (*O. euonymi*); **right**: ibid., thermophilous forest on slope in former ore mining area (Lower Jurassic, Terres rouges), 375 m, Brucherbierg, Kayl, collected between 1994–2014, phot. ?VII.2009, G. Marson; attached branches of *Cornus sanguinea* (*O. aristata*, *O. flagellispora*, *O. subaristata*, *O. vinosa*, H.B. 7005, 9163), *Quercus* (*O. obtusispora*, *O. ocellata*, *O. trapeziformis*, *O. vinosa*, H.B. 5079, 5104, 5111, 5112), *Rosa canina* (*O. vinosa*), *Salix caprea* (*O. aristata*, *O. vitalbae*, *O. xanthoguttulata*), *Clematis vitalba* (*O. euonymi*).

in these 9 states is obviously one reason for this disparity, another might be the widespread agriculture in some of them. Within the two southern states the large supratemperate zone of 100–700(–750 m altitude houses at present 75 spp. and the orotemperate zone (up to 1600 m) 29 spp. The low latter figure might be due to a more than 10× higher collection activity in the supratemperate zone and the comparative smallness of orotemperate areas in the two states.

Collections were made by D. Benkert (Brandenburg, 1967–1999), H.O. Baral (Baden-Württemberg, Oberpfalz etc., 1974–2018), L. Krieglsteiner (Bayern, Hessen etc., 1983–2007), N. Luschka (Bayerischer Wald, 1987–1990), W. Huth (Sachsen-Anhalt, 1987–2019), G. Marson (Baden-Württemberg etc., 1988–2005), T. Lohmeyer (Oberbayern, 1989–2014), W. Beyer (Oberfranken, 1992–2001), T. Richter (Mecklenburg, 1992–2019), A. Gminder (Baden-Württemberg, 1993–1999), E. Weber (mainly Tübingen, 1998–2017), P. Karasch (Oberbayern, 2001–2005), B. Mühler (Chemnitz, 2002–2015), S. Helleman (Thüringen, Niedersachsen etc., 2004–2016), B. Fellmann (München, 2005–2019), H. Bender (Mönchengladbach, 2007–2019), M. Bemmann (Heidelberg, 2009–2013), I. Wagner (Sonneberg, 2009–2018), and many others.

The most frequently collected species within Germany (> 20 samples) are *Hyalorbilia inflatula*, *H. juliae*, *H. subfusispora*, *Orbilia aprilis*, *O. aristata*, *O. aurantiorubra*, *O. auricolor*, *O. comma*, *O. crenatomarginata*, *O. eucalypti*, *O. leucostigma*, *O. sarraziniana*, *O. trapeziformis*, *O. vinosa*, and *O. xanthostigma*. Rarities are, e.g., *H. fomentarii* (also in Estonia), *H. oreadum* (also in Slovakia), *O. clavuliaristata* (also in eastern USA), *O. rosella* (also in Czechia), and *O. fissilis* and *O. zhongdianensis* (also in eastern Asia). *Liladisca acicola*, *O. flavovacuolata*, *O. jurana*, *O. rehmii*, and *O. solidaginis* are only known from the type collection.

1d. **Switzerland**, **Liechtenstein and Austria**: Höhnel (1907a) reported *O. xanthostigma* (as *O. botulispora*) for Austria, Rehm (1891: 453–457) *O. eucalypti* (as *O. coccinella*), '*O. luteorubella*' (?*H. inflatula* or *O. aprilis*), and *O. vinosa* for the Alps, and Breitenbach & Kränzlin (1981: figs 250–254, 261) about 8 orbiliaceous species for Switzerland: *O. auricolor* (as *O. curvatispora*), *O. eucalypti* and ?*O. tremulae* (as *O. coccinella*), *O. carpoboloides* & *O. comma* (as *Habrostictis rubra*), *O. crenatomarginata* (as *Hyalinia rosella*), *O. sarraziniana*, and *O. xanthostigma*. Records from Austria by Matočec et al. (2005: 324) include also *H. erythrostigma*, *H. inflatula*, and *O. luteorubella*, and those by Friebes (2011, 2017) and Friebes & Wendelin (2015) *O. abutilonis*, *O. crenatovinosa* (as *Orbilia* sp.), *O. leucostigma*, *O. pilifera*, *O. vinosa*, and *O. xanthoguttulata*.

Altogether 73 orbiliaceous species were encountered up to now in the three countries, 2 in *Lilapila*, 1 in *Amphosoma*, 12 in *Hyalorbilia*, and 59 in *Orbilia*. Of these 73 species, 20 occurred at least sometimes above 1350 m, and about 52 (71 %) are xerobiotic. When analysing the two main thermotypes separately, the orotemperate samples (> 800 m a.s.l.) included 39 spp. (4 in *Hyalorbilia*) and showed the same proportion of about 28 xerobionts (71 %) and 11 hygrobionts, whereas the supratemperate samples (< 800 m a.s.l.) included 54 spp. (11 in *Hyalorbilia*) and showed a slightly lower proportion of about 34 xerobionts (63 %) and 20 hygrobionts.

Collections from Switzerland were mainly made by H.O. Baral (1985–2018) and U. Graf (2006–2018), also by J. Breitenbach/T. Honermann/F. Kränzlin (1975–1980), P. Blank (1987–1991), E. Weber (2006, 2014), H. Aeberhard (2009–2014), E. Stöckli (2017–2018), B. Senn-Irlet (2017–2018) and others, from Liechtenstein solely by H.B. (1997), and from Austria mainly by W. Jaklitsch (1992–2003) and G. Friebes (2009–2019), also by F. v. Höhnel (1903–1916), W. Dämon (1990–1993), M. Mann

(2012–2018), R. Moosbeckhofer (2013–2018), A. Gallé (2013–2019), I. Wendelin (2014–2015) and others.

The most often collected species were in the supratemperate zone *H. inflatula*, *O. aurantiorubra*, *O. crenatomarginata*, *O. eucalypti*, *O. ficicola*, *O. sarraziniana*, *O. vinosa*, and *O. xanthostigma*, and in the orotemperate zone *Lilapila jurana*, *H. inflatula*, *O. alpigena*, *O. vinosa*, *O. rosea*, *O. subtrapeziformis* and others. Among the rare species is the type of *H. hergiswiliana* from Luzern, which was finally also found in Slovakia and Serbia. Remarkable is also the rare *O. jacaensis* from Pyrenees, discovered by B. Senn-Irlet in Graubünden. *O. crenatovinosa* was so far only found a few times in the orotemperate eastern Alps. *L. jurana* was at first only found in Swiss (and adjacent French) Jura, mainly by E. Stöckli, but was later detected by A. Polhorský in the Slovakian High Tatras.

1e. **Luxembourg**: During 1894–1902, the small country was investigated for *Orbiliomycetes* by J. Feltgen (and V. Noppeney), who recognized 9 species and 5 varieties (Feltgen 1899, 1901, 1903). A restudy of his specimens by one of us (H.B.) revealed 10 different orbiliaceous species (hygrobionts: *H. inflatula*, *O. auricolor*, *O. crenatomarginata*, *O. ?leporina*, *O. ?luteorubella*, *O. sarraziniana*, *O. xanthostigma*; xerobionts: *O. eucalypti*, *O. flavida*, *O. vinosa*), though with little correlation to Feltgen's species concept. G. Marson (1988–2019) and also H.O. Baral (1988–2001) thoroughly explored the country, but mainly regarding xerobionts. But hygrobionts have also been collected, especially on occasion of annual meetings held by the mycology group of Luxembourg between 1990 and 2000.

Luxembourg consists of two main natural regions: in the north the cooler, colline to submontane Oesling with its acidic soil (Devonian, in the south Buntsandstein), and in the south the warmer, colline Gutland, characterized by neutral to basic soil (Keuper and Lower Jurassic, the latter including iron-bearing rock = Terres rouges, = 'Minette') at the border to Middle Jurassic, Fig. 130 right). The climate is cold-temperate humid and subcontinental with some atlantic influence. Although the size of Gutland is only about 1.5 × that of Oesling, many more species of *Orbiliomycetes* were recorded in the former area. This could be due to the less favourable acidic soils in Oesling, but is perhaps only a result of the greater remoteness from G. Marson's home. Over 700 samples were studied, about 670 from Gutland and 40 from Oesling. The total species number was about 68 when disregarding unclarified genetic variants. All 68 occurred in Gutland, but only 25 in Oesling. The proportion between xero- and hygrobionts was 56 : 12 in Gutland and 20 : 5 in Oesling.

Remarkable rarities were, e.g., *Lecophagus ellipsoideus*, *Hyalorbilia latispora*, *H. rotifera*, *Orbilia fraxini*, and *O. poitevinica*, the latter otherwise only known from Marais Poitevin in western France.

1f. **Belgium and the Netherlands**: Arnolds et al. (1984: 309, 326) reported 9 orbiliaceous species for the Netherlands. The recent checklist for Flanders, Belgium (Declercq & Leysen 2017) gives 3 *Arthrobotrys*, 2 *Hyalorbilia*, and 17 *Orbilia* spp. Up to now, 10 *Hyalorbilia* spp. and 26 *Orbilia* spp. from almost 100 samples are recognized by us altogether in both countries (Belgium 9 hygro- and 11 xerobionts, Netherlands 15 hygro- and 15 xerobionts), most of them collected by B. Declercq (mainly Oost-Vlaanderen, 1993–2014) and S. Helleman (mainly Noord-Brabant, 2006–2015), some also by L. Rommelaars (mainly Noord-Brabant, 2002–2018) and others. The mild, overall supratemperate humid climate supports occurrence of atlantic species such as *O. rubrovacuolata*. Remarkable is the rare *O. xinjiangensis* which is otherwise only known from the type isolate in the continental Tian Shan Mts. in central Asia.

1g. **France**: In his 'Chamignons de France', Gillet (1881–83) reported about 9 orbiliaceous taxa of unclear identity in *Helotium*, *Lachnea*, and mainly *Mollisia*. From Bretagne Crouan & Crouan (1867) described 2 species: *O. carpoboloides* and *O. rubrovacuolata* (as *Peziza infixa*), and from southern France Saccardo (1883: pl. 1291) *O. luteorubella*, Rolland (1901) *O. hesperidea*, and Chenantais (1918) the unclear *Hyalinia ulicis*. From around Paris Boudier (1904–10: 265–270, pl. 459–467) reported 8 species: *O. aurantiorubra*, *O. auricolor* (as *O. cur-*

Figure 131: **left**: Mesotemperate humid, atlantic coastal shrubland dominated by the thorny evergreen gorse (*Ulex europaeus*), 80 m, St. Jugon, La Gacilly, Bretagne, France, collected 19.I.2006 & 17.II.2012, phot. 7.IV.2006, J.P. Priou; attached branches of *Taxus baccata* (*Orbilia vibrioides*) and *Ulex europaeus* (*Hyalorbilia ulicicola*, H.B. 8048); **right**: mesosubmediterranean semihumid shrubland with *Pinus maritima*, *P. pinaster*, *Cupressus macrocarpa*, *Quercus ilex*, *Fraxinus excelsior*, *Tamarix anglica*, *Atriplex hastata* etc., 7 m, Forêt de St. Clément, Île de Ré, Poitou-Charantes, France, 26.IV.2006 & 16.IV.2008, phot. H.O. Baral; attached or fallen branches and stems of various hosts (*H. fusispora*, *H. inflatula*, *H. ulicicola*, *O. aprilis*, *O. caulicola*, *O. eucalypti*, *O. fabacearum*, *O. obtusispora*, *O. subclavuliformis*, *O. subdelphinus*, *O. vinosa*, H.B. 8136–8158, 8807–8821).

Figure 132: **left**: Orosubmediterranean humid forest with *Pinus sylvestris* and *Larix* in calcareous Southern French Alps, Col de l'Iscle Annot, Alpes-de-Haute-Provence, France, 1050 m, 26.IX.2009, phot. G. Marson (#438); resinous wounds of living branches of *P. sylvestris* (*Lilapila* ?*oculisporella*). **right**: id., forest and shrubland with *Pinus sylvestris*, *Picea abies*, *Quercus pubescens*, *Acer monspessulanum*, 950 m, Pas de Pierre, Clue de Barles, 14.VIII.2009, phot. H.O. Baral; standing trunk of *Q. pubescens* (*H. fusispora*, H.B. 9156; 9 km eastwards at 1250 m, Col du Labouret, collected on attached *Pinus* and *Picea* branches: *Amphosoma atroolivaceum*, *A. resinicola*, *Lilapila* spp., *Orbilia alpigena, O. euonymi, O. flagellispora, O. patellarioides*, *O. subvinosa*, *O. vinosa*).

vatispora), *O. carpoboloides* (as *Habrostictis*), *O. crenatomarginata* (as *Hyalinia rosella* & *H. crystallina*), *O. eucalypti* (as *O. coccinella*), *O. rectispora* (as *Hyalinia*), *O. sarraziniana*, and *O. xanthostigma*. In his 'Discomycètes de France', Grelet (1948a: 49f.) added *O. leucostigma*, *O. luteorubella*, *O. polyspora*, and *O. vinosa*. Pacaud (2002: 88) reported 4 species for dépt. Vendée: *H. inflatula*, *O. auricolor* (as *O. curvatispora*), *O. eucalypti* (as *O. alnea*), and *O. xanthostigma* (as *O. delicatula*).

Over 1170 French orbiliaceous samples are treated in this study (excluding oversea provinces). The various administrative regions of France have very differently been investigated for *Orbiliomycetes*. To the well explored regions belong Bretagne (> 270 records, 57 spp.) mainly by J.P. Priou between 2000–2017, Provence-Alpes-Côte d'Azur (225 records, 57 spp.) and Rhône-Alpes (190 records, 69 spp.) mainly by G.M. and J.P. Priou between 1992–2017, and Poitou-Charente (147 records, 44 sp.) by various collectors (including H.B., J.P. Priou, P. Tanchaud, B. Capoen, M. Hairaud, S. Helleman, B. Coué etc.), especially during three meetings in dépt. Deux-Sèvres (2006, 2008, 2011). Better explored are also Alsace and Lorrain (mainly by J. Deny and H.B. 1990–2000) and Pays-de-la-Loire (mainly by J.P. Priou 2002–2016 and H.B. 2003). To the least explored regions belongs Corse, for which only one sample was available (*O. auricolor* on *Hedera*).

A total of 135 species were so far discovered in France, with 22% hygrobionts and 78% xerobionts: *Amphosoma* (3 spp.), *Hyalorbilia* (16 spp.), *Lecophagus* (3 spp.), *Lilapila* (4 spp.), *Orbilia* (109 spp.), *Pseudorbilia bipolaris*, and *Retiarius* ?*revayae* (anamorphic). Species so far exclusively known from France are *A.* aff. *resinicola*, *Lecophagus pini*, *L. subglobosus*, *Lilapila oculisporella* and *L. gallica*, *O. beatricis*, *O. cisti*, *O. cupressi*, *O. frullaniae*, *O. microlentiformis*, *O. myriolentiformis*, *O. olivacea*, *O. paracylindrospora*, *O. pseudocylindrospora*, *O. pyrenaica*, and *O. subdelphinus*. The North American *O. spermoides* was once also found in the Southern French Alps. *O. poitevinica* was named after its occurrence in Marais Poitevin

Figure 133: **left**: mesosubmediterranean semihumid shrubland (macchia) with *Quercus*, *Rosa*, *Pistacia*, *Acer*, *Ulex*, *Juniperus*, *Pinus*, 410 m, les Mouniers, Vallon-Pont-d'Arc, Ardèche, France, 8.X.2002, phot. G. Marson (#609); attached branches of *Ulex parviflorus* and *Quercus* (*Hyalorbilia subfusispora*, *Orbilia corculispora*, *O. montigena*, *O. vinosa*, H.B. 7317); **right**: supramediterranean semihumid *Juniperetum thuriferae*, 1040 m, Ermita de los Enebrales de Tamajón, Guadalajara, Spain, 14.V.1996, phot. H.O. Baral; attached twigs & branches of *Cistus ladanifer*, *Genista scorpius*, *Juniperus thurifera*, *Quercus rotundifolia*, *Rosa* (with *O. euonymi*, *O. gambelii*, *O. pleiogambelii*, *O. polyspora*, *O. rosicola*, *O. subaristata*, *O. subclavuliformis*, *O. subovoidea*, *O. trapeziformis*, *O. vinosa*, H.B. 5464, 5482, 5490, 5499, 5500, 5510, 5512, 5517).

in Poitou-Charantes, but a second sample was later made in Luxembourg. Remarkable is the presence of 4 different *Lilapila* spp. in mountainous regions of France.

Mainly J.P. Priou's collecting efforts raised the species number in Bretagne to now 51 (12 *Hyalorbilia* spp., 38 *Orbilia* spp., 1 *Pseudorbilia*). About 30 of them are xerobionts, and 6 of these xerobionts were presented by Priou (2005) as they had a published name at that time. 23 species (6 hygro- and 17 xerobionts) have been collected on *Ulex*, the most frequent being *H. ulicicola*, *O. corculispora* and *O. rubrovacuolata*. Remarkable rarities found in Bretagne are *Pseudorbilia bipolaris*, *H. herbicola*, *H. multiguttulata*, and *O. frangulae*. Because of the mild, atlantic climate various species from the mediterranean belt occur here, e. g., *O. corculispora*, *O. gambelii*, and *O. subovoidea*. Species with an exclusively atlantic distribution are *H. ulicicola*, *O. atlantis*, and *O. rubrovacuolata*.

In comparison to these lowland records at 1–320 m altitude, a similar number of 56 species was retrieved by comprehensive collecting in mountainous regions of the orotemperate to oro-submediterranean humid Southern French Alps (760–1950 m). 52 of these species are xerobionts, but the low number of hygrobionts is here due to a strong focus on xeric substrate. Some of the rarely collected species occurred here, and the region represents one of the main distribution areas of the genus *Lilapila*.

1h. **Iberian peninsula** (**Spain**, **Portugal**): 10 orbiliaceous species were treated by R. Galán in Pando & Hernández (2001: 121–126) in their 'Chorological basis of the mycological flora of Iberia': *Hyalorbilia inflatula* (as *Orbilia*), *O. auricolor*, *O. carpoboloides*, *O. eucalypti* s.l. (as *O. alnea*), *O. leucostigma*, *O. luteorubella*, *O. rubella*, *O. sarraziniana*, *O. vinosa*, and *O. xanthostigma* (as *O. delicatula*), and Rubio et al. (2005) added *O. crenatomarginata* (as *O. rosella*) and *O. eucalypti* s.l. under the name *O. coccinella* in their 'Provisional catalogue of macromycetes from Asturias'. In the present study, data from about 570 collections were available, comprising a total of 120 different species: 11 in *Hyalorbilia*, 106 in *Orbilia*, and 1 in each *Amphosoma*, *Bryorbilia*, and *Lecophagus*. Most of them (541 samples with 116 spp.) were made in Spain. Strongly underexplored are Portugal (28 samples with 5 *Hyalorbilia* spp. and 16 *Orbilia* spp.), but also Islas Baleares (4 samples with 4 spp.). Selected samples from the Natural Park of Somiedo in Asturias made in the 21th century were reported and illustrated in Rubio et al. (2010, 2015) and Rubio & Zapico (2018).

Our collections were made during a research visit in Alcalá de Henares in 1996 (H.B. & E.W., Madrid, Guadalajara), at the European Mycological Congress in Alcalá de Henares in 1999 (H.B. & G. M., Madrid, Guadalajara, Cuenca, Teruel, Castellón, Cataluña), and during two meetings in Somiedo in 2013 and 2017 and one in Jaca, Huesca in 2018 (H.B.). Various mainly Spanish collectors contributed with their collections and documentations, e. g., J. Linde & E. Rubio (Asturias, 2005–2019), J. Martin, I. Olariaga etc. (mainly País Vasco, 2012–2018), F.J. Balda (Navarra, 2013–2019), R. Tena (Teruel, 2010–2014), R. Blasco (Huesca, 2012–2019), J. Bometón (Cataluña, 2014–2017), F. Prieto (Madrid, Andalucía, 2001–2004), S. Tello (Andalucía, 2013–2017), and J.P. Priou (Portugal, 2006–2017).

The highest species number of 75 was observed in the eumediterranean zone, with 42 spp. in the supra- (Sm), 41 in the meso- (Mm), and 27 in the thermomediterranean subzone (Tm). An intermediate species number of 62 occurred in the submediterranean zone, with 33 spp. in the orosub- (Osm), 31 in the suprasub- (Ssm), and 21 in the mesosubmediterranean subzone (Msm). Only 54 spp. were found in the temperate zone, with 33 spp. in the oro- (Ot), 16 in the supra- (St), 17 in the meso- (Mt), and 18 in the thermotemperate subzone (Tt).

Many of the encountered species appear to be rare, and the following are exclusively known from the Iberian peninsula: *Bryorbilia arenicola* (Ssm), *O. asturiensis* (Ot), *O. crenatofalcata* (Sm, Ssm), *O. halimi* (Mm), *O. navicularis* (Sm), *O. octocorculispora* (Tm, Mm), *O. paramontigena* (Osm), *O. paravitalbae* (Tm, Mm, Osm), *O. pleioalbidorosea* (Sm, Osm), *O. pleistosphaera* (Sm), *O. rhamni* (Mm), *O. rosicola* (Sm), *O. somedana* (Ot), and *O. suberis* (Mm). Some other rare species have also been detected elsewhere: *O. jacaensis* (Ssm), described from Jaca at the base of the Pyrenees, was also found in the French Pyrenees and Swiss Alps (Ot), *O. angiosubvinosa* is known from different parts of Spain (Ot, Osm, Ssm) but apparently also occurs in North America (mild-maritime), and the insectivore *O. alba*, reported here from Asturias and Galicia (Tt), has variants in subtropical China and tropical South America.

1i. **Italy**: Saccardo (1883: pls 1289–1290, 1365) reported 3 orbiliaceous species from Italy (Südtirol): *O. eucalypti* (as *Calloria coccinella*), *Hyalorbilia* (?)*inflatula* (as *Calloria*), and *O. carpoboloides* (as *Habrostictis rubra*). Up to now, about 17 *Orbilia* spp. and two *Hyalorbilia* spp. are known from Italy, ~ 12 of them being xerobionts. They grew on woody angiosperms from orotemperate to mesomediterranean regions in the northern half of Italy, except for *O. auricolor* which was on dung in thermomediterranean Sicilia. More recent collections were, e. g., from Elba, by D. Triebel & G. Rambold in 1998, and Emilia-Romagna by J.P. Priou in 2004 and E. Camporesi in 2011. No collection from Sardinia was available.

1j. **Poland**, **Czechia**, **Slovakia**, **Hungary**: Schröter (1893: 120) reported for **Poland** 6 species for Silesia, viz. *O. aurantiorubra* (as *O. rubella*), *O.* ?*auricolor* (as *O. pannorum*), *O. carpoboloides* (as *O. lasia*), *O. eucalypti* (as *O. coccinella*), *O. vinosa*, and *O.* ?*xanthostigma* (as *O. chrysocoma*). Ginko (1986) added *O. auricolor* (as *O. curvatispora*) and *O.* ?*cejpii* (as *O. leucostigma*), and Chmiel's (2006) checklist of Poland includes also *O. luteorubella*, *O. sarraziniana*, and *O. xanthostigma*. Up to now, 10 *Hyalorbilia* spp. and 27 *Orbilia* spp. are known from Poland, besides *Amphosoma atroolivaceum*, 24 of them being xerobionts (63 %). Samples predominantly originate from Lower Silesia (Kłodzko county) where P. Perz collected between 2006–2013.

Velenovský (1934, 1940, 1947) reported for the former Czechoslovakia, mainly **Czechia**, 68 species and 12 varieties in *Orbilia*, and 1 in *Radotinea* (*R. caudata*). A restudy by Svrček (1954) accepted only 17 orbiliaceous species and 2 forms, and the present study about 41 species, the identities of which showing only moderate correlation with Velenovský's original concept. Six of them belong to *Hyalorbilia* and ~ 35 to *Orbilia*. Later Svrček (1977) added *O. polybrocha* (as *O. tenebricosa*). The relation between hygro- and xerobionts was about 55 : 45 %. During collecting in Czechia in 2008 and 2009 the first author (H.B.) found only *O. aprilis* and *O. vinosa*, but V. Halasů in 2019 *O. pseudoaristata*, which raises the species number of recorded species to 42. From **Slovakia** now 7 *Hyalorbilia* spp. and 24 *Orbilia* spp. are known, besides *Amphosoma atroolivaceum* and

Figure 134: Supratemperate humid forests with mediterranean influence at Fruška Gora mountain in suprasubmediterranean Vojvodina, Serbia; **left**: northern slope with steppe meadow vegetation (*Inulo-Chrysopogonetum grylli* with scattered small *Fraxinus ornus* trees) maintained by grazing, 235–270 m, Erdelj, 28.VIII.2012, phot. D. Savić; attached branches of *Colutea arborea*, *Fagus sylvatica*, *Quercus pubescens* (with *Hyalorbilia fusispora*, *H. juliae*, *Orbilia carpoboloides*); **right**: mountain top with *Aculeato-Querco-Carpinetum* (with *Ruscus aculeatus*), 420–510 m, Iriški venac, phot. 9.X.2007, D. Savić; attached twigs and branches of *Betula*, *Clematis*, *Larix*, *Picea*, *Populus*, *Prunus*, *Pseudotsuga*, *Quercus*, *Sorbus*, *Tamarix*, *Tilia*, *Ulmus* (with *H. orbiliicola*, *O. aprilis*, *O. aristata*, *O. carpoboloides*, *O. comma*, *O. clavuliformis*, *O. euonymi*, *O. ficicola*, *O. fraxini*, *O. montigena*, *O. nemaspora*, *O. subaristata*, *O. trapeziformis*, *O. vinosa*, *O. vitalbae*, *O. xanthoguttulata*), and on fallen substrate some hygrobiotic spp.

Lilapila jurana, most of them collected by A. Polhorský from the High Tatra Mts. and Danubian lowlands around Bratislava between 2016–2019.

The few collections from **Hungary** are all from the humid central north. Collections were made by L. Beenken in 1999 in the supratemperate Danube-Ipoly National Park at 200–285 m on *Quercus* and *Carpinus* xeric or hygric branches and logs (mainly on wood), by D. Magyar between 2007–2016 in the suprasubmediterranean Budapest urban area at 92–117 m on xeric trunk bark of mainly *Platanus*, rarely *Taxus*, and by A. Koszka in the supratemperate Vértes mt. at 266 m. Five xerobionts (*Lecophagus ellipsoideus*, *Hyalorbilia juliae*, *Orbilia aprilis*, *O. eucalypti*, *O. ficicola*) and two hygrobionts (*H. inflatula*, *O. xanthostigma*) were recorded. Four further xerobionts are only known from their anamorph (*Lecophagus vermicola*, *Mycoceros antennatissimus*, *Retiarius revayae*, *R. goenczoelii*).

Altogether about 75 orbiliaceous spp. have been recognized in the four countries up to now. 17 spp. came from the orotemperate zone of the Bohemian Forest, Sudetes mountains, and Carpathians (750–1800 m), and 68 spp. from the supratemperate to suprasubmediterranean hilly and lowland zone (25–700 m). Purely orotemperate species were *A. atroolivaceum*, *L. jurana*, *O. cylindrospora*, *O. filiformis*, and *O. subtrapeziformis*. The following species are so far only known from Czechia, all described by J. Velenovský: *O. acuum*, *O. cyparissias*, *O. leporina*, and *O. minutispora*. Remarkable is the occurrence of the predominantly mediterranean *O. gambelii* in the Danubian lowlands of southern Slovakia.

1k. Romania, Ukraine, Moldavia, Bulgaria, southwestern Russia: For **Romania** Pop (1994) listed a collection of *O. auricolor* (Cluj county). During our study three further species were recorded, *O. lentiformis*, *O. pleiolentiformis*, and *O. xanthostigma*. The former two species have been collected by R. Reuter in 1994 on the same xeric *Salix* branch in mesosubmediterranean humid southern lowlands at ~275 m, the latter by J.P. Priou in 2014 on a hygric *Salix* log in the supratemperate humid northern lowlands (280 m) at the foot of Carpathians.

Records from the supra- to orotemperate **Ukrainian** Carpathians were made by A. Pilát between 1929–1930 (*O. epipora*, *O. leucostigma*, *O. polybrocha*, *O. sarraziniana*, *O. xanthostigma*; names according to present study). Most of them were reported by Velenovský (1934), though under different names. Further species from this region were recorded in 2012 by A. Akulov (*Hyalorbilia fagi*, *H. inflatula*, *O. crenatomarginata*). From supratemperate humid, continental Ukrainian lowlands *O. xanthostigma* was collected by Z.K. Girzhitska (vid. E. Popov) in 1927 near Kyiv, and *O. aurantiorubra*, *O. carpoboloides*, *O. comma*, *O. crenatomarginata*, and *O. flavidorosella* between 2000–2012 around Kharkiv (Prylutskyi et al. 2017, Yatsiuk 2018, E. Popov pers. comm.).

In the west (Bryansk) and south (Rostov, Volgograd, Astrakhan) of **southwestern Russia** with a supra- to mesotemperate or suprasubmediterranean, humid to subhumid, continental climate, E. Popov collected 9 xerobiotic *Orbilia* spp. between 2002–2012. Among them is *O. cercidicola* on *Ulmus* which was otherwise only observed in mesomediterranean southern France on *Cercis*. The Volga floodplain represents the only site within Europe which is classified here by a subhumid ombrotype. Regarding the humid Caucasus region see under Asia (p. 177). No records are known to us from Moldavia and Bulgaria.

1l. Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro: Previous reports include *O. xanthostigma* (as *O. delicatula*) from Montenegro (Matočec & Focht 2000, apothecia yellow, N. Matočec pers. comm.) and *O. polyspora* from Croatia

(Tkalčec et al. 2008). Up to now, no records from Slovenia or Bosnia and Herzegovina are known to us.

Collections in **Croatia** were mainly made by N. Matočec, H.O. Baral and E. Weber between 1998–2000. 24 *Orbilia* spp. and one *Hyalorbilia* (*H. juliae*) are known at present. Most of them derive from Dalmatian islands, particularly Korčula, rarely Palagruža (*O. auricolor*) and Dugi Otok (*O.* ?*cotoneastri*). The low number of only 3 hygrobionts (12 %, the latter two and *O. xanthostigma*) is due to collecting mainly in summer on xeric substrate. The climate of the sites was mostly meso- to thermomediterranean semihumid at 1–450 m, mainly with *Quercus ilex* shrubland and maquis, rarely mesosubmediterranean (semi)humid at 635 m. Only one sample was from the supratemperate humid north of Croatia (*O. auricolor* on *Carex*). The substrates comprised a high diversity of mainly woody angiosperms, but also gymnosperms. The most often collected species were *O. vinosa*, *O. hesperidea*, *O. gambelii*, and *O. subaristata*. Rarities were *O. albovinosa* on *Lonicera* and the so far unique *O. dalmatica* on *Juniperus*.

From **Montenegro** so far 16 *Orbilia* spp. and 4 *Hyalorbilia* spp. were recorded, mainly by B. Perić in 2016 and D. Savić in 2019, 5 of them hygrobionts (*H. inflatula*, *H. ulicicola*, *O. auricolor*, *O. crenatomarginata*, *O.* ?*xanthostigma*). Most collections were from the mesosubmediterranean (semi) humid lowlands at 8–210 m, a minority from the supra- to orotemperate humid mountains (935–1725 m, e. g., *H. inflatula*, *O. crenatomarginata*, *O. subtrapeziformis*). Substrates were mainly woody angiosperms, also *Inonotus* (*H. ulicicola*) and *Orbilia* (*H. orbiliicola*). Rarities were *O.* ?*albovinosa* on *Euphorbia* and *O. mali* on *Punica*.

In northern **Serbia** (Vojvodina) D. Savić investigated Fruška Gora between 2013–2019 for ascomycetes, especially *Helotiales* and *Orbiliomycetes*. This mostly calcarean mountain range with an altitude of 200–540 m lies in the south of the Pannonian Plain in the very southeast of central Europe. The surrounding agricultural lowlands along the Danube river have a suprasubmediterranean (sub)humid, somewhat subcontinental climate and receive continuous but moderate rain throughout the year. The climate on the mountain is more supratemperate humid. Plant communities of Fruška Gora mainly belong to *Querco-Fagetea*, with *Aculeato-Querco-Carpinetum* as the most frequent forest type, but also beech and linden communities (*Tilio-Fagetum submontanum*) play an important role. Diversity is very rich (1500 plant species, ~50 being woody), providing great potential for ascomycete diversity. More or less omnipresent trees are *Quercus petraea*, *Q. cerris*, *Q. pubescens*, *Fagus sylvatica*, *Tilia tomentosa*, *T. platyphyllos*, *T. cordata*, *Fraxinus ornus*, *F. angustifolia*, *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *A. tataricum*, *Carpinus betulus*, *Sorbus torminalis*, *Staphylea pinnata* etc.

No previous reports of orbiliaceous taxa from Serbia are known to us. A total of 10 *Hyalorbilia* spp. and 42 *Orbilia* spp. were discovered in Fruška Gora including surrounding lowlands. Most of them are widely distributed in Central Europe, but some are rarities (e. g., *H. hergiswiliana*, *H. multiguttulata*, *O. clavispora*, *O. ficicola*, *O.*?*fraxini*, *O. nemaspora*, *O. sinensis*). *O. nemaspora* even represents a first record for Europe. About 33 species are xerobionts and 19 hygrobionts. Substrates were mainly woody angiosperms, also conifers and herbaceous stems.

1m. **Albania**, **North Macedonia**, **Greece**: No records are known to us from Albania, and only one from North Macedonia made by M. Theiß in 2006 (*O. xanthostigma*). Various collections were made in **Greece** by S. Helleman in 2009 in Attika (Athens) and mainly Peloponnese, by V. Kummer in 2010 in Rhodos, and by T. Giannakis (vid. B. Wergen) in 2015 in Central Macedonia (Thessaloniki, *O. gambelii*). Most of these places can be classified as semihumid and either meso- (Mm, 335–525 m) or thermomediterranean (Tm, 1–190 m). A total of 12 species were encountered on bark and wood of *Quercus*, *Pistacia*, *Anagyris*, *Myrtus* etc. All of them are xerobionts, because searching was only done on xeric substrate. Frequently collected were *O. subaristata* and *O. gambelii* at 12–525 m (Mm, Tm). Several species were only found in the thermomediterranean zone (e. g., *O. bicknellensis*, *O. hesperidea*). The single record of *O. serpentina* is the only which grew in a more semiarid region at 65 m (Tm). *O. myriosphaera* occurred at 1 m (Sm) and 855 m (Ssm), and *O. vinosa* at 30–185 m (Tm) and 565 m (Sm), the latter very probably occurring in Greece also at higher altitude (Ssm, Osm).

2. Africa (including islands near Madagascar)

Earlier records from the mainland of Africa comprise merely two species published in the 19th century, *Orbilia euphorbiae* (Ethiopia, Hennings 1891) and *O. serpentina* (Tunisia, Patouillard 1892a), and six further species which exist as unpublished herbarium specimens collected between 1920–1965 (see below). No previous record was known to us from the region of Madagascar. Also in the present study, collections were only sporadically available, therefore, a majority of African *Orbiliomycetes* diversity remain to be investigated.

For mainland Africa 30 orbiliaceous species are accepted by us up to now. The collection sites belong to the subtropical or rarely warm-temperate zone and comprise the northwestern ± coastal area (Maghreb), the afromontane Ethiopian highland and adjacent countries, the ± coastal region of southeastern and southern Africa, the Namib desert and savannah highland in southwestern Africa, and the coastal western Africa (Senegal). No collection was studied from tropical rainforests, but the occurrence of *O. blumenaviensis* in such a forest is proved by the type collection of its anamorph, *Arthrobotrys vermicola*, isolated from near Kampala (Uganda). For (sub)tropical sites on two islands near Madagascar 14 species are accepted.

Some of the recorded species might be endemic to mainland Africa (*Amphosoma natalense*, *O. aethiopica*, *O. caudimaeandrina*, *O. lobeliae*, *O. menageshae*, *O. myrioflexa*, *O. namibica*, *O. senegalensis*). Yet, considering the paucity of records compared to the rich species diversity observed in Macaronesia, there is little doubt that several hundreds of orbiliaceous species exist in mainland Africa with its diverse vegetation zones. The following arrangement of the different regions (phytochoria of mainland Africa according to White 1983, in Demissew 1988) gives an overview of the collection sites and recorded species.

2a. **Algeria**, **Morocco**, **Tunisia** (**Maghreb**) (mediterranean regional centre and transition to Sahara of northern Africa): The 7 orbiliaceous species known at present occurred in subtropical semihumid (eumediterranean) sites on mostly xeric bark and wood of angiosperms. All of them have been collected by French mycologists: Patouillard (1892a, b, *O. serpentina* on twig of *Artemisia herba-alba*), R. Maire (1920 in sched., *O. albovinosa* on *Lonicera etrusca*; *O.* ?*milinana* on *Ulmus*

Figure 135: Mesotemperate humid (winter-dry) evergreen afromontane forest with the tree-like (pachycaulous) herbs *Lobelia giberroa* (**left**) and *Solanecio gigas* (**below right**), 2520 m, Menagesha State Forest in subtropical Oromia region east of Addis Ababa, Ethiopia, 22.XII.2009 & 26.III.2010, phot. U. Lindemann; mesic stems and branches of *Solanecio*, *Lobelia*, indet. angiosperms (with *Hyalorbilia* ?*herbicola*, *H.* ?*brevistipitata*, *Orbilia aethiopica*, *O.* ?*caudata*, *O. euphorbiae*, *O. jugulospora*, *O. lobeliae*, *O. menageshae*, H.B. 9239–40, 9246, 9275–76, 9309–10, 9318).

campestris; *O. vinosa* on *Cistus crispus*), R. Bertault (1965 in sched.: *O. eucalypti* on *Acacia mollissima*), and G. Malençon (1934 in sched., *O. lentiformis* on *Thymelaea lythroides*; 1963 in sched., *O. auricolor* on *Acacia saligna*).

2b. **Eritrea**, **Ethiopia**, **Kenya** (Sudanian regional centre of eastern Africa): Only one orbiliaceous species was so far known from eastern Africa: the xerobiotic *O. euphorbiae* was described by Hennings (1891) on branches of *Euphorbia polyacantha* in the subtropical arid steppe of a high plateau in Eritrea.

Recent records from Ethiopia and Kenya were available from subtropical humid (winter-dry) afromontane evergreen forests with rainfalls in spring and mainly summer and a long dry period during autumn and winter (Fig. 135). Collections were mainly made by U. Lindemann (pers. comm.) from the Menagesha State Forest, an old volcanic area in the western Ethiopian highlands (Demissew 1988). Two tall trees, *Podocarpus gracilior* and *Juniperus procera*, constitute the forest. The collection site lies at 2500–2520 m a.s.l., and collections were made between 2009–2010 on fallen corticated branches of indet. angiosperms and on herbaceous stems of *Lobelia giberroa* and *Solanecio gigas* lying on the dry ground. The recorded eight species were either hygrobionts (*H.* ?*brevistipitata*, *H.* aff. *herbicola*) or showed a slight (*O. aethiopica*, *O. menageshae* s.l.) or more pronounced desiccation tolerance (*O.* aff. *caudata*, *O. euphorbiae*, *O. jugulospora*, *O. lobeliae*). Further collections of *O. menageshae* s.l. were made on *Yushania alpina* stems in a bamboo forest in southwestern Ethiopia (A. Gminder, 2014) and on a herbaceous *Euphorbia* stem in a highland forest of Kenya (O. Eriksson, vid. I. Olariaga, 1968).

2c. **Islands near Madagascar**: Samples belonging to 14 species were available from the islands of Mayotte (Comoros archipelago) northwest of Madagascar (M. Pélissier, vid. J.P. Priou, 2012–2014) and Réunion (Mascarene Islands) east of Madagascar (R. Reuter, 2011). They undoubtedly represent little more than an accidental spot check. From the tropical humid (winter-dry) Île de Mayotte the following 11, mainly hygrobiotic species were recorded at low altitude (90–440 m) on fallen hygric corticated to decorticated branches and logs of *Adansonia digitata* (*O. euphorbiae*), *Mangifera indica* (*O. vermiformis*), *Albizia lebbeck* (*O. blumenaviensis*, *Hyalorbilia* cf. *juliae*), indet. angiosperms (*H. citrina*, *H. ?japonica*, *O. ?fissilis*, *O. ?juruensis*, *O. nemaspora O. ?rosea*, *O. ?yuanensis*), and on stem of the bamboo *Dendrocalamus giganteus* (*O. nemaspora*). From La Réunion three xerobiotic species were observed at a subtropical humid (winter-dry) site at high altitude (2040 m) on an attached xeric corticated branch of *Acacia heterophylla* (*O.* cf. *aristata*, *O. eucalypti*, *O. vinosa*).

2d. **South Africa** (Kalahari-Highveld regional transition zone, eastern and southern part): seven species have been collected in the subtropical (winter-dry) savannah of southeastern Africa (D. Triebel & G. Rambold, 1990; V. Kummer, 2000 & 2006): in the subhumid Drakensberg Mts. and KwaZulu-Natal on a hygric angiosperm branch (*H. japonica*) and on xeric branches of ?*Vachellia* (*O. corculispora*) and ?*Pterocarpus* (*Amphosoma natalense*), and from the humid, more coastal Kranskloof Nature Reserve on fallen fruit of *Xylotheca kraussiana* (*O. auricolor*, *O. tenuissima*) and Oribi Gorge Nature Reserve on hygric indet. angiosperm wood (*O. xanthostigma*). A further species was observed in the warm-temperate humid Cape Mountains (Garden Route of southern Africa) on hygric indet. angiosperm bark (*O. jinguangsiensis*).

2e. **Namibia** (Kalahari-Highveld regional transition zone, western part): In 1995, R. Reuter collected in the warm-temperate arid highland savannah near Rehoboth an attached xeric branch of ?*Vachellia*, on which five different, highly desiccation-tolerant multispored *Orbilia* species occurred, three of them only known from this branch up to now: *O. caudimaeandrina*, *O. namibica*, *O. maeandrina*, *O. myrioflexa*, and *O. pluristomachia*. In the subtropical hyperarid Sossusvlei of the Namib desert, a piece of wood was taken by G. Parisot in 2007 from a decorticated branch of *Vachellia erioloba*, the famous upright tree corpses that died over 500 years ago from groundwater loss. On this piece of wood occurred *O. acaciae*, a species known before only from Australia and later from Macaronesia.

2f. **Senegal** (Guinea-Congolia/Sudania regional transition zone of western Africa): two drought-tolerant species have been collected by R. Reuter in 2000 and 2016 in tropical humid (winter-dry) open woodlands at low altitude on attached xeric branches of ?*Vachellia* (*O.* aff. *filiformis*, on wood) and *Citrus* (*O. senegalensis*, on bark).

3. Macaronesia

Korf (1992) reported 8 species of *Orbilia* s.l. (including *Hyalorbilia*) from the three archipelagos, but a restudy showed that he merged different species under one, so that he treated in fact min. 10 or 11 species. In their list of fungi of Canarian forests, Izquierdo et al. (2004: 29) reported 7 orbiliaceous species and Beltrán-Tejera et al. (2008: 183, 187) 3 for the National Forest Park of Garajonay in Gomera. Karasch et al. (2005) added 3 species on xeric branches of *Chamaecytisus proliferus* in La Palma. Later research, particularly in the islands of Tenerife and Madeira, mainly by L. Quijada & E. Beltrán-Tejera and J.P. Priou, raised the number of species to min. 61 for all Macaronesian archipelagos (54 from Canary Islands, 12 from Madeira, 1 from Azores), but none from Cape Verde. Of these 61 species, 28 are newly described in the present study, whereas most of the earlier published species have already been presented in Quijada et al. (2012, 2014a, b, 2016) and Quijada & Baral (2017, 2018). All 8 so far endemic *Orbilia* spp. (*O. adenocarpi*, *O. amarilla*, *O. asomatica*, *O. beltraniae*, *O. liliputiana*, *O. pisciformis*, *O. pseudeuphorbiae*, *O. succulenticola*) grew on plants endemic to this archipelago (*Adenocarpus viscosus Euphorbia canariensis*, *E. lamarckii*) but three of them occasionally or predominantly also on *E. balsamifera* which occurs as well in mainland Africa and the Arabian Peninsula.

3a. **Canary Islands**: The climate of the Canary Islands is very diverse due to the height of its volcanic mountains and the prevailing northeasterly trade winds that supply a humid climate to the northern slopes. It is classified as eumediterranean throughout, with different thermo- and ombrotypes ranging from inframediterranean hyper- to semiarid at the very lowlands, over thermo- to mesomediterranean in the region of the semihumid

Figure 136: Desert shrubs in Tenerife; **left**: inframediterranean arid tabaibal dulce (*Ceropegio fuscae-Euphorbietum balsamiferae*, adjacent to *Launaeo arborescentis-Schizogynetum sericeae*) with *Euphorbia canariensis* in foreground and *E. balsamifera*, *Plocama pendula*, *Kleinia neriifolia*, *Schizogyne sericea*, *Launaea arborescens* and *Cenchrus ciliaris* on the sides, 50 m, Montaña Centinela & Barranco la Vera, Abades, collected between 2009–2010, phot. 24.XI.2008, L. Quijada, lying xeric branches of *Euphorbia balsamifera* (*Orbilia pseudeuphorbiae*, *O. succulenticola*), *E. canariensis* (*O. acaciae*, *O. asomatica*, *O. pisciformis*, *O. pseudeuphorbiae*, *O. succulenticola*, H.B. 9153, TFC Mic. 22150 etc.), *E. lamarckii* (*O. pseudeuphorbiae*, TFC Mic. 22430), *Lavandula canariensis* (*O. pleioungulata*, TFC Mic. 22766); **right**: supramediterranean semihumid summit broom scrub (*Spartocytisetum supranubii*) with dead *Adenocarpus viscosus* in foreground, flanked by *Pterocephalus lasiospermus* and *Cytisus supranubius*, 2100–2160 m, Las Cañadas south of Teide, collected in 1978 and 2008–2012, phot. 27.XII.2009, L. Quijada; xeric twigs and branches of *Adenocarpus viscosus* (*O. adenocarpi*, *O. eucalypti*, *O. gambelii*, *O. macrodelphinus*, *O. microsoma*, *O. pleiogambelii*, H.B. 2280 etc., TFC Mic. 18428 etc.), *Carlina xeranthemoides* (*O. gambelii*, *O. ocellata*, TFC Mic. 23751, H.B. 9224), *Cytisus supranubius* (*O. euonymi*, *O. flavidorosella*, *O. subtrapeziformis*, H.B. 9225, TFC Mic. 24156 etc.).

Figure 137: Forests in Tenerife; **left**: mesomediterranean (sub)humid evergreen ridge-crest forest with *Erica platycodon*, *Laurus novocanariensis*, *Myrica faya*, *Viburnum rigidum*, *Pteridium aquilinum* etc., 860 m, Descansaderos de Tierra, Anaga, collected in 2012, phot. 27.V.2011, L. Quijada; lying log of *L. novocanariensis* (with *Orbilia xanthostigma*, TFC Mic. 23393; in 1976 at another place *O. dryadum* on *Myrica faya*, CUP-MM-434); **right**: mesomediterranean semihumid *Sideritido solutae-Pinetum canariensis* forest, Vilaflor, phot. 16.IV.1989, E. Weber; collected on xeric branches in pine forests close to these sites by L. Quijada at 1200–1600 m in 2012–2013 (*Aeonium arboreum*, *Chamaecytisus proliferus*, *Cistus* spp., *Pinus canariensis*, *Siderites soluta* (with *O. corculispora*, *O. flavida*, *O. ?paravitalbae*, *O. patellarioides*, *O. subaristata*, *O. vinosa*, TFC Mic. 23352–61, 23635–40, 23937, 23951) and by F. Bontemps at 1400 m in 1996 (*Acacia ?saligna*, *O. serpentina*, H.B. 5659).

(‘dry’) sclerophyllous shrublands or pine forests on the more southern slopes and the ± moist, (sub)humid cloud forests on the northern slopes, up to supra- (and oro-)mediterranean semihumid at the top. Rain falls during the winter months, with five dry months in summer.

Collections were available from Gomera, Gran Canaria, La Palma, and particularly Tenerife, the latter being thoroughly investigated by L. Quijada and E. Beltrán-Tejera between 2001–2015. Within Tenerife the recorded species show a remarkable adaptation to the humidity zones (Tab. 34). The highest number of species was observed in the semihumid zone (26 spp.), followed by the semiarid zone with 18 spp. (15 spp. in the lower and 10 spp. in the upper subzone), whereas in each of the remaining zones (hyperarid, arid, subhumid, humid) the number was 10 spp.

Table 34: Selected species of *Orbiliomycetes* collected in the Canary Islands (mainly Tenerife), sorted according to humidity (ombrotype) of the sites. The right column gives the observed thermotypes: Im = inframediterranean, Tm = thermomediterranean, Mm = mesomediterranean (i = lower, s = upper), Sm = supramediterranean. Numbers indicate the number of collections (only species with min. 3 collections are included). Ombro- and thermotypes according to Del-Arco et al. (2006); desiccation tolerance (x = xerobiotic, h = hygrobiotic).

Species	hyperarid	arid	lower semiarid	upper semiarid	semihumid	subhumid	humid	Thermotype	Desiccation tolerance
O. pseudeuphorbiae	7	11	5	–	–	–	–	Im23	x
O. acaciae	2	1	2	–	–	–	–	Im5	x
O. asomatica	2	1	2	–	–	–	–	Im5	x
O. pisciformis	2	5	5	–	1	–	–	Im13	x
O. pleioungulata	1	3	8	–	–	–	–	Im12	x
O. succulenticola	–	3	4	4	1?	–	–	Im11 Mms1?	x
O. pleiomicrosoma	–	1	2	1	1	–	–	Im3, Tm2	x
O. obtusispora	–	–	2	2	–	–	–	Im4	x
O. beltraniae	1	–	3	3	1	–	–	Im7	x
O. scolecospora	–	1	2	1	–	–	–	Im4	x
O. subaristata	–	–	1	1	1	–	–	Im2, Tm1	x
O. eucalypti	1	10	12	3	7	4	2	Im26, Tm2, Mmi6, Mms4, Sm1	x
O. hesperidea	–	–	1	1	1	–	–	Im3	x
O. gambelii	–	–	–	2	3	–	–	Im2, Mmi1, Mms1, Sm1	x
O. vinosa	–	–	4	–	4	1	–	Im5, Tm3, Mms1	x
O. adenocarpi	–	–	–	–	10	–	–	Mms4, Sm6	x
O. corculispora	–	–	–	–	3	–	–	Tm2, Mmi1	x
H. lunata	–	–	–	–	1	5	5	Tm7, Mmi4	h
H. tortuosa	–	–	–	–	–	2	2	Tm2, Mmi2	h
O. dryadum	–	–	–	–	–	6	4	Tm1, Mmi8	h
O. xanthostigma	–	–	–	–	–	~17	~29	Tm~40, Mmi~8	h
H. polypori	–	–	–	–	–	1	6	Tm6, Mmi1	h

According to Tab. 34, most of the drought-tolerant species occurred in varying frequency either in the hyperarid to lower semiarid zone or more in the lower and upper semiarid zone, or only in the semihumid ± south-facing slopes and summit zone. Solely *O. eucalypti* was found across all humidity zones, though especially in the arid to subhumid zones.

The inframediterranean lowlands (up to ~300–400 m altitude in the north and ~400–600 m in the south) comprises two main types of **succulent xerophytic scrublands** (tabaibal-cardonal, Fig. 136 left): (1) cardonal (*Periploco laevigatae-Euphorbietum canariensis*) in the semiarid (rarely semihumid or arid) north dominated by *Euphorbia canariensis*, and (2) tabaibal dulce (*Ceropegio fuscae-Euphorbietum balsamiferae*) in the (hyper)arid south (rarely north) dominated by *E. balsamifera*. Most records were on *Euphorbia* spp. and the number of observed species was 12 in the cardonal and 16 in the tabaibal dulce (a total of 21 spp., all belonging to *Orbilia* except for *Hyalorbilia fusispora*). Some of the more frequently collected species preferred the tabaibal (*O. acaciae*, *O. pseudeuphorbiae*), others the cardonal (*O. beltraniae*, *O. obtusispora*, *O. scolecospora*, and *O. succulenticola*). *O. pleioungulata* occurred more frequently in the cardonal, and *O. pisciformis* in both communities at equal frequency.

The thermo- and mesomediterranean (sub)humid **cloud forest** zone on the north-exposed upper slopes ranges at ~650–1900 m (Fig. 137 left). It houses *Orbiliomycetes* which never or only exceptionally appeared in drier zones. The vegetation types include remnants of the laurel (*Lauro novocanariensis-Perseetum indicae*) and ridge-crest forest (*Ilici canariensis-Ericetum platycodonis*), the more degraded fayal-brezal (*Myrico fayae-Ericetum arboreae*), and the natural and planted Canary pine forest (*Sideritido solutae-Pinetum canariensis*). Up to now (2019) 7 *Hyalorbilia* spp. and 7 *Orbilia* spp. were here recorded (Tab. S6). However, most collections were made on hygric branches and logs on the ground. Actually, most of these species show very little tolerance to drought, except for *O. eucalypti* (?collected on the ground) and *O. vibrioides* (on xeric branches). This low number of xerobiotic species in the cloud forests appears to be due to the neglect of attached branches (see under Madeira). Among the 14 species, *H. lunata* occurred also once in the dry Arbutus woodland (*Visneo mocanerae-Arbutetum canariensis*), and *O. eucalypti* across all climatic types (Tab. 34).

Only three species were so far collected in the **juniper shrubland** between xerophytic scrubland and cloud or pine forest, the thermomediterranean semiarid *Junipero canariensis-Oleo cerasiformis*, facies with *Pinus canariensis* at one site of the western slopes of Tenerife (*O. asomatica* on *Euphorbia lamarckii*, *O. pleioungulata* and *O. subaristata* on *Juniperus phoenicea* var. *turbinata*).

In the mesomediterranean semihumid **pine forest** (*Sideritido solutae-Pinetum canariensis*) on the west-, south- and east-exposed slopes (Fig. 137 right), which ranges at ~1200–2200 m, so far 11 species were recorded (*O. adenocarpi*, *O. corculispora*, *O. eucalypti*, *O. flavida*, *O. flavidorosella*, *O. patellarioides*, *O.* ?*paravitalbae*, *O. serpentina*, *O. subaristata*, *O.* ?*succulenticola*, *O. vinosa*). Some of them were only once found, so their ecological amplitude in the Canary Islands is unknown. Two (*O. eucalypti*, *O. vinosa*) occurred at equal frequency also in the succulent xerophytic scrubland, *O. eucalypti* also in the summit broom scrub and cloud forest.

The meso- to supramediterranean semihumid **caldera de las Cañadas**, around the Teide volcano is a high plateau of ~2000–2500 m altitude surrounded by a high rim (Fig. 136 right). The vegetation is mainly provided by the low summit broom scrub (*Spartocytisetum supranubii*), being treeless because of the low temperature due to the surrounding crater wall. A total of 10 orbiliaceous species were recorded, mainly on *Cytisus supranubius* and *Adenocarpus viscosus*, all being xerobiotic (see legend of Fig. 136). Most of them were only once found, even regarding the entire archipelago, but do also occur in Europe or North America. Outstanding is *O. adenocarpi* which was the only more frequently recorded species here, with overall 10 collections. It occurred only on *Adenocarpus viscosus* and only in this zone and once in the uppermost pine zone. Although the *Spartocytisetum supranubii* is endemic to Tenerife (del-Arco et al. 2016), *A. viscosus* (codeso de Cumbre) and *Cytisus supranubius* (retama) also occur at the top of La Palma, being endemic to the two islands.

3b. **Madeira**. The climate of Madeira is classified as submediterranean, semihumid to humid, except for the thermomediterranean semihumid southern lowlands. A total of 12 species are known at present. Korf (1992) reported *O. epipora* (= *H. inflatula* as reidentified by Quijada et al. 2014a) and *O. luteorubella* which requires reexamination. R. Reuter collected in 1997 *O.* ?*subulivinosa* and *O. vibrioides*, and K. Gilbert & B. Wergen in 2018 *O. cejpii*. A majority of records with overall 11 species were sampled and studied by J.P. Priou in 2009 and 2015, with emphasis on attached xeric twigs and branches. Most of the collections originate from the north-exposed (sub)humid cloud forests: the mesosubmediterranean laurel (*Lauro novocanariensis-Perseetum indicae*) and suprasubmediterranean ridge-crest forest (*Ilici canariensis-Ericetum platycodonis*). Here 3 *Hyalorbilia* spp. and 7 *Orbilia* spp. were recorded (5 xero- and 5 hygrobiotic species). Only one (*O. clavuliaristata*) came from the thermosubmediterranean semihumid lower zone.

3c. **Azores**. The islands of Azores comprise a temperate to submediterranean and only exceptionally eumediterranean climate. Only two samples are known which originate from thermotemperate semihumid areas of São Miguel and Flores, being reported by Korf (1992) under the name *O. inflatula* and reexamined by Quijada et al. (2014a, as *Hyalorbilia* spp.). One resembles European *H. ulicicola* and the other North American *H. texensis*.

4. Asia

Most Asian countries are badly explored until now, except for a few, in which either the xerobionts (China, Japan) or the hygrobionts (Mongolia, Turkey) were inadequately collected. Species diversity of Asia is at present 128, with about 22 *Hyalorbilia* spp., *Lecophagus muscicola*, 106 *Orbilia* spp., and *Pseudorbilia bipolaris*. This high number is mainly due to records from China. Despite this high number, the total diversity within Asia is probably two or three times higher. For the Ural region see p. 165, under boreal Europe (1a).

4a. **Central Asia**: Samples from the central Asian high- and lowlands were available for Tian Shan Mts. (Tajikistan) and especially Altay and Sayan Mts. and adjacent regions (Altay, Mongolia, Xinjiang, Tuva, Irkutsk). A total of 24 species were recorded until now, 3 in *Hyalorbilia* and 21 in *Orbilia*, about 12 of them being xerobionts.

During an excursion to cold-continental (sub)humid highland forests of western (Mongolian Altay Mts., 2200–2900 m a.s.l.) and northern (Yablonovy Mts., 1240–1600 m a.s.l.) parts of **Mongolia** in 2005, P. Karasch collected 13 xerobiotic *Orbilia* spp. on woody substrates. Two are only known from there (*O. basiflexa*, *O. mongolica*), the others were also recorded from Europe and North-America. Each species was only 1–2 × found, whereas *O. delphinus* was found at six localities. From the region of Tian Shan in **China** derives the type of *O. xinjiangensis* by X.Z. Liu in 2003, and from Chinese part of the Altay mountain range the hygrobiotic *O. juruensis* by Z.F. Yu in 2007 and *O. dryadum* by B. Liu in 2003.

A. Raitviir and others collected *Orbiliomycetes* at several sites between 1968–1980: *O. ?cardui* from the Tian Shan mountain range in **Kyrgyzstan** at the altimontane, cold-continental humid Lake Sary-Chelek; the type of *O. terrestris* from the Pamir-Alay mountain range in **Tajikistan** at the northwestern edge of Himalaya in a warm-continental semihumid (mediterranean) valley; *O. xanthostigma*, *O. sarraziniana*, *O. dryadum*, and the here described *H. sibirica* in humid angiosperm forests of the Sayan Mts. and Yenisey river in the **Tuva (Russia)**. E. Parmasto collected in 1975 in the eastern Sayan Mts. south of lake Baykal (**Irkutsk**, **Russia**) *H. ?fagi*, *O. tremulae*, and *O. xanthostigma*. In the cold-continental (sub) humid Altay mountains (**Altay**, **Russia**) E. Popov collected in 2008 4 xerobionts (*O. lentiformis*, *O. phragmotricha*, *O. arachnovinosa*, *O. aristata*) and 4 hygrobionts (*H. inflatula*, *O. epipora*, *O. fissilis*, *O. xanthostigma*).

4b. **Caucasus and Turkey**: In the **Caucasus** region, unpublished orbiliaceous samples were taken at several occasions between 1968–1977, particularly by B. Kullman in 1974, also by M. Murdvee, E. Parmasto, V. Puusepp, A. Raitviir and others. They are preserved at TAAM and were reexamined in the present study, resulting in 12 accepted, always hygrobiotic species. Further 3 samples collected in 1925, 2009, and 2012, 2 of them xerobiotic, were forwarded to us by E. Popov, resulting in overall 15 species. Due to the neglect of xeric substrate the actual diversity of orbiliaceous fungi in the Caucasus region remains largely unexplored.

A majority of collections derive from the **Russian** north-exposed slopes of the northwestern Caucasus (**Adygea**, **Krasnodar**, **Karachayevo-Cherkesiya**), and volcanic Beshtau Mt. (**Stavropol**), particularly from the orotemperate humid zone at 1000–1800 m, with forests composed of *Abies nordmanniana*, *Alnus*, *Carpinus*, *Fagus orientalis*, *Picea orientalis*, *Populus tremula*, *Pyrus caucasica*, and *Quercus*, but also from the supratemperate zone at 600–800 m, with *Carpinus*, *Fagus orientalis*, and *Ulmus*. Collections from the southeastern Caucasus were made at 700–900 m in the suprasubmediterranean humid south-exposed slopes of northwestern **Azerbaijan**, with *Carpinus*, *Corylus avellana*, *Fraxinus*, *Robinia pseudoacacia*, *Tilia platyphyllos*, and *Ulmus* as hosts. Further collections came from a marshy delta at 5 m in the mesotemperate (mt) humid Kolkheti National Park of western **Georgia** (near Poti at the Black Sea between Caucasus and Pontic Mts.), with the hosts *Platanus orientalis* and *Eucalyptus globulus*.

The following species were recorded (thermotype in parenthesis): hygrobionts include *Hyalorbilia caucasica* (Mt), *H. fagi* (Ssm, Mt), *H. inflatula* (St), *H. ?japonica* (Ssm), *H. polypori* (Ot), *Orbilia auricolor* (St or Ot), *O. epipora* (Ssm), *O. ?rosea* (St), *O. sarraziniana* (St, Ssm), *O. scolecospora* (Ssm), *O. sinensis* (Ssm), *O. tremulae* (Ot), and *O. xanthostigma* (Ot, Ssm, Mt); xerobionts include *O. aprilis* (Ot) and *O. subtrapeziformis* (Ot). Most frequently collected was *O. xanthostigma* (9 ×, but information on hymenial colour was absent in 5 samples), followed by *H. fagi* (4 ×) and *H. polypori* (3 ×). The rare *H. caucasica* is only known from the type collection, but not easily distinguished from *H. ulicicola*. Since several species were collected only once, their ecological amplitude in the Caucasus region remains unknown.

Akata & Doğan (2015) published for the first time orbiliaceous (hygrobiotic) species from **Turkey**, collected in the Pontic Mts. of the eastern Black Sea region: *O. auricolor* (as *O. curvatispora*), *O. sarraziniana*, and *O. xanthostigma*. In 2014 Y. Uzun collected *O. carpoboloides* on a xeric trunk of *Ulmus* in the same region, and A. Kaya and Y. Uzun *O. subaristata* on xeric twigs of *Pinus brutia* near Gaziantep (Y. Uzun pers. comm.).

In 2002–2003, T. Askun (unpubl.) collected xerobiotic *Orbilia* spp. around Balıkesir in the Marmara region (northwestern Turkey). The area lies at the border between the mediterranean and pontic floristic region and is tentatively classified here as supramediterranean. The altitude was 135–485 m and the geology calcareous. Both broad-leaved and mixed conifer forests were investigated, the broad-leaved trees comprising *Acer*, *Carpinus*, *Celtis*, *Fagus orientalis*, *Fraxinus*, *Mespilus germanica*, *Paliurus spina*, *Platanus orientalis*, *Populus*, *Quercus ilex*, *Salix alba*, and the conifers *Abies*, *Cedrus*, *Cupressus sempervirens*, *Juniperus*, *Picea orientalis*, *Pinus brutia*, *and P. nigra*. Collections were made on attached branches, predominantly of *Pinus brutia*, followed by *Quercus ilex* and many of the other genera. A total of 10 *Orbilia* spp. were encountered. The most frequent species were *O. euonymi* (7 ×) and *O. subaristata* (7 ×); the remaining included *O. eucalypti*, *O. flavida*, *O. gambelii*, *O. ovalis* (only anamorph), *O. pleiomicrosoma*, *O. subovoidea*, *O. subvinosa* (only anamorph), and *O. vinosa*.

4c. **Southern Asia**: Tewari & Pant (1966) reported *O. sarraziniana* from Uttar Pradesh (northern **India**) as first record of an identified *Orbilia* from India (unillustrated). Thind & Sharma (1980) added for India *O. auricolor* s.auct., *O. curvatispora*, *O. luteorubella,* and *O. xanthostigma*, and Thind et al. (1983) *O. rubrococcinea*, but all these reports are of doubtful identity, except for *O. curvatispora* (= *O. auricolor*) which was reexamined here. Unidentified up to now remained Batra & Batra's (1963) orbiliaceous collections from India (see p. 199).

Ahmad's (1978) unillustrated report of 3 hygrobionts for **Pakistan** includes *H. ?inflatula* (as *O. auricolor*), *O. ?auricolor* (as *O. curvatispora*), and ?*O. dryadum* (as *O. leucostigma*). Two xerobiotic species were examined in the present study (*O.* aff. *caudata*, *O.* cf. *trapeziformis*). From tropical humid (winter-dry) **Thailand** Ekanayaka et al. (2018) recorded *H. erythrostigma*, *H. arcuata* (as *H.* cf. *inflatula*), *O. caudata*, *O.* aff. *renispora* (as *O. leucostigma*), and the dubious *O. stipitata* (p.p. = *O. nemaspora*), and during the present study J.P. Priou in 2012 *H. tortuosa* and C. Peller in 1996 *O. milinana*.

Figure 138: Subtropical humid evergreen broad-leaved forests in Yunnan, southern China; **left**: with *Castanopsis orthacantha*, *Cinnamomum*, *Cyclobalanopsis*, *Lithocarpus variolosus*, *Rhododendron*, 2560 m, Jizushan, Dali, collected in 20.X.2008, phot. 18.VIII.2005, Y. Zhang; lying branches of indet. angiosperms (2300 m: *Orbilia ?battenii*, *O. cejpii*, *O. eucalypti*, *O. fissilis*, jz-34, 36, 41, 46; 2700 m: *Hyalorbilia japonica*, *H. macrohelicospora*, *H. multiguttulata*, *H. ulicicola*, *O. binchuanensis*, *O. ?cardui*, *O. latispora*, *O. laevimarginata*, jz-1, 3–7); **right**: with indet. *Taxodiaceae*, 1700 m, base of mountain Laifengshan, Baoshan, collected in VIII.2004, phot. 14.VIII.2005, Y. Zhang; hygric branches of indet. ?gymnosperms (*H. arcuata*, *O. hoana*, *O. tenuispora*, tc-22–23, 51).

From **Vietnam** N. Petit collected in 1995 *H. tortuosa* and *O. ?subfabacearum*. The type of *O. fici* (= *O. blumenaviensis*) comes from **Singapore**, and *O. pseudobrevistipitata* was collected by P. Wagner in 1995 from **Philippines**. From tropical humid **Indonesia** Penzig & Saccardo (1902) described *O. neglecta* and *O. sinuosa* (?= *H. inflatula*/*H. japonica*), and Rifai & Cooke (1966) the anamorph of *O. javanica*.

4d. **Eastern Asia**: The regions of eastern Russia, China, Korea and Japan are subjected to a humid, more or less continental, monsoon-dominated, winter-dry climate that ranges from the subarctic to tropical belt. Best explored is China, followed by Japan and Russia, whereas no collection of a teleomorph from Korea is known to us. A majority of the recorded species can more or less be classified as hygrobionts. The few xerobiotic taxa were mostly encountered by accident on fallen substrate, not by systematic search. In conclusion, the occurrence of xerobiotic *Orbiliomycetes* in eastern Asia remains largely unexplored. Due to the restriction to sampling in moist habitats, collecting was preferably done from June to November, following the rainy period which lasts from April-May to September-October.

The cold-continental to boreal **Russian Far East** (mainly **Primorje** and **Sachalin**) was treated by Raitviir (1991: 356–362) with at least 10 orbiliaceous species: *H. inflatula*, *O. auricolor*, *O. cardui*, *O. crenatomarginata* (as *Hyalinia crystallina*), *O. ?epipora*, *O. eucalypti* (as *O. microclava*), *O. luteorubella* (including *O. ?rosea*), *O. orientalis*, *O. ?sarraziniana*, and *O. xanthostigma* (as *O. delicatula*, ?including *O. leucostigma*). Only *O. orientalis* (type) was reexamined in the present study. We also saw photos of *O. ?umbilicata* from cold-continental Primorje (2005, E. Popov), and studied a sample of *O. crenatomarginata* from extremely continental and rather dry, boreal **Sakha** (Yakutia, 1968, H. Remm).

Until the end of the 20th century, **China** was poorly explored for *Orbiliomycetes*. The first report by Teng (1939: 167, see also Teng 1996) listed only one species, *O. sinuosa* (?= *H. inflatula*). More recent reports include *O. auricolor* (Zhuang & Korf 1989, as *O. curvatispora*; Wu 1998), *O.* aff. *umbilicata* (as *O. xanthostigma*, Zhuang 1997), *O. xanthostigma* (as *O. delicatula*) and *H. inflatula* (Wu 1998). Many further, often new orbiliaceous species were reported in the 21th century by Guo et al. (2014a, 2014b), Li et al. (2009), Liu et al. (2005a, b, 2007a, b), Mo et al. (2005b), Qiao et al. (2012, 2015), Qin et al. (2011), Su et al. (2011c), Wu et al. (2007), Yu et al. (2006, 2007a, b, 2009a, b, 2011), Zhang et al. (2006, 2007, 2009b, 2015, 2016, 2020a), Zhuang & Hyde (2011). For the region of Tibet, Liu et al. (2006b) reported *H. inflatula* and 9 *Orbilia* spp. (including *O. bomiensis* and *O. milinana*). In his comprehensive unpublished monograph on the *Orbiliaceae* of China, Liu (2006) reported over 350 samples made by him and X.Z. Liu mainly between 2002–2005, some also between 1994–1999 and earlier, including 8 *Hyalorbilia* spp. and 20 *Orbilia* spp.

Besides these reports on taxa with a known teleomorph, many papers on taxa without a known teleomorph appeared since 1994. The total number of species with known teleomorph lies up to now at almost 100 when including Taiwan. Species diversity was much higher in the warm-temperate to tropical southern parts (roughly south of 34° latitude) in comparison with the cooler, oro- to supratemperate northern parts of China (or high altitudes in more southern and western China), i. e., about 90 % of all recorded species occurred in the warmer regions and only about 28 % in the cooler zones. Among those species from cooler zones which were not recorded in the warmer parts of the country are *O. bomiensis*, *O. cejpii*, *O. epipora*, *O. nemaspora*, *O. quercus*, *O. tremulae*, *O. xinjiangensis*, and *O. zhongdianensis*.

A majority of collections came from subtropical, monsoon-influenced, often purely broad-leaved, evergreen highland forests in southern China, being composed of, e. g., *Castanopsis orthacantha*, *Cinnamomum glanduliferum*, *Lithocarpus variolosus*, *Magnolia campbellii*, *Quercus* (*Cyclobalanopsis*) *glauca*, *Rhododendron delavayi*, and *Schima* '*argentea*', based on data from two frequently visited areas in Binchuan county (Dali, Yunnan), Jinguangsi virgin forest (Golden Light Temple, ~2500 m) and Jizushan (Chicken-foot Mountain, ~2700 m, Fig. 138), or mixed with conifers, e. g., a *Quercus schottkyana* (= *Cyclobalanopsis glaucoides*) and *Pinus armandii* dominated forest in the Longquan (Dalongkou) National Forest Park in Yimen county (Yuxi, Yunnan, ~1700–1800 m). Fragments of many of these collections made between 2003–2010 were sent to us for study, and the results were published in various papers (see above references).

From orotemperate to cold-temperate ± humid northeastern China (Heilongjiang, Jilin, Beijing) derive about 5 *Hyalorbilia* and 10 *Orbilia* spp. Most of them are hygrobionts, except for *O. jugulospora* and *H. juliae* and perhaps *O. cejpii*. From cold-continental western China (Xinjiang, Tibet) are *H. inflatula* and 8 *Orbilia* spp., with *O. bomiensis* and *O. milinana* and possibly *O. xinjiangensis* being xerobiotic, and from orotemperate central and southern China 4 *Hyalorbilia* spp. and 4 *Orbilia* spp., with *H. juliae* and possibly *O. zhongdianensis* being xerobiotic. In sum there are about 8 *Hyalorbilia* and 20 *Orbilia* spp. from these cooler, deciduous or conifer forest regions. Several of these species are rarities, whereas the most frequently collected ones were *H. inflatula* and *O. xanthostigma* (Liu 2006).

From warm-temperate humid regions of China derive about 6 *Hyalorbilia* and 26 *Orbilia* spp., from subtropical regions (particularly humid highlands) *Pseudorbilia bipolaris*, 13 *Hyalorbilia* spp., and 50 *Orbilia* spp., and from tropical humid regions *H. polypori* and 15 *Orbilia* spp. In sum there are min. 17 *Hyalorbilia* and 66 *Orbilia* spp. from the warm-temperate and evergreen forest regions. Many of them appear to be rarities as they were only collected at one site, but some are known from different regions, such as *H. arcuata*, *H. japonica*, *O. dorsalis*, *O. hoana*, *O. laevimarginata*, or *O. tenuispora*. Here, too, *H. inflatula* was by far the most often collected species (Liu 2006), whereas *O. xanthostigma* was only sometimes encountered in the (sub)tropics and only once in Yunnan (Liu 2006). In addition, numerous anamorph-typified taxa, mainly without known teleomorph, were recorded as soil isolates particularly from these warmer regions.

From **Japan**, earlier reports include those of *Orbilia* ?*epipora* (as *H. inflatula*), *O. sarraziniana*, and *O. luteorubella* by Otani (1990). 33 collections by T. Hosoya (1990–1997) and W. Gams (1997) were revised in the present study, with 3 *Hyalorbilia* and 16 *Orbilia* spp., the most often collected taxa being *O. xanthostigma* and *H. japonica*. Rarities were, e. g., *O.* ?*battenii*, *O.* ?*renispora*, *O. spirospora*, and *O. umbilicata*. More or less all of these species are hygrobionts. Most collections were from temperate areas in Honshu and Hokkaido, but 3 from the warm-temperate (*O.* ?*cejpii*, *O. tenuispora*, *O.* ?*umbilicata*) and 2 from the subtropical zone (*H. citrina*, *O. spirospora*). Among the anamorphic taxa, Morikawa et al. (1993) isolated *Lecophagus muscicola* in the subtropical zone of Honshu.

5. Australasia and Melanesia

Previous **Australian** reports comprise totally 9 teleomorphic orbiliaceous species. Spooner (1987) accepted 8 spp. growing on wood and bark of *Eucalyptus*, *Melaleuca*, *Xanthorrhoea*, and unidentified plants collected from 9 different locations at 15–270 m altitude: 7 around Melbourne (Victoria) in warm-temperate humid southeastern Australia (*Orbilia xantho-* or *leucostigma*, 1914, collector unknown; *Hyalorbilia inflatula*, *O. auricolor*, *O.* ?*dryadum*, *O. flexispora*, *O. scolecospora*, '*O. vinosa*', 1962–64, G. or K. Beaton), and 2 near Brisbane (Queensland) in subtropical humid (winter-dry) eastern Australia (*O.* ?*carpoboloides*, undated, F.M. Bailey; *H. inflatula*, 1981, B.C. Sutton). No collection data were available for 2 samples reported by Bell (2005), cultured on Australian dung (*H. inflatula*, *O.* ?*cejpii*). A sample from tropical humid Solomon Islands referred by Spooner (1987) to *O. juruensis* (Fig. 163) requires reexamination.

Previous records from **New Zealand**, mainly by P.R. Johnston between 1989–2008 and J.A. Cooper between 2010–2012, comprise only 4 species when not differentiating cryptic, morphologically indistinguishable taxa of the *xanthostigma-leucostigma* complex, based on a total of 35 selected collections from 29 sites, some of which being revised in the present study: *H.* ?*ulicicola* (1 ×) *O. cunninghamii* (16 ×), *O.* ?*luteorubella* (2 ×), *O. xanthostigma* (16 ×). Included is the type of *O. cunninghamii* described by Sydow (1924). The 29 sites belong to low or medium altitudes (2–745 m) across the entire length of the country from the cold-temperate very south to the subtropical north, all with a humid (slightly summer-dry) oceanic climate.

Anamorphic records from Australasia include a forest litter isolate of *O. oxyspora* from **Papua New Guinea** (Matsushima 1971) and 19 predacious species of series *Arthrobotrys*, *Dactylellina*, and *Gamsylella* isolated from soil, moss, wood and dung in Western **Australia** (Park et al. 2002).

The low number of species known before 1996 is a result of the former neglect of xeric substrates. As a matter of fact, only one of those older records, the type of *O. decipiens* (?= *O. carpoboloides*) described by W. Phillips (in Cooke 1887), represents a xerobiotic species, and no such species is known so far from New Zealand. In contrast to this, the numerous Australian records presented here are almost exclusively from xeric substrates. They raised the number of species with a known teleomorph for Australasia to 154, which suggests that also in New Zealand many xerobiotic species remain to be discovered.

Within **Australia**, teleomorphs of *Orbiliomycetes* were studied in the present monograph from a total of ~460 individual populations, when counting each species recorded within each collection. About 3–10 orbiliaceous species were observed per site on a given host species, though sometimes only 1 or rarely up to 14. Collections derive from almost 100 sites at 2–1073 m altitude from all around Australia. Many of them represent woodlands and forests in a region less then ca. 100 km from the coastline, but numerous others are more or less desertic shrublands in the so-called 'outback' which in the west extends to the seaside. Except for two humid sites from which collections were sent to us by E. Batten (Tasmania, *H. polypori*, 1996) and T.R. Lohmeyer (Victoria, *O. xanthostigma*, 2008) and older samples mentioned above, all these sites were investigated by one of us (G.M.) during four collecting trips in 1998, 2001, 2006, and 2007.

A majority of collections derive from subtropical semihumid (summer-dry), mediterranean forests and open woodlands in the southwest (32 sites) and (sub)tropical (semi)arid shrublands in the west and centre of Australia (36 sites). Other sites are in monsoon-influenced (winter-dry) tropical savannahs in the northwest and north, in rain forests in the tropical humid

Table 35. Major vegetation groups in Australia evaluated for all reported collection sites, with indication of the number of populations/species, thermo- and ombrotype, biogeographic region (ecoregion), and collected substrate.

Vegetation group	Pop./spp.	Thermotype	Ombrotype	Ecoregion	Collected substrate
acacia forests and woodlands	11/9	subtropical	semiarid to arid	Carnarvon, Murchison	*Acacia* sp., *Psydrax latifolia*, *Vachellia farnesiana*
acacia open woodland	22/19	subtropical	semiarid	Gascoyne, rarely Murchison	*Acacia* spp., *A. cyperophylla*, *Eucalyptus* sp.
acacia shrublands	128/71	subtropical to tropical	semiarid to arid, rarely semihumid	Avon Wheatbelt, Burt Plain, Carnarvon, Pilbara, Yalgoo, Desert Uplands, Great Sandy Desert, McDonnell Ranges, Finke, Geraldton Sandplains etc.	*Acacia aneura*, *A. coriacea*, *A. georginae*, *A. jennerae*, *Allocasuarina decaisneana*, *Atriplex nummularia*, *Brachychiton gregorii*, *Psydrax latifolia*
	2/2	tropical	savannah	Dampierland	*Adansonia gregorii*, indet. tree
casuarina forests and woodlands	4/4	subtropical	semihumid	Geraldton Sandplains	*Acacia* sp.
eucalypt low open forest (karri-tingle)	5/5	subtropical	semihumid	Jarrah Forest	*Chamaelaucium ciliatum*, *Banksia grandis*
eucalypt tall open forests (karri-tingle)	6/6	subtropical	semihumid	Warren	*Eucalyptus* sp., *E. jacksonii*
	3/3	warm-temp.	humid	South Eastern Highlands	*Nothofagus cunninghamii*, indet. trees
eucalypt open forests (jarrah-marri)	5/4	subtropical	semihumid	Jarrah Forest	*Banksia grandis*
	11/11	subtropical to cold-temp.	humid	Sydney Basin to Tasmanian Northern Slopes	*Eucalyptus* sp., *Melaleuca* sp., indet. trees
(banksia-) eucalypt woodlands	54/26	subtropical	semihumid	Swan Coastal Plain, Jarrah Forest	*Acacia* sp., *Anigozanthos manglesii*, *Arbutus andrachne*, *Banksia cuneata*, *B. grandis*, *B. menziesii*, *B. sessilis*, *Eucalyptus* sp., *Jacksonia* sp., *Melaleuca rhaphiophylla*, *Ptilotus polystachyus*
	53/40	warm-temperate to tropical	savannah, subhumid, humid	Dampierland, Brigalow Belt, Einasleigh Uplands, Stuart Plateau, Naracoorte Coastal Plain, NSW South Western Slopes, Darling Riverine Plains	*Acacia aneura*, *A. cheelii*, *Adansonia gregorii*, *Casuarina cunninghamiana*, *Eucalyptus* sp., *Geijera parviflora*, *Livistona nitida*, *Melaleuca* sp., *Pittosporum phillyreoides*, *Salix babylonica*, *Xanthorrhoea australis*
eucalypt open woodlands	54/34	subtropical	semihumid, semiarid	Jarrah Forest, Swan Coastal Plain, Geraldton Sandplains, Avon Wheatbelt, Mallee	*Acacia* sp., *Agonis flexuosa*, *Allocasuarina campestris*, *Banksia cuneata*, *Calothamnus* sp., *Eremaea* sp., *Eucalyptus* sp., *Hakea* sp., *Jacksonia* sp. *Macrozamia riedlei*, *Nuytsia floribunda*, *Verreauxia reinwardtii*, *Xanthorrhoea preissii*
	9/8		savannah, subhumid	Brigalow Belt South	*Casuarina cunninghamiana*, *Melaleuca* sp.
hummock grasslands	15/11	subtropical	semiarid to arid	Pilbara, Carnarvon, McDonnell Ranges	*Acacia* sp., *A. aneura*, *A. estrophiolata*, *Solanum lasiophyllum*
other forests and woodlands	19/11	subtropical	semihumid	Swan Coastal Plain	*Adenanthos sericeus*, *Anigozanthos manglesii*, *Eremaea pauciflora*, *Hibbertia aurea*
other shrublands	27/24	subtropical	semihumid, semiarid	Yalgoo, Geraldton Sandplains etc.	*Acacia* sp., *Dodonaea angustissima*, *Lamarchea hakeifolia*, *Nuytsia floribunda*
rain forests and vine thickets	23/17	tropical	humid	Wet Tropics and Einasleigh Uplands	*Acacia* sp., *Bambusa* sp., *Barringtonia racemosa*, *Cocos nucifera*, *Hibiscus tiliaceus*, *Licuala ramsayi*, *Phragmites australis*, indet. climber
tropical eucalypt woodlands/grasslands	2/1	tropical	savannah	Arnhem Plateau, Daly Basin	*Acacia* sp.
tussock grasslands	6/6	subtropical to tropical	arid	Pilbara	*Acacia* sp., *Ipomoea costata*

northeast, and in woodlands and forests in the subtropical to warm-temperate (sub)humid east and southeast of Australia (39 sites). Collected substrates were mainly wood and bark of angiosperms, such as *Acacia*, *Adansonia*, *Allocasuarina*, *Atriplex*, *Banksia*, *Dodonaea*, *Eremaea*, *Eucalyptus*, *Jacksonia*, *Lamarchea*, *Melaleuca* and *Nuytsia*, but also herbaceous stems, particularly *Anigozanthos* and *Phragmites*, and the somewhat woody *Solanum lasiophyllum*, stems of bamboo, and petioles of *Cocos*, *Livistona*, and *Macrozamia* (Tab. 35).

Among the overall ~154 species, for which a teleomorph was recorded in Australia, at least 9 belong to *Hyalorbilia* and 146 to *Orbilia* as circumscribed here. Based on the evaluated humidity zones, the following species numbers were obtained. When starting clockwise in the southwest of Australia, 55 spp. occurred in the mediterranean zone, 73 spp. in the semiarid zone (68 in the subtropical and 10 in the tropical belt), 43 spp. in the arid zone (38 in the subtropical and 6 in the tropical belt), 24 spp. in the savannah (12 in the subtropical and 12 in the tropical belt), 18 spp. in the humid tropical zone, 17 spp. in the subhumid subtropical zone, 12 spp. in the humid subtropical zone, and 13 spp. in the humid warm-temperate zone. In summary, 37 spp. occurred in humid and 37 in subhumid (savannah-like) zones, whereas 55 were found in semihumid and 94 in semiarid to arid zones (see also Tab. 33). Among the 9 *Hyalorbilia* spp., 5 occurred in the humid (*H. arcuata*, *H. citrina*, *H. inflatula*, *H.* cf. *orbiliicola*, *H. polypori*), 1 in the semihumid (*H. juliae*), 2 in the subhumid (*H.* aff. *erythrostigma*, *H.* aff. *orbiliicola*), 2 in the semiarid (*H.* aff. *orbiliicola*, *H. pleioerythrostigma*), and 1 in the arid zone (*H.* aff. *orbiliicola*). Only about 13 of the 154 species can be classified as more or less hygrobiotic.

The majority of Australian species, mainly of series *Hemiorbilia* and *Habrostictis*, appear to prefer (semi)arid (sub)tropical regions. However, many of them were also often recorded in the semihumid zone (*O. australiensis*, *O.*

Figure 139: Subtropical semihumid forests and woodlands in Jarrah Forest ecoregion, southwestern Australia; **left**: eucalypt open forest (jarrah-marri), 307 m, Beelu National Park, Kalamunda, 13.XII.2001, phot. G. Marson (#547); 28 km NW from there (#546, 2001 & 2006): attached branches of *Banksia grandis* (with *O. aviceps*, *O. curvatinavajoana*, *O. eucalypti*, *O. microserpens*, H.B. 7322, 8659); **right**: Eucalypt woodland, 272 m, Udumung Nature Reserve, Wannamal, 3.–4.IX.2006, phot. G. Marson (#952–953); attached twigs and branches of *Acacia* sp. and *Eucalyptus* sp., xeric petioles of *Macrozamia riedlei* (with *Orbilia albidorosea*, *O. australiensis*, *O. austroocculta*, *O. austroregalis*, *O. coronohesperidea*, *O. eucalypti*, *O. kingsiana*, *O. myrioobliqua*, *O. nothovinosa*, *O. pleiocrescens*, H.B. 8391, 8582, 8604, 8662).

Figure 140: Subtropical semihumid Eucalypt woodlands in Swan Coastal Plain ecoregion, southwestern Australia; **left**: banksia-eucalypt woodland, 48 m, Kings Park in Perth, 7.IX.2006 & 14.XI.2007, phot. G. Marson (#965–957); lying xeric stems of *Anigozanthos manglesii* (kangaroo paw, with *Orbilia anigozanthi*, *O. kingsiana*, *O. ?nothoaprilis*, H.B. 8303, 8831), attached branch of *Banksia grandis* (with *O. astrovinosa*); **right**: eucalypt woodland dominated by *Jacksonia* sp., 37 m, Walyunga National Park, Perth, Swan Coastal Plain ecoregion, 23.XI.2001, phot. G. Marson (#501); attached branches of *Jacksonia* (both sites together with 14 *Orbilia* spp., e. g. *O. albidorosea*, *O. austroocculta*, *O. austroregalis*, *O. kingsiana*, *O. myrioaustraliensis*, *O. myriofusiclava*, *O. myrioobliqua*, H.B. 7284).

Figure 141: Subtropical shrublands in Geraldton Sandplains, western Australia; **left**: semihumid shrubland, 278 m, Northampton, 9.XII.2001, phot. G. Marson (#539); attached branches of *Nuytsia floribunda* (yellow-flowered, with *O. brachychitonis*) and *Acacia* sp. (with *O. commarosa*, *O. eucalypti*, *O. myriofusiclava*, H.B. 7237); **right**: semiarid wood- and shrubland, 292 m, Moora, 25.X.2007, phot. G. Marson (#1110); attached twigs of *Calothamnus* sp. (with *Orbilia australiensis*, *O. hesperidea*, *O. myrioobliqua*, H.B. 8966). Collecting in these semiarid shrublands requires protection against insects.

Figure 142. Subtropical semiarid acacia and other wood- and shrublands in western Australia; **left**: with *Acacia*, *Lamarchea*, *Dodonaea*, *Callitris* (northern mallee), 190 m, Nerren Nerren, Yalgoo ecoregion, 8.XI.2007, phot. G. Marson (#1129); attached branches of *Dodonaea viscosa* subsp. *angustissima*, *Acacia* sp., and *Lamarchea hakeifolia* (with *Hyalorbilia pleioerythrostigma*, *Orbilia fimbriata*, *O. gemma*, *O. lamarcheae*, *O. myriolilacina*, *O. pseudoflagellispora* and further 13 *Orbilia* spp., H.B. 8838, 9020, 9050); **right**: acacia shrubland (mulga), 67 m, Overlander Roadhouse, Carnarvon ecoregion, 7.XII.2001 & 6.XI.2007 (#533); attached branches of *Acacia* sp. (with *O. myriella*, *O. myrioauris*, *O. myriofusiclava*, *O. myrionanosoma*, *O. myriopseudoregalis*, *O. pleistoobliqua* and further 6 *Orbilia* spp., H.B. 7215, 8727).

pleioaustraliensis, *O. myrioobliqua* etc.). *O. myrioobliqua* belongs to a morphologically extraordinary group of 8 species with 32–128-spored asci within series *Vibrioides* which are so far only known from semihumid to arid western Australia. A number of species might be endemic to the mediterranean southwest, such as *O. anigozanthi*, *O. austroocculta*, *O. astrovinosa*, *O. aviaristata*, *O. aviceps*, *O. curvatinavajoana*, *O. nanosperma*, and *O. triangulispora*, but the low number of records is probably the reason for this restriction. The most often collected species in Australia, *O. eucalypti*, was so far exclusively found in the mediterranean zone. Other species, e. g. *O. myrioobliqua* and *O. myriofusiclava*, occur here but also in the semiarid zone, and various further ones, such as *O. pleioaustraliensis*, *O. multiserpens*, *O. myriella*, *O. pleioaustraliensis*, *O. pleioserpens*, and *O. pluristomachia*, were mainly found in the semiarid but also in the semi- to subhumid or arid zone.

A **subtropical semihumid** climate, reminiscent of the European mediterranean belt, characterizes the southwest of Australia and a large not investigated area around Adelaide in the southeast. Different main vegetation groups can be distinguished within this summer-dry region: in the very south of the hilly Darling Range it is the dense eucalypt tall open forest (karri-tingle) in the Warren ecoregion (Fig. 139 left), with a height of ~20–60 m and the highest humidity, with *Eucalyptus diversicolor* (karri) and *E. jacksonii* (red tingle) as typical species. Collections were made on *Eucalyptus* at 60–300 m a.s.l. and include *Orbilia aviaristata*, *O. lilacina*, *O. nanosperma*, *O. pseudoflagellispora*, and *O. subalbovinosa*, and in a eucalypt low open forest on *Banksia* and *Chamelaucium* at 75 m also *O. aviceps*, *O. triangulispora* and others. To the north follows the eucalypt open forest (jarrah-marri), characterized by *E. marginata* (jarrah) and *Corymbia calophylla* (marri), with records of *O. aviceps*, *O. curvatinavajoana*, *O. eucalypti*, and *O. microserpens* on *Banksia grandis* at 70–370 m a.s.l.

Around the Darling Range occur remaining fragments of the banksia-eucalypt woodlands, with a height of ~10–20 m, mainly composed of *Banksia grandis*, *B. menziesii*, *Eucalyptus marginata* and other eucalypt and acacia species (Fig. 139 right, 140 left) or *Jacksonia* (Fig. 140 right), besides casuarina and other forests and woodlands with various trees and shrubs, for instance *Nuytsia* (Fig. 141 left). Numerous species have been recorded here on these and various other substrates at 10–200 m a.s.l., including *O. anigozanthi*, *O. curvativitalbae*, *O. eucalypti*, *O. kingsiana*, *O. multicurvula*, *O. myriofusiclava*, *O. myrioobliqua*, and *O. nothovinosa*.

The region of **subtropical to tropical semiarid to arid** western and central Australia is represented by the Pilbara desert and the large centre of Australia which includes the McDonnell Ranges. The summer-dry region comprises two main types: (1) eucalypt open woodlands (mallee), in semiarid areas the dominant vegetation with multistemmed, ~10–20 m tall eucalypts, e. g., northern (Figs 141 right, 142 left) and southern mallee shrubland and heath (Nevill & McQuoid 1999), and (2) acacia shrublands (mulga) in semiarid and arid areas, dominated by

Figure 143: Tropical woodlands and forests in Northern Australia; **left**: subhumid Eucalypt open woodland (savannah) with tussock grass understory, 20 m, Fitzroy river, Dampierland ecoregion (Kimberley Plateau), 1.XI.2007, phot. G. Marson (#519); attached branch of *Adansonia gregorii* (baobab, with *Orbilia brachychitonis*, *O. carminorosea*, *O. euphorbiae*, H.B. 8777); **right**: humid rainforest and vine thicket, 15 m, Cape Tribulation, Wet Tropics ecoregion, 30.VIII.2006, phot. G. Marson (#936); originally vertical branch of *Hibiscus tiliaceus* (with *O. spirillospora*, *O. ?subfabacearum*, H.B. 8487).

Acacia aneura (Fig. 142 right), with multistemmed, up to ~5–10 m tall shrubs occurring in various ecoregions of the outback. Collections were made on *Atriplex*, *Allocasuarina*, *Acacia*, *Brachychiton*, *Dodonaea*, *Lamarchea* etc. at 5–700 m a.s.l. and include *O. australiensis*, *O. pleioserpens*, *O. multiserpens*, *O. myriomuscula*, *O. myrioobliqua*, *O. pleioaustraliensis*, *O. pluristomachia* and many others, a total of 94 *Orbilia* spp. The unexpected occurrence of rather dense and high acacia forests and woodlands as well as tussock grasslands in the semiarid to arid Pilbara desert is explained by a restriction to dry river flats.

The monsoon-influenced region of **tropical subhumid** northwestern and northern Australia (Fig. 143 left) in the Kimberley Plateau and Arnhem Plateau shows a savannah-like vegetation with dry but very mild winters. Typical are the scattered water-storing baobab trees (*Adansonia gregorii*) and *Acacia* spp., and a widespread tussock grass understory that grows during summer but is straw-coloured during winter. Collected substrates at 10–300 m a.s.l. include *Acacia aneura*, *Adansonia gregorii*, *Eucalyptus* sp. etc., with *Orbilia arachnopus*, *O. brachychitonis*, *O. carminorosea*, *O. euphorbiae*, *O. hesperidea*, and *O. paracaudata*.

Continuous and heavy summer rainfalls occur in the rainforests and vine thickets of **tropical humid** northeastern Australia at the northern end of the Great Dividing Range (monsoon-dominated evergreen forest, Fig. 143 right), though with a dry period during several months. Despite the high annual precipitation, drought-tolerant species occur in the dry season here. Collected substrates at 5–400 m a.s.l. include *Acacia* sp., *Bambusa*, *Cocos nucifera*, *Hibiscus tiliaceus*, and *Licuala ramsayi* in the Wet Tropics ecoregion, and *Barringtonia racemosa* and *Phragmites australis* in the more savannah-like Einasleigh Uplands, with 18 orbiliaceous species (4 in *Hyalorbilia*), e.g., *H. arcuata*, *O. bambusina*, *O. neocomma*, *O. nothoaprilis*, and *O. spirillospora*.

Records from **subtropical subhumid** (north)eastern Australia (winter-dry, monsoon-dominated savannah-like vegetation) derive from eucalypt (open) woodlands in the northern part of the Great Dividing Range at 100–300 m a.s.l., mainly in the large Brigalow Belt South ecoregion. Collected substrates were *Casuarina cunninghamiana*, *Eucalyptus* sp., *Geijera parviflora*, *Livistona nitida*, *Melaleuca* sp., and *Pittosporum phillyreoides*, on which more than 20 xerobiotic *Orbilia* spp. were observed, e.g., *O. angustoaristata*, *O. corculispora*, *O. geijerae*, *O. nothovinosa*, and *O. palmicola*. The holotype of *O. decipiens* (?= *O. carpoboloides*) from the coastal region of Brisbane also belongs to this climatic zone.

Collections from **warm-temperate (sub)humid** southeastern Australia (not or only slightly winter-dry forests and woodlands) in the southern part of the Great Dividing Range include 15 xerobiotic *Orbilia* spp. (e.g., *O. arachnopus*, *O. multinanosoma*, *O. myrioeuonymi*) which derive from eucalypt woodlands at two sites in the Central Tablelands west of the mountain range at 500–550 m a.s.l. and from eucalypt open forests at two sites in the Blue Mountains at 850–1050 m. Despite the high altitude the climate is warm-temperate there. Collections of hygrobiotic species from south and east of the southern Snow Mountains and Tasmania include eucalypt tall open forests at 100–600 m a.s.l. (*H. inflatula*, *O. dryadum*, *O. xanthostigma*), but also eucalypt open forests and eucalypt woodlands at 20–250 m (*H. polypori*, *O. flexispora*, *O. scolecospora*). Collected substrates include *Eucalyptus* sp., *Melaleuca* sp., *Salix babylonica*, and *Xanthorrhoea australis*.

6. North America

6a. **Northern America** (**including Greenland**): Previous reports of orbiliaceous teleomorphs include mainly those from eastern Northern America: from **Pennsylvania** (Schweinitz 1832, *Orbilia xanthostigma*, as *Peziza rufula*), **New Jersey** (Cooke 1875a, *O. cookei*, as *P. exigua*; Cooke & Ellis 1878, *O. regalis*; Rehm 1885, *O. occulta*), **Ohio** (Bachman 1909: 57, *H. inflatula*, as *O. auricolor*; *O. ?cejpii*, as *O. coccinella*; *O. ?dryadum*, as *O. xanthostigma*; '*O. vinosa*'), **Virginia** (Berkeley 1875, *O. carpoboloides*, as *P. fibriseda*), **Kentucky** (Rehm 1883, *O. carpoboloides*, as *Calloria rubrococcinea*), and **Alabama** (Berkeley (1875, *O. saccharifera*), **exceptionally** from the west, i.e., from **California** (Phillips & Harkness 1884, *O. eucalypti*). From the northwest are records from **Alaska** (Korf in Kobayasi et al. 1967, *O. ?eucalypti*, as *O. coccinella*?; *Orbilia* sp.), and from the northeast from **Québec** and **Ontario** (Haines & Egger 1982, *O. carpoboloides*, as *O. piloboloides*). Seaver (1951) included a few more or less unclear orbiliaceous species, such as *O. luteorubella* and *O. rubella*, but merged some of the above under *O. cruenta*.

About 120 records, mainly teleomorphic, made after 1990 by others than us in the northwest and particularly north- to southeast of Northern America came to our notice, either by receiving documents and/or molecular data or through personal studies by one of us (H.B.): from **Alaska** (D.H. Pfister & B. Liu in 2011, *O. ocellata*), **British Columbia** (O. & A. Ceska in 2013–2017, 7 spp.; C. Peller 1996, *O. canadensis*), **Ottawa** (J. Mack in 2013–2015, 2 spp.), **Quebec** (J. Cimon in 2009–2013, 3 spp.), **Greenland** (A. Raitviir in 2000, 3 spp.), **Prince Edward Island** (A. Carter in 2018–2019, 4 spp., two of them anamorphic), **Nova Scotia** (C. Peller 1996, 3 spp.), **Massachusetts**, **Maine** and **New York** (D.H. Pfister in 1994–96, Pfister 1997, B. Liu in 2011, D. Haelewaters, L. Quijada, A.C. Dirks, L.A. Kappler etc. in 2013–17, Haelewaters et al. 2018, E. Crenson in 2017–2019, ~25 spp.), **North Carolina** and **Tennessee** (Kohlmeyer et al. 1998, *O. junci*, W. Jaklitsch in 2003, 4 spp.), **Georgia** (Shao et al. 2018, 6 spp.), and **Florida** (1998, L. Ferron, 2 spp.; 2017, B. Kaminsky & D. Borland, R. Healy, 4 spp.).

All these records together represent about 50 different species (when omitting cryptic, morphologically indistinguishable taxa), all of which being from more or less humid (rarely semihumid, California) areas. They were mainly on woody gymno- and mainly angiosperms, rarely on herbaceous mono- and dicot stems. Despite the humid climate about 27 of these 50 species are xerobiotic.

A total of about 124 orbiliaceous purely xerobiotic species (including unnamed ones) were discovered during seven collecting trips in 1991, 1994, 1995, 1996, 1997, 2000, and 2003 by one of us (G.M.). A total of 127 collection sites were visited from which orbiliaceous species are reported here. Except for four sites from the Prairies of **Texas**, all are located in the western parts of Northern America in the region of the Canadian and mainly US-American Rocky Mountains, Colorado Plateau, and the deserts of Mojave, Sonora, and Chihuahua. Among these 127 sites, 46 lie in **Arizona** and 42 in **Utah**, but only 7 in **Colorado**, 6 in **British Columbia**, 4–5 in **New Mexico**, **Idaho**, and **Nevada**, and 1–3 in **California**, **Wyoming**, and **Montana**. The 127 sites embrace climatic zones with very diverse temperature and moisture parameters, ranging from hot arid deserts with different kinds of shrublands and succulent steppes

Table 36. Major vegetation groups tentatively evaluated for all collection sites in western United States, with indication of the number of recorded populations and species of *Orbiliomycetes*, thermo- and ombrotype of sites, biogeographic region, and collected substrate. ctmp = cold-temperate, wtmp = warm-temperate, wcont = warm-continental, subtr = subtropical; hum = humi, shum = subhumid, sar = semiarid, ar = arid; MRoMt = Middle Rocky Mountains, SRoMt = Southern Rocky Mountains, GrBas = Great Basin, ColumPl = Columbia Plateau, WyoBas = Wyoming Basin, ColPl = Colorado Plateau, MojDes = Mojave Desert, SonDes = Sonoran Desert, ChihDes = Chihuahuan Desert.

Vegetation group	Populations/ species	Thermo-type	Ombrotype	Ecoregion	Collected substrate
lodgepole pine forest	2/2	bor	hum	MRoMt	*Pinus contorta*
Engelmann spruce forest	16/11	ctmp bor	hum	ColPl SRoMt	*Picea* sp., *Pinus ponderosa*, *Populus tremuloides*, *Pseudotsuga menziesii*, *Ribes cereum*
Douglas fir forest (incl. Madrean biome)	51/25	ctmp bor	hum (shum)	MRoMt SRoMt ColumPl ColPl ChihDes	*Abies concolor*, *Acer glabrum*, *Amelanchier alnifolia*, *Arctostaphylos patula*, *Betula* sp., *Cercocarpus* sp., *Corylus cornuta*, *Picea* sp., *Picea sitchensis*, *Populus tremuloides*, *Pseudotsuga menziesii*, *Purshia tridentata*, *Quercus gambelii*
cottonwood-willow	9/9	ctmp bor	sar hum	ColPl	*Salix bebbiana*, *S. exigua*
ponderosa pine forest	33/24	ctmp	shum hum	ColPl	*Acer* sp., *Chrysothamnus viscidiflorus*, *Juniperus osteosperma*, *Pinus ponderosa*, *Populus tremuloides*, *Pseudotsuga menziesii*, *Quercus gambelii*
Mogollon cott.-willow	2/2	ctmp	sar	ChihDes	*Salix exigua*
Madrean cott.-willow	3/3	wtmp	sar	ChihDes	*Juglans major*
pinyon-juniper woodland	122/49	wtmp wcont ctmp	sar shum	ColPl (ColumPl GrBas)	*Amelanchier utahensis*, *Artemisia tridentata*, *Baccharis salicifolia*, *Cercocarpus* spp., *Chrysothamnus viscidiflorus*, *Fraxinus anomala*, *Juniperus osteosperma*, *Mahonia fremontii*, *Pinus edulis*, *P. ponderosa*, *Prunus virginiana*, *Purshia stansburyana*, *P. tridentata*, *Quercus gambelii*, *Ribes cereum*, *Salix* sp., *Shepherdia rotundifolia*
mixed chaparral	1/1	ctmp	shum	ColPl	*Cercocarpus betuloides*
manzanita chaparral	6/5	wcont	shum	ColPl	*Arctostaphylos patula*, *A. pungens*, *Fraxinus velutina*
sagebrush desert scrub	37/17	wcont ctmp	sar shum	ColPl (WyoBas GrBas)	*Amelanchier utahensis*, *Artemisia filifolia*, *A. tridentata*, *Elaeagnus angustifolia*, *Ericameria nauseosa*
blackbrush desert scrub	4/4	wtmp ctmp	sar shum	ColPl	*Coleogyne ramosissima*
saltbush desert scrub	14/7	wcont ctmp	sar shum	ColPl	*Artemisia tridentata, Sarcobatus vermiculatus*
winterfat desert scrub	4/3	wtmp wcont	sar	ColPl	*Krascheninnikovia lanata*
mixed grass-scrubld.	11/9	wtmp	sar	ChihDes	*Yucca elata*, indet. dicot
Mojave creosotebush	8/6	wtmp	ar	MojDes	*Atriplex* sp., *Larrea tridentata*, *Yucca schidigera*
Mojave saltbush	8/7	wtmp	ar	MojDes	*Atriplex confertifolia*, indet. angiosperm
creosote bush-tarbush	6/6	wtmp	sar	ChihDes (ColPl)	*Atriplex canescens*, *Koeberlinia spinosa*, *Larrea tridentata*
Sonoran paloverde-mixed cacti desert scrub	88/39	subtr wtmp	sar	SonDes	*Canotia holacantha*, *Carnegiea gigantea*, *Chrysothamnus* sp., *Cylindropuntia bigelovii*, *C. versicolor*, *Ephedra viridis*, *Fouquieria splendens*, *Glossopetalon spinescens*, *Krascheninnikovia lanata*, *Larrea tridentata*, *Olneya tesota*, *Opuntia* sp., *Parkinsonia microphylla*, *Sarcobatus vermiculatus*, *Stenocereus thurberi*
deciduous riparian scrub	4/4	wtmp	sar	SonDes	*Baccharis sarothroides*, *Prosopis velutina*
creosotebush-bursage	13/11	subtr	ar	SonDes	*Chrysothamnus* sp., *Cylindropuntia versicolor*, *Larrea tridentata*

up to cold-temperate or boreal humid conifer forests, according to the high variance in altitude and latitude in this mountainous western part of the continent.

The seven collecting trips yielded 460 here registered orbiliaceous records (populations), which increase the total species number for Northern America to around 162 (176 when including unnamed taxa). About 75 of these 162 species were so far exclusively observed in this continent,

Figure 144: **left**: Subtropical semiarid Sonoran paloverde-mixed cacti desert scrub, with *Carnegiea gigantea*, *Cylindropuntia versicolor*, *Fouquieria splendens*, *Larrea tridentata*, *Olneya tesota*, *Opuntia engelmannii* etc., 745 m, near Visitor Center, Saguaro National Park, Tucson, Arizona, 30.V.2003, phot. G. Marson (#716, H.B. 8085); xeric branches *Olneya tesota* (*O. ?barrowensis*, *O. maeandrina*, *O. multigambelii*, *O. multicreosoteris*, *O. myrioolneyae*, *O. myriourosperma*). **right**: Warm-continental semiarid sagebrush desert scrub with *Artemisia tridentata* and *A. filifolia*, 1813 m, near Hatch Rock, La Sal Mts. in background, Canyonlands National Park, Colorado Plateau, Utah, 16.VI.2000, phot. G. Marson (#263, H.B. 6736); collected nearby in dry riverbed, xeric branches of *Ericameria nauseosa* (*O. delphinus*, *O. dixiensis*, *O. lentiformis*, *O. mesaverdiana*, *O. multimaeandrina*, *O. plurilentiformis*, *O. phanosoma*, *O. multitrapezoidea*, *O. myriophanosoma*, *O. ocellata*).

Figure 145: Warm-continental semiarid shrubland with *Pinus*, *Juniperus*, *Artemisia* etc. in the pinyon-juniper woodland, 1590 m, Devils Garden, Arches National Park, Utah, 8.VI.2003, phot. G. Marson (H.B. 8051); xeric branches of *Fraxinus anomala* (*O. multimaeandrina*, *O.* aff. *paloverdensis*).

of which most are ± xerobiotic, except for *O. renispora* and *O. xanthoflexa* which represent the only seemingly endemic hygrobionts in Northern America.

Species diversity among the different climatic zones was found to be rather equal, although the proportion between xero- and hygrobionts strongly differs, being around 69 : 26 (= 2.65 : 1) in the temperate humid zones, 62 : 2 (= 31 : 1) in the subhumid zones, and 65 : 0 in the semiarid to arid zones (Tab. 33). The relation between population and species numbers indicate that on average about every second or third encountered population belonged to a different species. However, some of the species have been found much more often than others, the most frequent in the west of United States being *O. maeandrina* (25 ×), *O. delphinus* (22 ×), *O. lentiformis* (19 ×), *O. bicknellensis* (15 ×), *O. calyptrata* (13 ×), *O. multimaeandrina* (13 ×), *O. ocellata* (13 ×), *O. macrodelphinus* (12 ×), and *O. flexisoma* (10 ×).

Various species showed a restriction to a given climatic zone, based on the available data. For instance, *O. cactacearum* (5 ×), *O. cryptogena* (6 ×), *O. multigambelii* (9 ×), *O. myriourosperma* (5 ×), *O. pleiomesaverdiana* (5 ×), *O. pluristomachia* (7 ×), *O. sonorensis* (9 ×) and several others occurred only in different arid to semiarid grass- and shrublands at altitudes around 600–1700 m, *O. bicknellensis* (15 ×) and *O. calyptrata* (13 ×) in addition also in semiarid to subhumid shrub- and woodlands at altitudes around 1500–2000 m. The following species preferred humid forests at about 1800–2800 m: *O. aristata* (3 ×), *O. clavipisca* (3 ×), *O. coniferarum* (4 ×), *O. euonymi* (7 ×), *O. delphinus* (22 ×), *O. gambelii* (8 ×), *O. magnifica* (5 ×), and *O. vinosa* (3 ×). Others, particularly the more frequently collected ones, showed little adaptation, e. g., *O. lentiformis* (22 ×) and *O. maeandrina* (25 ×) occurred from the subtropical (semi)arid deserts up to the boreal humid conifer forests.

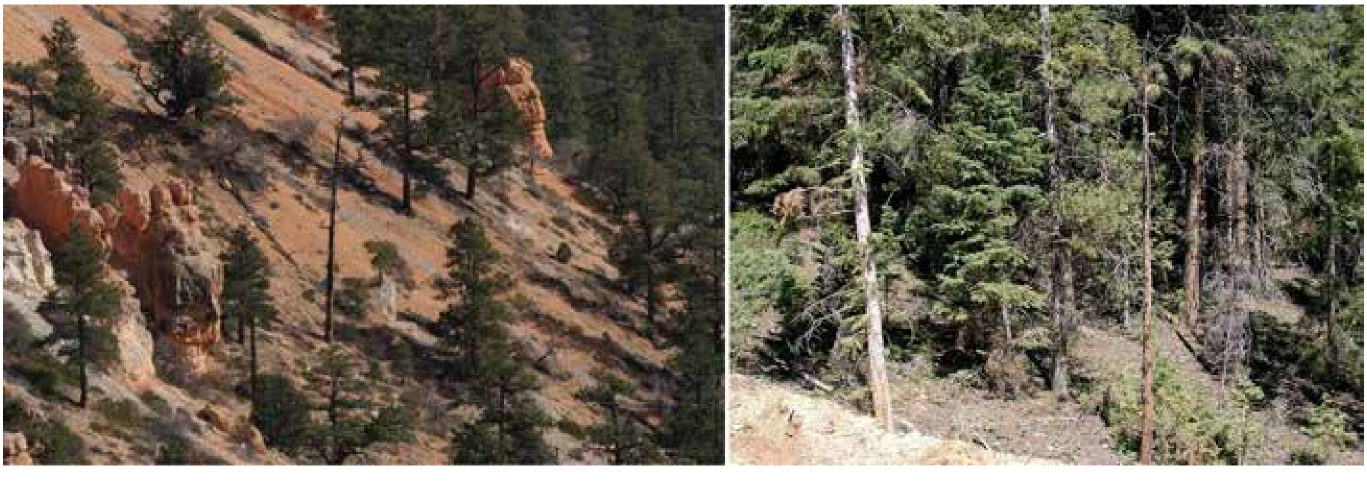


Figure 146: Cold-temperate (sub)humid Rocky Mountain montane conifer forests in Bryce Canyon, Utah; **left**: ponderosa pine forest with *Pinus ponderosa* and *P. edulis*, 2300 m, Navajo trail SE of Sunset Point, 25.VIII.1994 & 20.VI.2000, phot. G. Marson (H.B. 5164, 6744); xeric branches of *Cercocarpus ledifolius* (*O. pleionavajoana*) and *Acer* sp. (*Orbilia cupularis*, *O. microsoma*, *O. multimaeandrina*, *O. navajoana*). **right**: Douglas fir mixed forest with *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus* sp., 2500 m, near Trough Spring, 13.VI.2003, phot. G. Marson (H.B. 8095, 8864); xeric branches of *A. concolor* (*O. clavipisca*, *O. coniferarum*, *O. delphinus*, *O. maeandrina*, *O. ophiosoma*) and *Quercus gambelii* (*O. myriophanosoma*).

Figure 147: Boreal humid Rocky Mountain montane conifer forests; **left**: Douglas fir mixed forest in a broad glacier valley, with *Abies* sp. and *Populus tremuloides*, 1960 m, south of Grand Teton National Park, Wyoming, 6.VI.1996, phot. G. Marson (H.B. 5666, 6038, 6039); attached branches of *Purshia tridentata* (*Orbilia euonymi*, *O.* ?*obtusispora*, *O. vinosa*). **right**: Engelmann spruce forest at 2770 m on a high plateau (Rainbow Point) in Bryce Canyon, Utah, 20.VI.2000, phot. G. Marson (H.B. 7066, 6996, 6998); attached branches of *Abies concolor* (*Orbilia clavipisca*, *O. concoloris*, *O. coniferarum*, *O. delphinus*, *O. ophiosoma*, *O. phanosoma*, *O. pileosoma*).

Four belts have been recognized in the region of the Rocky Mountains and Colorado Plateau following the classification in Elmore & Janish (1976). They correspond to or comprise different plant comunities and differ from each other by ascending moisture and descending temperature. However, these belts and plant comunities are not sharply separated from each other because various, often characteristic plants occur across several of these belts, and mainly the predominance of a plant serves as a key character (GAP-reference).

The pinyon-juniper belt (1200–2100 m) is represented by the pinyon-juniper woodland, the pine-oak belt (1900–2800 m) corresponds to the ponderosa pine forest, the montane fir-aspen belt (2600–3100 m) to the Douglas fir mixed conifer forest, and the spruce-fir belt (3100–3800 m) to the Engelmann spruce forest and other subalpine conifer forests. The given altitudinal levels refer to the Colorado Plateau (see C. Hart Merriam). They depend on the geographical latitude and the exposition of the area: from the south to the north of the Rocky Mountains the elevation boundaries between these communities and between the corresponding climatic zones decrease, e. g. between the cold-temperate and boreal zone from about 2500–2700 m in the south to 1200–2000 m in the north of the United States (according to climate zones map); at the same altitudinal level, the cool north slopes and dry south slopes differ in vegetation density and composition, e. g., a pinyon-juniper woodland may occur on a south-exposed slope of a mountain and a ponderosa pine forest on its northern slope.

The treeless **semideserts** are characterized by a semiarid to arid ombrotype and occur particularly on dry plains and mesas, either at the base of these belts or also at higher altitude. Different types of sclerophyllous chaparral scrublands and desert scrubs but also grasslands grow in these regions. Depending on the geographical latitude and altitude, their thermotype is subtropical, warm-temperate, warm-continental, or cold-temperate. Semideserts are mainly located in the landscapes of the Colorado Plateau, Great Basin, Mojave Desert (including Death Valley), Sonoran Desert, and Chihuahuan Desert (Mexican highland). Climatic and geological conditions determine the plants by which these semideserts are dominated, such as *Arctostaphylos patula* (greenleaf manzanita), *Artemisia tridentata* (big sagebrush, Fig. 144 right), *Atriplex* spp. (saltbush), *Coleogyne ramosissima* (blackbrush), *Krascheninnikovia lanata* (winterfat), *Larrea tridentata* (creosote bush), *Sarcobatus vermiculatus* (greasewood) etc. However, some of these 'monocultures' are man-made, e. g., the expansion of grazing-resistant sagebrush was provoked by livestock grazing since the late 1800s which also suppressed wildfires. In the Sonoran Desert different *Cactaceae*, such as *Cylindropuntia* spp. (cholla), *Fouquieria splendens* (ocotillo), and the large *Carnegiea gigantea* (saguaro), but also *Parkinsonia* spp. (paloverde) and *Olneya tesota* (ironwood) are characteristic (Fig. 144 left). The second highest number of orbiliaceous records and species comes from this vegetation complex (Tab. 36). At the end of the Ice Age, the area of the desert scrubs was dominated by pinyon-juniper woodland and grassland which later retreated to the foothills of the nearby mountains.

The **pinyon-juniper woodland** (Fig. 145) includes a cold- to warm-temperate or warm-continental, semiarid to subhumid climate and typically consists of *Pinus edulis* (Colorado pinyon pine) and *Juniperus osteosperma* (Utah juniper). The shrubs and small trees grow scattered and develop on well-drained, mainly non-acidic soils. Pinyon-juniper woodlands are widespread in the Great Basin, Colorado Plateau, and Rocky Mountains. Many areas show desertification of understory conditions since the late 1800s through livestock grazing by suppressing former fire regimes. The highest number of orbiliaceous records and species comes from this vegetation complex (Tab. 36). Frequently recorded species were, e. g., *Orbilia arizonensis, O. flexisoma*, *O. lentiformis*, *O. macrodelphinus*, *O. maeandrina*, *O. multimaeandrina*, and *O. purshiae*.

The montane **ponderosa pine forest** (Fig. 146 left) includes a cold-temperate (subhumid to) humid climate and is typically composed of *Pinus ponderosa* and *Quercus gambelii* (Gambel oak). The trees are tall, straight and evenly spaced, allowing sunlight to penetrate to the forest floor. Ponderosa pine forests occur on slopes and high plateaus of the mountain ranges in Arizona and Utah. Also here wildfires play a dominant role, and grazing has altered the vegetation. Frequently recorded species were, e. g., *Orbilia delphinus*, *O.gambelii*, and *O.microsoma*.

The montane **Douglas fir mixed forest** (Fig. 147 left) occurs under a cold-temperate to boreal humid climate and typically consists of *Pseudotsuga menziesii* (Douglas fir), *Abies concolor* (white fir), and *Picea pungens* (blue spruce). On poor soil and after wildfires this forest may be replaced by pure stands of *Populus tremuloides* (quaking aspen). Frequently recorded species were, e. g., *Orbilia coniferarum*, *O. delphinus*, *O. euonymi*, and *O. maeandrina*.

The **Engelmann spruce forest** (Fig. 147 right) includes a boreal humid climate and forms the uppermost forest belt, in correspondence to the subalpine zone of the European Alps. It is mainly composed of *Picea engelmannii* and *Abies concolor*, sometimes associated with *Populus tremuloides*. Like the Douglas fir mixed forest, Engelmann spruce forests occur across the entire Rocky Mountains and Colorado Plateau above a critical altitude. Despite a high annual humidity, intense wildfires may temporarily replace these conifer forests by pure aspen stands. In this vegetation type occurred, e. g., *O. lentiformis*, *O. macrodelphinus*, and *O. maeandrina*.

In the boreal humid climatic zone occurs in the upper montane to subalpine Rocky Mountains, especially in their northern part (Montana), the **lodgepole pine forest**, which is dominated by *Pinus contorta*, a species that also requires wildfires for germination. Only *O. atrolentiformis* and *O. pileosoma* from near the Yellowstone National Park were recorded in this vegetation type. No records were available from another subalpine forest, being restricted to the southeast of Northern America, the **bristlecone pine forest** represented by *Pinus longaeva*, *P. aristata*, or *P. flexilis*. It occurs above the spruce-fir forests adjacent to the alpine tundra and is known for its very old trees.

6b. **Middle America**. Only a few species have previously been reported from the Carribean islands and the mainland of Middle America, namely *Hyalorbilia citrina* from **Dominica** (Smith 1901) and *Orbilia ?auricolor*, *?O. epipora*, and *O. juruensis* from **Panama** and **Cuba** (Dennis 1954 & 1970). From **Lesser Antilles** (**Guadeloupe** and **Martinique**) Patouillard & Gaillard (1889) reported *O. lancicula* as common (see also Dennis 1954), which from its type from French Guiana is a *Hyalorbilia* (*?H. inflatula*).

Sporadical collecting after 1970 revealed some other orbiliaceous species (see Appendix 2). The investigated regions include the mainly subtropical semiarid northwest of **Mexico** (**Baja California**, 1990–96, R. Galán et al., 4 spp.) and the tropical humid mainland and Carribean region: **Costa Rica** (1992, G. Kost, *O. aureocrenulata*), east of **Mexico** (**Cancun**, 2004, M. Eckel, *O. cocois*; **Veracruz**, 2018, L. Quijada, *O. aureocrenulata*), **Puerto Rico** (1970, R.P. Korf, 3 spp.; 1996, D.H. Pfister et al., 12 spp.; 2018, L. Quijada, *O. jesu-laurae* [Quijada et al. 2020], *O. milinana*), **Dominica** (1970, R.P. Korf, 3 spp.), **Jamaica** (1971, R.P. Korf, 4 spp.), **Guadeloupe** and **Martinique** (2005–6, C. Lechat, 10 spp.). This results in a total number of 23 species known from Middle America (when neglecting unclear literature reports). Four of them were so far only recorded here (*H. puertoricensis*, *O. cocois*, *O. jesu-laurae*, *O. subuliformis*), and only about six of them are desiccation-tolerant.

7. South America

For the South American continent only sparse records exist in the literature. From the more northern, (sub)humid subtropical highlands and tropical lowlands the following species were known (Dennis 1954, 1970, Patouillard & Gaillard 1889, Rehm 1895, Jeng & Krug 1977, Rubner 1996): from **Ecuador** *Hyalorbilia andina* (as *Orbilia auricolor*), *H. anonyma*, *H. citrina* (type of *O. andina* var. *lateritia*), and *O. elegans* (apothecia obtained in culture); from **Trinidad** *Orbiliaster pilosus* (type), *Orbilia alba* (type), and *O. ?crenatomarginata* (type of *O. curvatispora* var. *minor*); from **French Guiana** *?Hyalorbilia* sp. (type of *O. lancicula*); from **Venezuela** *H. ?inflatula* (as *O. lancicula*), *O. gaillardii* (type), *O. ?oxyspora* (type of *O. fimicola*), *O. tenuissima*, *O. xanthostigma*, and *Orbilia* sp. (the latter two not further specified by Dennis 1970).

From more southern, tropical to cold-temperate (sub)humid regions the following species were known (Hennings 1902a, Höhnel 1907b, Montagne 1853, Romero 1994, Spegazzini 1889, 1909, Starbäck 1899): from **Paraguay** *O. tenuissima* (type); from **Brazil**: *H. citrina* (type of *O. crenulatolobata*), *O. blumenaviensis* (type), *O. brasiliensis* (type), *O. caudata* (type), *O. disseminata* (type), *O. juruensis* (type); from **Argentina** *H. inflatula*, *O. carpoboloides* (as *O. chordicola* and *Helotium marmolense*), *O. nemaspora* (as *Orbilia* sp.), *O. ?scolecospora*, *O. xanthostigma* (as *O. delicatula*)); from **Chile** *O. xanthostigma* (as *Helotium persoonii*).

More recent records include those from tropical humid **Venezuela** (1996, D.H. Pfister et al., *H. citrina*) and **French Guiana** (C. Lechat in 2007, *H. citrina*, *O. guyanensis*), subtropical (sub) humid highlands of **Colombia**, **Ecuador**, **Peru**, and **Bolivia** (W. Jaklitsch in 1994, *O. ?caulicola*, *O. colombiana*, *O. eucalypti*, *O. ?flavidorosella*; L. Beenken & C. Hahn in 1998, *H. erythrostigma*, *O. gaillardii*; J.P. Priou in 2005, *O. colombiana*, *O. puyae*), and tropical humid rain forests in southern **Brazil** (M. Mann in 2011, *H. citrina*, *O. aureocrenulata*).

The total number of species known from South America at present lies at 31. Endemic taxa of the continent could be *H. anonyma*, *O. brasiliensis*, *O. colombiana*, *O. disseminata*, *O. gaillardii*, *O. guyanensis*, and *O. puyae*.

HISTORY OF TELEOMORPH GENERA

Generic concepts in the literature. In the course of the past 200 years, taxonomic concepts of genera and species of orbiliaceous fungi have undergone severe changes due to a different emphasis on special characters of the teleomorph. Characters nowadays considered as taxonomically less reliable, such as ascospore shape and septation, paraphysis shape, and hair characteristics, or macroscopic features, had a prevalent impact on the generic concepts of previous authors. At the time of the first reports of this group of fungi (Persoon 1801, Albertini & Schweinitz 1805, Fries 1815, Schweinitz 1832), macroscopic features such as colour, translucency, shape, and consistency of the apothecia, including structure of the margin and presence of a stipe, were the basis for the recognition of species in discomycetes and their division into genera. The name *Orbilia* is derived from the more or less circular and smooth outline of the usually sessile apothecia, a rather unspectacular feature. A somewhat waxy or gelatinous consistency and a certain translucency is often attested as characteristic of the group. Because species delimitation in the early times has mainly been a matter of apothecial pigmentation, most names of the older taxa of *Orbilia* refer to apothecial colour.

With the works of Berkeley & Broome (1860–75), Nylander (1869), Karsten (1861–85), Fuckel (1870–74) and others, microscopic features of ascomycetes, such as size and shape of the ascospores and shape of the paraphyses, were found to be taxonomically valuable and, therefore, briefly mentioned in the diagnoses. Such features were also described in some orbiliaceous fungi, in which spore characteristics were found to provide good species markers, whereas paraphysis characteristics were used more at the generic level. Boudier (1885) introduced the truncate apex and bifurcate base of asci and Rehm (1891: 453) their negative iodine reaction as more or less consistent key characters of the group. Boudier considered the presence of teeth at the apothecial margin as a generic character to distinguish *Hyalinia* from *Orbilia*.

Crouan & Crouan (1867), Berkeley & Broome (1873), Patouillard (1892b), and Boudier (1904–10) were the first to provide detailed illustrations of orbiliaceous fungi. Their microdrawings attest to the good quality of the microscopes of that epoch. Patouillard was the first to observe spore bodies in the living ascospores. Yet, this valuable character was almost completely neglected during the next hundred years.

Particularly in those early times, the orbiliaceous fungi were not clearly recognized as a well-defined natural group distinct from macroscopically similar taxa of *Helotiales* or *Pezizales*. Indeed, confusion with various quite distant genera frequently happened. During the 19th and 20th century, orbiliaceous fungi have been placed in not less than 30 different teleomorph-typified genera (for the many anamorph-typified genera see p. 214 ff.). According to their type species, 15 out of these 30 genera are today considered to belong to the *Helotiales* (*Calloria*, *Dasyscyphus*, *Helotiopsis*, *Helotium*, *Hymenoscyphus*, *Laetinaevia*, *Mollisia*, *Mollisiella*, *Ocellaria*, *Patinella*, *Pezicula*, *Pezizella*, *Pithyella*, *Pseudohelotium*, *Trichopeziza*), two in the *Phacidiales* (*Phacidium*, *Tympanis*), three in the *Pezizales* (*Lachnea*, *Humaria*, *Peziza*), and three in the *Basidiomycota* (*Craterocolla*, *Lachnella*, *Hirneola*).

The remaining seven genera are today considered to be orbiliaceous from their type species. Four of them achieved general acceptance during the 20th century: species with a dentate apothecial margin of agglutinated, non-septate glassy hairs were segregated in the genus *Hyalinia* Boud. (1885, paraphyses uninflated), species with non-agglutinated, septate hairs in *Orbiliaster* Dennis (1954, paraphyses uninflated) or *Habrostictis* Fuckel (1870, paraphyses inflated and beaked, apothecia erumpent), and species with a smooth margin in *Orbilia* Fr. (1836, paraphyses capitate, apothecia superficial). Two further genera were placed in synonymy: *Cheilodonta* Boud. (1885) with *Habrostictis*, and *Orbiliella* Kirschst. (1938) with *Orbilia*, and a third (*Radotinea* Velen. 1934) was not further regarded. Boudier's (1885) generic concept based on paraphysis shape and presence of hairs was adopted by Nannfeldt (1932) and accepted with little alterations by many subsequent authors. Velenovský (1934, 1940, 1947) and Seaver (1951), however, followed the system of Phillips (1887), Rehm (1891), and Massee (1895) of a broad concept of *Orbilia* which included *Habrostictis* and *Hyalinia*. In the present study, most of these seven genera were found to be more or less artificial. All their type species are considered here to belong to the same genus, hence, the oldest of these seven genera, *Orbilia*, is accepted while a number of species are segregated in the newly erected genus *Hyalorbilia* Baral & G. Marson (2001).

For a long time, the genus *Calloria* Fr. (1836) was thought to be closely related to *Orbilia*, until Nannfeldt (1932) segregated a family *Orbiliaceae* by excluding *Calloria*. Prior to Nannfeldt, the only delimiting character was seen in the ascospores, being 1-septate in *Calloria* and non-septate in *Orbilia*. Such an artificial system based on a single ascospore character was in vogue during the Saccardo era. Not only important ascus characters were often overlooked at that time, but also the fact that spore septation depends on the senescence of a population. In fact, members of *Calloria* and *Orbilia* usually eject non-septate spores which may become septate prior to germination in both genera. Within the orbiliaceous fungi a single exception is so far known: the spores of *Orbilia septispora* are generally 1-septate during ejection.

The genus *Orbilia* has frequently been characterized by asci and paraphyses being conglutinate by a gel matrix or at least apically immersed in an epithecial encrustation, also by an ectal excipulum of thin-walled, globose to angular cells (e.g., by Velenovský 1934, Korf 1973, Spooner 1987). However, a strongly gelatinized hymenium occurs only in the rather small genus *Hyalorbilia* (Baral & Marson 2001) though not in every species. This genus was segregated from *Orbilia* based on an ectal excipulum of usually elongate cells at the flanks, being oriented parallel to the surface (textura prismatica), also by more or less unstalked asci which consistently arise from croziers. It is astonishing that a textura prismatica has rarely been reported in the literature in orbiliaceous taxa. Unstalked asci were only used at some infrageneric level by Velenovský (1934), and croziers were entirely neglected within this group, as was generally the case in most other groups of ascomycetes.

Concerning the circumscription of genera and families by previous authors, our studies of *Orbiliaceae* soon provided evidence for an overestimation of features such as waxy, light-coloured apothecia, or capitate paraphyses (Baral 1994, Baral & Marson 2001). Such features obviously developed in various groups of fungi by convergent evolution. Instead, we found the following characteristics as better reflecting higher taxonomic units: (1) structure of the ascus apex, (2) ascogenous system (croziers versus simple septa), (3) presence of spore bodies (SBs) and their number and shape within the living ascospores, (4) type of ectal excipulum, (5) gel among and exudate over the paraphyses.

The genus *Hyalorbilia* is characterized by SBs that occur near both ends of the ascospores in most of the species (bipolar symmetrical arrangement), a more or less homopolar spore shape, and ± translucent apothecia of a whitish to chlorinaceous or yellowish colour. *Orbilia* subgenus *Hemiorbilia* Baral (1994) was established for a group of consistently desiccation-tolerant species with orange to rose-coloured apothecia, based on an apically thickened ascus wall in combination with a non-truncate ascus apex and predominantly uninflated paraphysis apices being often covered by a layer of thick exudate.

Although hardly detectable in herbarium material, SBs were found to belong to the most important characteristics at the species level, but also at higher levels up to the genus. SBs represent a very valuable aid for recognizing the entire class *Orbiliomycetes*, allowing a sharp delimitation from the *Helotiales* (see Baral 1992: 366: fig. 37, as 'VBs').

Confusion at the ordinal or class level due to a macroscopic similarity and neglect of vital characters. Quite a large number of species have erroneously been considered as orbiliaceous in the older literature. They have been misplaced in one or several of the above-mentioned seven orbiliaceous genera, but are today reclassified in genera that belong to very different fungal groups. Confusion occurred predominantly with helotialean genera, such as *Allophylaria*, *Antinoa*, *Ascocoryne*, *Bisporella*, *Calloria*, *Calloriella*, *Calycellina*, *Calycina*, *Dicephalospora*, *Diplonaevia*, *Duebenia*, *Epiglia*, *Hyaloscypha* (incl. *Parorbiliopsis*), *Hymenoscyphus*, *Laetinaevia*, *Mniaecia*, *Mollisia*, *Naeviopsis*, *Ombrophila*, *Pezicula*, *Ploettnera*, *Pseudohelotium*, *Psilachnum*, *Pyrenopeziza*, *Sarcotrochila*, and *Unguiculella*. Confusion also encompasses species now placed in genera of *Pezizomycetes* (*Iodophanus*, *Peziza*, *Pseudombrophila*), *Leotiomycetes* (*Thelebolus*), and *Lecanoromycetes* (*Agyrium*, *Caloplaca*, *Coenogonium*, *Sarea*, *Scutula*). Confusion concerns even non-stromatic members of *Hypocreales*, especially *Bionectriaceae* with light-coloured, soft-walled perithecia which collapse cup-shaped when dry.

Even basidiomycetes of the order *Dacrymycetales* may macroscopically appear so similar that only their strongly gelatinous consistency and microscopic construction reveal their true identity. As an example, specimens of *Orbilia* and *Dacrymyces* occur in Persoon's herbarium under the name *Peziza aurea* Pers. Similarly, *Peziza chrysocoma* Bull. was interpreted by some authors as a *Dacrymyces*, but by others as an *Orbilia*. Even conidial fungi that form apothecioid fructifications and small globose phialoconidia (*Peziza crocina* Mont. & Fr.) were mistaken for an *Orbilia*.

Species of *Orbilia* with hairy apothecia may strikingly resemble helotialean genera such as *Arachnopeziza*, *Lachnellula*, or the polyphyletic genus *Hyalopeziza* (*H. raripila* and '*Habrostictis*' *diaphana*, see p. 1669 under the latter name), so that they are easily confused. They also may be mistaken for members of *Octospora* (*Pezizales*), although *Orbilia* very rarely grows on bryophytes. The list of species ever placed in the seven orbiliaceous genera but now excluded from *Orbiliomycetes* is, therefore, fairly long (see p. 1660 ff.).

We repeatedly came across such deceptive doubles that macroscopically pretend to be an *Orbilia* but microscopically belong to the *Helotiales*. Conversely, we have at first neglected black discomycetes as presumably lecanoralean because of their colour, but an accidental microscopic examination revealed typical orbiliaceous characters. Quite a few here newly described taxa with dark-coloured, smooth apothecia (e.g., *Orbilia patellarioides*, *Liladisca acicola*) strongly resemble genera of *Leotiomycetes*, such as *Claussenomyces* s.auct. and *Durella*, *Dothideomycetes* like *Patellaria*, *Xylonomycetes* (*Symbiotaphrina*), or *Lecanoromycetes* such as *Amandinea*, *Sarea difformis*, or *Sclerococcum*. Likewise, the hairy, dark-coloured apothecia of *Lilapila* are easily mistaken for a *Trichopeziza* or *Perrotia* (*Helotiales*).

Frequently, confusion with the *Calloriaceae* (*Helotiales*) is noted in the literature. Nannfeldt (1932: 192, 253) considered five species originally described or early combined in *Orbilia* as belonging 'most probably' to *Laetinaevia*, though he did not propose new combinations for them, except for *O. rosella*. We found them to represent genuine members of *Orbilia*: *O. flavida* Feltgen, *O. flavidorosella* Rehm, *O. rosella* (Rehm) Sacc., *O. serpentina* Pat., and *O. uvispora* Mouton. *O. serpentina* is one of the very few species which was described with characteristic filiform, refractive spore bodies (see Fig. 151: 1). Based on this feature, the species is easily recognized as an *Orbilia* by a vital taxonomist, whereas Nannfeldt, unaware of SBs in *Orbilia*, tentatively placed those desiccation-tolerant species with often erumpent apothecia in his subfamily *Naevioideae* (= *Calloriaceae*).

The two genera *Patinella* and *Pithyella* are today assigned to the *Helotiales*, according to their type species. However, until recently they contained orbiliaceous species (*Patinella aterrima* Fuckel [≡ *Liladisca acicola*], *P. tenebricosa* Svrček [= *Orbilia polybrocha*], *Pithyella erythrostigma* (W. Phillips) Boud. [≡ *Hyalorbilia erythrostigma*], *P. anonyma* Rehm [≡ *H. anonyma*]). Whereas members of *Pithyella* have never been placed in the *Orbiliaceae* before, the type species of *Patinella* was believed to be orbiliaceous by Nannfeldt (1932) because of its capitate paraphyses.

Confusion up to the level of the class frequently occurred in the literature, mainly because of the rareness of vital studies. We assume that validly described orbiliaceous species still can be discovered in old genera such as *Calloria*, *Pezizella*, *Helotium*, or *Mollisia* (when bright-coloured), or in *Patellaria*, *Patinella* etc. (when dark-coloured).

Species concepts in the literature and misinterpretation. In addition to the inappropriate generic concepts that tempted workers to transfer a species to the genus *Orbilia* in the early times, concepts at the species level were frequently based on more or less unreliable, predominantly macroscopic, but also sporological, or even ecological characters. Whitish apothecia were referred to *O. leucostigma*, yellow ones to *O. xanthostigma*, orange-red ones to *O. coccinella* or *O. rubinella* and so on. Names such as *crenatomarginata*, *crystallina*, or *saccharifera* refer to the presence of whitish teeth or hairs at the apothecial margin. A simplified system of microscopical, mainly sporological characters likewise resulted in artificial concepts. For example, narrow curved spores were thought to point to a relationship with *O. curvatispora*, narrow straight spores to *O. luteorubella* and related species, and tailed spores to *O. occulta*.

Especially in the 19th century, identifications of orbiliaceous species are often dubious. Reexamination of some of the involved collections have demonstrated that different authors had different interpretations of a species, and that some authors mixed two or three different species under one name. Some of the oldest epithets of orbiliaceous fungi have been used over a long period of time in one or more ways different from what the revision of authentic material later revealed (Tab. 37).

Table 37. Five examples of old specific epithets in the genus *Orbilia* (left column) and their interpretation by different authors of the 19th and 20th century (right column, according to the present redefinition of these names based on the type or reference specimens). For *O. auricolor* and *O. coccinella* authentic material exists, which fixes *O. auricolor* as an earlier synonym of *O. curvatispora* and *O. coccinella* for a rare species with 16-spored asci and cashew-shaped spores. Neotypes are proposed in the present study for *O. leucostigma* and *O. xanthostigma* in accordance with the current usage, and *O. vinosa* in the sense of Rehm.

Old specific epithet	Identity of non-authentic collections according to present reexamination
leucostigma Fr.	*Orbilia leucostigma*, *O. eucalypti*, *O. crenatomarginata*, *Hyalorbilia inflatula*
xanthostigma Fr.	*O. xanthostigma*, *O. eucalypti*, *O. tremulae*, *O. auricolor*, *H. inflatula*, *O. ?umbilicata*
coccinella Fr.	*O. eucalypti*, *O. xanthostigma*
auricolor Berk. & Broome	*O. auricolor*, *H. inflatula*, *O. elegans*, *O. javanica*, *O. multiformis*, *O. oligospora*
vinosa Alb. & Schwein.	*O. vinosa*, *O. aurantiorubra*, *O. luteorubella, O. sarraziniana, O. tenuispora*

Similar to the situation noted for higher ranks, the reasons for erroneous species identifications must be sought in the current practice of studying dead herbarium specimens, as well as in the fact that species taxonomy at that time concentrated on spore size and shape.

However, the present research revealed that morphology of the anamorph, or molecular differences may necessitate further splits into species that can hardly be separated by teleomorph morphology alone (p. 16 ff., see also Baral et al. in prep. on the *xanthostigma-leucostigma* complex). Because many collections are without such information, our species concepts certainly includes misidentifications regarding such critical taxa.

Some workers named new species according to the host, perhaps because they believed that they were host-specific. For instance, *O. eucalypti*, *O. abutilonis* and *O. fici* were named after host genera. Also Velenovský named many species after the host. For nearly all such named taxa, the present study revealed a much wider host range than the epithet suggests. However, also we named many of our new taxa after the host, whenever their morphological features did not provide enough peculiarities (see also p. 19–20, Etymology).

Authors of the past centuries believed that the *Orbiliaceae* constituted a rather small family with only a few distinct species. As an example, a rather wide species concept was applied to taxa with a crenulate to hairy margin, which is briefly sketched below, represented by two authors, G. Massee and J.A. Nannfeldt.

Massee (1894b: 99) revised the types of *Peziza cruenta* Schwein. and some other North American taxa (*Peziza fibriseda* Berk. & Curt., *P. saccharifera* Berk., *P. rufula* Schwein., *P. regalis* Cooke & Ellis), all of which he considered to be conspecific because they share a reddish disc and a whitish, crenulate or pruinose to hairy margin. A sixth taxon (*P. conchella* Schwein.) he considered as a further possible synonym. Four of these authentic exsiccatae were reexamined in the present study and found to belong to four very different species. No type material could be located for *P. cruenta*, and in that of *P. conchella* only sporodochia of a hyphomycete could be found.

When Nannfeldt (1932: 252) was dealing with this group of taxa, he followed the opinion of Massee without personal studies. Moreover, he considered *O. cruenta* to belong to *Hyalinia* and to be possibly even conspecific with the European *H. rubella* (Pers.) Nannf. (≡ *O. rubella*) as represented in herb. P.A. Karsten (no. 834). Nannfeldt further believed that the type specimen of *Peziza rubinella* Nyl., which has rather glabrous apothecia, was conspecific with *H. rubella*. *P. rubinella* represents a special case of confusion: intrahymenial parasitism (see Baral 1999). According to a reexamination of the type, the asci described in the protologue belong to a parasite of the widespread genus *Helicogonium* that grows in the hymenium between the paraphyses of *O. vinosa* by lacking an own sporocarp. Parasites of that genus are not easily recognized as such, since their asci are inamyloid like the host asci, and often completely suppress the formation of the host asci. Species of *Helicogonium* are usually readily recognized by their ability to produce phialoconidia directly on the ascospores, a feature never seen in *Orbiliomycetes*.

Many cases of confusion are found in the studies by Feltgen and Velenovský. A revision of 38 specimens included in *Orbilia* in Feltgen's herbarium (LUX) revealed the presence of about 10 orbiliaceous and one helotialean species ('*Orbilia*' *rozei* = *Psilachnum rubicundum*, see p. 1683). Feltgen (1899, 1901, 1903) reported nine species and five varieties in *Orbilia*. However, the names applied by him show little correlation with the identities as evaluated here. For example, behind specimens carrying the name *O. coccinella* hides predominantly *O. xanthostigma* but also *O. eucalypti* and a single time *O.* cf. *luteorubella*. Under *O. luteorubella* he mainly preserved *O. sarraziniana*, while only one collection was *O.* cf. *luteorubella*, a further *O. auricolor*, and another *O. xanthostigma*. Although such discrepancy could in some cases be due to mixed populations, Feltgen's rather superficial microscopic work is obviously the main source for this confusion.

Velenovský's work (1934, 1940, 1947) is characterized by brief descriptions, to which often macro- and microscopic illustrations are added. For instance, he frequently gave only the length of spores while omitting spore width. Although his drawings are seemingly informative (he often illustrated asci with flexuous stalks and 2- to 4-furcate bases, see Fig. 154),

Table 38. Ascospore measurements [µm] of fifteen selected taxa described by Velenovský (1934, 1947) as new species: comparison of values of holo- or lectotypes in the protologue and/or manuscript plates (spore width was mostly omitted by the author and spores were not drawn to scale) to those evaluated by Svrček (1954) and Baral (present study, in KOH or KOH+CR) from the same material. Velenovský's values are often much smaller (75–85 % or even 35–50 %) than those of the revising authors, except for large-spored taxa (highlighted in grey) in which his values concur or exceed the revision values (probably because of the shrinking effect). Svrček's spore length values more or less agree with those of the present study, whereas spore width was in some species distinctly below the values of the present study. * = measurements appearing on manuscript plate.

Velenovský	present monograph	Velenovský (1934, 47)	Svrček (1954)	Present monograph	Approx. deviation
Orbilia connata	*O. epipora*	1–2.5*	3–4.5 × 0.5–0.8	3–4.2 × 0.7–0.8	35–50 %
O. minutispora	*O. minutispora*	1–2*	2.5–4 × 0.8–1	2.7–3.6 × 0.9–1.1	40–55 %
O. aprilis	*O. aprilis*	3–5	–	7–8 × 1.7	45–60 %
O. leporina	*O. leporina*	3–5 × 1	–	(6–)7–8(–9.2) × 1.1–1.3(–1.4)	50–60 %
O. acuum	*O. acuum*	2–3*	3–4 × 0.8–1	3.5–5.2(–6) × (0.8–)1–1.2	55 %
O. millispora	*O. xanthostigma*	1–2	–	2.3–2.6 × 1.1–1.3	50–75 %
O. parvula	*O.* (?)*luteorubella*	4–5*	7–8.5 × 1.2–1.5	5.5–7.5 × 1.4–1.7	60–75 %
O. pellucida	*O. cardui*	3–5	5.5–7 × 0.5–0.8(–1)	(4–)5–7(–7.5) × 1.1–1.2(–1.3)	65–75 %
O. cejpii	*O. cejpii*	2*	1.7–2.3 × 1.2–1.5	2–3.3 × 1.3–2	70 %
O. polypori	*Hyalorbilia polypori*	4–5*	5–7 × 0.8–1	5–7(–8) × 1.5–1.9	70–80 %
O. paradoxa	*O. xanthostigma*	1.8–2.2*	2–2.5 × 1–1.5	2.5 × 1	75–85 %
O. euonymi	*O. euonymi*	2–3*	–	2.5–3.6 × (1.4–)1.8–2(–2.3)	80 %
O. tricuspis	*O. vinosa*	12–15*	12.5–17 × 1.5	12–14.7 × 1.4–1.7	100 %
O. pulcherrima	*O. vinosa*	15–18*	14–15.5 × 1.5	13–15.3 × 1.5–1.7	115 %
O. cardui	*O. cardui*	6–8*	5–7 × 1–1.2	5–7 × 1.2–1.5	115–120 %

Table 39. Ascospore measurements [µm] of five selected taxa reported by Boudier (1904–10): comparison of the values in his descriptions to those evaluated from his plates (in situ length, magnification 820 ×) and from personal reexamination of the same specimens or, in square brackets, from recent collections of the same species. Boudier's values given in the description are partly too high, particularly spore width; values obtained from his drawings are more trustworthy as they often better match those obtained in the present study. § = perhaps measured along curvature (actual length).

	Boudier (text)	Boudier (plate)	Present study
Habrostictis carpoboloides (pl. 459)	15–20 × 2–3	15–19 × 2–2.9	[*(7.7–)8.5–14(–17) × (2–)2.2–2.8(–3.5)]
Orbilia sarraziniana (pl. 462)	7–8 × 1.5–2	7.2–8 × 1–1.2	[*(5.5–)6–8.5(–9) × (1.2–)1.3–1.6(–1.7)]
Orbilia aurantiorubra (pl. 464)	15–18 × 2 §	(11.5–)13–16.5 × 1.2–1.4	†12–14 × 1.1–1.2
Hyalinia roseola (pl. 465)	10–12 × 2 §	8.5–10.5 × 1–1.3	†6.5–9.5 × 0.7–0.8
Hyalinia crystallina (pl. 466)	8–11 × 2 §	8.5–10.2 × 0.9–1.1	[*7–8.5(–9) × (0.6–)0.7–0.8(–0.9)]

Velenovský made a large number of more or less severe errors. This can be concluded from the present reexamination of about 60 available type specimens in which apothecia could be found.

As a consequence, Velenovský's descriptions are often insufficient for the recognition of a taxon. Even in regard to rather well-defined species we were unable to identify them with Velenovský's descriptions. For instance, it was impossible to get an idea of what the protologues of *O. aprilis* or *O. euonymi* might represent, until the types were studied. As opposed to Svrček, who accepted only seven species and one form among Velenovský's 75 new species and varieties, we here accept 18 species which bear Velenovský's name (nine further species are of unclear identity). Our higher number of 18 can be explained by the fact that in some of the type specimens Svrček did no longer find apothecia although they still existed, therefore, he considered taxa as dubious which we here accept as valid. Nevertheless, under about seven different epithets Velenovský described what is here referred to *O. eucalypti*, under six epithets *O. leucostigma* and *O. xanthostigma*, under four epithets *O. cardui*, and under three epithets *Hyalorbilia inflatula*.

Velenovský's errors are manifold: (1) spore measurements of small-spored taxa are highly incorrect (see Tab. 38); (2) stray spores or algae were often misinterpreted as ascospores; (3) the septa of the paraphyses are drawn at rather equal distance in most of the illustrated species of *Orbilia* (Fig. 154), although in many of them the terminal cell was about 2–4 times longer than the lower cells; (4) the only taxon in his work with polysporous asci (*O. euonymi*, 32-spored) was reported by him as octosporous.

Orbilia euonymi and *O. aprilis* are two out of many examples of very inadequately described taxa. Both were gathered only once by Velenovský. The wrong spore number reported for *O. euonymi* later led to the misapplication of this name to the 8-spored *Hyalorbilia erythrostigma*, a very distant species. *O. aprilis* was misleadingly described with 3–5 µm long, ellipsoid ascospores. Reexamination of the rather immature type material revealed only a single (almost) mature ascus with narrowly fusoid, 7–8 µm long spores. Therefore, the name *aprilis* can only with some hesitation be applied to a previously unreported though very common taxon which is easily recognized in the living state. As a consequence, a highly constant and common species carries a somewhat uncertain name.

Tab. 38 illustrates errors in Velenovský's measurements, which are also apparent in other fungal groups treated in his works of 1934, 1940, and 1947. For a spore length in the range of 2.5–8 µm he often evaluated only 1–5 µm, i. e., ~75–85 or even 35–50 % of the true values. Longer spores, however, are more or less correctly reported (*O. tricuspis*, *O. pulcherrima*), and in one case (*O. cardui* s.l.) he reduced spore length from 6–12 µm (1934: 98) to 4–10 µm (1934: 401) which corresponded to the values obtained by later revisions. It seems that Velenovský used a combination of objective and ocular with a false calibration when he studied minute spores. Species published in 1947 (*O. aprilis*, *O. leporina*) show the same error. This is all the more surprising as Velenovský used to study living specimens in which spores are usually slightly larger than in dead specimens. More or less severe errors in calibration and scaling of illustrations are actually not infrequent in the literature.

As a further example, Boudier's (1904–10) values in his descriptions are often too high, whereas those calculated from his plates are more trustworthy (Tab. 39, see also Baral 1992: 347). This is especially true for the width of comparatively narrow elements: Boudier's spore width measurements are here often ~1.5–2 × higher than on his drawings, which in some cases is due to the fact that Boudier avoided to calculate steps smaller than 0.5 µm. In the case of strongly curved spores (Boudier l.c.: pls 464–466), a greater spore length in his descriptions might refer to the actual length (measured along the curvature) rather than to the in situ values (straight distance).

Although Velenovský (1934: 31) emphasized the preferential study of fresh living specimens, his figures usually show dead asci and spores, perhaps because he applied too much pressure on the cover slip in order to separate the hymenial elements. Actually, Velenovský never reported tear-shaped or vermiform SBs in those taxa which possess such bodies, e. g., *O. sarraziniana*, *O. aristata*, *O. aprilis*, *O. vinosa*, and *O. euonymi*. Only in one unpublished drawing of *O. sarraziniana* (as *O. luteorubella*, manuscript plate deposited in PRM) he illustrated vermiform SBs (see Fig. 156: b). Perhaps Velenovský omitted this drawing in his monograph because he considered the structure to be artificial. That the quality of his microscope was sufficient can be concluded, e. g., from his spore drawing of *O. paradoxa* (= *O. xanthostigma*, Fig. 154: 4) which perfectly shows the semicircular spore curvature, though it omits the dorsal warts and gives SBs at both spore ends.

In a number of taxa (*O. alnea* var. *vesiculosa*, *O. linata*, *O. microspora*, *O. paradoxa*, *O. pellucida*, *O. tiliacea*) Velenovský figured spores with two globose drops, one near each end. Such a bipolar (homopolar) guttular pattern is typical of the genera *Hyalorbilia* and *Amphosoma*. However, Velenovský's taxa are members of *Orbilia*, except for *O. linata* (= *Hyalorbilia inflatula*) in which case he reported stray spores. Bipolar globose drops as seen by him seem to refer to LBs in some of the taxa, but in others, e. g. *O. paradoxa*, they clearly represent spore bodies. At least in this species the bipolar arrangement of the drops obviously arose from Velenovský's phantasy.

Velenovský appears to have quite frequently mistaken spores of associated fungi or algal cells as the ascospores of *Orbilia*. This was also affirmed by Svrček (1954) in several cases. In 45 taxa of *Orbilia* (including *Radotinea*) Velenovský (1934) illustrated asci (Figs 154, 156, 174), but only exceptionally he depicted the spores within (*O. euonymi*, Fig. 156: a; *O. polypori*, Pl. 66). In *O. euonymi* he figured an eight-spored ascus although the holotype turned out to be 32-spored (Pl. 207: 5). This discrepancy could be due to a mixture in the type material, but this seems quite unlikely because all the other characters match very well. We conclude that Velenovský rarely saw living mature asci in his preparations, therefore, he only occasionally recognized spores within them and repeatedly reported stray spores in his diagnoses.

A further source of error concerns a mixture of different species in a single convolute. Although Velenovský recognized such a case in the type specimen of *O. fusispora* (≡ *Hyalorbilia fusispora*), which grew in close association with the type of *O. fusispora* var. *microscopica* (= *O. juliae*), it obviously escaped his notice in some other cases. For example, *O. carpathica* was described with long-tailed spores somewhat similar to *O. flagellispora*, but in the preserved type material only apothecia belonging to *O. sarraziniana* could be observed.

Number of accepted taxa (**teleomorph**). The above-mentioned high number of dubious epithets suggests that the total number of acceptable published taxa regarding the teleomorph is much lower than the works of authors like Velenovský suggest. Spooner (1987: 161) noted that 'of some 170 specific epithets' combined in *Orbilia* worldwide 'only about 30 species are reasonably well-known', but 'many of those published were inadequately described'. Kirk et al. (2008) gave the number of taxa of *Orbiliaceae* as 288. However, this calculation includes the anamorph-typified taxa of *Arthrobotrys* etc., whereas the number 'c. 58' under *Orbilia* refers only to the teleomorph taxa.

According to our present literature research, the total number of validly published epithets (including infraspecific, anamorph-typified, and non-orbiliaceous or doubtful taxa) ever combined with the generic name *Orbilia* Fr. up to now (including 2019/20) is about 270 (excluding species and combinations newly proposed in this monograph). Some epithets were invalidly proposed (*O. acicularis*, *O. albomarginata*, *O. albovinosa*, *O. inconspicua*, *O. lenticularis*, *O. quercus* var. *hainanensis*, *O. quercus* var. *hunanensis*). Much fewer epithets were combined with the remaining eight teleomorph-typified orbiliaceous genera. In the following, the first number indicates the total number of validly combined epithets, and the second number indicates, how many of them were also combined with *Orbilia*: *Cheilodonta* Boud. (2/2), *Habrostictis* Fuckel (16/3), *Hyalorbilia* (16/9), *Hyalinia* Boud. (63/28), *Orbiliaster* Dennis (2/1), *Orbiliella* Kirschst. (1/0), *Pseudorbilia* Ying Zhang et al. (1/0), and *Radotinea* Velen. (1/0).

After subtracting all those taxa for which two or more combinations in orbiliaceous genera exist, 51 epithets remain which have ever been placed in orbiliaceous genera other than *Orbilia*. As a consequence, ca. 270 + 51 = ca. 321 teleomorph epithets have ever been validly combined with 1 or more of these 9 orbiliaceous genera up to now. Out of these ca. 321 taxa, 113 either turned out to belong to other groups (predominantly in the *Helotiales*), or remained ambiguous as to their relationship, because authentic material could not be located and the descriptions are too inadequate. Further 15 epithets more or less probably concern orbiliaceous taxa, but their specific identity could not be clarified. Therefore, altogether ca. 128 taxa are treated in the 'List of excluded, doubtful or little-known taxa' (p. 1660 ff.) besides 27 further taxa of various other genera with potential affiliation in the *Orbiliomycetes*.

The remaining ca. 193 teleomorph-typified taxa are accepted here as belonging to the *Orbiliomycetes*, 197 when including 4 invalidly proposed orbiliaceous species (see Suppl. List of previously described taxa). 92 out of these ca. 197 are considered to represent heterotypic synonyms of accepted taxa (51 certain and 41 questionable synonyms). The rest of 105 epithets constitutes the basic stock of previously described teleomorph-typified taxa accepted in the present monograph. In addition to these 105 epithets, 7 further ones are accepted as validly described orbiliaceous species, which were assigned to different helotialean genera such as *Helotium*, *Pezizella*, *Pseudohelotium*, *Pithyella*, *Patinella*, and *Tympanis*, but never in any of the 9 orbiliaceous genera. Further 8 epithets were similarly never assigned to an orbiliaceous genus, but were referred by us to synonymy with accepted species of *Orbiliomycetes*. Hence, a total of ca. 112 epithets from the literature are accepted as validly described orbiliaceous species in the present monograph, and 100 epithets are listed as synonyms of these accepted taxa.

Since vital characters (SBs and SCBs) were not reported for most of these type collections, some critical taxa remain questionable as to their identity. This uncertainty concerns, e.g., *O. serpentina* which was described with subulate SBs in the spores, but for which the presence of crystalloid SCBs is unclear, or *O. fibriseda* and *O. rosella* for which neither SBs nor SCBs were reported. The identity of other taxa is questionable because their anamorph is unknown, and in some type specimens the apothecia are not mature enough (examples: *O. linata*, *O. uvispora*, *O. aprilis*). Until sequence data from old material might become available, we have chosen in such cases what seemed us the more probable identity.

The teleomorph-typified genera – Genera with orbiliaceous type species

Several teleomorph-typified genera show either a phylogenetic or historical relationship to the *Orbiliomycetes*. The more important 18 of these genera will be discussed in the following.

Orbilia Fr., Fl. Scan.: 343 (1836) – Lectotype species: *Peziza xanthostigma* Fr. (designated by Bachman 1909)

Prior to 1836. When the first orbiliaceous species were described in the years between 1791 and 1871, a rather small number of genera has been recognized within the non-lichenized discomycetes. For most species that form apothecia, a very wide concept of the genus *Peziza* Dill. ex Fr. was in use, which included at that time nearly all groups of both operculate and inoperculate discomycetes. Those species later referred to *Orbilia* were arranged by Fries (1822: 146) in a subgroup '*Ceracellae*' of the genus *Peziza*, which in turn was placed in the '*Ordo Cupulati*'.

The first species that clearly belong to the *Orbiliomycetes* were described by Persoon (1801: *Peziza aurea*, *P. rubella* and *P. vinosa* [the latter species is currently referred to Albertini & Schweinitz 1805]), Fries (1815: *P. leucostigma* and *P. xanthostigma*), and Sommerfelt (1826: *P. coccinella*). Also *Peziza chrysocoma* Bulliard (1791) was interpreted as orbiliaceous by some authors, but the taxon is now lectotypified on a basidiomycete (see p. 1665).

1836–1924. When erecting *Orbilia* in 1836, Fries included those two species described by him in 1815, and defined the genus by membranaceous-gelatinous apothecia and 'moniliform' asci. *Orbilia* is referred to the tribe '*Bulgariei*' of his family '*Discomycetes*', together with *Calloria* Fr., which he erected in the same paragraph a few words before, and which he separated from *Orbilia* by 'persistent' clavate asci. The tribe '*Bulgariei*' further comprised the genera *Bulgaria* Fr., *Leotia* Pers., and *Lemalis* Fr., but also *Exidia* Fr., a basidiomycetous genus.

Fries (1836) did not definitely associate the generic epithet *Orbilia* with the two epithets of the included species, as demanded by the Code (ICN Art. 35.2). Their combination in *Orbilia* was validated later, when Fries (1849: 357) added *Peziza coccinella* Sommerf. and *P. epiblastematica* Wallr. [≡ *Scutula epiblastematica* (Wallr.) Rehm, *Lecanorales*] to the genus. The generic diagnosis now reads 'apothecia round, ceraceous-membranaceous, saucer-shaped, marginate, 8 spores arranged in a moniliform row, without asci (at least without conspicuous asci), excipulum absent'. Fries incorrectly believed that the asci dissolved prior to spore liberation. With 'moniliform' he referred to senescent apothecia in which the spores occur in moniliform chains inside disintegrated asci (see, e. g., Pl. 842: 1b).

Orbilia was transferred by Fries (1849) to the family '*Helvellacei*', whereas *Calloria* remained in the '*Bulgariacei*'. Thereby, Fries's concept of *Calloria* was very heterogeneous (see p. 205). According to him, the name *Orbilia* is derived from '*orbis*', which infers to the circular apothecia. In a similar way, the obsolete word '*orbilla*' has been in use in the sense of 'apothecium', e. g., in Sprengel (1807, see Kirk et al. 2008).

Karsten (1861: 36–39; 1869: 106, 173–176) and Nylander (1869: 54–58) relied on the classical wide concept of *Peziza* when treating the discomycete flora of Finland. Nylander doubted Fries's concept of *Orbilia* and *Calloria*, since the microscopic characters provided by Fries appeared unreliable to him. Nylander's orbiliaceous species are, therefore, found in a subgroup of *Peziza*, named '*Orbilia* et *Calloria* Fr.'. Karsten (1861) placed orbiliaceous as well as helotialean taxa in *Peziza* subgenus *Phialea* section *Mollisia*. Later, Karsten (1869) accepted *Orbilia* as a section within *Peziza* (without using subgenera). The very same sectional diagnosis was reproduced in a 'repertorium' by Rabenhorst (1869), who named Karsten's 25 sections 'Untergattungen' (subgenera). Shortly afterwards, however, Karsten (1870: 248; 1871: 11, 97) adopted *Orbilia* at the generic level and placed it in the *Pezizaceae* subfamily *Bulgariaceae*.

Karsten (1861) listed three orbiliaceous species: *Peziza coccinella*, *P. leucostigma*, and *P. vinosa*. In 1869 he treated ten species in section *Orbilia*, nine of them being orbiliaceous: the three former, but also *P. delicatula*, *P. epipora*, *P. inflatula*, *P. luteorubella*, *P. rubinella*, and *P. xanthostigma*. Out of eight species which Nylander recognized in '*Orbilia* et *Calloria*', six are genuine members of *Orbiliomycetes*: *P. coccinella*, *P. epipora*, *P. leucostigma*, *P. luteorubella*, *P. rubinella*, and *P. vinosa*.

Karsten and Nylander were among the first to present more detailed microscopic features of orbiliaceous fungi. As characteristic of the majority of their species, the authors emphasized the capitate to clavate apices of paraphyses, the large, parenchymatous excipular cells, the small asci and spores, and the smooth, hyaline to bright-coloured apothecia without a visible subiculum. Although they introduced spore characters as a valuable means for species delimitation, they continued to attribute macroscopic features like apothecial colour a rather high taxonomic value.

Berkeley (1860: 370) recognized 15 species for Great Britain in *Peziza* subgroup *Mollisia*, three of which are orbiliaceous (*P. vinosa*, *P. xanthostigma*, *P. leucostigma*). Berkeley & Broome (1865) added *Peziza auricolor* which was misinterpreted in the following in the sense of *Hyalorbilia inflatula*, until Spooner (1987) redescribed the type material. The first authors providing detailed microscopic illustrations of orbiliaceous fungi were Berkeley & Broome (1866: pl. IV fig. 31, *Peziza erythrostigma*, subgroup *Mollisia*; 1873, *P. lasia*, subgroup *Dasyscyphae*, Fig. 168) and Crouan & Crouan (1867, *P. carpoboloides*, Fig. 169). Without illustration and microscopic data, Berkeley (1875: 157) described two North American species (*P. fibriseda*, *P. saccharifera*) in subgroup *Mollisia*, which are combined in *Orbilia* in the present monograph. For the British fungus flora, Cooke (1871) reported within the large genus *Peziza* five species that are today recognized as orbiliaceous (*P. leucostigma*, *P. xanthostigma*, *P. vinosa*, *P. auricolor*, *P. erythrostigma*).

Fuckel (1870, 1871, 1874) applied a narrower generic concept when treating the discomycetes of central Germany, but he did not adopt or even mention the generic name *Orbilia*. Fuckel reported five orbiliaceous species which he placed in four different genera (*Calloria chrysocoma* [s. Fuckel], *C. vinosa*, *Habrostictis rubra*, *Pezizella rubella*, *Pezicula aterrima*) and assigned to four different subgroups (*Stictei*, *Patellariacei*, *Bulgariacei*, *Pezizei*, respectively) of his '*Discomycetes*'. In *Calloria* he included two basidiomycetous taxa now recognized in *Dacrymyces* (*Dacrymycetales*), following Fries's (1849) heterogeneous concept of *Calloria*.

Also Gillet (1881–83) did not accept the genus *Orbilia*, but placed nine orbiliaceous species from France in *Helotium*, *Lachnea*, and mainly *Mollisia*. Although his work is rather rich

Figure 148. *Orbilia eucalypti* (Saccardo, Fungi italici, 1883: pl. 1289, as *O. coccinella*).

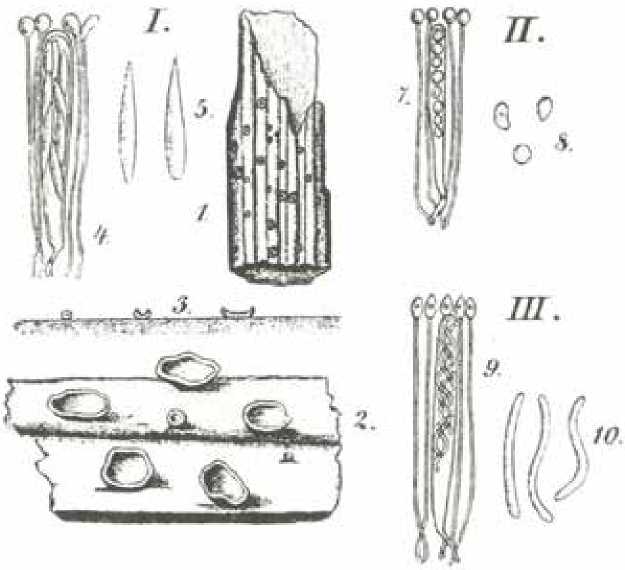


Figure 149. I. *Orbilia* sp. (as *O. vinosa*), II. *O. eucalypti* s.l. (as *O. coccinella*), III. *O. xanthoguttulata* (as *O. curvatispora*). From Rehm (1891: 447).

in illustrations, none of the orbiliaceous taxa are figured. Phillips (1887: 326–335) merged *Orbilia* with *Calloria* under the latter name, which he placed in the '*Bulgarieae*'. Phillips characterized the genus mainly by brightly coloured, gelatinous apothecia without a distinct excipulum. Nine of the 19 accepted British species are orbiliaceous: *Calloria auricolor*, *C. coccinella*, *C. inflatula*, *C. lasia*, *C. leucostigma*, *C. luteorubella*, *C. rubella*, *C. vinosa*, and *C. xanthostigma*.

When compiling diagnoses of the worldwide taxa in his 'Sylloge Fungorum', Saccardo (1889: 621–633) accepted 50 species in *Orbilia*, and disposed the genus in section '*Hyalosporae*' within the *Bulgariaceae* of his '*Discomycetae*'. The diagnosis of the genus (p. 608) includes apothecial characters such as subgelatinous, superficial, mostly red, yellow or white, and spore characters such as elongate-bacilliform or subglobose-ovoid. Only about 21 out of these 50 species are today recognized as orbiliaceous. These include, in addition to European taxa, some from North and South America (e. g., *O. rubrococcinea*, *O. occulta*, *O. gaillardii*, *O. brasiliensis*) and Australia (*O. decipiens*). One of them was reported as having multispored asci (*O. myriospora*), but reexamination of the type revealed that it belongs to the *Calloriaceae*, and that the oil drops in the immature asci were mistaken for ascospores (see p. 1679). In his colour atlas 'Fungi italici', Saccardo (1883: pl. 1289–1293, 1365) provided drawings of five species in the genus *Calloria* and one in *Habrostictis*, four of which are orbiliaceous: *C. coccinella* (Fig. 148), *C. inflatula*, *C. luteorubella*, and *H. rubra*.

In later volumes, Saccardo accepted about 40 further species in *Orbilia* (1892: 40, 2 spp.; 1895: 426–427, 6 spp.; 1899: 802–803, 5 spp., 1 var.; 1902: 767–768, 3 spp.; 1906: 137–140, 11 spp.; 1913: 722–725, 10 spp.; 1928: 1238–1239, 4 spp). In 1906 (p. 139) he enlarged the concept of the genus by adding a small group (*Orbilia* II *Orbiliopsis*) to accomodate a few species parasitic on living leaves (see p. 207).

In his survey of Austria, Germany and Switzerland, Rehm (1891: 453–462; 1896: 1224–5) accepted 15 species and one variety in *Orbilia*, 12 of these species are to be considered as orbiliaceous: *O. coccinella* s. Rehm (= *O. eucalypti*), *O. leucostigma* (incl. *O. xanthostigma*), *O. luteorubella* s. Rehm (?= *H. inflatula*/?= *O. aprilis*), *O. lasia* (= *O. carpoboloides*), *O. vinosa*, *O. chrysocoma* s. Rehm (?= *Hyalorbilia berberidis*), *O. curvatispora* (= *O. auricolor*), *O. rubella*, *O. occulta* s. Rehm (= *O. aristata*), *O. rosella*, *O. flavidorosella*, and *O. pannorum* (= *O. auricolor*). Rehm provided illustrations only for three of them (Fig. 149). He included species with erumpent and superficial, hairy and smooth apothecia with a waxy-gelatinous consistency. The genus is placed together with *Calloria* (which he segregated by septate ascospores following Karsten 1885: 138 and Saccardo 1889), *Agyrium* Fr., and *Stamnaria* Fuckel in the division '*Callorieae*' of the family *Bulgariaceae*.

For three species (*O. coccinella*, *O. luteorubella*, *O. curvatispora*) Rehm drew attention to a high variability in apothecial colour in contrast to a high consistency of their microscopic hymenial characters. For the first time the inamyloidity of the asci is mentioned for 'nearly all' species (except for the non-orbiliaceous *O. succinea* and *O. primulae* with a blue iodine reaction). Rehm also was the first to report the habitat of dry hanging branches as typical of rather many species of *Orbilia*. About seven of his orbiliaceous taxa inhabit xeric substrates, and the generic diagnosis emphasizes a reddish colour of the apothecia which is typical of desiccation-tolerant taxa.

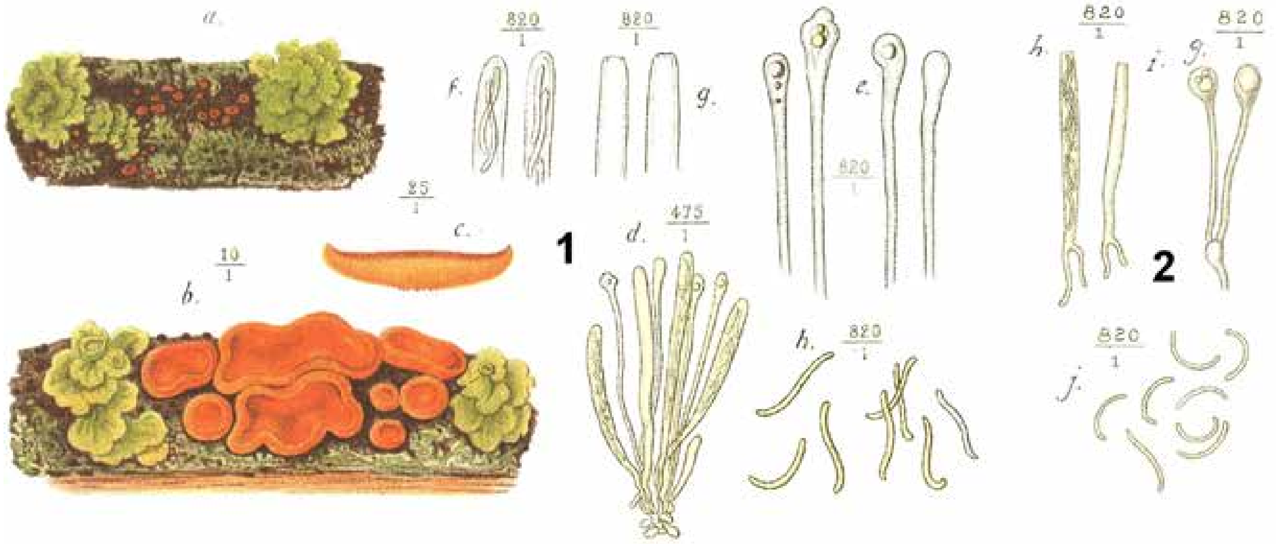


Figure 150: **1**. *Orbilia aurantiorubra*; **2**. *O. auricolor* (as *O. curvatispora*). From Boudier, Icones fungorum (1904–10: pl. 463, 464, from holotype).

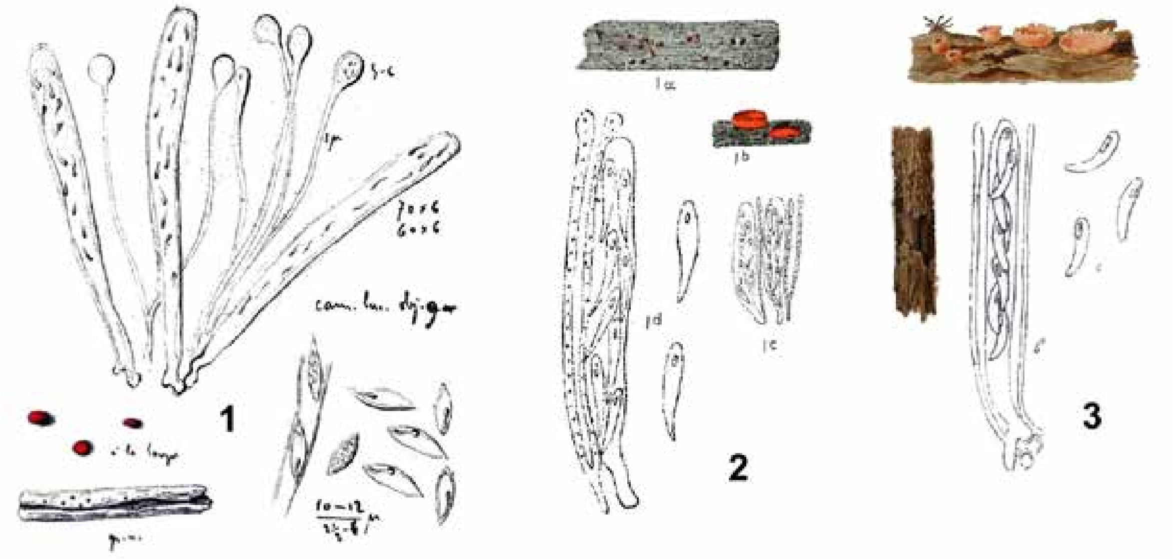


Figure 151. The first reports of spore bodies in the living spores that came to our notice (all from holotype). — **1**. *Orbilia serpentina* Patouillard (1892b, original drawing at PC); **2**. *Orbilia hesperidea* Rolland (1901); **3**. *Hyalinia ulicis* Chenantais (1918). The asci of *O. serpentina* are figured in the dead state, therefore, only the spore bodies are visible. Chenantais' watercolour drawing is taken from the unpublished original plate in the library of the Société Mycologique de France.

Boudier (1885: 114) placed *Orbilia* in the family '*Calloriés*' and characterized the genus by red to orange apothecia with a smooth margin, and capitate (button-shaped) paraphyses. Species with apically non-inflated paraphyses, flat apothecia with a dentate margin, and vermiform spores are treated in a separate genus *Hyalinia*, and those with apically lanceolate paraphyses and cupulate, dentate apothecia in *Cheilodonta* (see p. 201). In his survey on the European discomycetes, Boudier (1907: 102) listed 36 species within *Orbilia*, about 20 of which are to be considered as orbiliaceous.

Rehm was one of the first important herbarium taxonomists in discomycete systematics, and Boudier appears to be the first to have worked consistently on fresh collections with the microscope. Yet, although Boudier favoured the method of vital taxonomy and figured living asci, paraphyses and spores of many discomycetes, he never reported SBs in the ascospores in any of the nine orbiliaceous species treated in his 'Icones Fungorum' (1904–10: 265–270, pl. 459–467). This is astonishing at least regarding three species that have rather conspicuous SBs: *Habrostictis carpoboloides* (pl. 459, Fig. 167), *Orbilia sarraziniana* (pl. 462), and *O. aurantiorubra* (pl. 464, Fig. 150: 1).

Boudier (1886: 156; 1888: 80, pl. 16 fig. 6; 1907: 102; 1904–10: 265–270, pl. 459–467) introduced two new characters as typical of *Orbilia*, but also of *Habrostictis* (= *Cheilodonta*) and *Hyalinia*: (1) he precisely figured the bifurcate ascus base for ± all of the five species treated by him in *Orbilia,* by referring to one of the basal branches as spur-shaped or calcariform ('éperonnées', Fig. 150: 2); (2) he characterized the ascus apex as truncate, especially after discharge (Figs 150: 1g; 2h–i; 167: i).

Boudier's contemporary Patouillard (1892a: 11, b: pl. II fig. 6), likewise a very talented microscopic worker, described and figured living ascospores in a desiccation-tolerant 16-spored species from Tunisia, *Orbilia serpentina* (Fig. 151: 1). This is the first report of both polyspory and SBs in the *Orbiliomycetes*. Patouillard correctly depicted the subulate spore bodies of that species in free spores as well as within the asci. Regrettably he did not continue his essential approach to the vital micromorphology of *Orbilia*, and only two other French mycologists presented similar illustrations of living ascospores in two desiccation-tolerant, 8-spored taxa collected in southern France: *O. hesperidea* (Rolland 1901, Fig. 151: 2) and *Hyalinia ulicis* (≡ *O. ulicis,* Chenantais 1918, Fig. 151: 3).

Schröter (1893: 120) assigned the genus *Orbilia* to the '*Calloriei*' within the family '*Mollisiacei*', and reported six species for the Silesian flora (now Poland), among them the new species *O. pannorum*. Lindau (in Engler 1897) similarly placed both *Orbilia* and *Calloria* in the *Mollisiaceae* of the *Pezizineae.*

In his British Fungus Flora, Massee (1895: 143–149) listed 12 species within *Orbilia*, nine of which being orbiliaceous. He segregated *Calloria* by septate ascospores, but reported occasional occurrence of a spore septum in *O. lasia*. Concerning his study of North American taxa see p. 190.

Feltgen (1899, 1901, 1903) reported nine species and five varieties of *Orbilia* from Luxembourg, which were mostly confirmed to be orbiliaceous in the present reexamination. Illustrations of them can only be found in some of the preserved specimens. Feltgen's taxa concept was highly confusing and inconsistent (see p. 190). For instance, the new species *O. flavida* was described as 8-spored (Fig. 152), but is in fact 32-spored. When Feltgen made a second collection of his new taxon, he did not recognize it and again overlooked the polyspory of the asci.

Figure 152. Original sketch of *Orbilia flavida* Feltgen (in sched., holotype, from Luxembourg).

Hennings (1891, 1899, 1902a, 1902b, 1903, 1904, 1905, 1909) described seven new species in *Orbilia*, two further ones (*Ombrophila geralensis*, *Humaria euphorbiae*) which were later combined in *Orbilia*, and two (*Helotium blumenaviensis*, *H. disseminatum*) which were considered to be orbiliaceous by Dumont (1981: 323, 334). The type collections were from Europe, Africa, Indonesia, Australia, and especially Brazil, and each taxon was only recorded from a single collection. Hennings's rather brief descriptions are without illustration and hardly allow recognition of the species, and, in addition, his spore data are erroneous. Although the holotypes deposited in Berlin (B) were destroyed during the Second World War (see Hein 1988), nine specimens could be located in other herbaria and reexamined in the present study. Five of them (including those described in *Helotium* and *Humaria*) are confirmed to be orbiliaceous.

The three following species are likewise published without illustration: Lindau (1904) described *Orbilia drepanispora* which is a possible synonym of *O. auricolor* in its original sense, Höhnel (1907a) *O. botulispora* which is a synonym of *O. xanthostigma* as neotypified in the present study, and Ade (1924) *O. paradoxa* which is a possible synonym of *O. flavida*. The absence of illustrated microscopic features was detrimental particularly for *O. paradoxa*: the species was described in the living state with polysporous asci and an apical 'spot-like' body in each spore. Since a voucher specimen could not be located, it was impossible to clarify the shape of the spore body (globose or lens-shaped).

Höhnel (1918: 337) stressed the heterogeneity of the genus *Calloria* as emended by Fries (1849), which comprised some orbiliaceous species in Fries's treatment. On p. 343 Höhnel considered the parenchymatous texture of the entire ectal excipulum in *Orbilia* (*O. vinosa*) and *Calloria* to provide evidence for these genera to be simplified *Dermateaceae*. Later, Höhnel (1926a: 68) saw no clear limit between *Orbilia* and *Pezizella*, and found in *Pezizella teucrii* (?= *Calycellina chlorinella*, see p. 1665) an intermediate species with strong affinities to *Orbilia*.

Bachman (1909) provided a key to four species of *Orbilia* (*O. auricolor*, *O. coccinella*, *O. xanthostigma*, *O. vinosa*) found in Ohio, USA, but the identity of these records remains quite unclear. Bachman was apparently the first to select a lectotype of *Orbilia*, *O. xanthostigma*.

Migula (1913: 1293 ff.) mainly copied Rehm's (1891, 1896) descriptions of *Orbilia*. He supplied a key to 18 known species within central Europe, about 13 of which being orbiliaceous, among them *O. drepanispora* and *O. botulispora.*

1931–1976. Clements & Shear (1931: 314) selected *O. leucostigma* as lectotype of *Orbilia*, unaware of Bachman's (1909) study, and this selection was followed by all later workers. Clements & Shear referred *Hyalinia*, *Orbiliopsis* (Sacc.) Syd. and *Pteromyces* E. Bommer et al. to synonymy with *Orbilia*. As this work is a mere listing of taxa, the authors did not provide any discussion of this procedure. The genus *Orbilia* is listed in the *Bulgariaceae* of the *Pezizales*.

Nannfeldt (1932: 250 ff.) was the first to recognize a family *Orbiliaceae* separate from the *Dermateaceae* and *Bulgariaceae*, thus accentuating the microscopic differences between the macroscopically similar genera *Orbilia* and *Calloria* for the first time. All these three families he referred to the new order *Helotiales*.

Among the characters provided in the Latin diagnosis of the *Orbiliaceae*, the small, truncate asci are worth mentioning, but also the 'wax-like substance' that is exuded at the tip of the paraphyses and conglutinates them with the asci, and the apices of paraphyses being either uninflated or mostly subglobose-clavate. Neither of these characters are figured in his work, which predominantly illustrates excipular characteristics. Nannfeldt included three genera in the family: *Hyalinia* (2 spp.), *Orbilia* (min. 4 spp.) and *Patinella* (1 sp.). He followed Höhnel in separating *Hyalinia* from *Orbilia* on account of the presence of marginal hairs that are more or less agglutinated to form teeth.

Nannfeldt (1932: 191, 253) believed that the current concept of *Orbilia* was much too wide. He listed 14 species previously placed in *Orbilia* which he thought to belong to his new genus *Laetinaevia* in subfamily *Naevioideae* of *Dermateaceae*. Most of them have desiccation-tolerant apothecia, according to our knowledge, one being *O. serpentina* (with subulate spore bodies, see also p. 189). Nannfeldt's idea was partly based on a macroscopic similarity with such naevioid genera concerning their erumpent, more or less reddish apothecia growing on dead leaves and herbaceous stems. Nannfeldt (l.c.: 97) similarly retained the desiccation-tolerant genus *Habrostictis* near *Ocellaria* and *Pezicula* in the *Dermateaceae*. Today it is clear that his concept of the *Orbiliaceae* was artificial: several of the species placed by him in the *Dermateaceae* turned out to be orbiliaceous while, on the other hand, he assigned a clearly helotialean taxon (l.c.: fig. 40c, IVV: H.B. 7328, ?*Cistella* sp.) to the genus *Orbilia*.

Such controversial opinion can be explained by the fact that Nannfeldt attached great importance to the development and

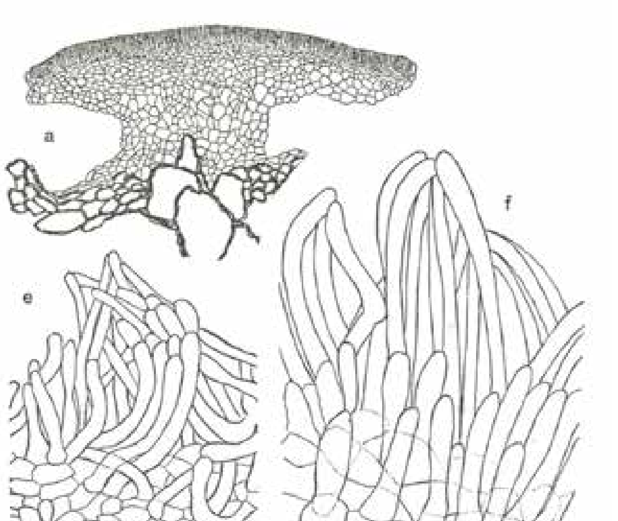


Figure 153: Excipular structure in *Orbiliaceae* as drawn by Nannfeldt (1932: fig. 40): *Orbilia epipora* [a], *O. phragmotricha* (as *Hyalinia rubella*, FFE 834) [e] and *O. crenatomarginata* (as *H. crystallina*) [f–g]. The hyphoid processes that form teeth at the margin are composed in [e] of septate, thick-walled hairs and in [f] of a solid glassy substance with a lumen only at the base, but this is neither obvious on Nannfeldt's drawings nor mentioned by him.

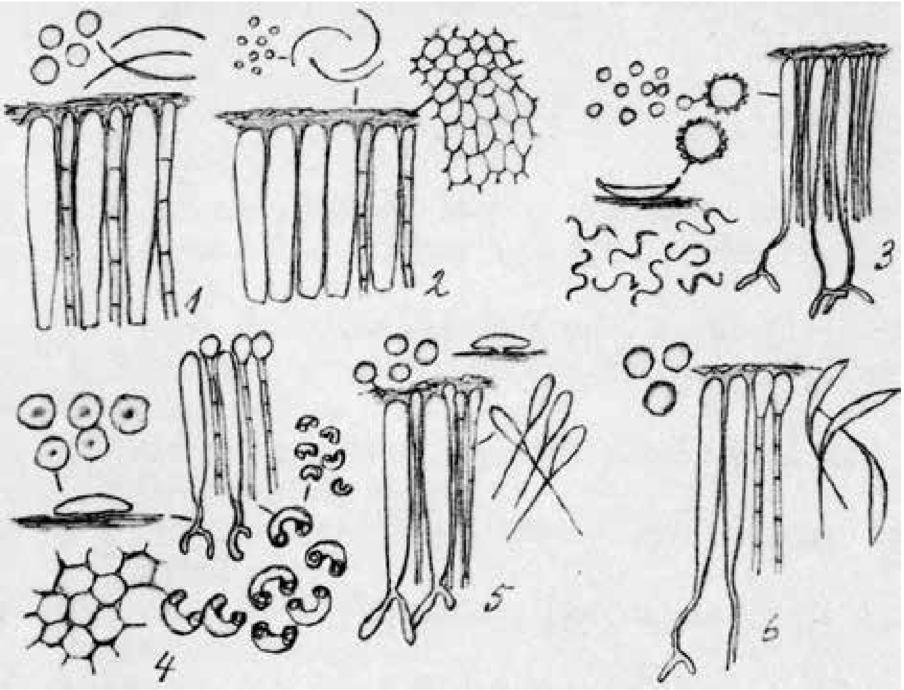
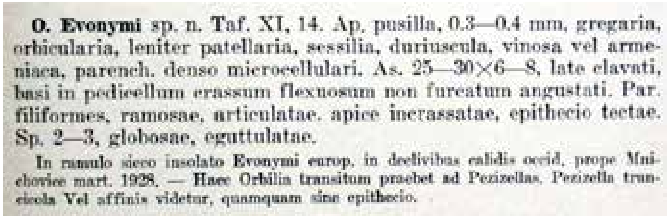


Figure 154: Examples of Velenovský's (1934) drawings regarding orbiliaceous species: pl. XI fig. **1**. *O. polyporacea* Velen. (?= *Hyalorbilia berberidis*), **2**. *O. berberidis* Velen. (≡ *H. berberidis*), **3**. *O. crenatomarginata* Höhn., **4**. *O. paradoxa* Velen. (= *O. xanthostigma*), **5**. *O. occulta* (Rehm) Sacc. (= *O. aristata*), **6**. *O. carpathica* Velen. (?= *O. flagellispora*). Note difference in ascus bases between *Hyalorbilia* (figs **1–2**) and *Orbilia* (figs **3–6**).

anatomical structure of the apothecia, following the tradition founded by Durand (1901). Therefore, Nannfeldt provided accurate and informative drawings of excipular textures (Fig. 153), but the hymenial characters are given much too little attention, if mentioned at all. For example, the absence of data about asci, paraphyses, and spores in his description of *O. inflatula* (l.c.: 254, ≡ *Hyalorbilia inflatula*) does not even allow recognition of the genus (the textura angularis shown on his fig. 40d might point to a member of *Orbilia* rather than *Hyalorbilia*).



O. Evonymi sp. n. Taf. XI, 14. Ap. pusilla, 0.3—0.4 mm, gregaria, orbicularia, leniter patellaria, sessilia, duriuscula, vinosa vel armeniaca, parench. denso microcellulari. As. 25—30×6—8, late clavati, basi in pedicellum crassum flexuosum non furcatum angustati. Par. filiformes, ramosae, articulatae, apice incrassatae, epithecio tectae. Sp. 2—3, globosae, eguttulatae.

In ramulo sicco insolato Evonymi europ. in declivibus calidis occid. prope Mnichovice mart. 1928. — Haec Orbilia transitum praebet ad Pezizellas. Pezizella truncicola Vel affinis videtur, quamquam sine epithecio.

Figure 155: Example of an *Orbilia* described as a new species by Velenovský (1934: 95; for his pl. 11 fig. 14 see Fig. 156: a).

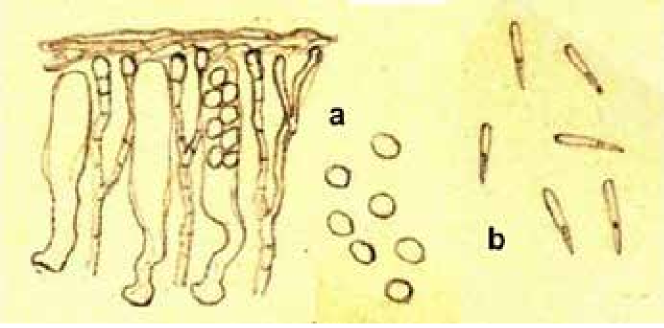


Figure 156: Examples of Velenovský's drawings on his unpublished manuscript plates. — **a**. *Orbilia euonymi* (holotype; the asci are in fact 32-spored, according to the present reexamination); **b**. *Orbilia* '*luteorubella*' (on *Cornus sanguinea*, 1.VII.1925; probably *O. sarraziniana*; the living ascospores contain subulate SBs at the acute end).

Velenovský (1934: 91–103, 1940: 177, 1947: 101–105) described by far the highest number of new taxa in *Orbilia*. For the region of Bohemia and Moravia (Czechia) and adjacent areas he reported a total of 69 species and 12 varieties. Although he supplied microscopic drawings for many of his taxa published in 1934 (see Fig. 154), he left all those unillustrated which he described later (however, drawings of two of his new taxa collected in 1942 and published in 1947 could be found among his manuscript plates, *O. vitrea* and *O. lupini*). The value of Velenovský's work was doubted by later workers, and many of his taxa were found to be synonyms. Nevertheless, his concept of the genus *Orbilia* is a rather natural one: just one verified case of a non-orbiliaceous species came to our notice (*Orbilia veratri* Velen., = *Calycellina* aff. *chlorinella*). It is also difficult to understand why he placed possibly the same desiccation-tolerant species with glassy processes (*O. aristata*) in two different families: in *Orbilia* subgroup *Aristula* (as *O. occulta* or *O. aristata*) in the *Orbiliaceae*, and in the monotypic genus *Radotinea* (as *R. caudata*) in the *Hyaloscyphaceae*.

The very high conformity in the circumscription of the genus is surprising, since Velenovský's work is full of errors regarding nearly every described taxon (see above). Similarly surprising is the fact that, like Boudier, Velenovský never reported (non-globose) spore bodies in the ascospores in any of the species treated, although he claimed to be an advocate of vital taxonomy (see p. 191).

74 out of these 81 taxa were proposed as new species or varieties (50 new species and 12 new varieties in 1934, 12 new species in 1940 & 1947). In 1934 Velenovský distinguished 56 species of *Orbilia*, but estimated that 'surely 200' exist within Europe.

Among the characters on which he based his generic concept, Velenovský stressed the inamyloid asci with their thin flexuous stipe and 2–3-furcate base, also the apices of the non-coherent (!) paraphyses which are either uninflated and covered by an epithecium (= exudate), or inflated and then without epithecium.

Velenovský (1934) proposed the family *Orbiliaceae* without being aware of Nannfeldt's (1932) study. Besides *Orbilia*, he

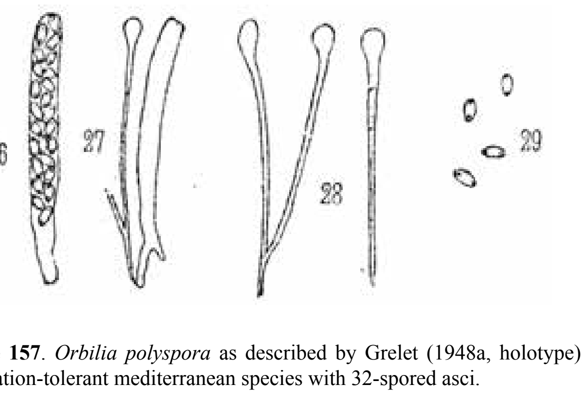


Figure 157. *Orbilia polyspora* as described by Grelet (1948a, holotype), a desiccation-tolerant mediterranean species with 32-spored asci.

Table 40. Infrageneric groups within *Orbilia* (rank not specified) as circumscribed by two Czech authors, based in the first place on spore shape. *Ascophorae* (VI) represents series *Habrostictis* in the present monograph, while *Spirospora* (IIa), *Spirospora* (II1) *Microsporae*, *Orbilia* (Ib) p.p., and *Euorbilia* (I2) *Stenosporae* correspond to the genus *Hyalorbilia*. *Soleina* concerns the single species *O. paradoxa* (= *O. xanthostigma*), *Euorbilia* (I1) *Ovatosporae* represents *O. xanthostigma* s. Svrček (= *O. tremulae*/*O. eucalypti*), and *Aristula* corresponds to series *Hemiorbilia*.

Velenovský (1934, 1940, 1947)	Svrček (1954)
(I) *Orbilia*: spores globose, ellipsoid to acicular, straight	(I) *Euorbilia*: spores not curved
(Ia) paraphyses clavate, without epithecium (25 spp.)	(I1) *Ovatosporae*: spores ovate (1 sp.)
(Ib) paraphyses not inflated, with epithecium (38 spp.)	(I2) *Stenosporae*: straight (8 spp.)
(II) *Spirospora*: spores very narrow, sickle-shaped	(II) *Spirospora*: spores sickle-shaped
(IIa) asci unstalked, not bifurcate (5 spp.)	(II1) *Microsporae*: spores small (2spp.)
(IIb) Asci stalked, bifurcate (6 spp.)	(II2) *Macrosporae*: spores large (2 spp.)
(III) *Hyalinia*: spores very narrow, strongly helicoid (1 sp.)	*Hyalinia* (recognized at the generic level)
(IV) *Soleina*: spores strongly allantoid-hemicircular ('soleiform', 1 sp.)	(III) *Soleina*: spores allantoid-hemicircular (1 sp.)
(V) *Aristula(e)*: spores fusoid, with a long thin tail (3 spp.)	(IV) *Aristula*: spores with a long and thin tail (1 sp.)
(VI) *Ascophorae*: asci min. 50 µm long, paraphyses with fusoid apex, without epithecium (1 sp.)	*Habrostictis* (recognized at the generic level)

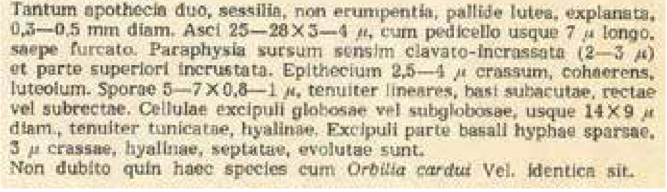
placed six further genera in that family: in 1934 *Agyrium* Fr., *Orbiliopsis* Velen., *Laricina* Velen., *Calloria* Fr., and *Stamnaria* Fuckel, and in 1940 *Algincola* Velen. Yet, almost all of the species assigned by him to these genera are clearly non-orbiliaceous (for *Algincola quercina* and *Laricina mollis* see p. 1682 and p. 1679).

Velenovský (1934) divided the large genus *Orbilia* into five subgroups, and in 1947 he added a sixth one (see Tab. 40). His infrageneric system is primarily founded on spore shape but also on paraphysis apex and ascus base features. His subgroup IIa comprises only species here referred to *Hyalorbilia*, while all those *Hyalorbilia* species with straight spores were placed in subgroup Ib. Subgroup VI corresponds to *Habrostictis*.

For the discomycetes of France, Grelet (1948a: 49f.) listed 16 species in *Orbilia*, 10 of which are with certainty orbiliaceous. The new species *O. polyspora* (Fig. 157) was reported with '24-spored' asci with a bifurcate base ('souvent éperonnées à la base').

Seaver's (1951: 152) account on the North American inoperculate discomycetes comprises 20 species in the genus *Orbilia.* About ten of these are non-orbiliaceous, and only one out of six species transferred by him to the genus (*O. cruenta*) appears to be orbiliaceous. The mentioned generic characters include brightly coloured, mostly smooth apothecia, often subglobose to pyriform tips of paraphyses (in *O. cruenta* rarely also lanceolate), and minute spores 'often difficult to diagnose'.

In Svrček's (1954) revision of 69 species and 12 varieties referred to *Orbilia* by Velenovský, he accepted 15 species and two forms in *Orbilia*, for which he provided a dichotomous key, and two species in two other genera: *O. vacini* in *Habrostictis* (as *H. rubra*), *O. crenatomarginata* and *O. roseohyalina* in *Hyalinia* (both as *H. crystallina*). Among Velenovský's new taxa (62 species and 12 varieties), Svrček accepted only seven species and two forms, while he considered the remaining taxa to be either dubious or synonymous. Svrček's descriptions (Fig. 158) are only insignificantly more detailed than those of Velenovský, but his observations are more reliable, though illustrations are completely lacking in this paper.



Orbilia luzularum Vel., Mon. Disc. Boh. p. 99, 1934.
Holotypus: Hrusice prope Mnichovice (Bohemia centr.), ad folium emortuum anni praecedentis Luzulae pilosae, VIII. 1924, leg. Velenovský (hMNP 150028).
Tantum apothecia duo, sessilia, non erumpentia, pallide lutea, explanata, 0,3—0,5 mm diam. Asci 25—28 × 3—4 µ, cum pedicello usque 7 µ longo, saepe furcato. Paraphysis sursum sensim clavato-incrassata (2—3 µ) et parte superiori incrustata. Epithecium 2,5—4 µ crassum, cohaerens, luteolum. Sporae 5—7 × 0,8—1 µ, tenuiter lineares, basi subacutae, rectae vel subrectae. Cellulae excipuli globosae vel subglobosae, usque 14 × 9 µ diam., tenuiter tunicatae, hyalinae. Excipuli parte basali hyphae sparsae, 3 µ crassae, hyalinae, septatae, evolutae sunt.
Non dubito quin haec species cum *Orbilia cardui* Vel. identica sit.

Figure 158: Example of a redescription by Svrček (1954) in his revision of *Orbilia* taxa erected by Velenovský.

The present revision confirms Svrček's species concept to a large extent, though in a number of taxa a different conclusion was attained. For instance, Svrček listed *O. juliae* and *O. polypori* as synonyms of *O. inflatula*, but we treat these three taxa as separate species within *Hyalorbilia*; in the type of *O. alnea* var. *vesiculosa* he observed ellipsoid spores, hence he assigned the taxon to *O. xanthostigma* s. Svrček (= *O. tremulae*/*eucalypti*), but the present examination revealed cashew-shaped warted spores typical of *O. xanthostigma*. For ten of Velenovský's new taxa Svrček could not trace type material. For further eleven taxa he was unable to detect any apothecia on the substrate, and for two he found only immature apothecia. Svrček probably did not rehydrate the dry specimens prior to scanning: in the present study mature apothecia could be detected in six of those apparently empty specimens (*O. euonymi*, *O. cardui* var. *farfarae*, *O. aristata*, *O. leporina*, *O. spinosae*, *O. vitrea*).

Svrček's arrangement of the accepted taxa of *Orbilia* follows Velenovský's system, but is more simplified since it is merely based on spore shape. He recognized four main groups (see Tab. 40). Svrček's arrangement is very different from the present system, and undoubtedly highly artificial. For instance, the three taxa *O. berberidis*, *O. inflatula* and *O. oreadum* are clear members of *Hyalorbilia*, whereas Svrček distributed them to three of his categories, which also include members placed by us in *Orbilia* subgenus *Orbilia*. Svrček's neglect of the ascus base (unstalked vs. stalked-furcate) is astonishing since Velenovský

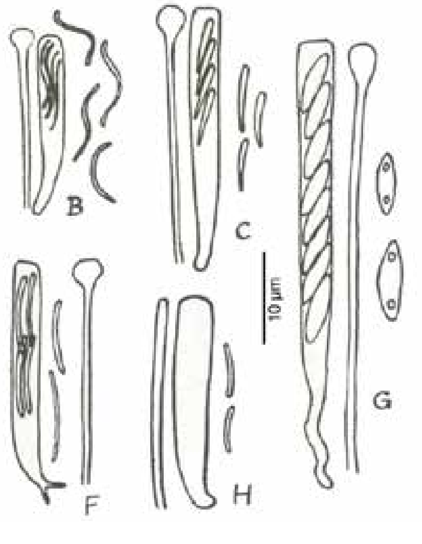


Figure 159: *Orbiliaceae* from tropical America, drawn by Dennis (1954: fig. 6), all from type material (except for C). B. *Orbilia curvatispora* var. *minor* (?= *O. crenatomarginata*), C. *O. juruensis*, F. *O. tenuissima*, G. *Helotium marmolense* (= *O. carpoboloides*), H. *O. andina* (≡ *Hyalorbilia andina*).

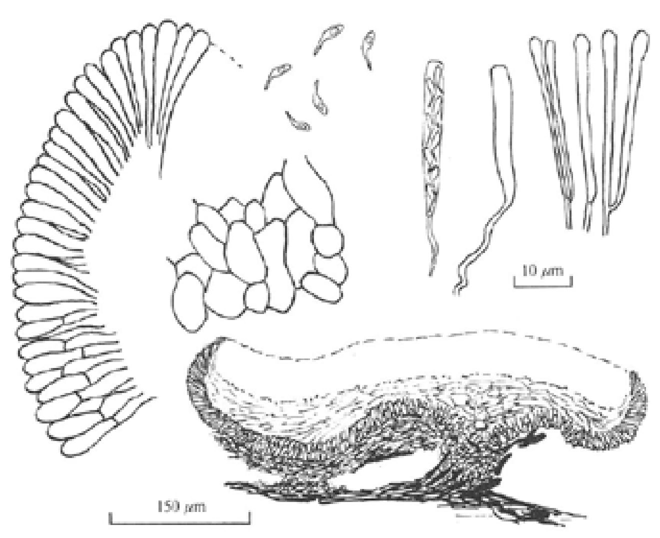


Figure 160: *Orbilia comma* (Great Britain, Warwickshire, holotype), drawn by W.D. Graddon (1977: fig. 17), spores in the living state.

already recognized to a certain extent the present concept of *Hyalorbilia* at some infrageneric level.

Dennis (1954: 295) provided a key to the seven orbiliaceous species known from the Caribbean region, with brief descriptions and illustrations (Fig. 159). When treating the fungi of Venezuela and adjacent countries, Dennis (1970: 351) reported nine species in *Orbilia*. All these Caribbean and South American taxa are obviously orbiliaceous (two of them belonging to *Hyalorbilia*), and most of them were reexamined in the present study. When Dennis studied *O. andina* (Fig. 159: H), he overlooked the isolated position of the genus *Hyalorbilia*, similar as Svrček did. According to the present reexamination, that species shows the typical characteristics of *Hyalorbilia*: unstalked asci arising from croziers, uninflated paraphyses, and a horizontal textura prismatica (see Pl. 75).

Moser (1963) included a key to the central European taxa of *Orbiliaceae*, with eight species recognized in *Orbilia* and three in *Hyalinia*. All of them are orbiliaceous according to the present knowledge. When using apothecial colour as a diagnostic character, Moser was apparently unaware of Rehm's (1891) statement that pigmentation in *Orbilia* is a rather unreliable character.

1977–2020. Jeng & Krug (1977) gave a brief history of the genus *Orbilia* when describing *O. fimicola*, a member of the difficult *O. auricolor* complex. The authors obviously viewed the coprophilous habitat as characteristic of their taxon, but did not notice its obvious similarity with *O. auricolor*.

For the British ascomycetes flora, Dennis (1968, 1978: 187, 196) treated seven species in *Orbilia*, apart from one in *Hyalinia* and one in *Habrostictis*. Among them is a non-orbiliaceous taxon (*O. marina*) with asci with amyloid apical rings, which was later transferred to *Laetinaevia* (Kirk & Spooner 1984: 568) and recently to *Calycina* (Baral & Rämä 2015). Dennis stressed the asci of *Orbilia* to be 'exceptionally small, often with a characteristically forked base and truncate tip, not blued by iodine', and the hymenial elements to 'cohere firmly to give the waxy texture peculiar to the family'. Ellis & Ellis (1985) keyed out twelve British species in *Orbilia*, while treating two others in *Habrostictis* and *Hyalinia*. One of them, *O. comma*, was described by Graddon (1977), who observed the spore body in the living spores (Fig. 160).

Ahmad (1978: 210) briefly described three species of *Orbiliaceae* from Pakistan: *O. auricolor* s.auct. (= *H. inflatula*), *O. curvatispora* (= *O. auricolor*), and *O. leucostigma*. Thind & Sharma (1980) gave detailed descriptions of species collected from the Indian subcontinent, which they identified with four European taxa: *O. auricolor* s.auct., *O. curvatispora*, *O. luteorubella*, and *O. xanthostigma*. However, the hymenial characters are illustrated with only slight deviations among these four taxa, so that their differentiation seems hardly possible. The spores of *O. curvatispora* are depicted nearly straight, although they are strongly curved on a sketch (possibly by A. Raitviir) on the label of the here examined duplicate in TAAM. The reported amyloidity of the asci was found to be an error (see p. 48). In the generic diagnosis the statement sounds strange that the asci of *Orbilia* usually have unbranched bases and non-truncate apices. This would point to members of *Hyalorbilia*, but the paraphyses are drawn with abruptly swollen apices and the ectal excipulum with isodiametric cells. Later, Thind et al. (1983) added a detailed description of a further species, *O. rubrococcinea* (Rehm) Sacc. Also Pande (2008) reported only five species for India: *O. auricolor* (s.auct., ?= *H. inflatula*), *O. coccinella*, *O. sarraziniana*, *O. vinosa*, and *O. xanthostigma*. Her descriptions are very brief and leave species identity quite unclear.

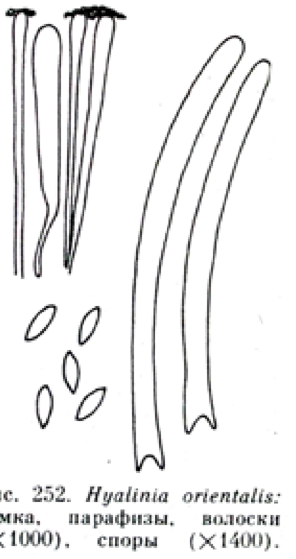


Figure 161: *Hyalinia orientalis* (Primorje, Russian Far East, holotype, ≡ *O. orientalis*), drawn by A. Raitviir (1991: fig. 252) in the dead state.

The apparent paucity of *Orbilia* species in Asia is in conflict with a statement by Batra & Batra (1963: 151) in a checklist on the Indian discomycetes, according to which many species of both *Orbilia* and *Hyalinia* are known from India. The authors

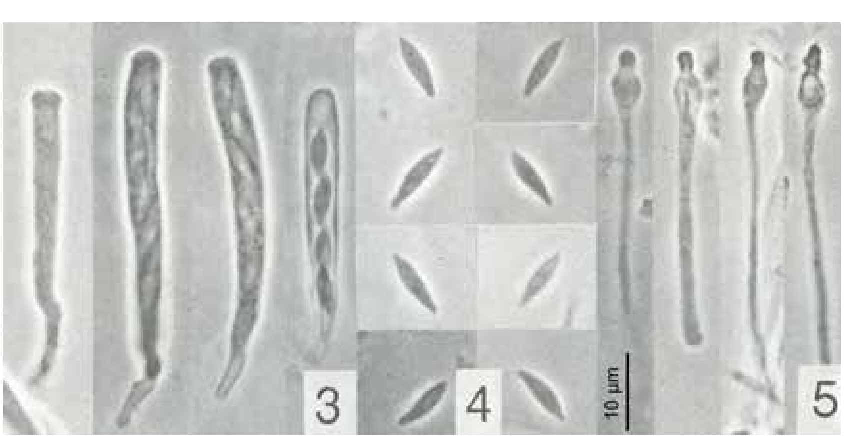


Figure 162: *Orbilia piloboloides* (Québec, Canada, holotype, = *O. carpoboloides*), photographed by Haines & Egger (1982) in the dead state.

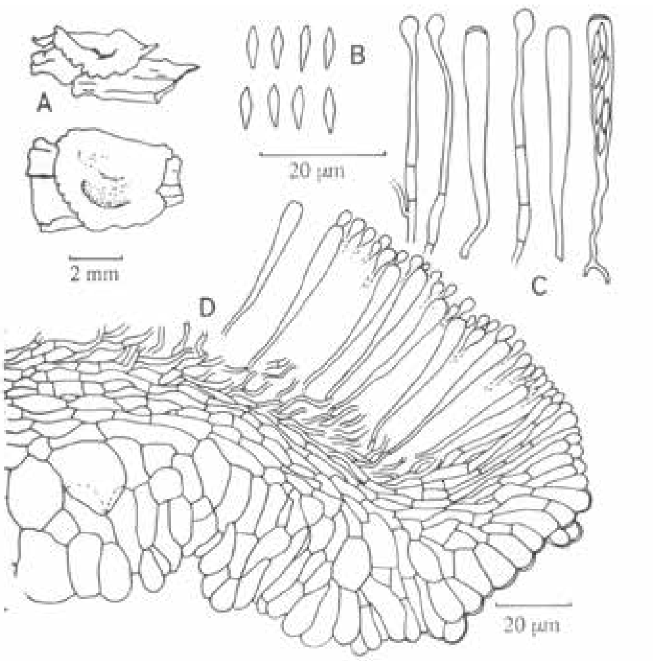


Figure 163: *Orbilia juruensis* (Solomon Islands, Melanesia), drawn by Spooner (1987: fig. 24) in the dead state.

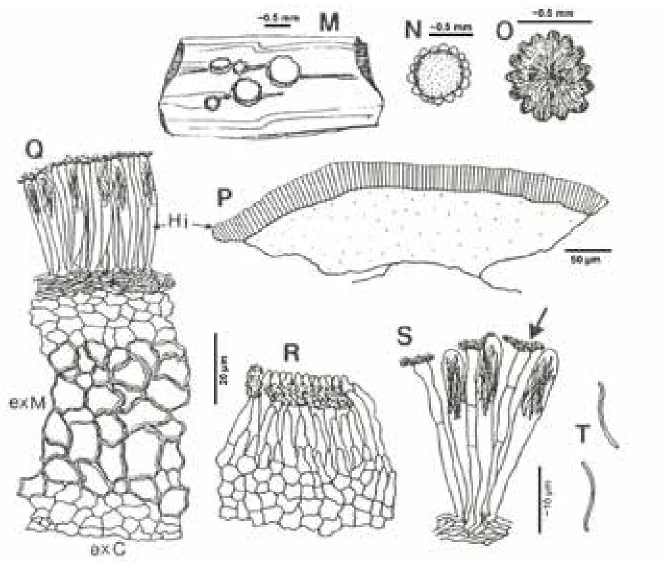


Figure 164: *Hyalinia scolecospora* (Buenos Aires, Argentina, ≡ *Orbilia scolecospora*), drawn by Romero (1994, some scale bars adjusted).

stated that they did not determine specific names since no authentic material for comparison was available. Regrettably, they did not present descriptions, and did not cite any voucher material.

In their ascomycetes flora of Switzerland, Breitenbach & Kränzlin (1981: figs 250–254, 261) presented colour photographs of four species in *Orbilia* (*O. coccinella*, *O. curvatispora*, *O. sarraziniana*, *O. xanthostigma*), one in *Hyalinia* (*H. rosella*), and one in *Habrostictis* (*H. rubra*). Although these species were photographed in the fresh state, the authors made their microscopic drawings consistently from dead, dried material.

For the Russian Far East, Raitviir (1991: 356–362) provided descriptions and a key to eight orbiliaceous species in the genus *Orbilia* (one of them, *O. inflatula*, belonging to *Hyalorbilia*), and two species with glassy processes in *Hyalinia*. One of his rather schematic sketches is shown in Fig. 161.

Haines & Egger (1982) described the North American *O. piloboloides* (Fig. 162), a desiccation-tolerant species on bark

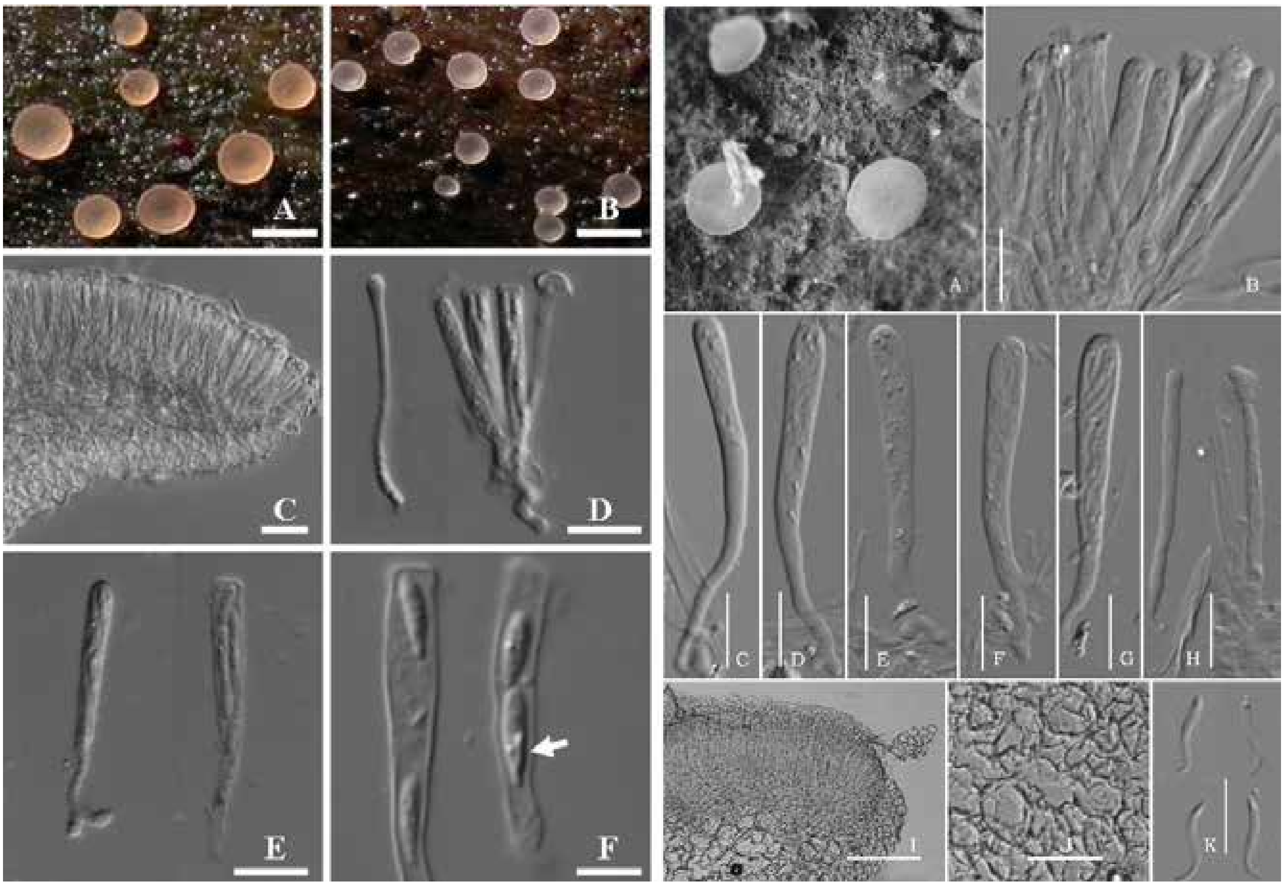


Figure 165: **left**: *Orbilia sarraziniana* (Beijing, China, from Liu 2006: fig. 41); **right**: *O. vermiformis* (Yunnan, China, holotype, from Yu et al. 2007a).

of *Ulmus*. The authors stressed the extraordinary shape of the *Pilobolus*-like apices of paraphyses, and reported an anamorph obtained in pure culture. They obviously overlooked that their species is very similar to the European *Habrostictis rubra* (= *O. carpoboloides*, likewise often found on bark of *Ulmus*), with which it even appears to be conspecific (see p. 1033). The examination of a later collected topotype of *O. piloboloides* in the living state (Pl. 573: 1) supplies the vital characters of this species, which were previously not reported due to unfavourable preparation methods.

When treating the *Helotiales* of Australasia (including Melanesia), Spooner (1987) provided detailed descriptions and illustrations of seven species accepted in *Orbilia* (Fig. 163), one in *Hyalinia*, and one in *Habrostictis*, most of them being collected by G. & K. Beaton in the warm-temperate humid southeast of Australia. *Orbiliaster* was accepted as a further genus of the *Orbiliaceae* unknown in Australasia. Spooner's generic concept is mainly based on the presence and construction of the hairs, and the shape of paraphysis apices. For the first time the warted dorsal surface of the ascospores of *O. delicatula* (= *O. xanthostigma*) is reported.

Baral (1989) described *O. septispora*, which remained until now the only known species of the large genus *Orbilia* having septate ascospores within the living asci (Pl. 683). The remarkable subulate SBs in the spore apices of this and some other species gave the impetus to the present monograph.

Korf (1992) investigated the *Orbiliaceae* of Macaronesia, with *Orbilia* as the only known genus. He presented a key to eight species, two of which (*O. inflatula* and the new species *O. lunata*) are assigned to *Hyalorbilia* in the present study. Korf followed a rather wide species concept, according to the present reexamination: for instance, under *O. epipora* he merged specimens belonging to *H. inflatula* and *O. ?dryadum*, and under *O. occulta* specimens that belong to *O. pisciformis* and *O. euphorbiae*.

In an unpublished poster, Baral (1993b) provided an overview of 29 mainly European species of *Orbiliaceae*. In another poster (Baral & Marson 1994) 35 desiccation-tolerant North American species were presented, 33 of which being considered as undescribed, thereby extending the concept of *Orbilia* to include species with olivaceous-black apothecia. Baral (1994) divided the genus *Orbilia* in two subgenera based on the structure of the ascus apex when viewed in the dead state. *Orbilia* subgenus *Hemiorbilia* was defined by hemispherical apices with an apical thickening, and *Orbilia* subgenus *Orbilia* by thin-walled, more or less truncate (shouldered) apices. *Habrostictis*, *Hyalinia*, and *Orbiliaster* were referred to synonymy with *Orbilia*, and within this genus all were thought to belong to subgenus *Orbilia*. Baral segregated a small group around *O. inflatula*, which was later described as a new genus *Hyalorbilia* (Baral & Marson 2001). The truncate, shouldered, thin-walled type of ascus apex was also described by Descals et al. (1999, see Fig. 32: a), and the rounded type with a pronounced apical thickening was reported by Kohlmeyer et al. (1998, Pl. 390: 4).

In her floristic and ecological study about micromycetes on *Eucalyptus viminalis* stumps in Argentina, Romero (1994) reported four desiccation-sensitive species (three in *Orbilia*, one in *Hyalinia*). An example of her study is given in Fig. 164. Similar as in Nannfeldt's drawing of *Hyalinia crystallina* (Fig. 153), the glassy nature of the marginal processes (Fig. 164: R) is not clearly recognizable.

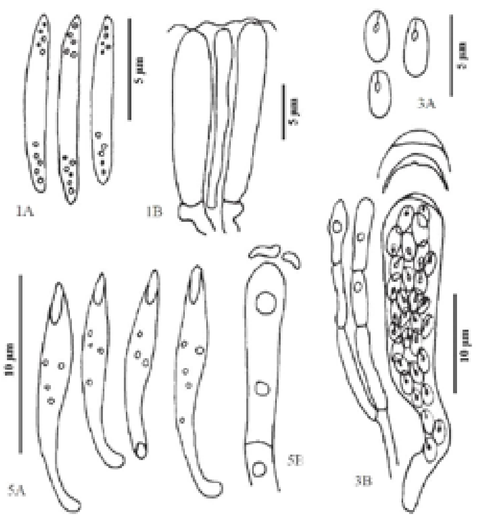


Figure 166: *Hyalorbilia juliae* (1), *Orbilia euonymi* (3), *O. aurantiorubra* (5), drawn by Priou (2005) in the living state.

Since 1994 a series of papers was published on connections between anamorphs and teleomorphs within the *Orbiliomycetes*, mainly from Chinese isolates (see Tab. 41). Various new species of *Orbilia* s.str. were published during these years, predominantly from living material and often dealing also with their anamorphs (Kohlmeyer et al. 1998, Webster et al. 1998, Karasch et al. 2005, Liu et al. 2005a, Liu et al. 2006b, Yu et al. 2007a, b [see Fig. 165 right], Zhang et al. 2009b, Su et al. 2011c, Friebes 2011, Ekanayaka et al. 2018, Shao et al. 2018, Zhang et al. 2020a).

Priou (2005) reported six desiccation-tolerant species of *Orbiliaceae* (five of *Orbilia*, one of *Hyalorbilia*) in the living state, all from atlantic Europe, and emphasized their restricted occurrence on xeric substrate. Quijada et al. (2014b) investigated by morphological and molecular methods *O. aurantiorubra* and three new species, *O. jugulospora*, *O. xanthoguttulata*, and *O. succulenticola*. Quijada et al. (2016) presented descriptions, images, and a key to 18 *Orbilia* species recorded in Tenerife, but he included only described species, whereas many further species, being newly described in the present monograph, were recorded from this island.

Liu et al. 2006b provided a key to the species of *Orbiliaceae* known from Tibet (two of *Hyalorbilia*, eleven of *Orbilia*). In his unpublished thesis, Liu (2006) presented keys and descriptions of 20 species and one variety of *Orbilia* known from China (see Fig. 165 left). For the identification of taxa, such as *Orbilia aprilis*, *O. euonymi*, or *O. orientalis*, these authors had the unpublished type studies of the present monograph at their disposal.

Cheilodonta Boud., Bull. Soc. Mycol. Fr. 1: 114 (1885) –
Lectotype species: *Peziza carpoboloides* P. & H. Crouan (indirectly designated by Höhnel 1917: 333)

The genus was erected for two species, *Peziza carpoboloides* (on rotten cord) and *P. lasia* Berk. & Broome (on bark of *Ulmus*). It was characterized by apothecia with a dentate margin (from this the name *Cheilodonta* is derived), being first closed and cupulate when young, and by the acuminate-spathulate tips of paraphyses. Lindau (in Engler 1897: 217) considered *Cheilodonta* to be a possible synonym of *Orbilia*. Boudier placed *Cheilodonta* in his '*Calloriés*' near *Orbilia* and *Hyalinia*. Later (1907: 102, 1908: 265) he placed *P. carpoboloides* and *P. lasia* in *Habrostictis*, a name which he obviously had overlooked, and retained this genus close to *Orbilia* (the name *Cheilodonta* is not

Figure 167: *Habrostictis carpoboloides* (≡ *O. carpoboloides*), drawn by Boudier (1904–10, pl. 459), ascospores in the dead state.

further mentioned). Höhnel (1917: 330f.) suggested to maintain the genus *Cheilodonta* based on *P. carpoboloides* as distinct from *Habrostictis*, since he saw no teeth at the apothecial margin in the type material of *H. rubra* (on bark of *Ulmus*), which he considered to be undoubtedly synonymous with *O. lasia*, although Fuckel described them as 'margine lacerato-fimbriato'. However, Nannfeldt (1932: 96) accepted the synonymy of *Cheilodonta* with *Habrostictis*. Based on type studies, Baral (1994: 119) found that *P. carpoboloides* and *H. rubra* represent the same species. Because of a similar ascus structure he placed *Habrostictis* (= *Cheilodonta*) in synonymy with *Orbilia*. *P. lasia* was already found by Rehm (1891: 456) to be a synonym of *H. rubra*.

Habrostictis Fuckel, Jahrb. Nassau. Ver. Naturkd. 23/24: 249 (1870) – Lectotype species: *H. rubra* Fuckel, designated by Höhnel (1917: 330).

The genus was named after the resemblance to a *Stictis* (the prefix habro means soft-fleshed). It was defined by soft, translucent apothecia and fusiform('lanceolate')-cylindric or egg-shaped ascospores. Besides *H. rubra*, Fuckel included three further taxa: *Stictis ocellata* (Pers.) Fr. [≡ *Pezicula ocellata* (Pers.) Seaver], which he validly transferred to *Habrostictis* a year later (Fuckel 1871), *Schmitzomia chrysophaea* (Pers.) Fr. [as 'Rbh.', ≡ *Ramonia chrysophaea* (Pers.) Vězda], and '*Stictis lecanora* (Pers.) Fr.'. The protologue was apparently influenced by the broadly ellipsoid-ovoid ascospores of *P. ocellata*.

Fuckel (1870) described the type species with erumpent, at first closed, then lacerate-fimbriate apothecia, and apically capitate-ovate paraphyses. He placed *Habrostictis* in the '*Stictei*' between *Naevia* and *Stictis*. Boudier (1907, 1904–10) accepted *Habrostictis* with *H. carpoboloides* and *H. lasia* (the name *H. rubra* was not mentioned). He placed the genus close to *Orbilia* and modified the circumscription by including truncate asci (after spore discharge) and correcting the shape of paraphysis apices to markedly lanceolate (Fig. 167). Phillips (1887), Massee (1895), Rehm (1891) and others did not hesitate to include a species in *Orbilia* (under the synonym *O. lasia*) which has hairy, erumpent apothecia that open rather late, and acute paraphyses. Also Haines & Egger (1982) did so with their *O. piloboloides* (= *O. carpoboloides*). Nevertheless, later authors followed Höhnel (1917: 330f., 1926b: 96) who accepted *Habrostictis* as a genus distinct from and not even related to *Orbilia*.

Höhnel (1917) excluded *Stictis ocellata* and *Schmitzomia chrysophaea* from *Habrostictis* by stating that *H. rubra* is the type of the genus. On account of an ectal excipulum composed of isodiametric cells and erumpent, orange apothecia in the type of *H. rubra* and, as he believed, a similar anamorph, Höhnel transferred *Habrostictis* to the '*Dermateen*' (1917) or '*Stictideen*' (1926b) in the vicinity of *Ocellaria* and *Dermatea.* Höhnel, followed by Nannfeldt (1932: 96), included in *Habrostictis* a non-orbiliaceous species, *H. roseoflavida* (Rehm) Höhn., which is considered here to belong to *Cistella* (see p. 1683).

The placement of *Habrostictis* close to *Ocellaria* was followed, e.g., by Nannfeldt (l.c.), who had both in the *Peziculoideae* of *Dermateaceae*, Korf (1973), Sherwood (1977), and Breitenbach & Kränzlin (1981). Grelet (1948a), however, placed *Habrostictis* close to *Orbilia*, following Boudier.

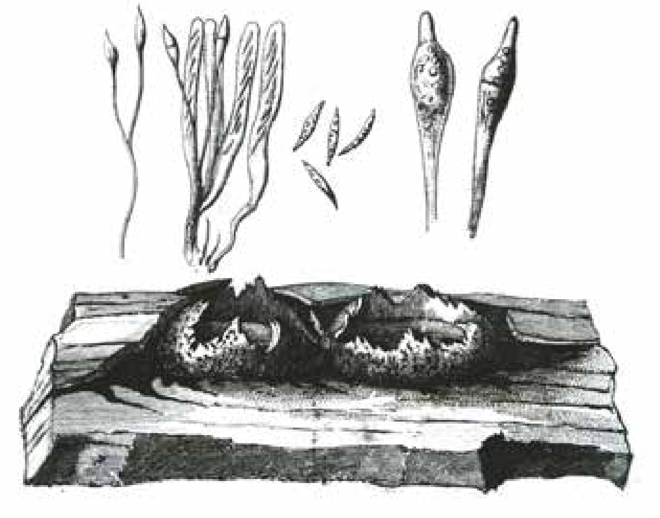


Figure 168: Holotype of *Peziza* (*Dasyscypha*) *lasia* (= *Orbilia carpoboloides*, on bark of *Ulmus*), drawn by M.J. Berkeley in the dead state (from Berkeley & Broome 1873: pl. VIII fig. 10).

Figure 169: Holotype of *Peziza carpoboloides* (≡ *O. carpoboloides*, on decayed twine), drawn by H.M. Crouan in the dead state (**left**: from Crouan & Crouan 1867: pl. suppl. fig. 10; **right**: unpublished watercolour sketch).

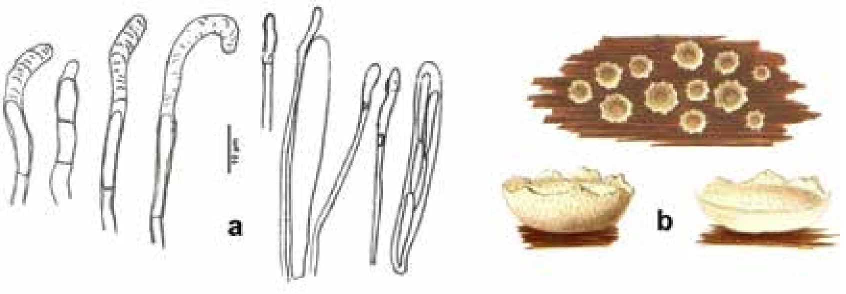


Figure 170: **a**. *Orbilia albovinosa*: dead asci, paraphyses, marginal cortical cells terminated by glassy processes, drawn by Maire (in sched., as *Hyaloscypha albovinosa*); **b**. *Hyalinia crystallina* (= *O. crenatomarginata*): apothecia with a dentate margin, drawn by Boudier (1904–10: pl. 466).

Dennis (1960a: 111; 1968: 176; 1978: 187, 196) recognized a similarity with the *Orbiliaceae* but retained *Habrostictis* in the *Dermateaceae*. Hein (1976: 9) gave a history of the genus which he excluded from the *Naevioideae* (= *Calloriaceae*). Spooner (1987: 159, 192) considered *Habrostictis* as clearly orbiliaceous, mainly because of the ascus characters (truncate apex, base sometimes forked), but he kept the genus separate from *Orbilia* on account of 'lanceolate to flame-shaped' apices of paraphyses, asci mostly exceeding 50 µm in length, and erumpent, fimbriate apothecia, with a marginal ectal excipulum composed of parallel septate hyphae. Verkley (1999: 151) accepted placement of *Habrostictis* in *Orbiliaceae* by emphasizing that it is 'not even remotely related' to *Dermateaceae*. This high phylogenetic distance is also seen in Phyl. 1.

Habrostictis was placed in synonymy with *Orbilia* subgenus *Orbilia* by Baral (1994), because very closely related species (e.g., *O. serpentina* and *O. trapeziformis*) deviate in having capitate paraphyses and non-fimbriate apothecia, though featuring strikingly similar characters of asci and ascospores, particularly the same type of vermiform-subulate or filiform spore bodies.

In the present monograph, species with lanceolate to spathulate-lageniform paraphyses similar as in *O. carpoboloides* are assigned to a small group (series *Habrostictis*, p. 1024) within the very large section *Habrostictis*, which exclusively comprises desiccation-tolerant species. At the subgeneric level we here use the name *Habrostictis* by inclusion of sections *Aurantiorubrae* and *Helicoon* which likewise mostly possess elongate SBs. Placement of series *Habrostictis* within the present large concept of *Orbilia* is demonstrated by molecular phylogenetic methods (see p. 1025).

Hyalinia Boud., Bull. Soc. Mycol. Fr. 1: 114 (1885), nom. illegit. (Art. 53.2 ICN), non *Hyalina* Stackh. 1809 (= *Desmarestia* Lamouroux 1813, nom. cons., *Phaeophyceae*) – Type species: *Helotium crystallinum* Quél.

The name of this genus refers to the translucency of the slightly pigmented apothecia. Boudier (1885) differentiated *Hyalinia* from *Orbilia* by subhyaline apothecia with a dentate margin (Fig. 170: b), non-inflated apices of paraphyses, and vermiform ascospores. In his survey on the European discomycetes, Boudier (1907: 103) enlarged the concept of *Hyalinia* to include species with an even margin, e.g., *H. rectispora*. Here he treated in *Hyalinia* no less than 45 species, but only about five of them are with certainty orbiliaceous. Among the remaining ones, many are members of *Helotiales* (often related to *Calycina*, *Calycellina* and other genera of *Hyaloscyphaceae*), some belong to *Lecanorales*, and many are nomina dubia (see p. 1660 ff.). Filiform paraphyses and vividly coloured ('gaie'), usually translucent apothecia with an often denticulate margin are mentioned by Boudier as characteristic of *Hyalinia*. Because of the marginal teeth, Lindau (1897: 205) referred *Hyalinia* to synonymy with *Cyathicula*.

In contrast to Boudier, Höhnel (1907a: 133) reduced the differences between *Hyalinia* and *Orbilia* to the marginal teeth, since the paraphyses were capitate in his *Hyalinia crenatomarginata*. However, no apical inflation of the paraphyses was seen in the type material of this taxon, which is considered to be conspecific with *Hyalinia crystallina* (Quél.) Boud. in the present study. Saccardo (1889 and later volumes of Sylloge Fungorum) never adopted *Hyalinia* as different from *Orbilia*, and also Clements & Shear (1931) listed *Hyalinia* as a synonym of *Orbilia*.

Nannfeldt (1932: 251), however, accepted *Hyalinia* in the modified sense of Höhnel by neglecting the shape of the paraphyses, but further included all species with hyphoid marginal processes, irrespective of being agglutinated as teeth (*H. crystallina*) or not (*H. rubella*). Kanouse (1939) appears to have treated a *Hyalorbilia* when she combined *Orbilia breviasca* Henn. into *Hyalinia* by stressing the non-inflated paraphyses as characteristic of *Hyalinia*. Grelet (1948b: 105) treated 14 species in *Hyalinia*. However, only five of them are with certainty orbiliaceous. Contrary to Höhnel and Nannfeldt, Grelet delimited the genus by apically non-inflated paraphyses and considered the marginal processes as unimportant at the generic level.

Moser (1963: 68) and Dennis (1978: 189) accepted *Hyalinia* in Nannfeldt's (1932) circumscription, and recognized three and one species, respectively. Spooner (1987: 159, 188) reexamined the type material of *Hyalinia crystallina* and also *H. scolecospora* G.W. Beaton, an Australian species described in Beaton & Weste (1978). Spooner accepted *Hyalinia* as distinct from other orbiliaceous genera on account of the marginal 'hairs', which he was the first to describe with a solid, glassy apical portion (in the present monograph referred to as 'glassy processes') and a lumen confined to the base of the 'hairs'. The absence of a lumen and the frequently observed stratification in the glassy part of the processes was precisely depicted already by Maire (in sched.) in *O. albovinosa* (Fig. 170: a), possibly in 1920, but was overlooked by other authors prior to Spooner, including Nannfeldt. For those species with septate hairs with a lumen up to the tip, Spooner (l.c.: 159) accepted the genus *Orbiliaster* Dennis. Among the seven species of *Hyalinia* recognized in the Checklist of the British Ascomycetes (Cannon et al. 1985) only one is surely orbiliaceous (*H. rubella*).

Hyalinia was placed in synonymy with *Orbilia* subgenus *Orbilia* by Baral (1994) because of the thin-walled, truncate ascus apices. The value of the glassy processes as a generic character was questioned because they were found to vary strongly in length. Moreover, very closely related species or even different collections of a single species often differ in this character between long, short, and completely absent. In the present monograph, *Hyalinia* comprises only species with helicoid ascospores and is accepted as a series of subgenus *Habrostictis* section *Aurantiorubrae*. The original key character, the glassy processes at the margin, is only present in some of

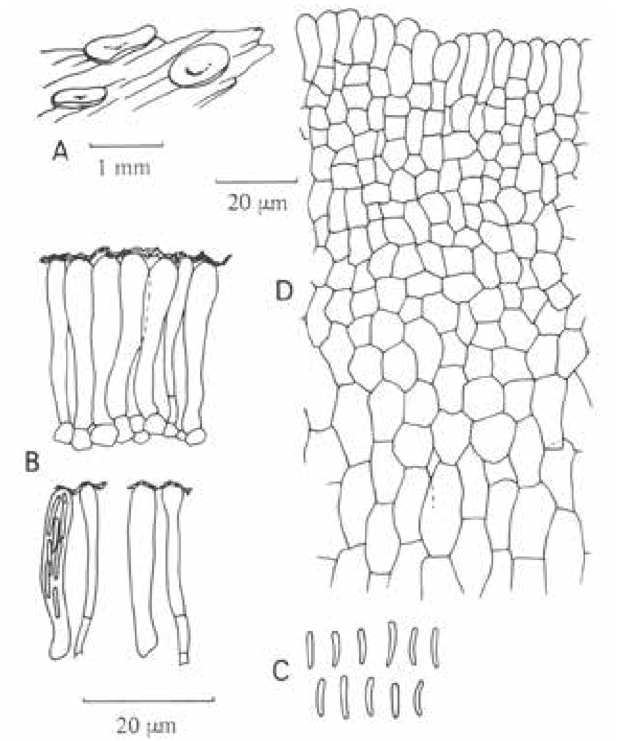


Figure 171. *Orbilia inflatula* (≡ *Hyalorbilia inflatula*). Victoria, Australia (Beaton 176), drawn by Spooner (1987: fig. 23) in the dead state.

the included species, while they occur in many other series of *Orbilia* as well.

The name *Hyalinia* Boud. is considered to be an illegitimate homonym of the older *Hyalina* Stackh. (brown algae), a name which is in concordance with the Code (ICN Art. 53.2; see, e.g., Kirk et al. 2008). The similarity of the two differently spelled names and their ease of confusion is illustrated by the fact that different listings erroneously spell both taxa in the same way. For example, Kirk et al. (l.c.) wrote '*Hyalinia*' for both names, whilst the Index Nominum Genericorum wrote '*Hyalina*' for both. In fact, Stackhouse's genus was originally spelled *Hyalina* and Boudier's *Hyalinia*. To our knowledge, *Hyalinia* has never been conserved against *Hyalina*, hence it must be considered as illegitimate.

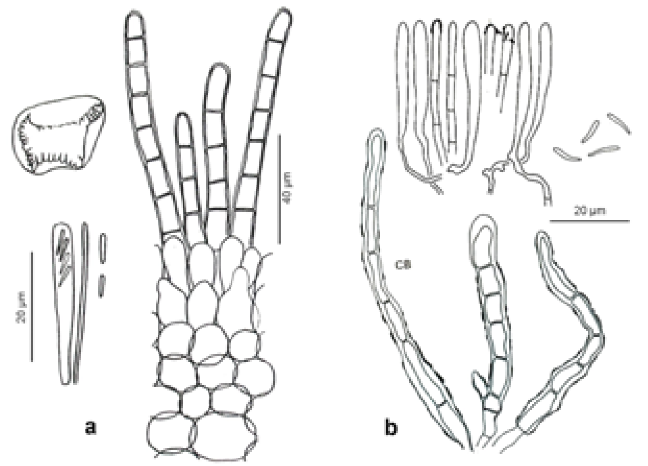


Figure 172: Septate hairs are the key character of *Orbiliaster* (drawings from holotypes in the dead state). — **a**. *O. pilosus* (≡ *Orbilia pilosa*), from Dennis (1954), from Lesser Antilles, Trinidad; **b**. *O. paradoxus* (≡ *Orbilia phragmotricha*), from Huhtinen (1992), from Finland, Varsinais-Suomi.

Hyalorbilia Baral & G. Marson, Micologia 2000: 44 (2001) – Type species: *Orbilia berberidis* Velen.

The genus was named after the pale colour and translucency of the apothecia. It was erected for five species, including *Orbilia inflatula* (P. Karst.) Sacc., based on a number of characteristics: asci with hemispherical apices without wall thickenings, base ± unstalked, arising from croziers, hymenial elements conglutinate in a gelatinous matrix, exudate on the surface of apothecia frequently forming minute warts, ascospores with a ± homopolar shape and in most species also with a homopolar guttule pattern formed by the SBs, ectal excipulum of horizontally oriented textura prismatica, and paraphyses apically not or only slightly inflated. Since type material of the well-known *O. inflatula* could not be located, a less known but well typified taxon, *O. berberidis* Velen., was chosen as type species. Although Spooner (1987) described most of these characteristics in a specimen identified as *O. inflatula* (Fig. 171), with exception of ascus croziers and guttules in living spores, he did not consider the possibility of a separate genus.

Liu et al. (2005b), Wu et al. (2007), and Su et al. (2011c) described four new species in the genus. Liu et al. (2006a) supported separation of *Hyalorbilia* from *Orbilia* at the generic level for the first time by molecular phylogenetic data. In his unpublished thesis, Liu (2006) presented a key to eight species of *Hyalorbilia* known from China, with descriptions and photo plates, and Quijada et al. (2014a) did so with six species and two unidentified *Hyalorbilia* spp. from Macaronesia. Liu et al. (2007b) presented three species of *Hyalorbilia* from China and Guo et al. (2014a, 2014b) eight. In all these works, *Hyalorbilia andina*, *H. erythrostigma*, *H. fusispora*, *H. juliae*, *H. oreadum*, and *H. polypori* were identified using the unpublished type studies of the present monograph.

Orbiliaster Dennis, Kew Bull. 9: 294 (1954) – Type species: *O. pilosus* Dennis

The genus was erected for a single tropical collection from Trinidad (Fig. 172: a). It is named after the long septate marginal hairs that may give the apothecia a star-like appearance. Later, Dennis (1970: 351) stated that the genus was perhaps not sufficiently distinct from *Hyalinia* emend. Nannf., probably because both have hair-like structures and apically uninflated paraphyses.

Huhtinen (1992) added a temperate species to the genus, *Orbiliaster paradoxus*, based on a recent record from Finland (Fig. 172: b). However, he was unaware of the presence of this species in Karsten's herbarium under the name *Orbilia rubella*. In fact, Karsten (1870, 1871) and Nannfeldt (1932: fig. 40e, see Fig. 153: e) overlooked septa in the hairs of their specimens (s. Karsten, e.g., FFE 834, see Pl. 429: 5). Nannfeldt treated *O. rubella* in *Hyalinia*; however, we propose the new name *Orbilia phragmotricha* for *Orbiliaster paradoxus* by keeping *O. rubella* as a close but separate species.

Baral (1994) placed *Orbiliaster* in synonymy with *Orbilia* subgenus *Orbilia*, because the presence of hairs was not found to be correlated with any other character that would support a separate genus. A later examination of the holotype of *Orbilia pilosa* and some other, apparently conspecific collections (Pl. 1001) confirmed the minor taxonomic value of hair-like structures in *Orbiliomycetes*. *Orbiliaster* is referred here to synonymy with series *Drechslerella* (section *Arthrobotrys* of subgenus *Orbilia*), because one of the specimens referred to

O. pilosa produced constricting rings in pure culture (Pfister 1997: 16, as *Orbilia* sp.; see also p. 1630).

Orbiliaster paradoxus (≡ *Orbilia phragmotricha*, = *O. rubella* s. Karsten) and *O. rubella* are treated in the present monograph in series *Rubellae* of subgenus *Habrostictis* section *Aurantiorubrae*. In Baral (1994) a close relationship between *Orbiliaster paradoxus* and *Hyalinia crystallina* (= *O. crenatomarginata*) was assumed, but our phylogenetic analyses indicate that the latter species is better placed in a separate series *Hyalinia* of section *Aurantiorubrae*.

Dennis used the name *Orbiliaster* as having a feminine gender. However, the traditional use of the suffix *-aster* is masculine, therefore, we believe that the two epithets need to be corrected to *pilosus* and *paradoxus* (Art. 62.1, Turland et al. 2018).

Orbiliella Kirschst., Ann. Mycol. 36: 374 (1938) – Type species: *O. armeniaca* Kirschst.

According to Kirschstein, *Orbiliella* differs from *Orbilia* mainly in the presence of a subiculum (*Orbiliella* is a diminutive of *Orbilia*). The genus was cited as a possible synonym of *Orbilia* by Spooner (1987). The presumed anamorph, referred by Kirschstein to *Trichothecium* Link, could be rediscovered close to the apothecia in the type specimen and is identified here as *Arthrobotrys* cf. *superbus*. It matches the anamorph obtained in pure culture of *Orbilia auricolor* by Pfister & Liftik (1995) who referred it to the very similar *A. cladodes* var. *macroides.* The teleomorph of *Orbiliella armeniaca* concurs with *Orbilia auricolor* as redefined by Spooner (1987). Since *O. auricolor* turned out to be an aggregate of several, more or less cryptic taxa, sequence data would be necessary to clarify the identity of *Orbiliella armeniaca*.

Pseudorbilia Ying Zhang, Z.F. Yu, Baral & K.Q. Zhang, Fungal Diversity 26: 306 (2007) – Type species: *P. bipolaris* Ying Zhang, Z.F. Yu, Baral & K.Q. Zhang

The genus was recently erected for a single species which shares characters of both *Orbilia* and *Hyalorbilia* (see p. 305). Because of the lack of DNA data, the phylogenetic affiliation of *Pseudorbilia* is unknown, but a close relationship to *Hyalorbilia* seems probable.

Radotinea Velen., Monogr. Discom. Bohem.: 298, pl. 17 figs 57, 58, 70 (1934) – Type species: *R. caudata* Velen.

The genus *Radotinea* was named after Radotín, now a village discrict in the southwest of Praha. Velenovský thought the type species to be intermediate between *Orbilia* and *Olla* Velen. (= *Unguicularia* s.auct.), but placed it in the *Hyaloscyphaceae* because of solid (glassy), 15–35 µm long 'hairs' with a lumen only at the very base (Fig. 173). Although the holotype was found to be empty by Svrček (in sched.) and also in the present study, the described and illustrated flexuous, bifurcate ascus bases and the exudate over the paraphyses clearly assign this taxon to the genus *Orbilia*, as was already stated by Baral (in Eriksson et al. 2003). The figured spermoid ascospores with a filiform tail of about the length of the ellipsoid upper part (total length 15–20 µm) and the glassy processes fit *O. aristata* as already noted by Svrček (in sched., as *O. occulta*) or perhaps *O. subaristata* (p. 719). These species belong to series *Hemiorbilia* of *Orbilia* subgenus *Hemiorbilia*, but also *O. pseudoaristata* (p. 947), a member of series *Albovinosae* (subgenus *Habrostictis*), cannot be excluded with certainty, although it has much less exudate over the paraphyses contrary to Velenovský's sketch. Mainly *O. subaristata* and *O. pseudoaristata* have long glassy processes comparable to those depicted for *R. caudata*. This might explain why Velenovský (1934: 102, 1947: 104) assigned *O. aristata* to *Orbilia* subgroup *Aristula*, without reference to *Radotinea*, as his genus concept of *Orbilia* excluded taxa with marginal hairs. In fact, Velenovský's type specimen of *O. aristata* has only very indistinct marginal teeth with 8–15 µm long glassy processes. However, one of Velenovský's (1947) later collections assigned by him to *O. aristata* has longer glassy processes (15–25 µm) which, however, form distinct teeth, but Velenovský appears to have overlooked this feature as he did not mention it.

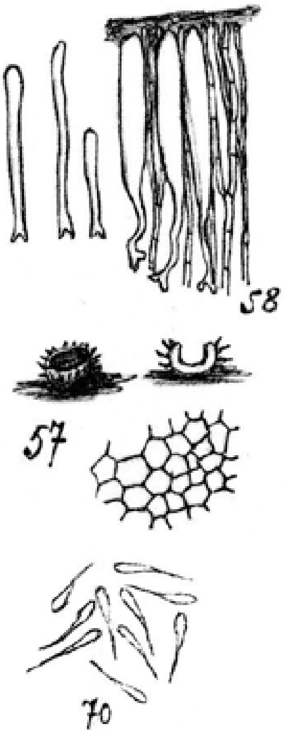


Figure 173: *Radotinea caudata* [(?)= *Orbilia aristata*], holotype, drawn by Velenovský (1934) in the dead state.

The genus *Radotinea* is placed here in synonymy with *Orbilia*. It would offer a valid name for *Orbilia* subgenus *Hemiorbilia* Baral (type *O. occulta*) if one prefers to attribute that group generic rank, but we recommend to use *Hemiorbilia* instead of *Radotinea*, because of the uncertain identity of the type species of *Radotinea* (Baral et al. 2017b).

Genera with non-orbiliaceous type species

Calloria Fries, Fl. Scan.: 343 (1836) – Lectotype species: *Peziza fusarioides* Berk. (designated by Clements & Shear 1931, = *Calloria urticae* (Pers.) J. Schröt.)

The first, very brief description by Fries (1836) placed the genus *Calloria* together with *Orbilia* in the '*Bulgariei*' (see p. 192). Later, Fries (1849: 359) listed nine species in *Calloria*: three basidiomycetous taxa now assigned to *Dacrymyces*, four ascomycetous taxa today recognized in the *Helotiales* [*Calloria urticae*], *Phacidiales* [*Claussenomyces atrovirens* (Pers.) Korf & Abawi], *Orbiliomycetes* [*Orbilia vinosa*], and *Pezizales* [*Iodophanus testaceus* (Moug.) Korf], besides two dubious taxa.

For a long time, *Calloria* was placed in vicinity of *Orbilia*, or it was even united with it. Nylander (1869) doubted the limits as outlined by Fries, and Phillips (1887) united both genera under *Calloria*. Karsten (1885), Saccardo (1889), and Rehm (1891) segregated *Orbilia* by its permanently non-septate ascospores from *Calloria* in which the spores are finally 1(–3)-septate (see also p. 188). In doing so, the authors included in *Calloria* only non-orbiliaceous taxa. They placed the two genera in the subfamily *Callorieae* of *Bulgariaceae*, while Boudier (1885), who characterized *Orbilia* by capitate paraphyses, recognized a separate family ('Famille XI. – *Calloriés*'), followed by Marchand (1894, 1896) who used the name *Calloriacés*. Also Höhnel (1907b, 1918) followed Karsten's concept, but placed the two genera in the *Dermateaceae*. Nannfeldt (1932) erected the new family *Orbiliaceae* and retained *Calloria* in the *Dermateaceae*. Although *Orbilia* and *Calloria* are today segregated in different classes, Velenovský (1934) still saw a close relationship between them by retaining *Calloria* in the *Orbiliaceae*. *Calloria* was accepted by Hein (1976) with three species in the *Naevioideae* of the *Dermateaceae*. Johnston et al. (2014b) changed the current name *Calloria neglecta* to *C. urticae*, the older name of its anamorph *Cylindrocolla urticae*, but proposed to keep the name *Calloria* instead of adopting the younger *Cylindrocolla* Bonord.

A molecular analysis presented by Baral & Rämä (2015) placed *Calloria urticae* and *Laetinaevia carneoflavida* (Rehm) Nannf. ex B. Hein in a supported clade within the *Helotiales*. Their sequences and one of *Duebenia compta* (Sacc.) Nannf. ex B. Hein, all gained by G. Marson from apothecia and representing typical species of the respective genera, provide arguments for raising the *Naevioideae* to family level (see also Phyl. 1). Consequently, Baral (in Jaklitsch et al. 2016) resurrected the family '*Calloriaceae* Marchand' by tentatively including various naevioid genera. However, the family names *Calloriés* Boud. and *Calloriacés* Marchand are invalid because of their non-Latin termination. Since this family has never been validly published, validation was done recently:

Calloriaceae Baral & G. Marson, Index Fungorum 407: 1 (2019)
≡ *Calloriaceae* Marchand [as '*Calloriacés*'], Bull. Soc. mycol. Fr. 10(3): 153 (1894), nom. inval., Art. 32.1 ICN (see also Art. 18.4)
Type: *Calloria* Fr., Fl. Scan.: 343 (1836)
Diagnosis: see Baral in Jaklitsch et al. (2016: 171).

The high molecular similarity of *Laetinaevia carneoflavida* with *Pezizella epithallina* (W. Phillips & Plowr.) Sacc. and with species of the anamorph-typified genus *Tetracladium* De Wild., and the relative phylogenetic distance of *Duebenia compta* need further attention (see Phyl. 1), as do the relationship to *Vandijckellaceae* and the unexpected placement of *Naevala perexigua* (= *N. minutissima*) in *Discinellaceae* (Johnston et al. 2019).

Deltopyxis Baral & G. Marson, Andrias 19: 176 (2012) – Type species: *Deltopyxis triangulispora* Baral & G. Marson

The fungicolous *Deltopyxis triangulispora* is the only species known in the genus. It was compared with *Orbiliomycetes* by Baral & Marson (2012) because of its triangular spores in multispored inamyloid asci, but was excluded based on rDNA data. The present analysis of the 5.8S+LSU region revealed a relationship with the *Ostropomycetidae* (*Lecanoromycetes*), in which it clustered in a medium supported clade with *Coenogonium* Ehrenb. (*Gyalectales*) and *Cryptodiscus* Corda (*Ostropales*) (Phyl. 1). *Deltopyxis* was recently included with *Phaeopyxis* in a new family *Deltopyxidaceae* by Ekanayaka et al. (2019) who proposed a relationship with *Cyttariales*. Also '*Patinella*' *abietina* belongs in this family (see p. 1660).

Gelatinopsis Rambold & Triebel, Notes R. bot. Gdn Edinb. 46(3): 375 (1990) – Type species: *Gelatinopsis geoglossi* (Ellis & Everh.) Rambold & Triebel

The genus includes discomycetes with inamyloid asci growing parasitic on other fungi or lichens. *Gelatinopsis geoglossi* differs from members of *Hyalorbilia* in having asci without croziers and spores with large glycogen bodies, but otherwise strongly resembles that genus. However, the species is up to now only documented in the dead state (for a redescription see Baral & Marson 2001). Some other members recognized in *Gelatinopsis* were studied in the living state (Baral & Marson l.c.), and they always lacked spore bodies. Problematic is that a few taxa which undoubtedly belong in *Hyalorbilia* tend to lack spore bodies (e.g., *H. rotifera*, *H. pleioerythrostigma*), or possess inconspicuous SBs.

ITS and LSU rDNA data were available for *Gelatinopsis exidiophila* Baral & G. Marson (MN047447), *G. fungicola* (Kirschst.) Baral (GU727556), and *G. hysteropatellae* Baral & G. Marson (MF322772), but none for *G. geoglossi*. *G. fungicola* was uploaded in GenBank as *Mollisia incrustata* (New York, on *Trametes versicolor*), but a sequence of *G. fungicola* from Switzerland on the same host (MH221520, MH485386) deviates by only two gaps in the ITS and is thus conspecific. *M. incrustata* is a *Hyphodiscus*, *H. incrustatus* (Ellis) Raitv. with coarsely warted hairs (see p. 1674 and IVV).

In our analysis of the 5.8S+LSU region (Phyl. 1), the three *Gelatinopsis* species clustered in the *Leotiomycetes*, each of them highly supported with another taxon: *G. exidiophila* with *Fulvoflamma eucalypti* Crous, *G. fungicola* with *Geltingia associata* (Th. Fr.) Alstrup & D. Hawksw., and *G. hysteropatellae* with an unnamed member of *Cordieritidaceae*. From this analysis it appears that *Gelatinopsis* is heterogeneous: *G. exidiophila* and *G. fungicola* belong in the *Phacidiales* in the wide sense as adopted by Baral (in Jaklitsch et al. 2016), whereas *G. hysteropatellae*, which forms its minute apothecia intrahymenially, belongs in the *Cordieritidaceae* (*Helotiales*).

In Jaklitsch et al. (2016) the family *Helicogoniaceae* was recognized for fungicolous genera with inamyloid asci, either forming superficial to immersed apothecia (*Gelatinopsis*, *Geltingia* Alstrup & D. Hawksw. etc.) or living as intrahymenial parasites which entirely lack apothecia (*Helicogonium*). For the bryophilous genus *Mniaecia* a separate lineage was proposed. In the present analysis, *G. exidiophila* and *Fulvoflamma* formed a sister clade of *Mniaecia*, while *G. fungicola* and *Geltingia* clustered unresolved within the *Phacidiales*. No sequence data were available for any of the species of *Helicogonium*.

Habrostictis Clem., Gen. Fungi: 63, 174 (1909), nom. illegit. (Art. 53.1 ICN), non *Habrostictis* Fuckel – Type species: *Pseudopeziza pallida* Fuckel
≡ *Naevia* subgroup *Habrostictis* Fuckel s. Rehm, Rabenh. Krypt.-Fl. 1.3: 137 (1888)

Rehm (1888: 137) adopted *Habrostictis* Fuckel in a sense very different from Fuckel: he reduced it to an infrageneric group of *Naevia* Fr. to accomodate 16 species [including *Naevia pallida* (Fuckel) Rehm] which today reside mainly in the *Calloriaceae* and the *Hysteropezizella* complex (*Helotiales*). In the same volume of Rabenhorst's Kryptogamen-Flora, Rehm (1891: 456) placed the type of *Habrostictis* (*H. rubra*) in *Orbilia*, as a synonym of *O. lasia*. It remains a mystery why Rehm (1888) disregarded the nomenclature rules, and not even commented in 1891 on his 1888 concept of *Habrostictis* as a subgroup of *Naevia*.

Clements (1909: 174), followed by Clements & Shear (1931: 310), relied on Rehm's (1888) interpretation of *Habrostictis*

Fuckel when stating that *H. pallida* (Fuckel) Clem. (≡ *Pseudopeziza pallida* Fuckel, ≡ *Naevia pallida*) is the type of that genus. However, selection of a taxon as lectotype, which was not included in the original concept, is against the Code (Art. 10.2, Turland et al. 2018). The reason why Clements considered this rather poorly known species as type of *Habrostictis* might be sought in the fact that it is the only one within *Habrostictis* s. Rehm that was described by Fuckel. Clements's (1909) procedure was interpreted as the erection of a new genus, *Habrostictis* Clem., because the author treated *Habrostictis* under his 'List of new genera and types', although later Clements & Shear (1931) explicitly refer to '*Habrostictis* Fkl.'.

Rehm (1888: 139) stated that the iodine reaction in *N. pallida* was unknown. Nevertheless, he listed this species within his subgroup *Habrostictis*, which he characterized as 'Ascus pore in iodine stained violet or blue'. Apparently therefore, Clements (1909: 63) keyed *H. pallida* under 'ascus pore blue with iodine'. Based on this statement, Hein (1976: 9) listed *Habrostictis* Fuckel under genera with a positive iodine reaction. Concerning the identity of *Habrostictis pallida* see also p. 1681.

Ombrophila Quél., Compt. Rend. Associated Franç. Avancem. Sci. 11: 402 (1883) ['1882'] [nom. illegit., Art. 53.1] – Type species: *Ombrophila rubella* (Pers.) Quél.

This illegitimate genus, which is a later homonym of *Ombrophila* Fr., is listed in Index Fungorum and MycoBank with one species, *O. rubella* (Pers.) Quél. [≡ *Orbilia rubella* (Pers.) P. Karst.]. Quélet (1883) did not intend to erect a new genus when he proposed the new combination *Ombrophila rubella*. In a footnote he gave a clear reference to the genus *Ombrophila* Fr. ('l'ancien genre de Fries'), by mentioning *Ombrophila lilacina* (Fr.) P. Karst. (≡ *Ascocoryne lilacina* (Fr.) Baral et al.), described and illustrated by him in Quélet (1873: 413 [erroneously as 409], pl. V fig. 12) as *Ombrophila lilacina* Wulfen. Quélet interpreted the genus *Ombrophila* Fr. as basidiomycetous ('espèces exosporées'), i.e., a member of *Auriculariales* (= *Tremellales*, as 'Trémellinées') close to *Exidia* Fr., and his illustrations of *O. rubella* and *O. lilacina* show basidia and basidiospores. Species with gelatinous ascomata and ascospores ('endosporées') he referred to the genera *Calloria* Fr. and *Helotium* Tode. Thus, he did not erect a new genus but changed the interpretation of *Ombrophila* Fr.

Orbiliopsis Höhn., Ber. Dtsch. Bot. Ges. 37: 109 (1919), nom. inval. (ICN Art. 38.11) – Type species: *Peziza subcarnea* Schumach. [≡ *Phaeohelotium carneum* (Fr..) Hengstm.]
≡ *Orbiliopsis* Höhn., Mitt. bot. Inst. tech. Hochsch. Wien 3: 101 (1926), nom. inval. (ICN Art. 38.11) et illegit. (ICN Art. 53.1) – Lectotype species: *Peziza subcarnea* Schumach. (designated by Nannfeldt 1932)

The genus *Orbiliopsis* Höhn. was established for three species, *O. austriaca* (Höhn.) Höhn., *O. pudica* (Rehm) Höhn., and *O. subcarnea* (Schumach.) Höhn. Although mentioned at the third place by Höhnel (1926), *O. subcarnea* was named by Nannfeldt (1932: 194) 'pseudotypus' of the genus, a term used by this author mostly in the sense of the first species rule (Nannfeldt 1932: 8). This exception could be explained by the fact that the new genus was already proposed by Höhnel (1919: 109), who included there solely *O. subcarnea*. However, Nannfeldt did not mention Höhnel's (1919) very brief and hidden first publication of the genus. No diagnosis was supplied by Höhnel in either work, and his indirect reference to the included species is not sufficient (ICN Art. 38.11), therefore, the name *Orbiliopsis* Höhn. is invalid. This was the reason why Spooner & Dennis (1986) erected the genus *Parorbiliopsis* (see below).

O. subcarnea was transferred by Dennis (1971) to *Phaeohelotium* Kanouse. However, the original identity of the species is not very clear, though it was extensively treated by Hengstmengel (2009). In general agreement it is a member of *Helotiales*. Similarly unclear is *O. pudica*. *O. austriaca* is found to be a synonym of *Leptodontidium trabinellum* (P. Karst.) Baral, Platas & R. Galán, according to a restudy of type material (see p. 1686). Based on molecular methods, *Phaeohelotium trabinellum* (P. Karst.) Dennis was found to be a synonym of *Leptodontidium elatius* (F. Mangenot) de Hoog, the type of *Leptodontidium* de Hoog which is of unclear relationship within the *Helotiales* (Baral 2015).

Orbiliopsis (Sacc.) Syd., Ann. Mycol. 22: 308 (1924) – Lectotype species: *Orbilia coleosporioides* Sacc. (designated by Sydow 1924)
≡ *Orbilia* subgroup *Orbiliopsis* Sacc., in Sacc. & D. Sacc., Syll. Fung. 18: 139 (1906)

The unranked infrageneric taxon was introduced by Saccardo for two orbilia-like species parasitic on living leaves: *Orbilia coleosporioides* (on *Didymaea mexicana* from Mexico) and *O. myristicae* P. Henn. (on *Myristica fragrans* from Java). Sydow (1924) raised the group to generic level and selected the type species, but did not explicitly mention *O. myristicae*. He added a third species, *Orbiliopsis callistea* Syd. (on *Hebe subalpina* from New Zeeland, as *Veronica subalpina*), which he believed to be very similar to the type species. The genus is characterized by broadly sessile, irregularly-shaped, confluent apothecia with a reduced excipular tissue, developing subcuticular, and by large, ellipsoid ascospores surrounded by a gel sheath. Also Nannfeldt (1932: 253) assumed from the description of *O. callistea* that the genus resembles *Orbilia* merely by its yellow to yellow-red colour and fleshy consistency, and that it could instead be of the ascolocular type. Clements & Shear (1931: 314), however, placed *Orbiliopsis* in synonymy with *Orbilia*.

Orbiliopsis callistea was recently rediscovered in New Zealand on the type host by P.R. Johnston (pers. comm.), who made a detailed unpublished study on it. Among other features are the inamyloid asci with an overall slightly thickened wall which is thinner at the very apex (comparable to *Pithyella*, see Fig. 174). A sequence taken from the apothecia (PDD 97932: HQ533049, HQ533050) referred the species to the *Helotiales* incertae sedis. *O. myristicae* was found in the present study to resemble the genus *Micropeziza* Fuckel (*Pezizellaceae*), according to the reexamination of an isotype (see p. 1679), whereas *O. coleosporioides* never seems to have been redescribed.

Orbiliopsis Velen., Monogr. Discom. Bohem.: 103, pl. 17 figs 35–37 (1934), nom. illegit. (ICN Art. 53.1) – Type species: *O. graminum* Velen.

Velenovský placed this genus in the *Orbiliaceae*. However, the 3-septate, fusoid ascospores and clavate asci with obtuse apices appear to exclude *Orbiliopsis graminum* from the

Orbiliomycetes. A pronounced 'epithecium' covers the filiform, apically uninflated paraphyses. The author failed to indicate the iodine reaction of the asci, and compared the species with genera such as *Durella* and *Orbilia*. The relationship of *O. graminum* is certainly to be sought within the *Helotiales*, but assignment to a family requires reexamination of the type.

Parorbiliopsis Spooner & Dennis, Sydowia 38: 303 (1986). –
Type species: *P. minuta* Spooner & Dennis
(?= *Hyaloscypha intacta* Svrček)

In order to avoid heterogeneity in the genus *Phaeohelotium* Kanouse, and because of the homonymy with the older *Orbiliopsis* (Sacc.) Syd., the new genus *Parorbiliopsis* Spooner & Dennis (1986) was erected to replace *Orbiliopsis* Höhn. The authors chose a new species as type, *P. minuta* Spooner & Dennis. They placed also *Phaeohelotium extumescens* (P. Karst.) Dennis in the genus, but left the generic position of *Orbiliopsis subcarnea* open (see under *Orbiliopsis* Höhn.).

We have found *P. minuta* to be a desiccation-tolerant species that is very common on various woody angiosperms in central Europe. Contrary to Spooner & Dennis who described *P. minuta* as hairless, the apothecia have actually very short, more or less flask-shaped hairs (also in the holotype, IVV: H.B. 5753). Due to variation among the collections in the length of the bristle-like part of the hairs, some doubt remains as to whether or not *P. minuta* and *Hyaloscypha intacta* are distinct at the species level. In both taxa the asci are inamyloid and arise from simple septa. Because of this strong similarity we consider *Parorbiliopsis* as a synonym of *Hyaloscypha* Boud. Molecular data confirm this view (Phyl. 1), therefore, *P. minuta* was combined in *Hyaloscypha* (Baral 2015). The type material of *P. extumescens* (IVV: H.B. 5249) was found to be strongly overmature, but proved to have very distinct hairs typical of *Hyaloscypha*, and the taxon might be a synonym of *Hyaloscypha albohyalina* (P. Karst.) Boud.

Patinella Sacc., Grevillea 4: 22 (1875) – Type species:
P. hyalophaea Sacc.

The genus was named after its dark pigmented apothecia. Saccardo characterized *P. hyalophaea* (Italy, on wood of *Fagus*) by strongly inflated, globose, dark brown apices of paraphyses (misidentified as conidia), and by small, ovoid, hyaline, non-septate ascospores. The genus was later enlarged, e. g., by Saccardo (1889: 769–774), Rehm (1889: 310–313), and Massee (1895: 92–95), to include many dark-coloured discomycetes that also resemble members of the genus *Patellaria* Fr. (*Patellariales*). Generic concepts at that time were mainly based on spore characters. Among the hyaline-spored genera, *Patinella* was defined by non-septate spores, *Patellea* (Fr.) Sacc. by 1-septate spores, and *Patellaria* by at least 2-septate spores. Migula (1913: 889) provided a key to nine central European species of *Patinella* in this sense.

Clements & Shear (1931: 315) designated *Patinella sanguineoatra* (Rehm) Sacc. as lectotype, a decision which is against the Code (Art. 10.2, Turland et al. 2018), and recognized the genus in the *Patellariaceae* of the *Pezizales*. Nannfeldt (1932: 256) discussed the genus in detail and accepted only two species with apically inflated paraphyses (*P. hyalophaea*, *P. aloysii-sabaudiae* Sacc.). With some hesitation, he placed *Patinella* in his new family *Orbiliaceae* close to *Orbilia*, mainly because of the shape of the paraphyses and the construction of the ectal excipulum made up of isodiametric (paraplectenchymatic), angular cells (obviously by mistake, the protologue of *Patinella* says 'excipulo minute prosenchymatico'). The dark brown pigmentation, especially of the subhymenium and tips of paraphyses, was quite unusual at that time in orbiliaceous fungi, therefore, Nannfeldt took *Patinella* as a link to the *Mollisioideae* in the *Dermateaceae*.

Because of similar truncate thin-walled asci, Bellemère (1968: 474) saw a close relationship between typical *Orbiliaceae* with light-coloured apothecia and a specimen tentatively referred by him to *Patinella*. It cannot be excluded that this specimen of unclear identity might, in fact, represent a dark-coloured member of *Orbiliomycetes*.

Spooner (1987: 158) reexamined the type material of *P. hyalophaea*, apparently the only known collection of that species at that time, but did not present a detailed redescription. He excluded it from the *Orbiliaceae* because the asci have a rounded apex and a simple, unforked base, and referred it to the *Dermateaceae*, apparently because of the dark brown excipulum of textura angularis.

The present reexamination of the type and a recent perfectly corresponding Canadian collection on coniferous wood (Baral & Carter 2013) revealed asci with basal croziers and inamyloid apical wall thickenings, and paraphyses with strongly capitate to clavate apices with dark brown apical wall thickenings (0.5–2 µm thick). A sequence of rDNA (ITS and LSU, KT876978) taken from the Canadian sample surprisingly revealed a very close relationship to the type species of *Holwaya* Sacc., *H. mucida* (Schulzer) Korf & Abawi (3.5 % distance in the ITS region, 0.5 % in the D1–D2 of LSU, see Phyl. 1), a genus referred to the new family *Tympanidaceae* of the *Phacidiales* (Baral et al. 2015, Jaklitsch et al. 2016). Although *H. mucida* has phragmosporous ascospores and a synnematal anamorph, *H. mucida* and *P. hyalophaea* indeed share several characters, such as black apothecia with a brownish, non-ionomidotic ectal excipulum of textura angularis, capitate paraphyses with brown exudate, and inamyloid 8-spored asci with croziers and with a rounded, thick-walled apex.

A few of the many taxa being combined in *Patinella* were reexamined in the present study. They are treated in the Excluded list, except for two which were found to be orbiliaceous: *P. aterrima* (Fuckel) Rehm and *P. tenebricosa* Svrček. The former is placed here in the new genus *Liladisca*, whereas the latter was found to belong to series *Drechslerella* of *Orbilia* subgenus *Orbilia*, because it forms constricting rings in culture (Pfister 1997: 14f.). Svrček (1977) thought *P. tenebricosa* to belong to *Orbiliaster* by misleadingly describing the marginal glassy processes as clavate hyphae (see under *O. polybrocha*, p. 1634).

Pithyella Boud., Bull. Soc. Mycol. Fr. 1: 118 (1885). – Type species: *Mollisia hypnina* Quél.
= *Helotiopsis* Höhnel, Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 119: 623 (1910) – Type species: *Peziza apicalis* Berk. & Broome

Probably because of the globose ascospores, Boudier (1885) believed that *Pithyella* was related

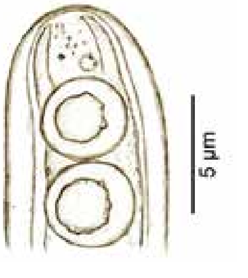


Figure 174: Apex of submature ascus of *Pithyella apicalis* (type, in KOH).

to *Pithya* Fuckel which he both placed in the 'Inoperculés'. Later (1907), Boudier enlarged *Pithyella* to include seven species and retained it near *Trichoscypha* Boud. (= *Lachnellula* P. Karst.), while he treated *Pithya* in the 'Operculés' (*Pezizales*). Nevertheless, Clements & Shear (1931: 328) reduced *Pithyella* to synonymy with *Pithya* in the *Pezizaceae*.

Sherwood & Korf (1976) and Korf & Zhuang (1987) reassessed *Pithyella* to comprise finally five species with globose to subglobose spores. Sherwood & Korf used the name *Helotiopsis* and defined the genus, e. g., by the inamyloid ascus apex with a rather thick apical wall. The two type species, *Pithyella hypnina* (Quél.) Boud. and *P. apicalis* (Berk. & Broome) Korf & Zhuang, are bryophilous and possibly conspecific (Korf & Zhuang, l.c.), and the pteridicolous *P. jenkinsii* (Sherw. & Korf) Korf & Zhuang is also very similar. Both *P. apicalis* and *P. jenkinsii* have globose spores with prominent warts.

Two of the species included by Korf & Zhuang (l.c.) in *Pithyella*, *P. erythrostigma* (Berk. & Broome) Boud. and *P. anonyma* (Rehm) Korf & Zhuang, are found to be orbiliaceous in the present monograph, according to the study of type material and of recent collections of the former species including molecular data (see Phyl. 2). The two taxa are very similar in having subglobose, smooth ascospores and lacking any apical or lateral ascus wall thickening. A refractive, globose, eccentric spore body characterizes the living ascospores of *P. erythrostigma* (see Pl. 126: 1, 5, 7), and this previously neglected character is faintly perceptible in the type specimens of both taxa (see Pls 126: 2a; 132: 1a). It clearly refers these two taxa to the *Orbiliomycetes*, and here to the genus *Hyalorbilia*, where *P. erythrostigma* was transferred by Baral & Marson (2001) based, e. g., on the hemispherical ascus apex and presence of croziers. This and a third very similar species with subglobose spores, *H. brevistipitata* Bin Liu et al., were confirmed to be orbiliaceous by molecular methods, and they cluster in *Hyalorbilia* not far from each other (Liu et al. 2005b, 2006a).

Reexamination of the type material in K (VV: H.B. 5352) indicates that *Pithyella apicalis* is not orbiliaceous but possibly a member of *Helotiaceae*. The inamyloid asci with a hemispherical apex have a laterally thickened wall, 1–1.2 µm in KOH thick in their subapical part, whereas the apical region is thin-walled (Fig. 174). This is in contrast to Sherwood & Korf's (1976) report of a thick-walled apex in an isotype (FH) of the same collection. The eight ascospores are subglobose, prominently warted, and contain a single large LB (perhaps by confluence). The paraphyses are filiform and very distantly septate, apically without any exudate. Especially the laterally thickened ascus wall and the large amount of lipid in the spores exclude this species from the *Orbiliomycetes*.

Döbbeler (2004) added a further bryophilous species, *Pithyella frullaniae* (Chal.) Döbbeler (= *P. chalaudii* Priou), which was here studied from a recent living collection (IVV: H.B. 7288). The finely warted spores each contain one eccentric LB, the inamyloid asci arise from croziers and have nearly no apical thickening (dead state, also the lateral wall is thin), and the living paraphyses and marginal hairs are densely filled with globose, medium refractive VBs (multiguttulate). Closely related with this species is probably *Muscicola dubia* (Velen.) Svrček, a bryophilous discomycete with ellipsoid, warted ascospores, an ascus apex with an euamyloid apical ring, and long uncinate hairs (IVV: H.B. 3570, 3878).

Pithyella in its restricted sense clearly belongs to the *Helotiales*. It was placed in the *Leotiaceae* by Sherwood & Korf (1976), but resides in the *Hyaloscyphaceae* in Lumbsch & Huhndorf (2010). Even though *Muscicola dubia* looks hyaloscyphaceous, it might rather be related to genera of the *Helotiaceae*, such as *Bryoscyphus* and *Cyathicula*, on account of its guttulate paraphyses and *Hymenoscyphus*-type of apical ring.

Pteromyces E. Bommer, M. Rousseau & Sacc., in Saccardo, Ann. Mycol. 3: 507 (1905) – Type species: *P. ambiguus* E. Bommer, M. Rousseau & Sacc.

Pteromyces was tentatively placed in the *Bulgariaceae* near *Orbilia* by Bommer et al. (in Saccardo 1905). The authors segregated the genus by apothecia having indistinct margins though remaining 'urceolate for apparently a long time', and by an extraordinary substrate, rotten pins from feathers of a pheasant, after which the genus was named. Clements & Shear (1931: 314) were apparently unimpressed by these characters when referring *Pteromyces* to synonymy with *Orbilia*.

P. ambiguus was described with densely gregarious, minute (0.07–0.1 mm diam.), pale brownish-rose apothecia developing subcuticular, a reddish-brown paraplectenchymatous ('pseudoparenchymatous') excipulum, asci 18–22 × 7–8 µm, 8-spored, young obovoid, then clavate, with rounded apices and short, narrow bases, spores ovoid, hyaline, 3–4 × 1.5–2 µm, outside asci 6 × 3 µm, paraphyses bacillar, apically slightly clavate, often curved.

The holotype of *P. ambiguus* (Belgium, Furnes, La Panne, III.1904, M.H. Rousseau, IVV: H.B. 8917a) contains a number of quite undecayed feathers. Near the basal end of the quill the apothecia grew in groups together with pycnidia of *Phoma ornithophila* E. Bommer, M. Rousseau & Sacc. Due to their minuteness (rehydrated 0.05–0.1 mm diam.) they are easily overlooked under the dissecting microscope. While the associated pycnidia remain subcuticular, the rehydrated apothecia are superficial and show a distinct, somewhat crenulate, hardly protruding, bright brown margin and a brownish-cream, slightly convex disc. The saccate 8-spored asci measure 23–27 × 9.5–11 µm and are not stained in IKI. They have a hemispherical apex with a 1.2 µm thick apical dome when immature, and a very short base that arises from croziers. The ellipsoid, firm-walled, smooth ascospores are eguttulate in KOH and measure 7–8.8 × 4–4.8 µm. The paraphyses have strongly capitate, partly asymmetrical apices 3.5–5 µm wide, with light brown walls. The ectal excipulum is of a textura angularis with small, irregularly tangentially elongated cells embedded in bright ochraceous exudate.

All these characters fit well ***Thelebolus microsporus*** (Berk. & Broome) Kimbr., a mainly coprophilous species which is known from dung of various animals but also from intestines and feathers of birds (De Hoog et al. 2005: 63, fig. 12). Consequently, *Pteromyces* becomes a synonym of *Thelebolus* Tode. The small spore measurements in the protologue might refer to the protoplast of the dead spores which had a size of 5–6.5 × 2–3 µm in the present reexamination.

Table 41. Chronological list of anamorphs connected to teleomorphs of the genera *Orbilia* and *Hyalorbilia* as being reported in the literature up to now, with indication of the current holomorph name, mainly based on cultural studies (except for Kirschstein 1938 and Korf 1992). See also tab. 1 in Zhuang & Mo (2006: 21).

Reference	Anamorph	Teleomorph	Holomorph name in present study
Brefeld 1891, Butterfield 1972, Pfister 1997, Liu 2006, Shao et al. 2018	*Dicranidion fragile* Harkn. (Brefeld s.n.)	*O. coccinella* (Brefeld, Liu), *O. xanthostigma* (Butterfield), *O. alnea* (Pfister)	*O. eucalypti* (W. Phillips & Harkn.) Sacc. s.l.
Kirschstein 1938 Pfister 1994	*Arthrobotrys ?superbus* Corda (as *Trichothecium* sp.) *Arthrobotrys superbus*	*Orbiliella armeniaca* *O. fimicola*	*O. auricolor* (A. Bloxam) Sacc. s.l.
Berthet 1964a	*Dicranidion ?inaequale* Tubaki & T. Yokoyama (s.n.)	*O. xanthostigma*	*O. tremulae* Velen.
Webster & Descals 1979, Descals et al. 1999, Pfister 1997 Liu 2006	*Anguillospora rosea* J. Webster & Descals (partly as *Anguillospora* sp.) *Dactylella* sp.	*Orbilia* sp. (Webster & Descals, Descals), *O. ?luteorubella* (Pfister) *O. luteorubella*	*O. rosea* (J. Webster & Descals) Baral & E. Weber
Haines & Egger 1982, Pfister 1997	*vermispora*-like (as *Idriella*-like)	*O. piloboloides*	*O. carpoboloides* (P. & H. Crouan) Baral
Zachariah 1983	*Drechslerella dactyloides* (Drechsler) M. Scholler et al. (*as Arthrobotrys dactyloides*)	(*Orbilia* sp.)	*Orbilia* sp.
Thakur & Zachariah 1989	*Dactylella rhopalota* Drechsler	*Orbilia* sp.	*O.* aff. *cardui* (Boud.) Baral
Korf 1992	*Dicranidion* sp.	*O. alnea*	*O. cejpii* Velen.
Pfister & Liftik 1995	*A. cladodes* var. *macroides* Drechsler	*O. auricolor*	*O. auricolor* s.l. (*O. cladodes*)
Pfister & Liftik 1995, Liu 2006	*Arthrobotrys oligosporus* Fresen. (var. *oligosporus*)	*O. auricolor*	*O. oligospora* (Fresen.) Baral s.l.
Rubner 1996	*Arthrobotrys oudemansii* M. Scholler et al. (as *Monacrosporium psychrophilum*)	*O. auricolor*	*O. elegans* Baral et al.
Matsushima 1995	*Trinacrium* sp. (perhaps a contamination)	*O. trinacriifera*	*H.* aff. *erythrostigma* (Berk. & Broome) Baral & G. Marson
Pfister 1997	*Drechslerella polybrocha* (Drechsler) M. Scholler et al. (as *M polybrochum*)	*Patinella tenebricosa*	*O. polybrocha* (Drechsler) Baral & E. Weber
Pfister 1997	*Drechslerella* aff. *doedycoides* (Drechsler) M. Scholler et al. (as *M. ?doedycoides*)	*Orbilia* sp.	*O. pilosa* (Dennis) Baral
Pfister 1997, Liu 2006	*Dicranidion gracile* Matsush. (Liu as *D. tenue*)	*O. delicatula*	*O.* cf. *xanthostigma* (Fr.) Fr.
Pfister 1997	*Helicoon sessile* Morgan	*O. luteorubella*	*O. luteorubella* (Nyl.) P. Karst.
Pfister 1997 Liu 2006	*Dactylella* sp. *Dactylella* cf. *coccinella* Ying Yang & X.Z. Liu	*O. ?alnea* *O. epipora*	*O. dryadum* (Velen.) Baral & E. Weber
Webster et al. 1998, Liu 2006, Liu et al. 2007a	*Dactylella oxyspora* (Sacc. & Marchal) Matsush. (Liu as *D. rhombospora*)	*O. fimicoloides*	*O. oxyspora* (Sacc.& Marchal) E. Weber & Baral s.l.
Kohlmeyer et al. 1998	*Dwayaangam junci* Kohlm. et al.	*O. junci*	*O. junci* Kohlm. et. al.
Liu et al. 2005a	*Dactylellina quercus* Bin Liu et al.	*O. quercus*	*O. quercus* Bin Liu et al.
Mo et al. 2005a	*Arthrobotrys yunnanensis* M.H. Mo & K.Q. Zhang	*O. auricolor*	*O. multiformis* (Ts. Watan.) E. Weber & Baral
Mo et al. 2005b	*Dactylella lignatilis* M.H. Mo & K.Q. Zhang	*Hyalorbilia* sp.	*Hyalorbilia lignatilis* (M.H. Mo & K.Q. Zhang) E. Weber & Baral
Liu et al. 2005b	*Brachyphoris brevistipitata* (Bin Liu et al.) Juan Chen et al. (as *Dactylella brevistipitata*)	*Hyalorbilia brevistipitata*	*Hyalorbilia brevistipitata* Bin Liu et al.
Yang & Liu 2005	*Dactylella coccinella* Ying Yang & X.Z. Liu	*O. coccinella*	*O.* aff. *dryadum* / aff. *tremulae*
Yu et al. 2006	*Drechslerella* aff. *brochopaga* (Drechsler) M. Scholler et al. (as *D. brochopaga*)	*O. orientalis*	*O.* cf. *tonghaiensis* Z.F. Yu, Baral & E. Weber and *O. orientalis* (Raitv.) Baral
Liu 2006	*Trinacrium incurvum* Matsush.	*O. brasiliensis*	*O.* aff. *farnesianae*
Liu 2006	*Dactylellina lysipaga* (Drechsler) M. Scholler, Hagedorn & A. Rubner	*O. quercus var. hunanensis*	*O. lysipaga* (Drechsler) Bin Liu, Baral & E. Weber
Liu 2006	*Dactylellina ellipsospora* (Preuss) M. Scholler, Hagedorn & A. Rubner	*O. quercus var. hainanensis*	*O. ellipsospora* (Preuss) Bin Liu, E. Weber & Baral
Liu 2006	*Arthrobotrys cladodes* Drechsler	*O. auricolor*	*O. cladodes* (Drechsler) E. Weber & Baral
Liu 2006	*Arthrobotrys javanicus* (Rifai & R.C. Cooke) Jarow.	*O. auricolor*	*O. javanica* (Rifai & R.C. Cooke) Bin Liu, Baral & E. Weber
Liu 2006 Yu et al. 2009b	*Drechslerella* cf. *brochopaga* (Drechsler) M. Scholler, Hagedorn & A. Rubner *Drechslerella yunnanensis* Z.F. Yu & K.Q. Zhang	*O. orientalis* *O.* cf. *orientalis*	*Orbilia yunnanensis* (Z.F. Yu & K.Q. Zhang) Bin Liu, E. Weber & Baral
Liu 2006	'*Anguillospora sarraziniana*'	*O. sarraziniana*	*O. sarraziniana* Boud.
Liu 2006	*Dactylella* sp.	*Orbilia* sp.	*Orbilia nemaspora* Baral, Bin Liu, A.I. Romero, Healy & Pfister
Yu et al. 2007a	*Dactylella vermiformis* Z.F. Yu et al.	*O. vermiformis*	*O. vermiformis* Baral et al.
Yu et al. 2007b	*Dactylella dorsalis* Ying Zhang et al.	*O. dorsalis*	*O. dorsalis Ying* Zhang et al.
Yu et al. 2009a	*Dactylella alba* Z.F. Yu & K.Q. Zhang	*O. alba*	*O. alba* Dennis
Li et al. 2009	*Arthrobotrys nonseptatus* Z.F. Yu et al.	*Orbilia* sp.	*Orbilia* sp.
Yu et al. 2011	*Pseudotripoconidium sinense* Z.F. Yu & K.Q. Zhang	*O.* aff. *luteorubella*	*O. sinensis* (Z.F. Yu & K.Q. Zhang) Baral, Z.F. Yu & E. Weber
Qin et al. 2011	*Dactylella pseudobrevistipitata* L. Qin et al.	*Orbilia* sp.	*O. pseudobrevistipitata* (L. Qin, M. Qiao & Z.F. Yu) Baral & E. Weber
Su et al. 2011b	*Arthrobotrys latisporus* H.Y. Su & X.Y. Yang	*Orbilia* sp.	*O. latispora* (H.Y. Su & X.Y. Yang) Baral & E. Weber

Reference	Anamorph	Teleomorph	Holomorph name in present study
Su et al. 2011c	*Pseudotripoconidium*	*O. acicularis*	*O. acicularis* Baral & Hong Y. Su
Qiao et al. 2012	*Arthrobotrys vermicola* (R.C. Cooke & Satchuth.) Rifai	*O. blumenaviensis*	*O. blumenaviensis* (Henn.) Baral & E. Weber
Guo et al. 2013	*Trinacrium incurvum* Mats.	(*Orbilia* sp.)	*O.* aff. *bannaensis* Ying Zhang, Z.F. Yu & K.Q. Zhang
Ren et al. 2014b	trinacrium-like	*O. corculispora*	*O. corculispora* Baral & G. Marson
Zhang et al. 2015	dactylella-like	*O. laevimarginata*	*O. laevimarginata* Baral, Y. Zhang & Z.F. Yu
Qiao et al. 2015	anguillospora-/vermispora-like	*O. yuanensis*	*O. yuanensis* Baral, Z.F. Yu & H.Y. Su
Zhang et al. 2016	dactylella-like	*O. tianmushanensis*	*O. tianmushanensis* Baral, Y. Zhang & Z.F. Yu
Shao et al. 2018	phragmoconidia		*O. georgiana* Y.Y. Shao, Baral & Bin Liu
Shao et al. 2018	dicranidion-like		*O. renispora* Y.Y. Shao, Quijada, Baral, Haelew. & Bin Liu
Shao et al. 2018	dicranidion-like		*O.* cf. *xanthoguttulata* Baral
Shao et al. 2018	trinacrium-like		*O. occulta* (Rehm) Sacc.
Zhang et al. 2020	drechslerella-like		*O. tonghaiensis* Z.F. Yu, Baral & E. Weber
Zhang et al. 2020	drechslerella-like		*O. pseudopolybrocha* Z.F. Yu & M. Qiao
Zhang et al. 2020 in press	*Arthrobotrys latisporus* H.Y. Su & X.Y. Yang		*O. latispora* (H.Y. Su & X.Y. Yang) Baral & E. Weber
Zhang et al. 2020 in press	dactylellina-like		*O. apiculata* Z.F. Yu & M. Qiao
Zhang et al. 2020 in press	dactylellina-like		*O. biforma* Z.F. Yu & M. Qiao

HISTORY OF ANAMORPH GENERA

The *Orbiliomycetes* are characterized by a pleomorphic life cycle which comprises two very different states: in addition to the apothecial state (teleomorph), many species of this class are known to form a conidial state (anamorph). Conidia are asexual propagules. In the *Orbiliomycetes* they are freely formed on short to long conidiophores which arise from superficial hyphae of effuse mycelia, often in more or less close association with the apothecia, sometimes from apothecial tissue, but almost never in conidiomata. Conidiophores and conidia are always hyaline and thin-walled, and conidiogenesis is consistently holoblastic (see also p. 109 ff., Morphology of the anamorph).

Connections between anamorph and teleomorph are as yet uncertain or unknown for many of the recognized species, however. This means that a lot of teleomorph-typified taxa are without a known anamorph and, vice versa, a lot of anamorph-typified taxa are without a known teleomorph. Our research suggests that most if not all species with teleomorph are able to produce an anamorph, but it is often very difficult in this class to obtain conidia in pure culture. Because apothecia are not easily formed in pure culture, the question is still open whether anamorph-typified taxa exist which have actually lost their sexual reproduction ability.

Anamorphs previously connected to orbiliaceous teleomorphs. Tab. 41 lists all connections between anamorph and teleomorph within the genera *Orbilia* and *Hyalorbilia* known to us from the literature until now. These reports predominantly concern desiccation-sensitive species growing in continually moist habitats.

Schulzer v. Müggenburg (1878) was apparently the first to report conidia associated with a species of *Orbilia.* He described spindle- to club-shaped conidia on apothecia which he identified as *Peziza leucostigma*. Such conidia are typical of the genus *Dactylella*. However, the identity of his specimen is unclear concerning both anamorph and teleomorph (*Hyalorbilia* or *Orbilia*). The second was Costantin (1888) who examined ascocarps of an *Orbilia* which he thought to be *O. vinosa*, an ambiguous name at that time which included species of section *Helicoon* as well as section *Hemiorbilia*. Quite probably Costantin's fungus belonged in the scope of *O. luteorubella*. However, the ovoid conidia observed by him most likely do not belong to an *Orbilia*. Costantin suspected that they arise by detachment of the upper parts of the moniliform heads of the paraphyses, but this interpretation seems to be erroneous, as we never observed natural detachment of paraphysis heads in any species of *Orbiliomycetes*.

Brefeld (1891: 304, pl. XI fig. 69) obtained an anamorph in pure culture from a specimen identified by Rehm as *O. coccinella* (= *O. eucalypti* in the present monograph). This produced at first unbranched, subcylindrical and later forked conidia which appears to represent *Dicranidion fragile*. The illustrated asci with cashew-shaped spores (l.c.: fig. 68) belong to another collection (probably *O. leuco-* or *xanthostigma*) which did not form a mycelium.

Velenovský (1934: 97, pl. 11 fig. 29) described *O. tricuspis* Velen. (= *O. vinosa*) with tricuspidate structures growing out of the basal excipulum. These could no longer be found in the type material, but they very probably represent conidia of the trinacrium-like anamorph of *O. vinosa* which we have repeatedly obtained in pure culture and observed on the natural substrate (see Pls 258, 261).

Drechsler (1937a: 458, fig. 18 R) obtained apothecia of an unidentified discomycete (obviously an *Orbilia*) in a single nematode-infested culture of *Arthrobotrys superbus*. However, he could not exclude a contamination (see p. 1530, *O. auricolor*).

Kirschstein (1938) observed two-celled conidia emerging from the subiculum of his new genus and species *Orbiliella armeniaca* Kirschst., a later synonym of *Orbilia auricolor*, according to our study of the type (Pl. 950: 2). He regarded this imperfect fungus as the anamorph, and tentatively referred it to *Trichothecium* Link. Our restudy of this anamorph showed that it is a species of *Arthrobotrys* (*A. ?superbus*) and undoubtedly the anamorph of the associated *Orbilia*.

In their overview of connections of the anamorphs and teleomorphs in discomycetes, Hennebert & Bellemère (1979) listed only two credible connections within the *Orbiliaceae*. Since that time various further connections were published (see Tab. 41 and under the different anamorph-typified genera). For instance, Mo et al. (2005a) listed 19 and Zhang et al. (2011a) 32 connections. However, the identity of the reported taxa is not always clear, and in several cases the same name of a teleomorph appears as being connected to different anamorphs. Such cultural differences from seemingly conspecific teleomorphs are mostly supported by deviating molecular data, which indicate that different species are involved.

The present monograph accepts about 145 connections between anamorphs and teleomorphs as certain. Out of these 145 connections, ca. 45 have earlier been reported in the literature, and 14 of these 45 reports were affirmed in the present study from recent collections. Further ca. 90 connections are reported as presumed, because conidia were observed on the natural substrate only, being not assured by pure culture and/or molecular data (see Appendix 4).

In the following, an overview of the anamorph-typified genera (including form genera) is given, in which species were placed for which a connection to the *Orbiliomycetes* could be demonstrated (20 genera) or is presumed (*Haptocara*, *Tripoconidium*). A large number of the known anamorph-typified species belongs to five of these genera (*Arthrobotrys*, *Dactylella*, *Dactylellina*, *Drechslerella*, *Gamsylella*), which represent the anamorphs of *Orbilia* section *Arthrobotrys* (p. 1432). These usually have long conidiophores (much longer than the conidia) and ellipsoid-ovoid, fusiform or cylindric-clavate, almost exclusively unbranched conidia, and are mainly desiccation-sensitive, including their teleomorphs. The remaining genera belong to other sections of *Orbilia* or other genera of *Orbiliomycetes*. Those with unbranched conidia include *Anguillospora*, *Brachyphoris*, *Helicoon*, *Lecophagus*, *Microdochiella*, and *Vermispora*, whereas *Curucispora*, *Dicranidion*, *Dwayaangam*, *Descalsia*, *Mycoceros*, *Retiarius*, *Tridentaria*, and *Trinacrium* are defined by branched conidia. All these remaining genera have often more or less short conidiophores, and the conidia or conidial arms and stipes are usually comparatively long and narrow. Many of the species are desiccation-tolerant, including their teleomorphs.

A further genus, *Pseudotripoconidium*, occupies a morphologically isolated position. The conidia are obpyramidal, with more or less prominent denticle-like protuberances, and are formed on rather long conidiophores. Molecular data indicate a close relationship to those anamorphs of *Orbilia* with narrow, unbranched anguillospora-like phragmoconidia.

For most of these anamorph-typified genera a teleomorph has been reported. *Microdochiella* and *Vermispora* are placed here in synonymy with *Hyalorbilia* based on molecular similarities of a typical *Hyalorbilia* teleomorph (*H. rotifera*) that clustered in the so far purely anamorphic *Vermispora* clade. *Curucispora*, *Descalsia*, and *Tridentaria* are reported here for the first time as anamorphs of *Orbilia*, and also for *Lecophagus* a connection to an orbiliaceous teleomorph is established. *Haptocara* shows affinities with *Lecophagus* regarding similar very broad mycelial cells containing cubical bodies and conidiophores bearing phragmoconidia in an apical cluster. Its conidia are characterized by a filiform subapical appendage and an apical adhesive knob.

Judging from its morphology, also *Tripoconidium* is very probably an orbiliaceous anamorph. It combines long conidiophores with branched (staurosporous) conidia, a feature also noted in a few species assigned to *Arthrobotrys*, *Dicranidion*, and *Tridentaria*. Only for a single taxon with this combination of characters, *Arthrobotrys iridis* (= *Dactylella ramiformis*), a connection to a teleomorph is so far known (see p. 1547, *Orbilia multiformis*). For the similar genus *Pseudotripoconidium* a connection to a number of teleomorphs have been established, but its conidia with short protuberances can hardly be termed staurosporous.

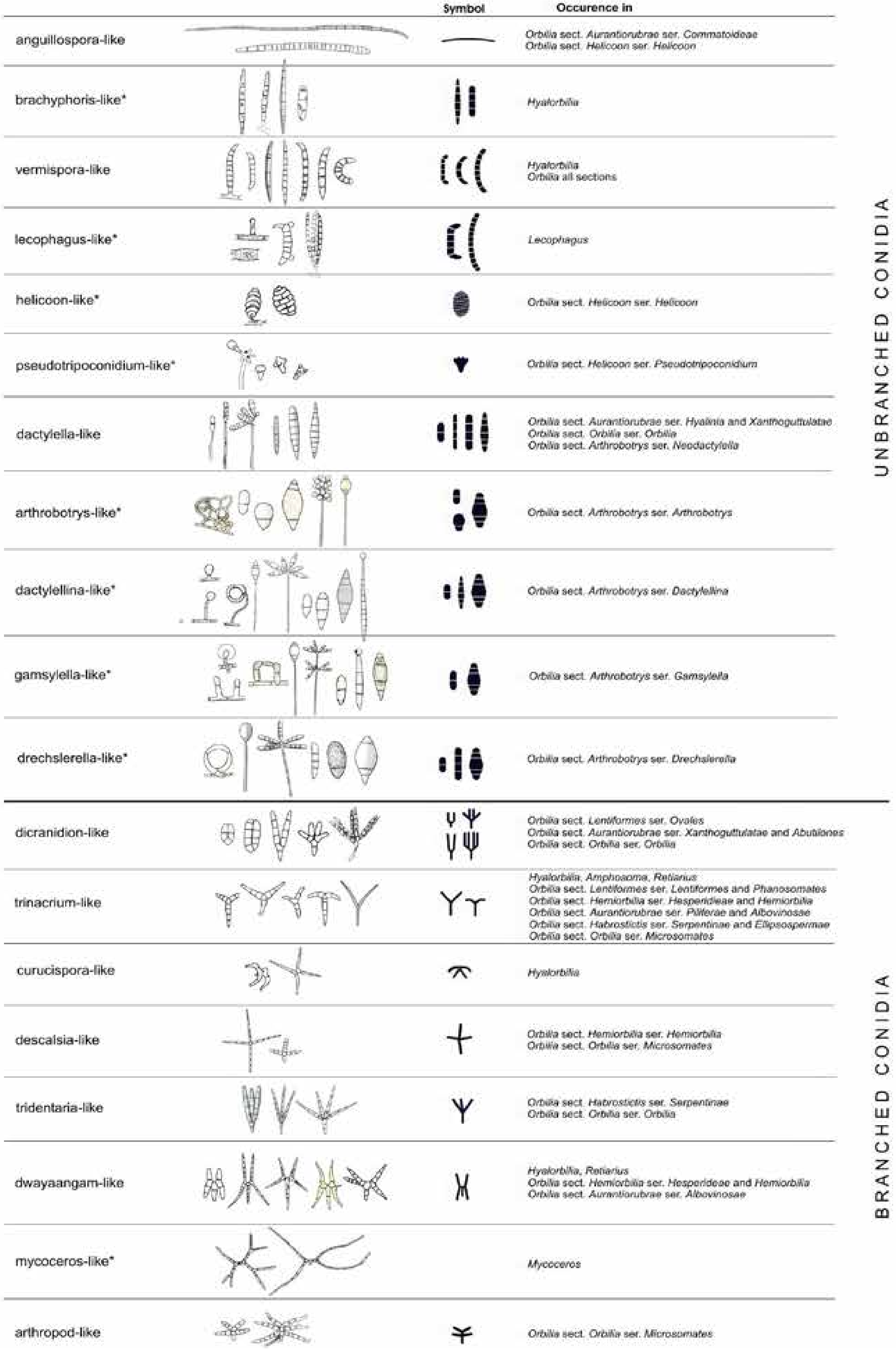
Five of the mentioned anamorph-typified genera (*Arthrobotrys*, *Dactylellina*, *Drechslerella*, *Gamsylella*, and *Lecophagus*) are characterized by the ability of every included species to prey by means of trapping organs on nematodes or other invertebrates such as rotifers, tardigrades, springtails, and copepods. Yet, also a species of *Tridentaria* and the type species of *Tripoconidium* and *Haptocara* are reported as nematophagous. Parasitism on eggs of nematodes, rotifers, or insects is known in some species referred to *Brachyphoris*, *Dwayaangam*, *Trinacrium*, and *Vermispora*. Rhizopods are captured by some species referred to *Brachyphoris*, *Dicranidion*, *Dwayaangam*, *Gamsylella*, *Trinacrium*, and *Tridentaria*. Parasitism on spores of oomycetes and zygomycetes is known in some species referred to *Brachyphoris*, *Dactylella*, *Tridentaria*, and *Vermispora*. Parasitism on pollen grains was reported for *Mycoceros* and *Retiarius*, a genus with conidia very similar to either *Dwayaangam* or *Trinacrium*. Apart from *Lecophagus*, which is named after its ability to trap rotifers by means of adhesive pegs, the etymology of most of these names of anamorphs refers to the morphology of conidia or conidiophores.

Classification. Phylogenetic studies by Liou & Tzean (1997), Ahrén et al. (1998), Scholler et al. (1999), Hagedorn & Scholler (1999), Li et al. (2005), and Yang & Liu (2006) using rDNA sequence data of predominantly nematophagous species revealed that within this group, assigned to section *Arthrobotrys* in the present monograph, trapping devices provide the main morphological criterion for a natural delimitation of phylogenetic groups. Scholler et al. (1999) obtained four well-separated clades, which differ among each other in their mode of trapping nematodes, but hardly so in conidial or conidiophore morphology. Thereupon they accepted four anamorph-typified genera and reassessed their circumscription: *Arthrobotrys* with adhesive networks, *Drechslerella* with constricting rings, *Dactylellina* with stalked adhesive knobs and non-constricting rings, and *Gamsylella* with adhesive columns, loops, bridges, and adhesive knobs which are predominantly unstalked. The large genus *Monacrosporium* is treated as a synonym of *Arthrobotrys* from their type species, while many members of both genera were reallocated, mainly to *Arthrobotrys*, *Dactylellina*, and *Drechslerella*. Moreover, the concept of *Dactylellina* and *Drechslerella* is strongly enlarged, each of which formerly containing only a single species. Li et al. (2005) and Yang & Liu (2006) did not accept *Gamsylella* as a separate genus, but assigned its members partly or altogether to *Dactylellina*. In this monograph we accept the concept of *Gamsylella* in a restricted sense.

In a similar way, Chen et al. (2007a–c) presented a new generic concept within the *Dactylella* complex, in which conspicuous organs of capture are unknown, based mainly on sequence data (ITS). The authors segregated three well-founded groups: *Dactylella* for anamorphs belonging to *Orbilia* in the present circumscription (with straight, rarely slightly curved conidia and predominantly long conidiophores), *Vermispora* without known teleomorph (with slightly curved conidia and short to long conidiophores), and *Brachyphoris* as anamorph of *Hyalorbilia* (with straight to slightly curved conidia and short conidiophores).

In most of the remaining anamorph-typified genera conspicuous trapping devices have so far likewise never

Table 42. Conidial types including conidiophores and trapping organs of *Orbiliomycetes* recognized in this monograph, with their symbols as used in Baral et al. (2017b). Only those types marked by an asterisk are used by us in a phylogenetic sense, whereas the others represent form genera. The conidial symbols shown here were included in some phylograms of our phylogenetic analyses.



		Symbol	Occurence in
UNBRANCHED CONIDIA	anguillospora-like		Orbilia sect. *Aurantiorubrae* ser. *Commatoideae* Orbilia sect. *Helicoon* ser. *Helicoon*
	brachyphoris-like*		*Hyalorbilia*
	vermispora-like		*Hyalorbilia* Orbilia all sections
	lecophagus-like*		*Lecophagus*
	helicoon-like*		Orbilia sect. *Helicoon* ser. *Helicoon*
	pseudotripoconidium-like*		Orbilia sect. *Helicoon* ser. *Pseudotripoconidium*
	dactylella-like		Orbilia sect. *Aurantiorubrae* ser. *Hyalinia* and *Xanthoguttulatae* Orbilia sect. Orbilia ser. Orbilia Orbilia sect. *Arthrobotrys* ser. *Neodactylella*
	arthrobotrys-like*		Orbilia sect. *Arthrobotrys* ser. *Arthrobotrys*
	dactylellina-like*		Orbilia sect. *Arthrobotrys* ser. *Dactylellina*
	gamsylella-like*		Orbilia sect. *Arthrobotrys* ser. *Gamsylella*
	drechslerella-like*		Orbilia sect. *Arthrobotrys* ser. *Drechslerella*
BRANCHED CONIDIA	dicranidion-like		Orbilia sect. *Lentiformes* ser. *Ovales* Orbilia sect. *Aurantiorubrae* ser. *Xanthoguttulatae* and *Abutilones* Orbilia sect. *Orbilia* ser. *Orbilia*
	trinacrium-like		*Hyalorbilia*, *Amphosoma*, *Retiarius* Orbilia sect. *Lentiformes* ser. *Lentiformes* and *Phanosomates* Orbilia sect. *Hemiorbilia* ser. *Hesperideae* and *Hemiorbilia* Orbilia sect. *Aurantiorubrae* ser. *Pilferae* and *Albovinosae* Orbilia sect. *Habrostictis* ser. *Serpentinae* and *Ellipsospermae* Orbilia sect. Orbilia ser. *Microsomates*
	curucispora-like		*Hyalorbilia*
	descalsia-like		Orbilia sect. *Hemiorbilia* ser. *Hemiorbilia* Orbilia sect. *Orbilia* ser. *Microsomates*
	tridentaria-like		Orbilia sect. *Habrostictis* ser. *Serpentinae* Orbilia sect. *Orbilia* ser. Orbilia
	dwayaangam-like		*Hyalorbilia*, *Retiarius* Orbilia sect. *Hemiorbilia* ser. *Hesperideae* and *Hemiorbilia* Orbilia sect. *Aurantiorubrae* ser. *Albovinosae*
	mycoceros-like*		*Mycoceros*
	arthropod-like		Orbilia sect. *Orbilia* ser. *Microsomates*

been observed. Our culture studies suggest that a majority of *Orbiliomycetes*, especially the desiccation-tolerant species, do not produce trapping organs in the presence of nematodes or rotifers. Some of the recognized, apparently non-predacious anamorph-typified genera are highly heterogeneous. For instance, a majority of *Anguillospora* species, including the type, are not connected to the *Orbiliomycetes*. The circumscription of these anamorph-typified genera is based merely on conidial morphology, e. g., in the case of branched conidia on the number and type of branching, or on the curvature of conidia and length of conidiophores when conidia are unbranched.

These more or less artificial genera are not even sharply differentiated from each other by their morphology. Their application is complicated by different kinds of variation which were quite frequently encountered during our study and also by other authors: generic limits may be obscured by (1) strong variability in conidial shape within a species, (2) frequent but inconsistent simultaneous occurrence of different conidial types within a single isolate, such as branched and unbranched conidia, or micro- and macroconidia, and (3) the existence of intermediate conidial types. For instance, straight and distinctly curved conidia, or Y-shaped (*Trinacrium*) and tunefork-shaped conidia (*Dicranidion*), do not represent clear-cut character states, but are connected by intermediate forms. Likewise, the number of arms in *Dicranidion* is often not consistent within a strain.

Our molecular phylogenetic analysis of *Orbiliomycetes* in Baral et al. (2017b) coincides to a large extent with the classification we have achieved from teleomorph morphology. Concerning the anamorphs, however, the analysis indicated that the different conidial types frequently show a scattered, polyphyletic distribution, i. e., they are often not significantly correlated with the mono- or paraphyletic clades which we here classify as subgenera, sections and series. Actually, very similar conidial types, e. g., referable to *Trinacrium*, occur scattered in rather distant infrageneric groups of *Orbilia*, and even in separate genera (*Hyalorbilia* and *Amphosoma*). Vice versa, different conidial types were found to belong to very closely related teleomorphs. For instance, vermispora- and trinacrium-like conidia occur in section *Lentiformes*, even within a species complex (*O. lentiformis*, *O. ocellata*) that shows hardly any differences in the teleomorph.

All these observations indicate the minor systematic value of morphology in most of the conidial types. With the new rules (ICN, Turland et al., 2018) the anamorph-typified genera lose their subordinate status concerning priority. Most of the anamorph-typified orbiliaceous genera are now to be treated as synonyms, mainly of the genus *Orbilia* which is older than all of them, or of a few anamorphic genera when applying a narrow generic concept. For practical reasons we continue to use anamorphic names, but in an informal, descriptive way with the suffix '-like', being aware that several of them represent polyphyletic form genera, which might reflect some ecological adaptation by convergent evolution rather than phylogenetic entities. For instance, the statement 'anamorph trinacrium-like' may either refer to triradiate conidia of series *Hemiorbilia*, to which the type of *Trinacrium* probably belongs, or to an anamorph with morphologically similar conidia but more or less distant position. This form of typography follows suggestions by Cannon & Kirk (2000) and Hawksworth (2011: 14), and makes clear that these designations are not scientific names governed by the Code. With this kind of approach, a given species may simultaneously produce two or three different anamorph-typified form genera within a single Petri dish, mainly regarding different types of conidial branching (see Tab. 42).

Only in some groups a striking morphological homogeneity in the anamorphs was noted. In two sections of *Orbilia* the included series show homogeneity with respect to either trapping organs (section *Arthrobotrys*) or conidial shape (section *Helicoon*). In *Lecophagus* the anamorph shows homogeneity in the trapping organs as well as conidial shape. The anamorph-typified genus *Brachyphoris* includes rather homogeneously shaped conidia which are always ± straight and unbranched, and comparatively short conidiophores. We accept it here in a phylogenetic sense restricted to the teleomorph-typified genus *Hyalorbilia*, to which it is a synonym. However, there is evidence that some species of *Hyalorbilia* form branched conidia, e. g., curucispora-like, dwayaangam-like or trinacrium-like ones, the latter strongly resembling in their curved arms conidia of *Amphosoma* and some species of *Orbilia*, apparently by convergent evolution.

The anamorph-typified genera

Anguillospora Ingold – (Pl. 1)

The genus was erected in 1942 for the single species *A. longissima* (Sacc. & P. Syd.) Ingold. It is characterized by filiform, multiseptate, hyaline conidia which resemble an eel (= *anguilla*). *Anguillospora* is heterogeneous in the present circumscription, because of different patterns of conidial secession (rhexolytic vs. schizolytic, i. e. with or without a separating cell that splits during secession) and teleomorphs belonging to different orders (Webster & Descals 1979, Descals et al. 1999, Belliveau & Bärlocher 2005, Baschien et al. 2006). Belliveau & Bärlocher (l.c.) support the polyphyletic origin of *Anguillospora* by sequence analyses of nSSU rDNA. The eight species included in their study were distributed among the classes *Dothideomycetes* (2), *Leotiomycetes* (5), and *Orbiliomycetes* (1). According to Belliveau & Bärlocher (l.c.) the genus includes ten generally accepted species and three poorly known taxa.

In the type species conidial secession is rhexolytic, whereas in most of the remaining species secession appears to be schizolytic. The rhexolytic conidial secession in *A. longissima* was observed by Ingold (1942), Willoughby & Archer (1973) and Webster & Descals (1979) in British strains, and by Baschien et al. (2006) in strains from an alpine stream in Germany. In the original description of the type collection from Belgium by De Wildeman (1894, as *Fusarium elongatum* De Wild., non *F. elongatum* Cooke) this feature is not visible, however, instead percurrent extensions growing from central cells of the detached conidia were drawn, which are reminiscent of those percurrent extensions at the conidial base as reported, e. g., in *A. rubescens* Gulis & Marvanová (*Dothideales*) and which appear to represent germ tubes. The latter species was classified by Gulis & Marvanová (1999) as schizolytic, and showed percurrent proliferations at the conidiogenous tips. But also Baschien et al. (2006) illustrated basal percurrent extensions in conidia of *A. longissima*.

The observation of proliferation by De Wildeman might tell that the type species of *Anguillospora* is not orbiliaceous. However, Baschien et al. (2006) and Descals et al. (1999) stated that also *A. rosea* shows percurrent proliferation, and L. Marvanová observed this feature in her isolates of *A. rosea*. Whether the current interpretation of *A. longissima* is correct we

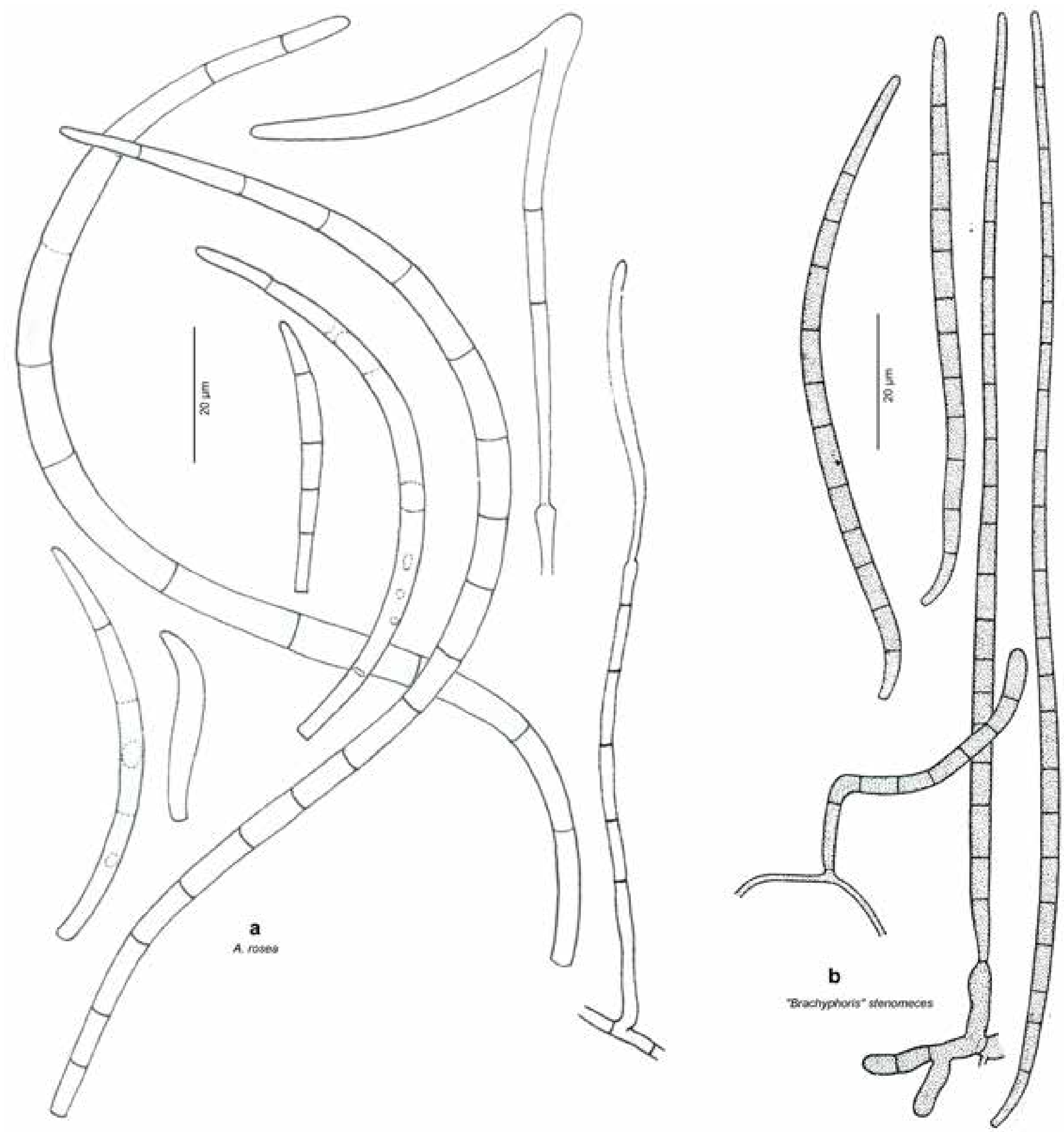


Plate 1. Two orbiliaceous species referable to the form genus *Anguillospora* (conidiophores and conidia). — **a**. from Descals et al. (1999), with microconidia; **b**. from Drechsler (1963). The scale of the two right elements of *A. rosea* was enlarged to 168 % of that given by Descals et al., because we believe that their fig. 4 has a wrong scale, the correct scale being that on their fig. 6.

cannot comment. Baschien et al. (2006) found great variability in conidial size and considered that *A. longissima* might be a species aggregate. Willoughby & Archer (1973) and Webster & Descals (1979) determined a connection of *A. longissima* to a teleomorph (as *Massarina* sp., *Massarinaceae*, *Pleosporales*). However, Baschien et al. (2006) believed that it could rather be a *Lophiostoma*. Morphological and molecular data supplied by Zhang et al. (2009a) indicate that *A. longissima* represents a fourth species of the genus *Amniculicola* Y. Zhang ter & K.D. Hyde, which was recently erected to accomodate three newly described species in the new family *Amniculicolaceae*, which is a segregate of *Lophiostomataceae*. Rossman et al. (2016) combined *A. longissima* in *Amniculicola* and suggested to change the type species of *Anguillospora*. That Zhang et al. (2009a) did not obtain conidia in their cultures of *Amniculicola* spp. can be explained by the fact that they did not submerge them in sterile water, a method found by Webster & Descals (1979) to be essential for conidial induction. Based on the similarity in the analysed gene regions and in the observed teleomorphs, a congruence between *Anguillospora* s.str. and *Amniculicola* seems highly probable.

Only for one species of *Anguillospora*, *A. rosea* Webster & Descals (Pl. 1: a), an *Orbilia* teleomorph was reported (Webster & Descals 1979, Descals & Chauvet 1992, Descals et al. 1999, as *Orbilia* sp.), apart from the unnamed anamorph of *O. yuanensis* (Qiao et al. 2015) with anguillospora-(to vermispora-) like conidia. Pfister (1997) connected *Anguillospora* sp. with an *Orbilia* which he tentatively identified as *O. luteorubella*. Descals et al. (1999) assumed that Pfister's *Anguillospora* is *A. rosea*, but they hesitated to link *O. luteorubella* to *A. rosea*, because Pfister did not provide a full description of the anamorph and none of the teleomorph. In both reports, much shorter, pauciseptate microconidia occur along with the macroconidia. The connection of *A. rosea* to the genus *Orbilia* is confirmed by Belliveau & Bärlocher (2005) by molecular analysis of a paratype strain from England. Molecular data are unavailable for two further species, *Dactylella stenomeces* Drechsler and *D. helminthodes* Drechsler, which were recently placed in *Brachyphoris* by Chen et al. (2007b) mainly because of their short conidiophores. However, especially *D. stenomeces* (Pl. 1: b) with its long and slender conidia might instead belong to *Orbilia* series *Helicoon* (section *Helicoon*) or to *O. caulicola* of series *Commatoideae* (section *Aurantiorubrae*, see also under *Brachyphoris*, p. 217–219).

Anguillospora-like species have mostly been sampled in aquatic environments. Pfister (1997) emphasized the similar conidial morphologies in *Anguillospora* as pointing to convergent evolution in aquatic or semiaquatic habitats.

In the present study we accept typification of *Anguillospora* as a member of *Dothideomycetes*. We obtained anguillospora-like anamorphs in pure culture only in a few species, particularly in those of series *Helicoon* (section *Helicoon*), including *A. rosea* which is confirmed to be the anamorph of an *Orbilia* of the *O. luteorubella* aggregate (*O. rosea*). Similar anamorphs with shorter, anguillospora- to vermispora-like phragmoconidia are found in *O. hoana* and *O. yuanensis*. Also in *O. caulicola* (section *Aurantiorubrae*) we obtained anguillospora-like conidia in pure culture.

In their short conidiophores these orbiliaceous anamorphs resemble those of *Vermispora* and *Brachyphoris*, which are, however, genetically quite distant from *Orbilia* and here included in *Hyalorbilia* (see p. 311).

Arthrobotrys Corda – (Pl. 2, Tab. S7)

The genus *Arthrobotrys* was erected in 1839 by Corda for the single species *A. superbus* Corda. Numerous investigators worked on the genus, e.g., Drechsler (1937a, 1944a), Haard (1968), Jarowaja (1970), Schenck et al. (1977), Van Oorschot (1985), and many others. For a long time, the main characteristics of the genus were the didymosporous conidia formed on swollen fertile nodes in roundish clusters, combined with the ability of trapping nematodes. The Greek suffix *botrys* describes these clusters, and the prefix *arthro* refers to the chain-like arrangement of the clusters along the very elongate conidiophore in the type species. However, Liou & Tzean (1997), Ahrén et al. (1998), Scholler et al. (1999), and Yang & Liu (2006) have shown by molecular phylogenetic methods that the morphology of the trapping devices provides more valuable key characters to circumscribe natural groups. Scholler et al.'s (l.c.) concept of *Arthrobotrys* is no longer restricted to 1-septate conidia, but includes non-septate and multiseptate forms, and conidia borne singly at the tip of long conidiophores. A number of species were found to produce microconidia (see p. 113). All of the included species trap nematodes by means of more or less 3-dimensional adhesive networks. Molecular data in GenBank are available for numerous *Arthrobotrys* species (see p. 1515, Phyls 28–31, Tab. S7).

According to Scholler et al. (l.c.), eight further generic names are synonyms of *Arthrobotrys* (see p. 1513). The reasons for their original erection were manifold: *Candelabrella* was proposed for species with pronounced denticles in a candelabrum-like terminal arrangement (candelabrelloid), *Didymozoophaga* because of two-celled conidia, *Duddingtonia* based on absent nodules, *Geniculifera* (= *Genicularia*) because of the geniculate conidiophore apex, *Monacrosporiella* and *Monacrosporium* based on conidiophores that produce a single acrogenous conidium, and *Nematophagus* and *Woroninula* because of conidiophores with nodules aggregated on ± swollen nodes (arthrobotryoid) and conidia with predominantly more than one septum. However, all these genera form adhesive networks in culture, and molecular data show that they cluster within the *Arthrobotrys* clade (no sequence was available for the type of *Nematophagus*, *N. azerbaijanicus*). Seifert et al. (2011) added the genus *Roigiella* as a ninth synonym of *Arthrobotrys* in the narrow sense. This is confirmed by comparison of an unpublished sequence of the type strain (CBS 222.85) of the type species *R. lignicola* which forms synnemata on wood. No trapping organs were reported in pure culture, probably because no nematodes were added.

Despite these results, some modern authors (e.g., Li et al. 2005, Su et al. 2005, Kim et al. 2006) retained *Monacrosporium* as circumscribed by Subramanian (1964), Liu & Zhang (1994), and Rubner (1996). This genus was separated from *Arthrobotrys* based on frequently broadly fusiform conidia with usually more than one septum and an inflated middle cell, which are formed only singly or in small groups at the tip of the conidiophore.

The following connections between anamorphs and teleomorphs have been reported in *Arthrobotrys* until now. In seven of them the morphologically hardly distinguishable teleomorph is the collective species *O. auricolor*: *A. cladodes* var. *cladodes* (Liu 2006), *A. cladodes var. macroides* (Pfister & Liftik 1995), *A. oligosporus* var. *oligosporus* (Pfister & Liftik 1995, Liu 2006); *A. elegans* (Rubner 1996, as *Monacrosporium psychrophilum*); *A. javanicus* (Liu 2006); *A. multiformis* (Mo et al. 2005a, as *A. yunnanensis*); *A. superbus* (Pfister 1994, as *O. fimicola*). Li et al. (2009) reported *A. nonseptatus* as anamorph for an unidentified *Orbilia* with subglobose ascospores and Qiao et al. (2012) connected *A. vermicola* to *O. blumenaviensis*.

Within the *O. auricolor* complex, problems exist in morphological delimitation between *A. oligosporus*, *A. superbus*, and *A. cladodes* (see under *O. auricolor*, p. 1531), or between *A. psychrophilus* and *A. oudemansii* (see under *O. elegans*, p. 1554). Shenoy et al. (2007) suggested significant phenotypic variation within a species caused by external factors as one reason for these problems. The authors also imagined that one teleomorph (*O. auricolor*) may produce several different anamorphs at a time by occurring in all possible combinations. This idea is contradicted by the absence of, e.g., any isolate that produced both *A. oligosporus* and *A. psychrophilus* anamorphs. Today's available molecular data suggest a high phylogenetic diversity within the *O. auricolor* complex and the existence of a number of different species.

Arthrobotrys species live in moist habitats, in soil, on decaying plant material, or on dung. They are capable of capturing nematodes, and show a worldwide distribution. Because of the large number of publications and described taxa concerning *Arthrobotrys* (Scholler et al. 1999 accepted 46 species) we refrain here from a detailed listing (but see Tab. S7).

In the present study, the genus *Arthrobotrys* was reduced to a section and series of *Orbilia*. Besides the above-mentioned connections between anamorphs and teleomorphs we here add the new species *O. menageshae* with a known anamorph. With regard to the rather high number of known *Arthrobotrys* species we expect for the future a distinct increase of newly reported

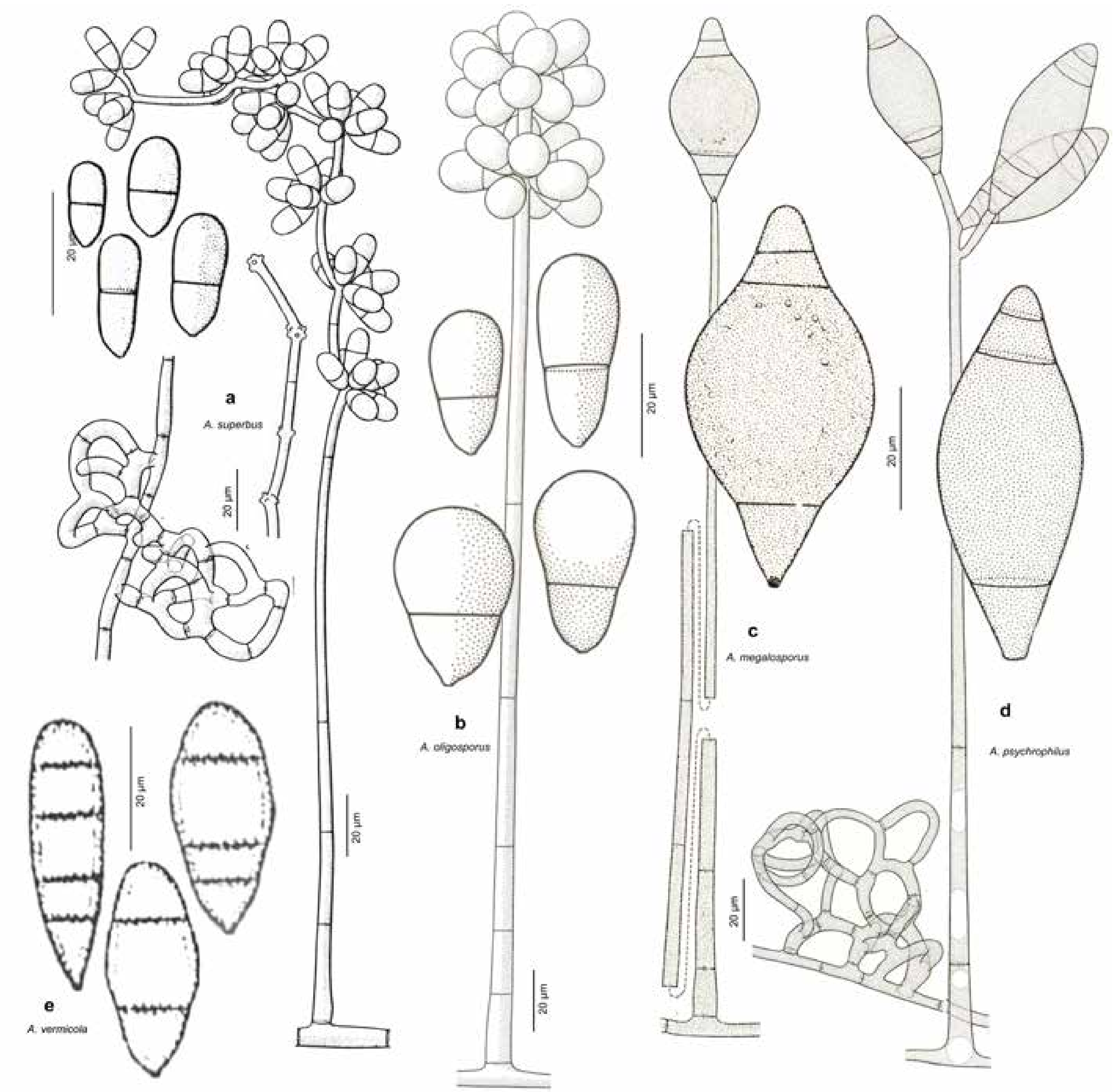


Plate 2. Some selected species of *Arthrobotrys* (conidiophores, conidia, and adhesive networks). — **a–b**. from Drechsler (1937a), **c**. from Drechsler (1954), **d**. from Drechsler (1944a), **e**. from Cooke & Satchuthananthavale (1965).

connections. The teleomorphs are often nearly identical or without striking morphological differences, e.g., between *O. auricolor*, *O. elegans*, and *O. oligospora*. Species distinction without the anamorph or genetical data is, therefore, impossible. But even cryptic species appear to exist, therefore, it could not be clarified which *Arthrobotrys* species belongs to *O. auricolor* in its original sense.

Brachyphoris Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu – (Tab. 43, Pl. 3)

In a phylogenetic analysis of 37 dactylella-like isolates, Chen et al. (2007a: fig. 1) obtained three distinct groups which were morphologically supported to some extent: the largest clade (*Dactylella* s.str.) comprised most of the species previously assigned to *Dactylella*, with the exception of *D. oviparasitica*, *D. brevistipitata*, *D. tenuifusaria*, and *D. spermatophaga*. Whereas *D. spermatophaga* formed a distinct clade with the newly described *Vermispora fusarina* and *V. leguminacea* (see p. 246, under *Vermispora*), the other three *Dactylella* species formed a third group. For this group the authors described the genus *Brachyphoris* (with *B. oviparasitica* as type species), with the following main characteristics (Chen et al. 2007c): conidiophores simple or occasionally branched, very short or at least distinctly shorter than conidia, producing mostly a single conidium at the tip, conidia spindle-shaped, filiform or elongate-fusoid, straight or slightly curved [3–22-septate]. The name *Brachyphoris* refers to the short conidiophores. Chen et al. distinguished *Vermispora* from *Brachyphoris* by often somewhat curved conidia formed on sympodially proliferating conidiophores. Based on morphological similarities of conidiophores and conidia it cannot be excluded that the genus *Paradactylella* Matsush. represents an earlier synonym of

Table 43. Overview of the accepted species of *Brachyphoris* (*B. stenomeces* is also treated under *Anguillospora*).

Species	Conidial size (in µm)	Number of septa	Spore shape	Habitat	References
‘*Dactylella*’ *lignatilis* M.H. Mo & K.Q. Zhang (≡ *Hyalorbilia lignatilis*)	25–51 × 2.5–6.3	(1–)3–4(–6)	fusiform to cylindrical	on decayed *Pinus* twig, China	Mo et al. 2005b
B. brevistipitata (Bin Liu et al.) Juan Chen et al. (≡ *Hyalorbilia brevistipitata*)	23–52 × 3–4	3–5	narrowly fusoid	on decaying twigs of broad-leaved tree, China	Liu et al 2005, Chen et al. 2007c
B. oviparasitica (G.R. Stirling & Mankau) Juan Chen et al. **Type species** (≡ *Hyalorbilia oviparasitica*)	31–65 × 2.7–5	4–7	fusiform	from roots of *Prunus persica*, USA, parasitic on eggs of *Meloidogyne* sp.	Stirling & Mankau 1978, Chen et al. 2007a, c
B. helminthodes (Drechsler) Juan Chen et al.	53–84 × 2.8–3.7	7(–8)	elongate fusiform	leaf mould, USA, parasitic on *Pythium* oospores and *Cochlonema* zygospores	Drechsler 1952, Chen et al. 2007b
‘*Dactylella*’ *passalopaga* Drechsler	60–80 × 4.5–6	6–8	elongate fusiform	in decaying plant roots, in soil, and leaf mould, capturing rhizopods, *Pythium* oospores, USA, Japan	Drechsler 1936, Morikawa & Saikawa 1992, Barron 2008
B. tenuifusaria (Xing Z. Liu et al.) Juan Chen et al. (≡ *Hyalorbilia tenuifusaria*)	88–120 × 4–6	9–14	elongate-fusoid	soil, rhizopod-capturing, China	Liu et al. 1996, Chen et al. 2007c
[*B. stenomeces* (Drechsler) Juan Chen et al.]	55–170 × 2.5–3.2	8–22	filiform	on decaying leaves, USA, parasitic on *Pythium* oospores	Drechsler 1963, Chen et al. 2007b

Brachyphoris (but see p. 220, under *Dactylella*).

In Chen et al.’s circumscription, *Brachyphoris* contains five species, all of which were previously included in the genus *Dactylella*. Liu et al. (2005) described *D. brevistipitata* as anamorph of *Hyalorbilia brevistipitata*, therefore, *Hyalorbilia* was regarded by Chen et al. to be the teleomorph of *Brachyphoris*. In the same year, Mo et al. (2005b) described as anamorph of a *Hyalorbilia* sp. the similar *D. lignatilis*, which is obviously also brachyphoris-like (see under *H. lignatilis*, p. 359). Sequence data are lacking in two species with medium to very long, vermiform, multiseptate conidia, *B. helminthodes* and *B. stenomeces*. Chen et al. assigned them to *Brachyphoris* obviously because of the short conidiophores and parasitic habit, although the morphology of conidia and conidiophores, especially in *B. stenomeces*, resembles also the anamorph of species of series *Helicoon* or *Commatoideae* of the genus *Orbilia*, to which they might instead belong. *B. stenomeces* is, therefore, figured on the *Anguillospora* plate. Possibly, further species listed at present in *Dactylella* are anamorphs of *Hyalorbilia*. Potential candidates would be the four species with short to medium long conidiophores which parasitize *Pythium* oospores: *D. arrhenopa*, *D. polyctona*, *D. anisomeres*, and *D. stenocrepis*. In the conidia of the former three species as figured by Drechsler (1943, 1952, 1963) one can discern small globose/cubical bodies which would be typical of *Brachyphoris*.

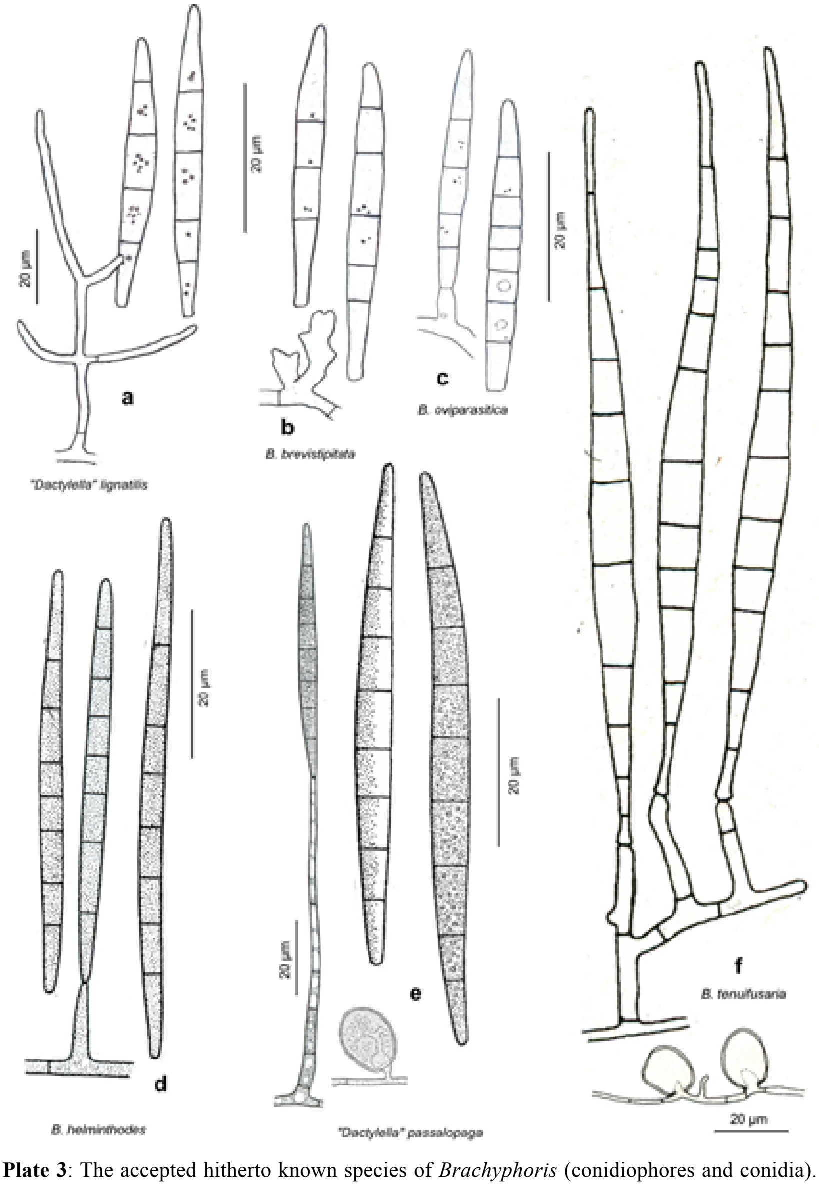


Plate 3: The accepted hitherto known species of *Brachyphoris* (conidiophores and conidia). — **a**. from Mo et al. (2005b), **b**. from Liu et al. (2005b), **c**. from Chen et al. (2007c), **d**. from Drechsler (1952), **e**. from Drechsler (1936), **f**. from Liu et al. (1996); **e** and **f** with captured rhizopods on adhesive pegs.

When isolating DNA from wood, litter and soil, Smith & Jaffee (2009) found in their phylogenetic analysis of the 28S rDNA eleven unidentified *Brachyphoris* species which formed a monophyletic group with *B. oviparasitica*. The employed method did not include pure cultures, therefore, morphological features are unknown for all these DNA isolates, and only two of the sequences were similar enough to existing sequences in order to give them specific names (see under *Hyalorbilia*, p. 317).

Brachyphoris species live in moist but also xeric habitats on decaying plant material, and are known from Asia, Europe and North Amer-

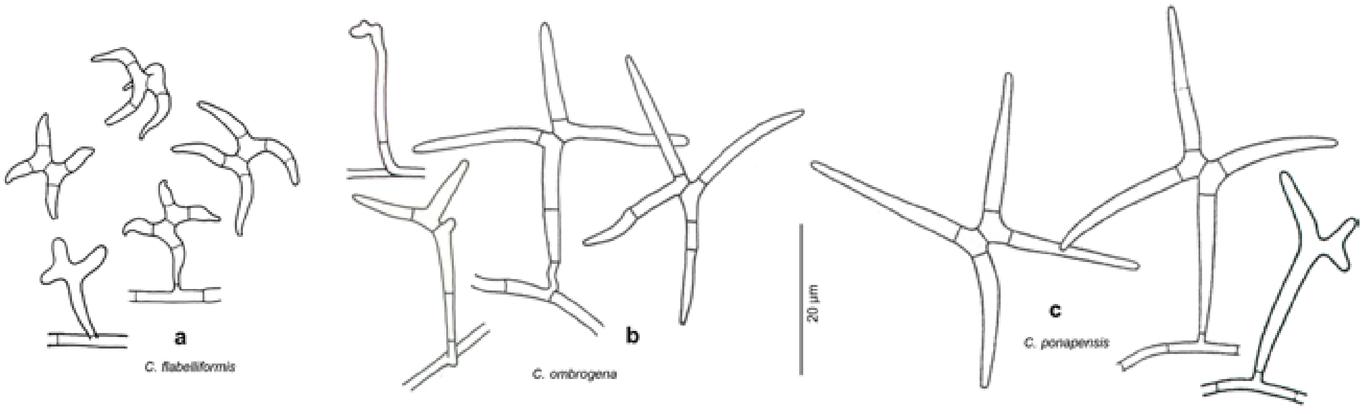


Plate 4. The accepted, hitherto known species of the form genus *Curucispora* (conidiophores and conidia). — **a**. from Ando (1993), **b**. from Ando & Tubaki (1984a), **c**. from Matsushima (1981).

ica. Some are capable of invading nematode eggs or cysts, '*D.*' *passalpoaga* forms adhesive knobs that capture rhizopods, and *B. helminthodes* and *B. stenomeces* are parasites on spores of oomycetes and zygomycetes.

In the present study, the term brachyphoris-like is exclusively used for anamorphs of *Hyalorbilia*. *Brachyphoris* and also *Vermispora* are synonymised with *Hyalorbilia* (but note that we use 'vermispora-like' for morphologically similar anamorphs in *Orbilia*). In addition to the known connections in *H. brevistipitata* and '*D.*' *lignatilis*, brachyphoris-like anamorphs are reported by us from cultures of four species: *H. fagi*, *H. inflatula*, *H. polypori*, and *H. tortuosa*. In contrast to those taxa included by Chen et al. (2007a–c), the conidiophores in these anamorphs sometimes attained a length of over 100 µm. Because of morphological similarities of the conidia, *D. passalopaga* is considered by us to belong to *Hyalorbilia*, possibly to *H. inflatula* (see p. 349). No sequence data are available for this brachyphoris-like anamorphic species, but the striking similarity of the conidia and the capacity to capture rhizopods as reported by Drechsler (1936) and Barron (2008) leave no doubt about its relationship with *Hyalorbilia*. We observed in *Hyalorbilia* also trinacrium-like (*H. erythrostigma*, *H. orbiliicola*) and curucispora-like (K-shaped) conidia (*H. subfusispora*, *H. latispora*) as hitherto undescribed anamorphs. A dwayaangam-like anamorph, *D. quadridens*, was combined in *Hyalorbilia* by Baral et al. (2017b).

A conspicuous small organelle of the living conidia was seen in several species and appears to be characteristic of the genus. It is referred here to as cubical body, because it resembles those more or less cubical bodies seen in *Lecophagus*, although the light microscope does not permit to decide whether it is globose or angular (see p. 94–95). This refractive organelle is also clearly visible on Barron's (2008) photos of *D. passalopaga* (see Pl. 59: a).

Curucispora Matsush. – (Tab. 44, Pl. 4)

Matsushima (1981) erected the genus for one species, *C. ponapensis*. Ando & Tubaki (1984a) described *C. ombrogena*, and Ando (1993) *C. flabelliformis*. The main characteristics of the genus are the tetraradiate, ┼-shaped conidia, to which the generic name refers which derives from the Latin *crux*. The conidia consist of three arms and a similarly shaped stipe, and develop from short denticles on intercalary conidiogenous cells. A teleomorph has not been reported so far, and molecular data are not available.

There is some confusion about the generic name *Curucispora*. Matsushima (1993) changed it to *Crucispora*, whereas Ando (1993) believed that the linguistically wrong but legitimate original spelling *Curucispora* must be retained. Because *Crucispora* Horak antedates this genus, Matsushima (2005: 145) proposed the new name *Cruciconidiifera* for it, obviously as he considered the original spelling *Curucispora* to be an 'orthographic' or 'typewriting error'. We follow Ando (l.c.) in maintaining the name *Curucispora*, because Matsushima did not change the original spelling in a corrigendum of the 1981 volume, and because the correction proposed in 1993 affects the first syllable of the generic name (Art. 60.3 ICN).

The three conidial arms do not emerge from one point because the conidium develops by dichotomous branching, thereby one of the two arms very early undergoes a second branching. Indeed, the three arms are formed almost simultaneously, as can be seen from the sketches by Matsushima (1981, see Pl. 4: c right), Ando & Tubaki (1984a, Pl. 4: b left), and Ando (1993, Pl. 4: a, lower left). Matsushima believed that in *C. ponapensis* one arm belongs to the main axis, and later the two other arms emerge from the centre of the main axis like a 'V'. However, an initial stage with a main axis without branches is only seen on his schematic sketch (Matsushima 1981: fig. 62). Ando & Tubaki believed that in *C. ombrogena* one arm is a later lateral outgrowth below the 'V', but their fig. 5A (Pl. 4: b, upper left)

Table 44. Overview of the accepted hitherto known species of the form genus *Curucispora* (*data evaluated from illustration).

Species	Conidial total size (in µm)	Arm width (in µm)	Habitat	Reference
C. flabelliformis K. Ando	15–20 × 13–18.5*	1.5–2	on fallen leaves of *Livistona chinensis*, Japan	Ando 1993
C. ombrogena K. Ando & Tubaki	~27–35 × 25–35 µm	1.3–2*	in rainwater from *Phyllostachys bambusoides*, Japan	Ando & Tubaki 1984a
C. ponapensis Matsush. **Type species**	~35–50 × 35–50 µm	2–2.5(–3)	decaying petioles of *Cocos nucifera*, Ponape, Caroline Islands, Micronesia	Matsushima 1981

shows that initial stages of all three arms may very early be present as small protuberances.

Similar tetraradiate conidia occur in *Descalsia* and *Tridentaria* (see there), and in *Arborispora paupera* Marvanová & Bärlocher (1989). In *Arborispora* the lateral arms insert in the middle of the main axis and are always very strongly constricted at their base, and sometimes a third arm emerges from another cell of the main axis or from one of the primary branches. The basidiomycetous anamorph-typified genus *Cruciger* Kirschner & Oberwinkler (1999) has similar but non-septate conidia, and conidiophores with clamps.

Species of *Curucispora* were isolated from decaying palm leaves, bark and leaves of broad-leaved trees, or from rainwater draining from the tree canopy. Collections are from eastern Asia, Micronesia, South America (Matsushima 1993), and Europe (Gönczöl & Révay 2006).

In the present study, *Curucispora* is treated as a possible synonym of *Hyalorbilia*, because we observed curucispora-like conidia in two *Hyalorbilia* species: *C. ponapensis* is reminiscent of the presumed anamorph of *H. subfusispora*, and *C. flabelliformis* strongly resembles the anamorph of *H. latispora*.

Dactylella Grove – (Tab. 45, Pls 5–6, see also Tab. S8)

The generic name was derived from *Dactylium candidum* Nees, a species characterized by 3–4 conidia at the conidiophore apex, resembling fingers (Greek *daktylo*) of a hand. In contrast to this, the monotypic genus *Dactylella* (Grove 1884), based on *D. minuta*, was described as forming always only a single terminal conidium (Pl. 6: e). *Dactylium* Nees is a nomen utique rejiciendum (ICN: appendix V) following a proposal by Gams & Rubner (1997), who argued that the type species *D. candidum* was a nomen dubium and an earlier synonym of the widely used *Monacrosporium* (an interpretation of *D. candidum* by Drechsler 1937a concerns *Dactylellina haptotyla*). The circumscription of *Dactylella* was emended several times by different authors (e. g., Subramanian 1964, Van Oorschot 1985, Zhang et al. 1995, Rubner 1996, Chen et al. 2007b). The main characteristics are: conidiophores ± long, sometimes branched, conidia clavate, ellipsoid or fusiform, straight, produced singly at the apex of conidiophores or on short branches.

Zhang et al. (1995) included 34 species in *Dactylella*, part of which are predacious (nematophagous). Rubner (1996: 105) provided a checklist of epithets used in *Dactylella*. She excluded all nematophagous species and transferred them to *Monacrosporium*, because *D. minuta* is most probably not capable of capturing nematodes. Based on molecular and morphological analyses, Chen et al. (2007a, b) found that *Dactylella* is a phylogenetically heterogeneous group. The authors accepted 28 species in *Dactylella* (s.str.) which are saprobic, though sometimes capable of invading oospores or nematode eggs, whereas they transferred six species with short conidiophores to the genera *Brachyphoris* (five spp.) and *Vermispora* (*V. spermatophaga*). The monotypic genera *Drechsleromyces* and *Gangliophragma*, which Subramanian (1978) separated from *Dactylella* because of sympodially proliferating conidiophores, were considered to be synonyms of *Dactylella* by Zhang et al. (1995) and Chen et al. (2007b). According to Seifert et al. (2011), the genus *Paradactylella* Matsush. (1993) is a synonym of *Dactylella*. The shortness of the conidiophores would rather point to *Brachyphoris*, for which *Paradactylella* could provide an earlier name. However, in our opinion, on the original drawing of *P. peruviana* and on the drawing in Seifert et al. conidial secession seems to be rhexolytic, a feature which we have never observed in any of the orbiliaceous anamorphs reported here, so at present we hesitate to accept placement of *Paradactylella* in the *Orbiliomycetes*. An overview of ca. 30 *Dactylella* species accepted by us is given in Tab. 45 and Pls 5–6, see also Tab. S8. Yet, it cannot be excluded, that some of these species are anamorphs of *Hyalorbilia* (see above, under *Brachyphoris*).

D. zhongdianensis was described by Zhang et al. (2005) as a predacious fungus that forms three-dimensional adhesive networks. Chen et al (2007b), however, found this species unable of producing organs of capture when nematodes were added. This was supported by their neighbour-joining analysis (Chen et al. 2007a), in which the species clustered near *D. rhopalota* in the *Dactylella* clade. For the dubious *D. rhombica* Matsush. (1971) no type material was available (see Rubner 1996); the large fusiform conidia [50–70 × 14–20 µm, (5–)6(–8)-septate], with enlarged middle cell rather point to *Dactylellina*.

Some authors relied after 1999 on the traditional generic concept based on conidial morphology and placed new species with cylindric-clavate to fusoid, phragmosporous conidia and three-dimensional adhesive networks in the genus *Dactylella*. For instance, *D. shizishanana* (Liu & Zhang 2003) and *D. pseudoclavata* (Miao et al. 2003) belong to *Arthrobotrys*, where they were transferred by Chen et al. (2007b), and also *D. crassa* Miao et al. (1999) would better be placed in *Arthrobotrys.* The recently described South African *D. bolusanthi* (Crous 2019) with rather short conidiophores is not included in the plates.

Dactylella is reported several times as anamorph of *Orbilia* (see also Tab. 41): Thakur & Zachariah (1989) obtained apothecia of '*Orbilia* sp.' (possibly *O. cardui*) from a culture identified as *D. rhopalota* (see p. 1472). Pfister (1997) figured a *Dactylella* sp. obtained from an ascospore isolate of *O. dryadum* (as *O.* ?*alnea*). Yang & Liu (2005) described *D. coccinella* as anamorph of a teleomorph with unknown morphology but identified as '*O. coccinella*'. However, this anamorph is very different from *Dicranidion fragile*, the anamorph of *O. eucalypti* (= *O. coccinella* s.auct.). It agrees to Pfister's anamorph of *O. dryadum*, although the ITS-sequences are quite different (see p. 1389). Webster et al. (1998) reported *D.* (cf.) *oxyspora*, an isolate identified as *D. atractoides* by Zhang et al. (2011a), in pure culture of *O. fimicoloides* (= *O. oxyspora*). A report of *D. lignatilis* as anamorph of a *Hyalorbilia* sp. by Mo et al. (2005b) refers to a species of *Brachyphoris* (= *Hyalorbilia*, see p. 359), that of *D. dorsalis* as anamorph of *O. dorsalis* by Yu et al. (2007) is difficult to distinguish from *O. oxyspora* (see p. 1500), that of *D. alba* as anamorph of *O. alba* by Yu et al. (2009a) is referred here to *Gamsylella* (see p. 1615), and that of *D. pseudobrevistipitata* as anamorph of *Orbilia* sp. by Qin et al. (2011) is combined in *O. pseudobrevistipitata* by Zhang et al. (2015) (see p. 864). *O. tianmushanensis* with a dactylella-like anamorph was reported by Zhang et al. (2016). Zhang et al. (ined.) reported us two further species with dactylella-like anamorphs, *O. longquanensis* and *O. dehongensis* nom. prov.

Species of *Dactylella* probably have a worldwide distribution. They were isolated at wet habitats from decaying plant material and soil, and were found to be sometimes parasitic on oospores of oomycetes and eggs of nematodes, one also on rhizopods.

In the present study, dactylella-like anamorphs were mainly found in series *Neodactylella* of section *Arthrobotrys*, but also in series *Hyalinia* and *Xanthoguttulatae* (section *Aurantiorubrae*),

Table 45. Overview of the accepted species of the form genus *Dactylella* (nematophagous species and species with coloured conidia or conidiophores, or phialidic conidiogenesis are excluded; see also Rubner 1996: 105f. and Chen et al. 2007b); * = values corrected according to scale (published as 13.3–39 × 3.5–5.6 µm); ** = values corrected acccording to Z.F. Yu (pers. comm., published erroneously as 22–30.3 × 3.3–4 µm).

Species	Conidial size [µm]	Number of septa	Conidial shape	Habitat	Reference
D. polyctona (Drechsler) K.Q. Zhang et al.	12.7–21 × 2.3–2.8	1	clavate to ellipsoidal	on leaf mould, USA, parasitizing *Pythium* oospores, rhizopods, cysts of myxobacteria	Drechsler 1952
D. arrhenopa (Drechsler) K.Q. Zhang et al.	17–25 × 2.6–3.7	1	clavate to ellipsoid	in soil of a wood, USA, parasitc on *Pythium* oospores	Drechsler 1943a
D. tenuis Drechsler	25–41 × 6.3–8.2	(1–)3(–4)	cylindrical	on leaf mould in deciduous woods, USA, parasitic on *Pythium* oospores	Drechsler 1937a,
D. clavispora Juan Chen et al. (≡ *Orbilia clavispora*)	18–32.5 × 7.5–11	1–3	clavate or cylindrical to ellipsoid	living leaf of *Betula*, U.K.	Chen et al. 2007b
D. coccinella Y. Yang & Xing Z. Liu (Pfister as *Dactylella* sp.)	22.5–32.5 × 5–6.5	1–7	cylindrical	?	Yang & Liu 2005 Chen et al. 2007b
D. zhongdianensis J. Zhang & K.Q. Zhang (= *Orbilia zhongdianensis*)	17.5–37.5 × 5–8	(2–)3(–6)	cylindrical to clavate	soil, China	Zhang et al. 2005, Chen et al. 2007b
D. vermiformis Z.F. Yu et al. (≡ *Orbilia vermiformis*)	20–36.8 × 5.8–8.1	(0–)1	clavate	on rotten root of angiosperm tree, China	Yu et al. (2007a)
D. pseudobrevistipitata L. Qin et al.(≡ *Orbilia pseudobrevistipitata*)	18–39 × 3.8–6.7*	1–5	cylindrical	from bark of angiosperm tree, China	Qin et al. 2011
D. anisomeres Drechsler	20–43 × 3.5–4.5	(1–)3(–5)	± cylindrical	leaf mould, USA, parasitic on *Pythium* oospores	Drechsler 1962
D. cylindrospora (R.C. Cooke) A. Rubner	22.5–45 × 6.5–8.5	1–4	obconical to clavate to cylindrical	in soil, Western Samoa	Cooke 1969, Rubner 1996, Chen et al. 2007b
D. pulchra (Linder) de Hoog & Oorschot	(27–)34–45 × (7–)9–11	5–7	clavate to slightly fusiform	flower pots, from greenhouse lettuce seedlings, USA	Linder 1934, De Hoog & Van Oorschot 1985, Chen et al. 2007b
D. stenocrepis Drechsler	29–46 × 4.6–7.8	mainly 3	fusiform	decaying plant material, USA, parasitic on *Pythium* oospores	Drechsler 1962
D. heptameres Drechsler	29–52 × 8–10.8	3–7	mostly fusiform	on leaf mould, USA	Drechsler 1943b Chen et al. 2007b
D. ramosa Matsush.	32–54 × 4.2–6	3–9	cylindrical to clavate	on decaying *Ficus* leaf, Micronesia	Matsushima 1971, Chen et al. 2007b
D. xinjiangensis Juan Chen et al.(≡ *Orbilia xinjiangensis*)	39.5–54 × 7–12	4–7	clavate	soil, China	Chen et al. 2007b
D. clavata R.H. Gao et al.	20–64 × (4–)6–8	(1–)3–7	clavate	from soil, China	Gao et al. 1995, Chen et al. 2007b
D. strobilodes Drechsler	30–60 × 11–18	1–9	elongate ellipsoidal	on leaf mould in deciduous woods, USA	Drechsler 1950b
D. rhopalota Drechsler (≡ *Orbilia rhopalota*)	36–60 × 6.7–9.6	3–10	mostly clavate to cylindrical	on leaf mould, USA; decaying wood and leaf litter, Europe	Drechsler 1943b, Chen et al. 2007b
D. submersa (Ingold) Sv. Nilsson	35–65 × 6–9	1–6	cylindrical to clavate	decaying *Quercus* leaves in water, UK	Ingold 1944
D. nuorilangana X.F.Liu & K.Q.Zhang (= *Orbilia rectispora*)	42–62 × 4.5–7.5	1–7	cylindric (-fusoid)	from soil, China	Zhang & Mo 2006
[*D. rhombospora* Grove] *D. rhombospora* s.auct. (?= *O. dorsalis*)	[~52–70 × 14.5–19] 40–71 × 8.5–13	[7] 5–10	fusiform	[wood & bark], leaf litter, [U.K.], USA, Macaronesia	[Grove 1885], Drechsler 1937a, Chen et al. 2007b
D. minuta Grove **Type species**	60–70 × 14–15	6–8	clavate	on dead wood, England	Grove 1884 (Rubner 1996, Chen et al. 2007b)
D. attenuata R.H. Gao et al.	42–62 × 3–4	4–9	elongate-fusoid to cylindrical	in rainforest soil, China	Gao et al. 1997, Chen et al. 2007b
D. dorsalis Y. Zhang et al. (≡ *Orbilia dorsalis*)	51.8–75.5 × 7.8–12.3**	5–9	elongate fusoid	on dead bark, China	Yu et al. 2007b
D. atractoides Drechsler (= *D. oxyspora* fide Chen et al. 2007b)	26–76 × 7.2–10.2	3–13	mostly fusiform	decaying leaves of *Solanum lycopersicum*, USA	Drechsler 1943b
D. chichisimensis Ts. Watan.	20–78 × 5–8	3–9	clavate, cylindrical, or ellipsoid	from forest soil, Japan	Watanabe et al. 2001
D. bolusanthi Crous	42–75 × 5–6	5–11	elongate fusoid	leaf litter of *Bolusanthus speciosus*, South Africa	Crous 2019
D. intermedia T.F. Li et al.	40.5–82 × 8–13	5–8	fusiform	soil, litter of *Ziziphus spina-christi* and *Ficus religiosa*, China	Li et al. 1998, Chen et al. 2007b
D. panlongana X.F. Liu & K.Q. Zhang (Chen et al. as '*panlongna*')	42.5–97.5 × 4.5–8	3–12	oblong fusiform to cylindrical	soil, China	Zhang & Mo 2006, Chen et al. 2007b
D. oxyspora (Sacc. & Marchal) Matsush.	60–105 × 9–13	6–12	± elongate fusoid	dung, soil and plant debris, Germany, Netherlands, Tenerife, Ecuador, USA	Marchal 1885, Rubner 1996, Chen et al.2007b
= *D. arnaudii* Yadav (≡ *Orbilia oxyspora*)	29.5–92 × 3.3–9.9	3–12	fusiform, (partly rostrate)	on decaying stems of *Heracleum sphondylium*, U.K.	Yadav 1960, Chen et al. 2007b
D. yunnanensis K.Q. Zhang, Xing Z. Liu & L. Cao (= ?*D. oxyspora*)	66.5–106 × 8.5–13.5	7–10	elongate fusoid, somewhat rostrate	from forest soil, China	Zhang et al. 1995, Chen et al. 2007b
D. qiluensis H.Y. Su & M.H. Mo	89–143 × 8.7–11.2	5–9	elongate fusoid, rostrate	from waterlogged soil from a lake, China	Su et al. 2011a

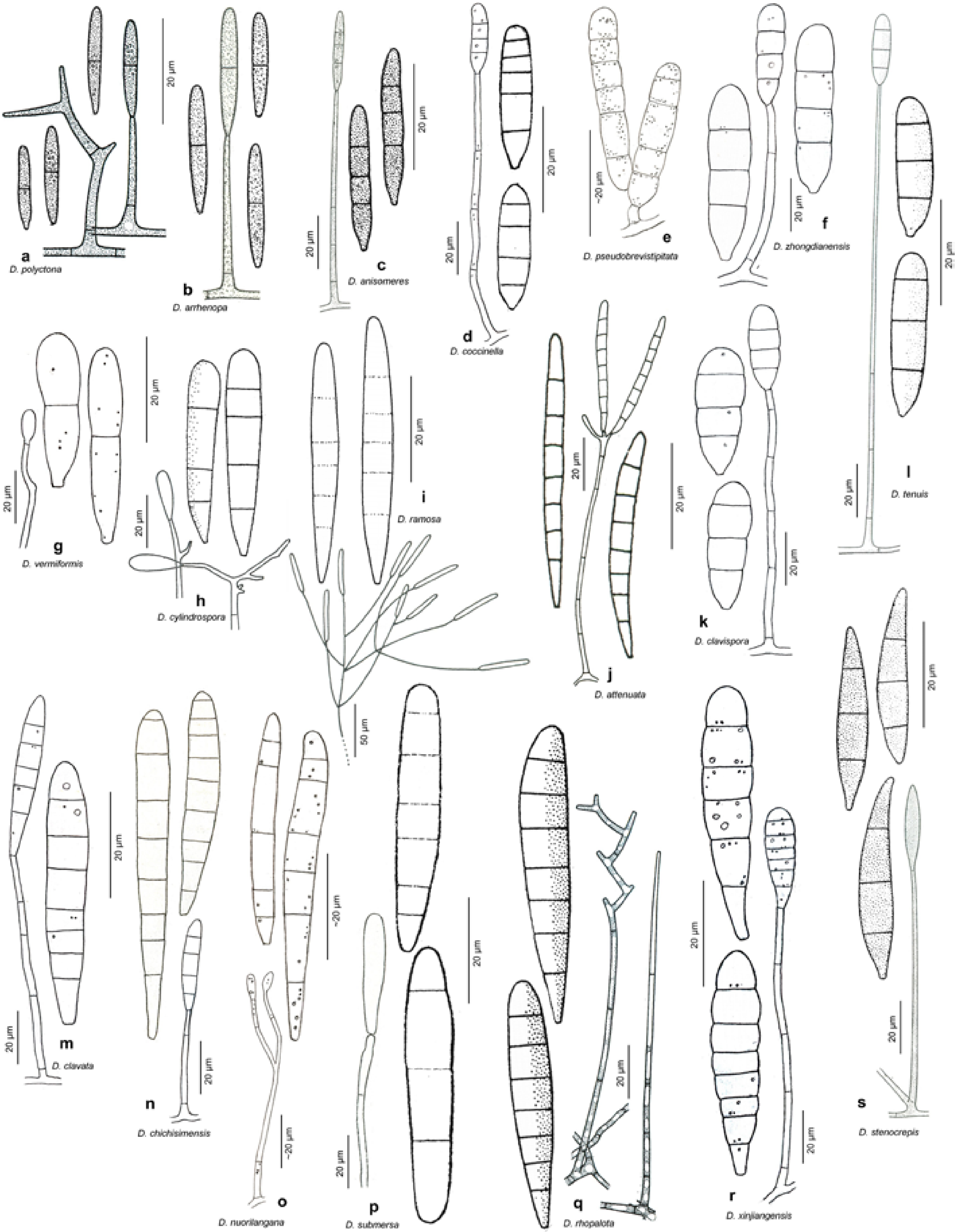


Plate 5. The accepted, hitherto known species of the form genus *Dactylella* I (conidiophores and conidia). — **a**. from Drechsler (1952), **b**. from Drechsler (1943a), **c**. from Drechsler (1962), **d**. from Yang & Liu (2005), **e**. from Qin et al. (2011)*, **f**. from Zhang et al. (2005), **g**. from Yu et al. (2007a), **h**. from Cooke (1969), **i**. from Matsushima (1971), **j**. from Gao et al. (1997), **k**. from Chen et al. (2007b), **l**. from Drechsler (1937a), **m**. from Gao et al. (1995), **n**. from Watanabe et al. (2001), **o**. from Zhang & Mo (2006)*, **p**. from Ingold (1944), **q**. from Drechsler (1943b), **r**. from Chen et al. (2007a, b), **s**. from Drechsler (1962). * = The size of conidia and conidiophores is somewhat modified according to the size given in the description.

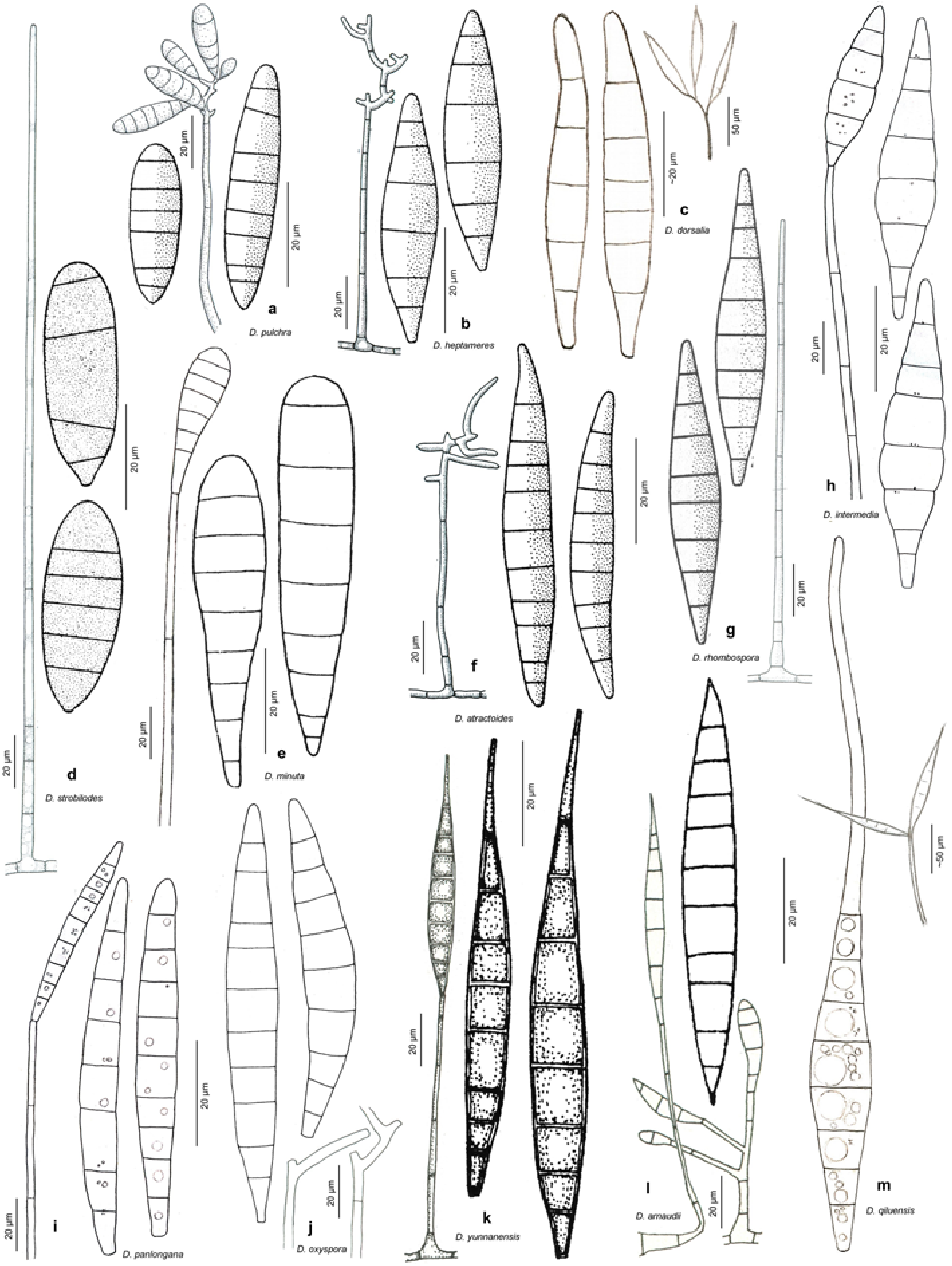


Plate 6. The accepted, hitherto known species of the form genus *Dactylella* II (conidiophores and conidia). — **a**. conidiophore from Linder (1934), conidia from Drechsler (1943b), **b**. from Drechsler (1943b), **c**. from Yu et al. (2007b), **d**. from Drechsler (1950b), **e**. from Rubner (1996), **f**. from Drechsler (1943b), **g**. from Drechsler (1937a), **h**. from Chen et al. (2007b), **i**. from Liu & Zhang (2006), **j**. from Rubner (1996), **k**. from Zhang et al. (1995), **l**. from Yadav (1960), **m**. from Su et al. (2011a).

and series *Orbilia* (section *Orbilia*). No sequence is available for the type of *Dactylella*, *D. minuta*. From its morphology, this species could either belong to series *Neodactylella* or in series *Hyalinia*. The type species of *Gangliophragma* (*D. rhopalota*) and *Drechsleromyces* (*Drm. atractoides*, = *D. oxyspora* fide Chen et al. 2007b) are assumed to belong to series *Neodactylella*. Species delimitation within *Dactylella* is problematic in several cases. Based on molecular analyses by Chen et al. (2007a) and the present study we conclude that *D. arnaudii*, *D. yunnanensis*, and *D. atractoides* s. Li et al. (2006) are conspecific with *D. oxyspora*. *D. rhombospora* s. Chen et al. (2007b) and *D. dorsalis* are morphologically similar to *D. oxyspora*, but form a separate clade.

Dactylellina M. Morelet – (Tab. 46, Pls 7–9, see also Tab. S9)

Mekhtieva (1967) proposed the genus *Dactylosporium* as a segregate of *Dactylella* for a single species (*D. leptospora*) because of its nematophagy by means of stalked adhesive knobs and non-constricting rings, and denticulate conidiophores. Eleven years later, Mekhtieva (1978) erected *Kafiaddinia* for a new taxon, *K. fusariispora*, with fusarium-like conidia with

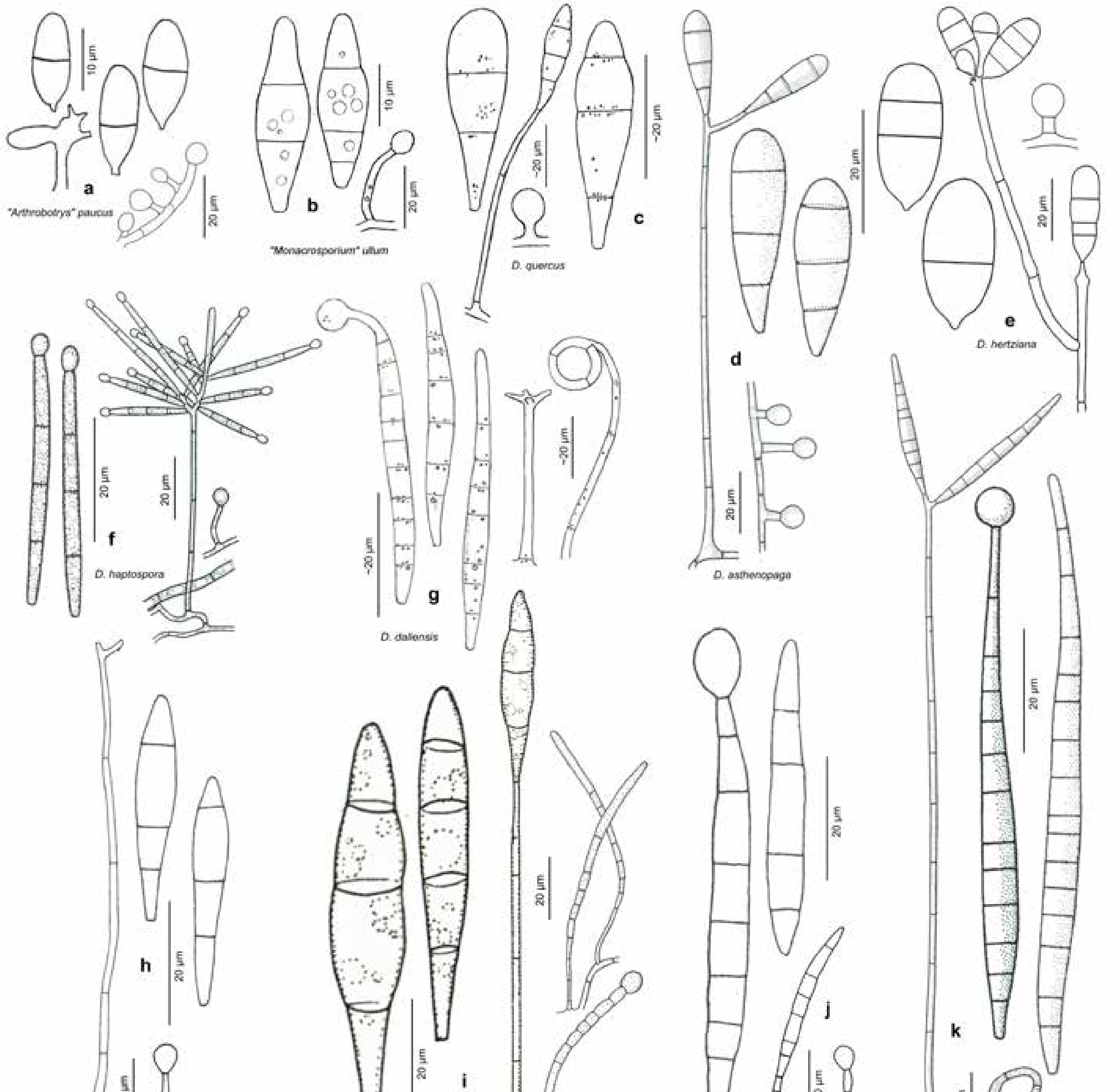


Plate 7: The accepted, hitherto known species of *Dactylellina* I (conidiophores, conidia, adhesive knobs and non-constricting rings). — **a**. from McCulloch (1977), **b**. from Kim et al. (2006), **c**. from Liu et al. (2005a)*, **d**. from Drechsler (1937a), **e**. from Scholler & Rubner (1999), **f**. from Drechsler (1940), **g**. from Su et al. (2008)*, **h**. from Chen et al. (1998), **i**. from Barron (1990), **j**. from Liou et al. (1995) (= *D. leptospora*), **k**. from Drechsler (1937a). * = The size of conidia and conidiophores is somewhat modified in reference to the size given in the description.

Table 46. Overview of the accepted species of *Dactylellina*.

Species	Conidial size [µm]	Number of septa	Conidial shape	Noncon-stricting rings	Habitat	Reference
'*Arthrobotrys*' *paucus* J.S. McCulloch	12–19 × 4–7	1	(cylindric-) ellipsoid		soil around strawberry, Australia, nematophagous	McCulloch 1977
D. hertziana (M. Scholler & A. Rubner) M. Scholler et al.	(16–)16.5–27.5(–28.5) × 7.5–11.5(–12)	(0–)3(–4)	obovoid to ellipsoid-cylindrical		plant debris, Canary Islands, nematophagous	Scholler & Rubner 1999
D. huisuniana (J.L. Chen et al.) M. Scholler et al.	29.5–41 × 4.5–7.5	3	mostly fusiform		decaying leaves of a dicot tree, Taiwan, nematophagous	Chen et al. 1998
D. quercus Bin Liu, Xing-Z. Liu & Zhuang (≡ *Orbilia quercus*)	25–40(–50) × 8–12	3	fusiform		on rotten *Quercus*-wood, China, nematophagous	Liu et al. 2005a
'*Monacrosporium*' *ullum* D.G. Kim et al.	17–44 × 7–10	(1–)2(–4)	fusiform		decaying plant material in soil, Korea, nematophagous	Kim et al. 2006
D. drechsleri (Tarjan) M. Scholler et al.	29.5–48.7 × 10.7–15.4	3	somewhat fusiform		from soil, USA, nematophagous	Tarjan 1961, Rubner 1996
D. mammillata (S.M. Dixon) M. Scholler et al. (≡ *Orbilia mammilata*)	29–44 × 9–14	3–4	ellipsoid to fusiform		decaying wood, soil, leaf litter, Canada, Germany, UK, nematophagous	Dixon 1952, Rubner 1996
D. asthenopaga (Drechsler) M. Scholler et al.	20–46 × 6.5–9.5	(1–)3(–5)	obconical or (fusoid-) clavate		forest soil, leaf mould, decaying wood and acorns, Australia, Netherlands, UK, USA, nematophagous	Drechsler 1937a, Rubner 1996
D. parvicollis (Drechsler) Y. Li (as '*parvicolle*', = *D. phymatopaga*)	35–45 × 8–14	4	fusiform		leaf litter, dead grass, soil, horse dung, Ecuador, Germany, Sweden, USA, nematophagous	Drechsler 1962, Rubner 1996
D. ellipsospora (Preuss) M. Scholler et al. (≡ *Orbilia ellipsospora*)	(24–)35–52(–65) × (7.5–)12–17(–19)	(2–)4	fusiform		soil, wood, leaf-litter, Germany, Spain, UK, nematophagous	Drechsler 1937a, Rubner 1996
D. daliensis H.Y. Su	28.7–51.5 × 3.2–5.2	(1–)6–8(–13)	elongate fusoid	+	from soil, China, nematophagous	Su et al. 2008
D. candida s. Drechsler (= *D. haptotyla* s.l.)	26–52 × 5.5–11.5	(2–)4(–6)	fusiform	+	from leaf mould, USA, nematophagous	Drechsler 1937a
D. haptotyla (Drechsler) M. Scholler et al.	(29–)33–56 × (7–)8–13.3	(3–)4(–5)	fusiform		soil, decaying leaves and culms of *Poa pratense*, wood, France, Germany, Sweden, UK, USA, nematophagous	Drechsler 1950a, Rubner 1996
D. lysipaga (Drechsler) M. Scholler et al. (≡ *Orbilia lysipaga*)	28–55 × 9–14	(2–)4	fusiform	+	on leaf mould in deciduous woods, USA, nematophagous	Drechsler 1937a, Rubner 1996
D. haptospora (Drechsler) M. Scholler et al.	35–60 × 2.2–3.2	4	cylindrical		woody remnants of *Ambrosia trifida*, USA, nematophagous	Drechsler 1940
D. varietas Y. Li et al.	25–61.5 × 6.5–10	(1–)7–8(–9)	fusoid	+	from forest soil, China, nematophagous	Li et al. 2006
D. mutabilis (R.C. Cooke) M. Scholler et al.	37.5–60 × 12.5–17.5	(3–)4(–5)	ellipsoidal to fusiform		in soil, Samoa, nematophagous	Cooke 1969, Rubner 1996
D. phymatopaga (Drechsler) Y. Li	40–60 × 11–18	4	fusiform		from soil, from mosses, Germany, Ecuador, Sweden, nematophagous	Drechsler 1954, Rubner 1996
D. formosana (J.Y. Liou et al.) M. Scholler et al. (= *D. leptospora*)	30–70 × 5–7.5	(2–)4–7(–8)	fusoid – cylindrical		decaying leaves of dicot tree, Taiwan, nematophagous	Liou et al. 1995
D. yunnanensis (K.Q. Zhang et al.) M. Scholler et al. (= *D. hyptotyla* s.l.)	34–81 × 8.5–12.5	(3–)4–6(–9)	fusiform	+	from forest soil, China, nematophagous	Zhang et al. 1996
D. sichuanensis Y. Li, K.D. Hyde & K.Q. Zhang (= *D. lysipaga*)	(35–)47–74(–82.5) × (7.5–)12.5–15.5(–17.5)	(3–)4(–6)	fusiform	+	from forest soil, China, nematophagous	Li et al. 2006
D. copepodii (G.L. Barron) M. Scholler et al.	56–97 × 8.5–16	(1–)4(–6)	fusiform		composted manure, New Zealand, capturing copepods	Barron 1990, Rubner 1996
D. leptospora (Drechsler) M. Morelet **Type species**	40–105 × 4–5.8 (primary conidia)	5–15	elongate fusoid, also cylindrical	+	soil, leaf mould in deciduous woods, USA, nematophagous	Drechsler 1937a, Rubner 1996
D. appendiculata (Anastasiou) M. Scholler et al.	57–108 × 9.3–14.5	4–7	fusiform, with lateral arms		from leaves in water, Hawaii, nematophagous	Anastasiou 1964, Rubner 1996
D. illaqueata D.S. Yang & M.H. Mo (?= *D. lysipaga*)	25.5–117.5 × 5.5–15.2	3–8	elongate fusiform	+	from soil, China, nematophagous	Yang et al. 2006
D. multiseptata (H.Y. Su & K.Q. Zhang) Z.F. Yu	67.5–132.5 × 13.8–17.5	4–9	fusiform to clavate		from soil, China, nematophagous	Su et al. 2005

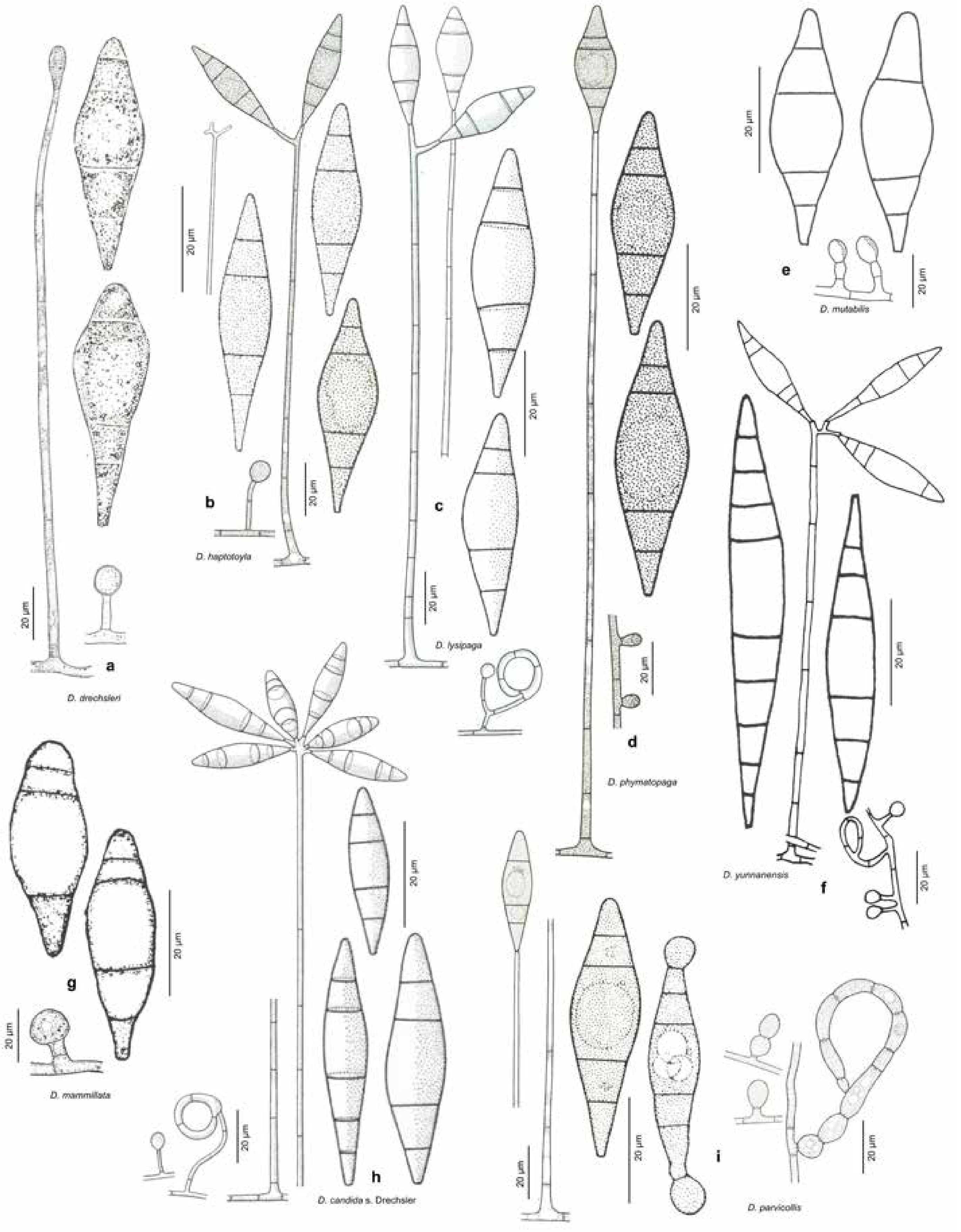


Plate 8. The accepted, hitherto known species of *Dactylellina* II (*D. candida* s. Drechsler = *D. yunnanensis* ?= *D. haptotyla*, *D. parvicollis* = *D. phymatopaga*) (conidiophores, conidia, adhesive knobs and non-constricting rings). — **a**. from Tarjan (1961), **b**. from Drechsler (1950a), **c**. from Drechsler (1937a), **d**. from Drechsler (1954), **e**. from Cooke (1969), **f**. from Zhang et al. (1996), **g**. from Dixon (1952), **h**. from Drechsler (1937a), **i**. from Drechsler (1962).

sometimes an adhesive knob at one end, along with the characters mentioned for *Dactylosporium*. This species was considered as synonymous with *D. leptospora* by Rubner (1996). Because of the illegitimacy of *Dactylosporium*, Morelet (1968) proposed

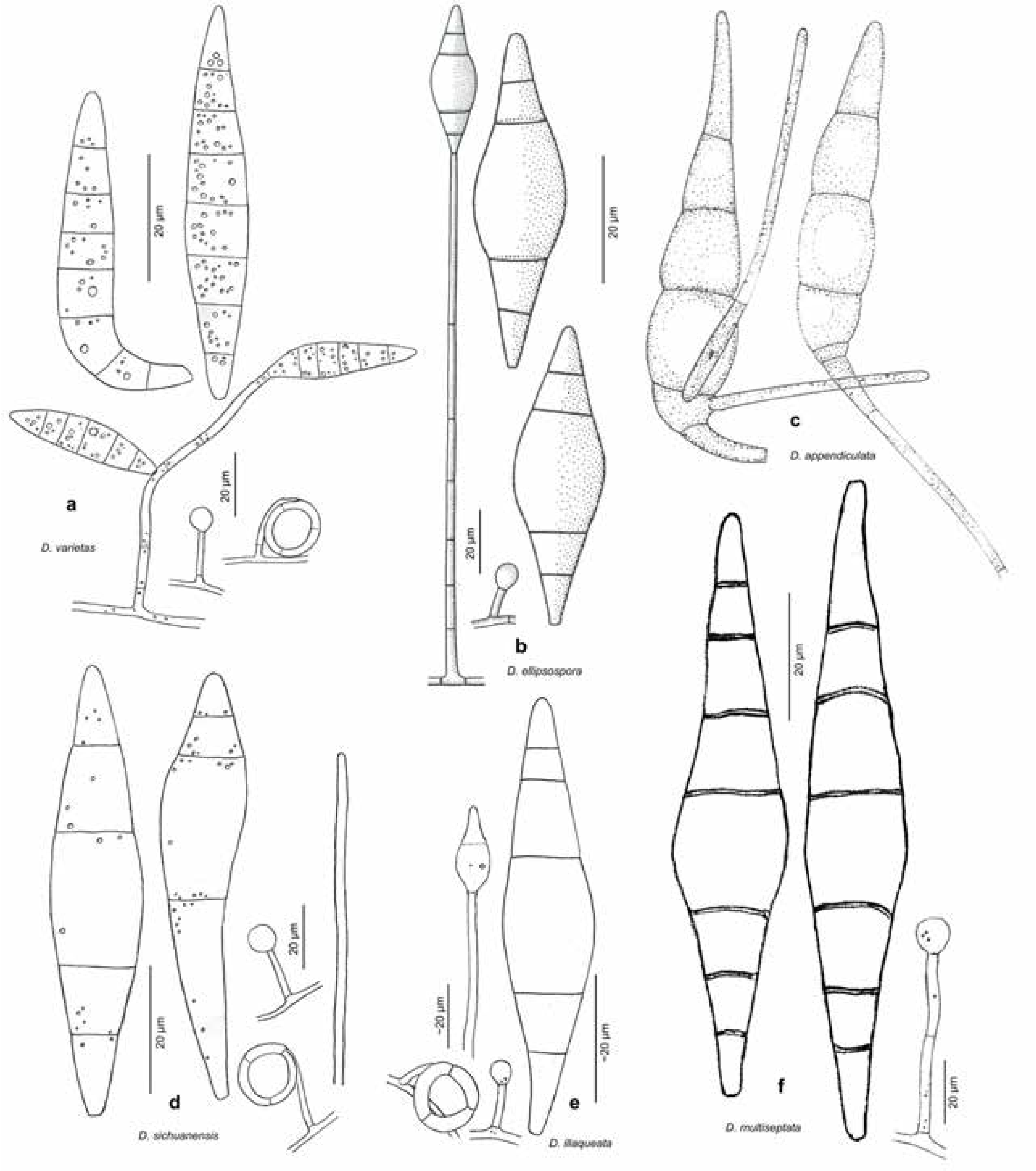


Plate 9. The accepted, hitherto known species of *Dactylellina* III (*D. sichuanensis* = *D. lysipaga*) (conidiophores, conidia, adhesive knobs and non-constricting rings). — **a**. from Li et al. (2006), **b**. from Drechsler (1937a), **c**. from Anastasiou (1964), **d**. from Li et al. (2006), **e**. from Yang et al. (2006)*, **f**. from Su et al. (2005). * = The scale is estimated in reference to the conidial size given in the description (the scale bar in the protologue seems to be 8 µm rather than 10 µm long).

the new name *Dactylellina*. In 1979, Mekhtieva considered her genus *Kafiaddinia* as a replacement name for the illegitimate *Dactylosporium*, unaware of the new name *Dactylellina* proposed by Morelet. The later synonym *Laridospora* was erected by Nawawi (1976a) with the type species *Dactylella appendiculata* based on long and filiform conidial branches that resemble appendages, also because of the semiaquatic habitat and being non-predacious when adding nematodes and rotifers (Anastasiou 1964, Nawawi 1976a). Yet, Rubner (1996: 98) obtained stalked adhesive knobs in a syntype culture of this species, but no conidia.

Dactylellina was emended by Scholler et al. (1999) who combined 16 species to the genus. Li et al. (2005) and Yang & Liu (2006) transferred further eight species to *Dactylellina*, which mainly comprise those previously assigned to *Gamsylella* by Scholler et al.

An overview of the 22 species of *Dactylellina* accepted in the new circumscription is given in Tab. 46, and Pls 7–9 (see also Tab. S9). The main characteristics are the nematode-trapping organs: stalked adhesive knobs which sometimes occur in combination with non-constricting rings, but also sessile adhesive knobs or two- to multicelled superimposed knobs or rarely adhesive columns or loops occur (*Dactylellina phymatopaga*). Conidia are hyaline, one- to multiseptate, predominantly fusoid to fusiform, formed singly or in clusters on the tip of long conidiophores. Scholler et al. (1999) listed *Kafiaddinia*, and *Laridospora* as synonyms of *Dactylellina*, and *Anulosporium* and *Dactylium* as possible synonyms. Also *Monacrosporium ullum* Kim et al. (2006) and *Arthrobotrys paucus* McCulloch (1977) with stalked adhesive knobs should be regarded as belonging to *Dactylellina*.

The genus *Anulosporium* with the single species *A. nematogenum* was described by Sherbakoff (1933) from a moist chamber culture with strawberry plants from Tennessee, with stalked adhesive knobs and non-constricting rings. The author misinterpreted the stalks as conidiophores, the rings as conidia, and the knobs as early stages of the rings. Because no authentic conidia were observed, the identity of the fungus at the species level cannot be clarified, and Rubner (1996: 36) could not classify the species in her generic system which was based on conidiophore and conidial morphology. For this reason, Scholler et al. (1999: 109) considered the genus as doubtful, although it is a clear synonym of *Dactylellina* in their classification and would have priority over that genus. However, since the specific identity of *A. nematogenum* is uncertain, the genus should be rejected (see also Baral et al. 2017b).

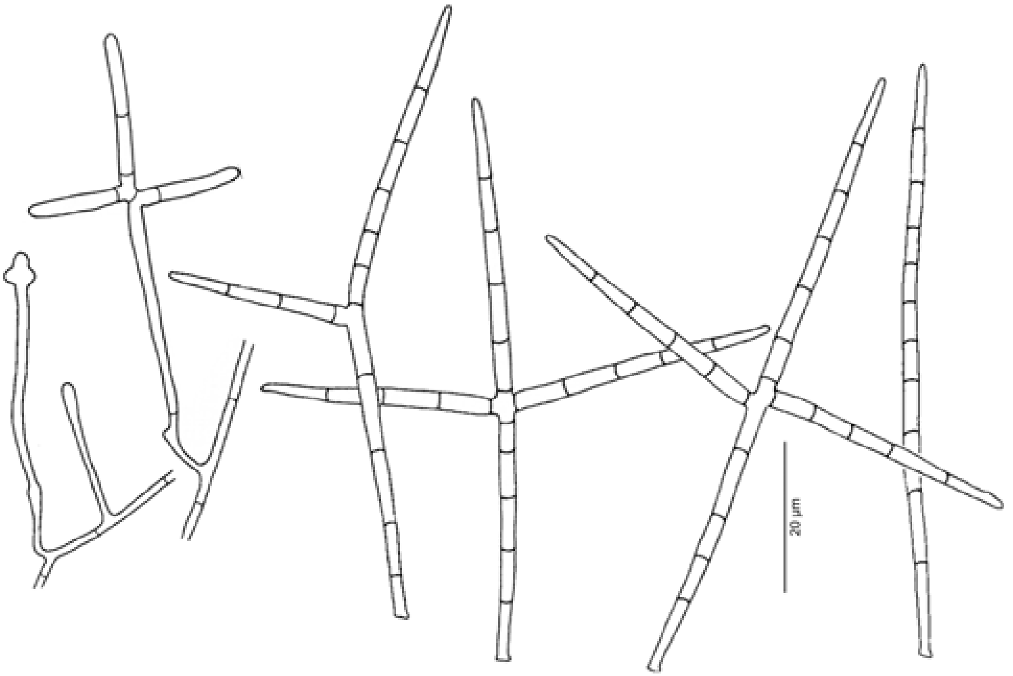


Plate 10: The single known species of the genus *Descalsia*, *D. cruciata* (conidiophores and conidia). From Roldán & Honrubia (1989).

'*Dactylellina*' *entomopaga* and '*D.*' *ferox* (Pl. 14: b–c) deviate from typical species of *Dactylellina* in adhesive knobs with voluminous mucilage which mainly trap insects. They are treated here under *Gamsylella* because of a close similarity in the trapping organ to *Orbilia alba* (Pl. 14: a), which we found to cluster in the *Gamsylella* clade.

The first connection of teleomorph and anamorph in *Dactylellina* was reported by Liu et al. (2005a): *Orbilia quercus* and *D. quercus* (both as *querci*). For two further taxa Liu (2006) reported connections to anamorphs: *O. quercus* var. *hunanensis* with *D. lysipaga* and *O. quercus* var. *hainanensis* with *D. ellipsospora*. In an abstract, Liu et al. (2002, cited in Mo et al. 2005a and Zhang & Mo 2006) reported *O. cunninghamii* as teleomorph of *Monacrosporium parvicolle*, but this refers to *O. quercus*/*D. quercus*, as B. Liu (pers. comm.) treated in that abstract his new species temporarily under those names. Zhang et al. (in prep.) described *O. apiculata* and *O. biforma* with anamorphs and teleomorphs. Species delimitation within *Dactylellina* is highly problematic, and various misidentifications and synonymies could be detected based on rDNA sequences (see p. 1584 ff.).

Dactylellina species have been collected in wet habitats like soil, decaying herbal material and wood, or on bryophytes. They prey on nematodes or arthropods and are distributed worldwide.

In the present study, *Dactylellina* was reduced to a series of section *Arthrobotrys* of *Orbilia*. New reports of connections between anamorphs and teleomorphs are given for *O. rubrovacuolata* and *O. mammillata*. The genus *Gamsylella* is accepted in a modified sense based on molecular as well as morphological reasons (see p. 235).

Descalsia A. Roldán & Honrubia – (Pl. 10)

The name of the genus refers to the mycologist Enrique Descals. Roldán & Honrubia (1989) described the only known species, *Descalsia cruciata*, a hyphomycete isolated from foam in a Spanish stream, with branched, septate conidia formed on short conidiophores. Conidia are mainly tetraradiate (┼-shaped), with a stipe and three arms, more rarely with only two arms or unbranched. Usually, the arms emerge from a single central cell, but sometimes there are two contiguous cells separated by an oblique septum (Pl. 10 left), which is a key character of the similar genus *Curucispora*. A sequence of this species was not available.

Roldán & Honrubia compared their genus with *Curucispora, Isthmotricladia* Matsush.*, Enantioptera* Descals*, Hexacladium* D.L. Olivier, and *Articulospora* Ingold.

Articulospora inflata Ingold (1944) has very similar though much larger conidia. In addition, in *Articulospora* the third and fourth arm is constricted at the point of insertion (see also under *Tridentaria*, p. 242).

In the present study we consider *Descalsia* as a possible synonym of *Orbilia*, particularly of series *Hemiorbilia*. We observed descalsia-like conidia in *O. aristata* and some related further species of series *Hemiorbilia* which closely resemble *D. cruciata* but occurred on xeric branches.

Dicranidion Harkn. – (Tab. 47, Pl. 11)

The name of the genus, which was erected for the single species *Dicranidion fragile* (Harkness 1885), refers to the shape of conidia resembling a tuning fork (from Greek 'dikranos'). Peek & Solheim (1958) emended the description of *Dicranidion* and synonymised *Pedilospora* Höhn. The genus is characterized by branched, U- to V- or Y-shaped, septate, hyaline conidia, borne on usually short conidiophores. Typically, the two arms are parallel, often touching each other, and the stipe is mostly short or ± absent. Young conidia are heart-shaped. In addition, unbranched phragmoconidia were observed in association with the bilobed conidia (Tubaki & Yokoyama, 1971, Butterfield

1973, Matsushima 1981), and also tri- or tetralobed conidia occurred (Ando & Tubaki 1984b, Bubák 1916, Butterfield 1973, Matsushima 1971, 1975, 1981, 1993). As an exception within *Dicranidion*, *D. incarnatum* forms conidia with regularly 3–8 arms (Martin 1948, as *Tetracrium incarnatum*). Conidia of *Dicranidion* with more than two arms are formed by repeated dichotomous branching (Pl. 11: a, l). In *D. fragile* and its possible synonym *D. argentinense* the conidiophores may be aggregated in sporodochia-like structures (Peek & Solheim l.c., Spegazzini 1911).

Twelve species of *Dicranidion* are tentatively accepted here (see Tab. 47), differing mainly in the length of conidial arms and stipes and in the number of septa, also in the number of arms. The two most often reported species are *D. fragile* and *D. gracile*. Peek & Solheim (1958) synonymised *Pedilospora ramularioides* Bubák with *D. fragile.* Furthermore, they assumed that *P. parasitans* Höhn. (the type species of *Pedilospora*) and *P. episphaeria* Höhn. are synonyms of *D. fragile*. Another possible synonym of that species is *D. argentinense* Speg. fide Matsushima (1981). *D. dactylopagum* deviates in extraordinarily long conidiophores, and in its ability to trap testaceous rhizopods similar as in *Brachyphoris* (= *Hyalorbilia*). The conidia of *D. macrosporum* closely resemble those of *D. amazonense* except for the higher number of septa. We consider *D. tenue* and *D. dactylopagum* as possible synonyms of *D. gracile* by reducing the number of accepted species to ten.

According to Matsushima (1987), *Dicranidion* species vary strongly in conidial morhology depending on the substrate: on the natural substrate, e.g., *D. ontariense* formed longer conidia (24–28 µm) than on PDA (14–18 µm). Likewise, Butterfield (1973) reported for *D. fragile* that different agar media caused an extensive variation in conidial morphology, for which reason he synonymised *D. inaequale* with *D. fragile*. Variation is also observed concerning diverging of the arms: in *O. xanthostigma* we observed dicranidion gracile-like conidia with strongly diverging arms only on the natural substrate, whereas in our culture the arms mostly did not diverge at all. Yet, Matsushima (1971, 1975, as *D. gracile*) and Pfister (1997: fig. 7, *Dicranidion* sp. of the gracile type) obtained conidia with diverging arms in culture. Especially if such V-shaped conidia possess an elongate 1-septate stipe, they are hardly separable from the form genus *Trinacrium*.

So far it has been known that *Dicranidion* anamorphs were connected with two *Orbilia* species. For *O. eucalypti* (as *O. coccinella*), anamorphs referable to *D. fragile* were reported by Brefeld (1891) and Liu (2006). Reports by Korf (1992) and Pfister (1997: fig. 8) under the name *O. alnea* (= *O. eucalypti*) rather resemble *D. gracile* and might relate to *O.* cf. *xanthoflexa*, *O. cejpii*, or *O. renispora*. For *O.* cf. *xanthostigma* (as *O. delicatula*) Pfister (1997) and Liu (2006) observed a dicranidion-like morph which Pfister referred to *D. gracile* and Liu to *D. tenue* (note that Pfister erroneously applied on p. 13 the epithets '*fragile*' and '*gracile*' in contradiction to what he wrote in the legends to his figs 7 and 8). Berthet (1964a) figured as anamorph of '*O. xanthostigma*' conidia (9–12 × 6–7 µm) with somewhat asymmetrical septation (i.e., without distinct basal cell) reminiscent of *D. inaequale*, and a sequence of this strain confirmed that the collection was *O. tremulae*, a species closely related to *D. inaequale.* Shao et al. (2018) reported *O. renispora* with dicranidion fragile- and *O.* (cf.) *xanthoguttulata* with dicranidion-like anamorph.

Species of *Dicranidion* were usually isolated from decaying plant material (wood, leaves etc.). The morphology of the staurosporous conidia led Pfister (1997) to speculate about an aquatic habitat. However, with the exception of *D. fissile* which was isolated from rainwater draining from intact trees (Ando & Tubaki 1984b), no reports of *Diranidion* species from water or foam came to our attention. Only for one species (*D. dactylopagum*, Drechsler 1934) the ability of capturing and

Table 47. Overview of the accepted species of the form genus *Dicranidion* (values partly corrected or completed acccording to the author's illustrations).

Species	Conidial total size [µm]	Stipe [µm]	Arms [µm]	Habitat	Reference
D. inaequale Tubaki & T. Yokoyama	9–17 × 6–7	—	~(5–)8–13.5 × 2.4–3.3	on decaying *Diaporthe*-like fungus, Japan	Berthet 1964a, Tubaki & Yokoyama, 1971
D. fragile Harkn. **Type species** (= *Orbilia eucalypti*)	8–23(–25) × 6–9.5	4–9 × 5–8	8–17 × 3–4.5	rotten wood and bark or petioles of *Cryptomeria japonica*, *Eucalyptus globulosus*, *Nerium oleander*, *Quercus*, in mycelium of *Bispora pusilla*, Argentina, Japan, Peru, Micronesia, USA	Harkness 1885, Saccardo 1886, Spegazzini 1911, Bubák 1916, Peek & Solheim 1958, Butterfield 1973, Matsushima 1971, 1975, 1981
D. fissile K. Ando & Tubaki (≡ *Orbilia fissilis*)	12–22.5 × 5.5–13	7.5–10.5(–12) × 2.4–4	6.5–11 × 2–2.8	on leaves of *Quercus myrsinifolia*, Japan	Ando & Tubaki 1984b
D. ontariense Matsush.	14–28 × 8.5–12	4.5–10 × 3–5	6–24 × 3–5	dead bark of *Acer saccharinum*, USA	Matsushima 1987
D. amazonense Matsush.	16–32 × 10–14	0–8	10–28 × 4.5–7	rotten palm leaf, decaying leaves, Peru	Matsushima 1981 1993
D. tenue Matsush. (?= *D. gracile*)	18.5–35 × 7.5–9	4.5–12 × 4–6	(9–)10–25.5 × 3–4.5	palm petioles, rotten leaves, Peru, South Africa	Matsushima 1993, 1996
D. macrosporum Prasher et al.	21–37 × ~12–15	—	~22–26 × 5-7	on bark of *Cassia fistula*, India	Prasher et al. 2008
D. gracile Matsush.	25–41 × 9–17	8–14(–18) × 3.2–5(–6)	(14–)16–33 × (3–)3.5–4	decaying leaves, wood of *Quercus*, Cuba, Japan, Peru, Micronesia, USA	Matsushima 1971, 1975, 1981, 1987, 1993
D. dactylopagum (Drechsler) Peek & Solheim (?= *D. gracile*)	20–40 × 6–8	8.5–18 × 2.7–4.2	10–22 × 2.3–3.5	decaying plant material, USA, capturing testaceous rhizopods	Drechsler 1934
D. parapalmicola Matsush. (1981 as *Dicranidion* sp., M.F.C. 9432)	25–47 × 9–14	4–9(–12) × 5–8	20–40 × 4–6.5	petioles of palms, bark of *Quercus*, Peru, USA	Matsushima 1981, 1993
D. palmicola Matsush.	30–60 × 10–12.5	6.5–20 × 3.8–7	11–50 × 4–6	decaying palm petioles, Taiwan, Guam	Matsushima 1981
D. incarnatum (G.W. Martin) Peek & Solheim	~45–50 × 13–24	~3.5–6 × 3.5–6	~(23–)31–43 × 3.5–4.5	dead stem of *Opuntia*, Galapagos Islands	Martin 1948

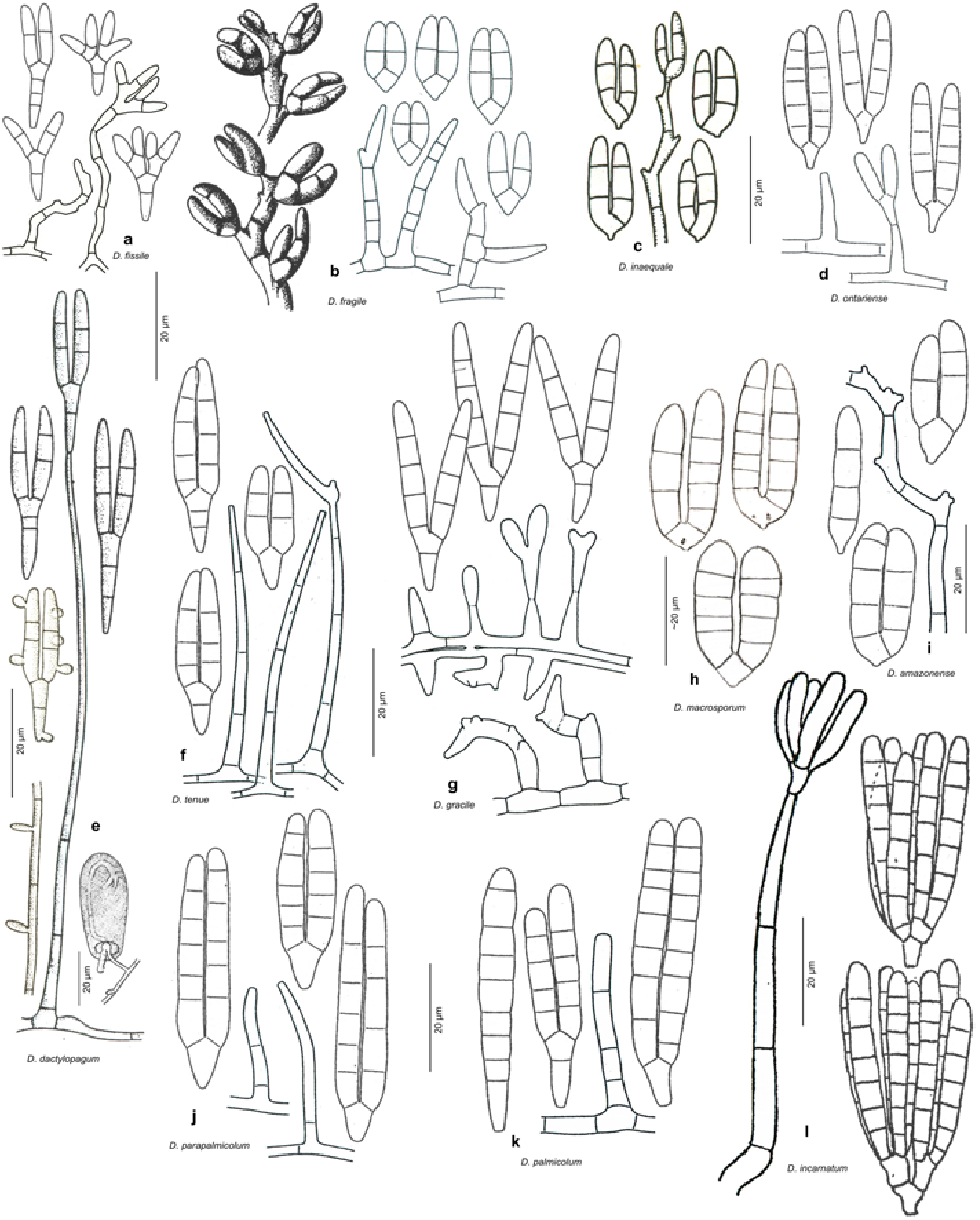


Plate 11: The accepted, hitherto known species of the form genus *Dicranidion* (conidiophores and conidia, **e**. with captured rhizopod). — **a**. from Ando & Tubaki (1984b), **b**. left from Harkness (1885), right from Matsushima (1975), **c**. from Tubaki & Yokoyama (1971), **d**. from Matsushima (1987), **e**. from Drechsler (1934), **f**. from Matsushima (1993), **g**. from Matsushima (1971), **h**. from Prasher et al. (2008, scale estimated), **i**. from Matsushima (1981), **j–k**. from Matsushima (1981), **l**. from Martin (1948).

consuming invertebrates (testaceous rhizopods) is proved. *Dicranidion* species were reported from Asia, North and South America, Oceania, and Europe.

In the present study we treat *Dicranidion* as a synonym of *Orbilia* section *Orbilia* series *Orbilia*, and the type species *D. fragile* as a synonym of *O. eucalypti*. Dicranidion-like anamorphs mainly occur in series *Orbilia*, but also in sections *Lentiformes* (*O. ovalis*) and *Aurantiorubrae* (*O. xanthoguttulata*, *O. siculispora*). Judging from their morphology alone, *D. gracile* and *D. tenue* might be conspecific. On the other hand, *O. xanthostigma*, *O. leucostigma*, *O. battenii*, *O. cejpii*, and *O. renispora* all have anamorphs referable to *D. gracile*, and the *xanthostigma-leucostigma* complex is comprised of various cryptic taxa. We accept *D. inaequale* as a species different from *D. fragile* based on its frequently asymmetrical basal cell (see also under *O. tremulae* p. 1377).

Drechslerella Subram. – (Tab. 48, Pl. 12, see also Tab. S10)

Subramanian (1964) erected *Drechslerella* for the single species *Dactylella acrochaeta* based on a long, filiform apical appendage of its conidia, and named the genus after the author of the species, Charles Drechsler. Liu and Zhang (1994) treated *Drechslerella* as a synonym of *Monacrosporium* Oudem. Scholler et al. (1999) resurrected and emended the genus, accepted 13 species, and synonymised the genera *Dactylariopsis* and *Golovinia* under *Drechslerella*. Another species, '*Monacrosporium*' *obtrulloides*, is close to *D. bembicodes* (see Castaner 1968, Rubner 1996) but was never combined in *Drechslerella*. The present survey tentatively accepts 16 species (see Tabs 48 & S10), but further, mainly cryptic taxa without a name for the anamorph are accepted in the taxonomic part of this study. The genus is characterized by three-celled constricting rings that trap nematodes by active and sudden swelling of the cells, and by hyaline, one- to four-septate, cylindric, ellipsoid, obovoid, fusiform, or top-shaped conidia, formed singly or, more rarely, in clusters at the tip of long conidiophores. Only in one species a mucilaginous sheath around the conidia is reported (*D. polybrocha*). Many of the species were found to produce microconidia (see p. 113).

Pfister (1997) reported the anamorph-teleomorph connection between *D. polybrocha* and *Patinella tenebricosa* and between *D. ?doedycoides* and *Orbilia* sp. (= *O. pilosa*). Yu et al. (2006) reported *D. brochopaga* as anamorph of *O. orientalis*, and Yu et al. (2009b) *D. yunnanensis* as anamorph of *O. ?orientalis*. Zhang et al. (2020a) described *O. tonghaiensis* and *O. pseudopolybrocha* with anamorphs and teleomorphs. Species delimitation within *Drechslerella* is very difficult, and different cryptic taxa need to be separated based mainly on their rDNA sequences, particularly in the *D. brochopaga* complex (see p. 1624).

Species of *Drechslerella* were isolated from decaying herbal material, mainly leaf mould, and from soil. They were reported from North America, Asia, and Europe. From western Australia no *Drechslerella* could be found among 37 isolates of fungi referable to section *Arthrobotrys* (Park et al. 2002).

In the present study, the genus *Drechslerella* was reduced to a series of section *Arthrobotrys*. A further connection of anamorph and teleomorph is reported for *O. naumburgensis*.

Table 48. Overview of the accepted species of *Drechslerella*. – §: larger (1–)3-septate conidia of (16–)20–32 × 5.0–6.5 µm occurred in another isolate of this species (HMAS 139691), indicating that the small conidia are microconidia.

Species	Conidial size [µm]	Number of septa	Conidial shape	Habitat	Reference
D. yunnanensis Z.F. Yu & K.Q. Zhang (≡ *Orbilia yunnanensis*)	7.8–12.9(–17.8) × 3.3–4.2(–5.5) §	(0–)1	cylindric-ellipsoid	on decaying bark of broad-leaved tree, China, nematophagous	Yu et al. 2009b
D. polybrocha (Drechsler) M. Scholler et al. (≡ *Orbilia polybrocha*)	33.5–41 × 20–25	1	broadly obovoid	decaying rootlets of *Spinacea oleracea*, decaying wood, USA, nematophagous	Drechsler 1937a, Rubner 1996
D. doedycoides (Drechsler) M. Scholler et al.	28–39(–50) × 14–24	2(–3)	ellipsoid-fusiform	leaf mould in deciduous woods, soil in *Acacia* forest, Portugal, UK, USA, nematophagous	Drechsler 1940, Rubner 1996
D. acrochaeta (Drechsler) Subram. **Type species**	30–42 × 13.2–22.6	2	fusiform	leaf mould in deciduous woods, USA, nematophagous	Drechsler 1952, Rubner 1996
D. anchonia (Drechsler) M. Scholler et al.	29–43 × 15–19	1(–2)	elongate obovoid	decaying plant residues, USA, nematophagous	Drechsler 1954
D. brochopaga (Drechsler) M. Scholler et al. (≡ *Orbilia brochopaga*)	26–46 × 5–9	(2–)3(–4)	cylindrical (-ellipsoid)	leaf mould in deciduous woods, USA, nematophagous	Drechsler 1937a
D. hainanensis Jian Y. Li & Z.F. Yu	32.5–43 × 17–25	(0–)1–2	ellipsoid(-cylindrical)	forest soil, China, nematophagous	Li et al. (2013)
'*Monacrosporium*' *obtrulloides* Castaner	39.5–46 × 10.5–17.5	2	fusiform (-clavate)	rotting wood, USA, nematophagous	Castaner 1968
D. dactyloides (Drechsler) M. Scholler et al.	(25–)32–48 × 7–9.5(–18)	1(–2)	cyl.-ellipsoid (rarely fusiform)	decaying leaves and roots, leaf mould, USA, nematophagous	Drechsler 1937a
D. heterospora (Drechsler) M. Scholler et al.	35–47 × 13–20	2	ellipsoid	decaying leaves of *Poa pratensis*, USA, nematophagous	Drechsler 1943b, Rubner 1996
D. bembicodes (Drechsler) M. Scholler et al. (≡ *Orbilia bembicodes*)	34–48 × 16–23	3	fusiform	leaf mould, in decaying acorns (*Quercus prinus*), USA, nematophagous (and rotifers)	Drechsler 1937a, Rubner 1996
D. effusa (Jarow.) M. Scholler et al.	30–50 × 17–26	(1–)2	ellipsoid	from marsh soil, rotten wood, Poland, Canada, nematophagous	Jarowaja 1968b, Rubner 1996
D. aphrobrocha (Drechsler) M. Scholler et al.	41–55 × 17–26	3–4	top-shaped	leaf mould, USA, nematophagous	Drechsler 1950a
D. stenobrocha (Drechsler) M. Scholler et al.	34–56.5 × 12.5–16.5	(1–)2–3	cylindric-ellipsoid	leaf mould, USA, nematophagous	Drechsler 1950a
D. coelobrocha (Drechsler) M. Scholler et al.	46–64 × 18–25	(2–)4(–5)	top-shaped	decaying leaves of *Fagus grandifolia*, USA, nematophagous	Drechsler 1947, Rubner 1996
D. inquisitor (Jarow.) M. Scholler et al.	50–65 × 18–24	3	fusiform	forest litter, Poland, nematophagous	Jarowaja 1971, Rubner 1996

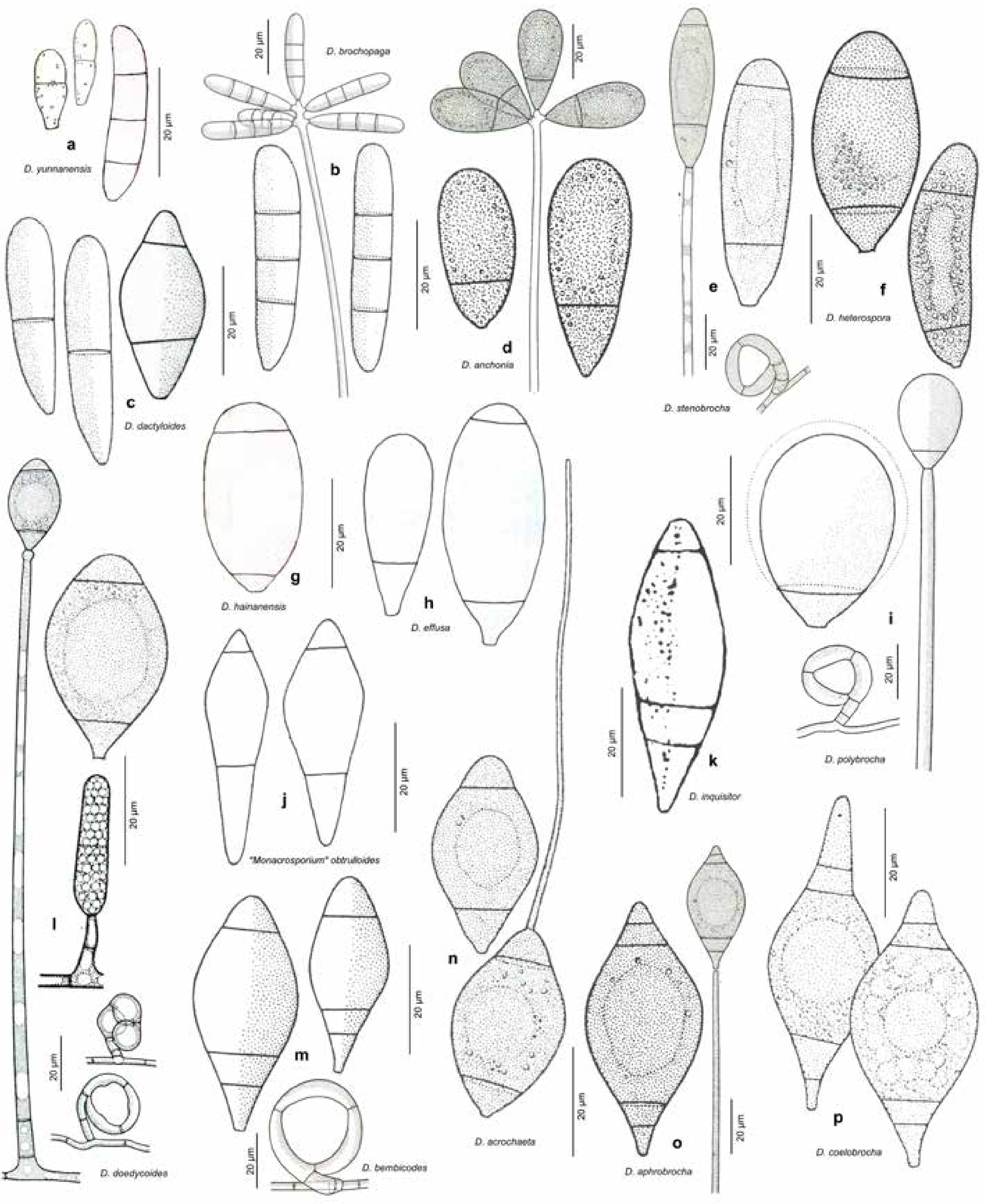


Plate 12. The accepted, hitherto known species of *Drechslerella* (conidiophores, conidia and constricting rings, **l**. with microconidium). — **a**. from Yu et al. (2009b, left) and Liu (2006, right), **b–c**. from Drechsler (1937a), **d**. from Drechsler (1954), **e**. from Drechsler (1950a), **f**. from Drechsler (1943b), **g**. from Li et al. (2013), **h**. from Rubner (1996), **i**. from Drechsler (1937a), **j**. from Castaner (1968), **k**. from Jarowaja (1971), **l**. from Drechsler (1940), **m**. from Drechsler (1937a), **n**. from Drechsler (1952), **o**. from Drechsler (1950a), **p**. from Drechsler (1947).

Dwayaangam Subram. – (Tab. 49, Pl. 13)

Species of *Dwayaangam* are characterized by staurosporous, hyaline conidia arising from short conidiophores, with normally four arms formed by repeated dichotomous branching (the name is derived from Sanskrit: *dwaya* = two, *angam* = branch, Subramanian 1978). Eight species have to date been validly described, with *D. quadridens* (Drechsler) Subram. as type species (see Tab. 49). *D. quadridens* was combined into

Table 49. Overview of the accepted species of the form genus *Dwayaangam*; **D. colodena* is phylogenetically related to *Arachnopezizaceae* (*Helotiales*).

Species	Total size of conidia (length × width at the widest part) [µm]	Habitat	Reference
D. yakuensis (Matsush.) Matsush.	~20–34 × 12–20	from soil and leaf mould, decaying leaves of *Machilus*, *Quercus*, *Archontophoenix*, *Fagus* bark, Australia, Japan, USA	Matsushima 1975, 1981, 1989, Kitz & Embree 1980, Ando & Tubaki 1984a
D. heterospora G.L. Barron	~36–39 × 16–22	organic debris, New Zealand, parasitic on eggs of rotifers and nematodes	Barron 1991c
D. junci Kohlm. et al. (= *Orbilia junci*)	~30–50 × 20–28	on *Juncus roemerianus*, USA	Kohlmeyer et al. 1998
Dwayaangam sp. (as '*D. cornuta*')	~40–57 × 13–25	on decaying leaves of angiosperm tree, Ecuador	Matsushima 1993
D. gamundiae Cazau et al.	~51–58 × 20–42	from bark in a river, Argentina	Cazau et al. 1993
D. dichotoma Nawawi	~42–61 × 60–83	foam of a river, Malaysia	Nawawi 1985a
D. quadridens (Drechsler) Subram. **Type species** (= *Hyalorbilia quadridens*)	~80–90 × 62–80	organic material, USA, parasitic on testaceous rhizopods (*Euglypha levis*)	Drechsler 1962
D. cornuta Descals	~50–90 × 35–70	decaying twig in water, Great Britain	Descals & Webster 1982
D. colodena Sokolski & Bérubé*	~80–110 × 80–110	needles of *Picea mariana* in water, Canada	Sokolski et al. 2006

Hyalorbilia recently (Baral et al. 2017b). Cazau et al. (1993) and Kohlmeyer et al. (1998) provided an overview of five and seven species, respectively. Several authors (e.g., Ingold 1942, 1958, 1959; Sinclair et al. 1983) have published dwayaangam-like conidia from streams in Africa and Great Britain, some of which they regarded as belonging to the genera *Tripospermum* Speg. or *Triposporina* Höhn.

Matsushima (1993) figured a collection from Ecuador under the name *D. cornuta* (Pl. 13: c) which represents, in our opinion, an undescribed species resembling *D. junci* (see also under *O. junci*, p. 767).

Drechsler (1937a, 1962) described *Triposporina aphanopaga* and *T. quadridens.* When Deighton & Pirozynski (1972) examined the type species of *Triposporina*, *T. uredinicola* Höhn., a hyperparasite with short bilabiate arms growing on uredospores of a rust fungus, they found that the conidiogenesis is annellidic, whereas it is not annellidic in Drechsler's two *Triposporina* species. Based on this and on differences in conidial shape, Subramanian (1978) erected two new genera, *Dwayaangam* with *D. quadridens* as type species, and *Tripoconidium* with *T. aphanopagum* (Drechsler) Subram. (see p. 246).

The type species of the genus *Retiarius*, *R. superficiaris* D.L. Olivier (Pl. 20: a) has dwayaangam-like conidia though the number of arms varies

The conidia of *Dwayaangam* normally branch twice dichotomously at the tip of the main axis, thus resulting in four arms, but this feature varies in some species. *D. heterospora* (Barron 1991c) and *D. yakuensis* (Matsushima 1981, Ando & Tubaki 1984a) show intraspecific variation in producing morphologically different types of conidia: typical conidia with four arms (dwayaangam-like), conidia with two arms (trinacrium-like), and unbranched phragmoconidia (Barron 1991c). *D. cornuta* develops up to eight arms (Descals & Webster 1982), and *D. colodena* has usually six arms (Sokolski et al. 2006). That the limits between the form genera *Dwayaangam* and *Trinacrium* are rather artificial is also shown in the reports of Drechsler (1938) and Ando (1992) (see under *Trinacrium*, p. 243–245).

Only for one *Dwayaangam* species, *D. junci*, an *Orbilia* teleomorph was reported up to now: *O. junci* (Kohlmeyer et al. 1998). For *D. colodena* (with 5–6 arms) Sokolski et al. (2006) demonstrated by molecular analysis that this species is phylogenetically remotely related to *Arachnopeziza* (*Helotiales*), although conidial morphology strongly resembles other species of *Dwayaangam*, like *D. dichotoma*. Possibly, further species of the form genus *Dwayaangam* will turn out to belong to classes other than *Orbiliomycetes*.

Matsushima (1993) mentioned a similarity to *Hydrometrospora* Gönczöl & Révay (1984). In the single species *H. symmetrica* Gönczöl & Révay a large H-shaped part of the conidium emerges laterally from the main axis, whereas in *Dwayaangam* the apex of the main axis divides dichotomously. *Monogrammia* F. Stevens (1918) with the single species *M. miconiae* F. Stevens resembles *Dwayaangam* but was considered to be the anamorph of *Paranectriella miconiae* (F. Stevens) Rossman (*Pleosporales*), with which it was found to co-occur on the natural substrate (Rossman 1987).

Some species of *Dwayaangam* were isolated from water or foam, some from decaying plant material. Because of the staurosporous form of the conidia, the habitat of *D. junci* at the sea shore, and the occurrence of other *Dwayaangam* species in freshwater, Kohlmeyer et al. (1998) considered this species as an Ingoldian fungus adapted to water dispersal. Yet, later research (Kohlmeyer & Volkmann-Kohlmeyer 2001) indicated that *O. junci* forms its conidia on recently dead dry tips of standing culms, where later the apothecia occur (see p. 767). Gönczöl & Révay (2006) reported nine different species (*D. cornuta*, *D. dichotoma*, *D. yakuensis*, and *Dwayaangam* spp. 1–6) from rainwater collected from different trees. *D. heterospora* was found to grow parasitically on eggs of rotifers and nematodes (Barron 1991c) and *D. quadridens* as predacious on a rhizopod (Drechsler 1962). *Dwayaangam* species have been collected in North and South America, Asia, Africa, New Zealand, and Europe.

In the present study we consider the genus *Dwayaangam* in a very narrow sense, restricted to its type species *D. quadridens*, as synonym of *Hyalorbilia* (see below). We obtained dwayaangam-like anamorphs in pure culture of three species in two different sections of *Orbilia* (*O. aristata* and *O. subvinosa* in section *Hemiorbilia*, *O. albidorosea* in section *Aurantiorubrae*). But also *O. subaristata*, *O. flagellispora*, and *O. arachnovinosa* (section *Hemiorbilia*) are presumably connected to dwayaangam-like anamorphs. In section *Hemiorbilia* the dwayaangam-like conidia frequently occur mixed with trinacrium- and descalsia-like conidia. All this indicates that *Dwayaangam* is a form genus when defined merely by conidial shape. Actually, the predacious capability of the type species of *Dwayaangam*, *D. quadridens*, points to a relationship with *Hyalorbilia*, in which rhizopod traps occur in *Brachyphoris tenuifusaria* and '*Dactylella*' *passalopaga*

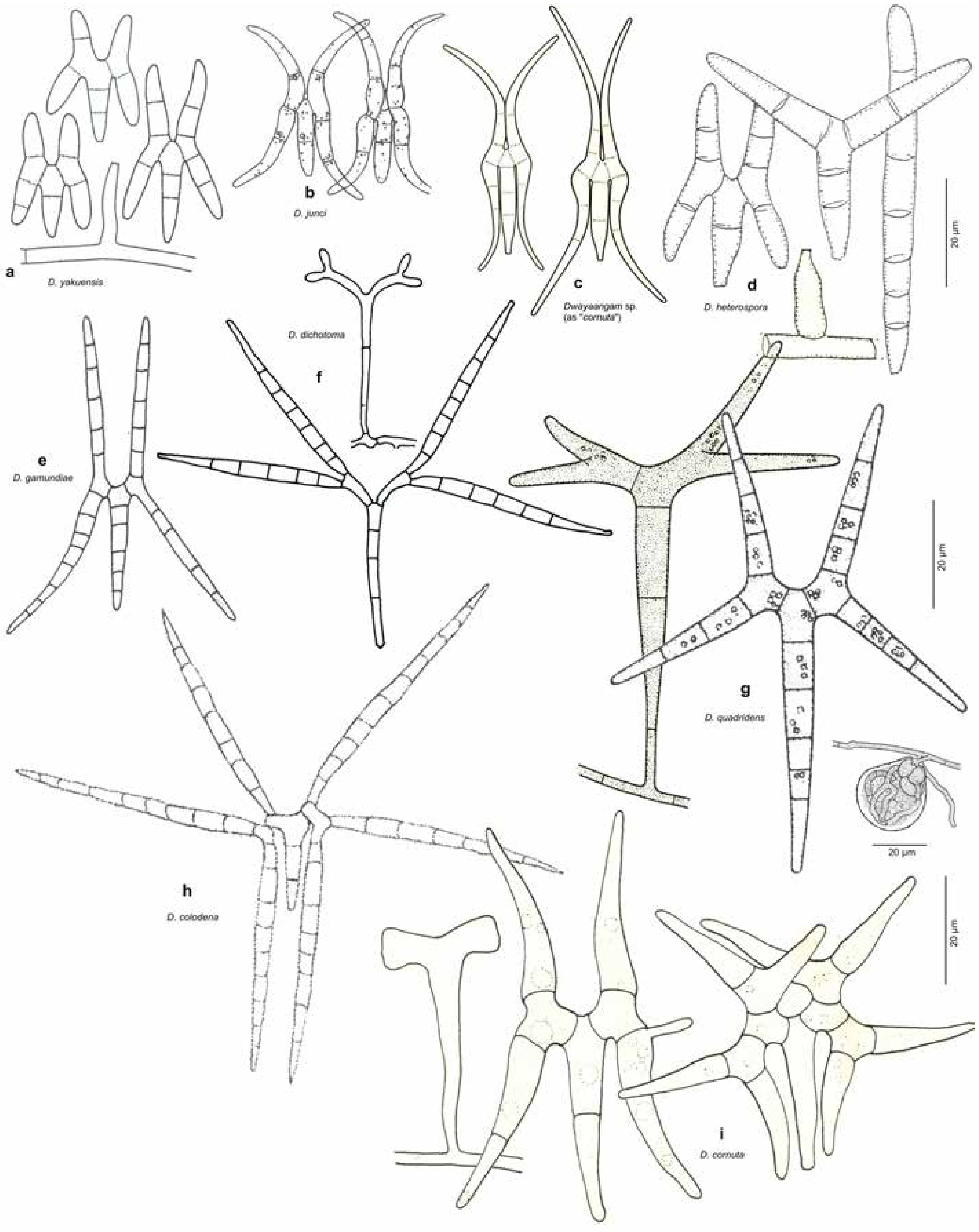


Plate 13. The accepted, hitherto known species of the form genus *Dwayaangam* (conidiophores and conidia, **g**. trapped rhizopod). — **a**. from Matsushima (1975), **b**. from Kohlmeyer et al. (1998), **c**. from Matsushima (1993), **d**. from Barron (1991c), **e**. from Cazau et al. (1993), **f**. from Nawawi (1985a), **g**. from Drechsler (1962), **h**. from Sokolski et al. (2006), **i**. from Descals & Webster (1982).

(see under *Brachyphoris*, p. 218). Moreover, the droplets in the rather broad cells of the living conidia of *D. quadridens* as drawn by Drechsler should be of non-lipidic nature and point to a relationship with *Hyalorbilia*, in which these droplets were found to be characteristic and branched conidia occur in some species.

Gamsylella M. Scholler, Hagedorn & A. Rubner – (Tab. 50, Pl. 14, see also Tab. S11)

This genus was erected by Scholler et al. (1999) for six species that trap nematodes by means of sessile adhesive knobs or two- to multicelled columns which tend to form arches or scalariform bridges: *G. arcuata* (type species), *G. gephyropaga*, *G. lobata*, *G. parvicollis*, *G. phymatopaga*, and *G. robusta*. According to Rubner (1996) and Scholler et al. (1999), '*Dactylella*' *cionopaga* is a synonym of *G. gephyropaga*, but this synonymy is questioned by molecular data. The generic name was chosen in honour of the famous mycologist Walter Gams.

The circumscription of the genus is problematic because of a high diversity in the trapping organs. The limits between sessile and stalked adhesive knobs are gradual, and strong variation in the constriction of sessile knobs and columns complicate their classification. As a consequence, trapping organs with a strong constriction, i. e., globose sessile knobs that occur one above another (Fig. 106: h, i), could be treated as a modification of either stalked adhesive knobs (by proliferation) or adhesive columns. One species (*G./D. parvicollis*, Pl. 8: i) forms different types of trapping organs, some of which are reminiscent of *Gamsylella* and others of *Dactylellina*. Scholler et al. (l.c.) placed it in *Gamsylella* because of sessile adhesive knobs that proliferate to form adhesive columns of roundish cells similar to *G. lobata*, or adhesive arches of elongate cells with only slight constrictions at the septa similar as in *G. arcuata*. However, *D. parvicollis* predominantly forms very short- to long-stalked adhesive knobs (see Drechsler 1962, pls 4–5; Jarowaja 1968a; Rubner 1996: fig. 44). This feature was not mentioned when Scholler et al. placed *D. parvicollis* in *Gamsylella*, whereas Yang et al. (2007: fig. 3), who classified it in *Dactylellina*, listed for this species only stalked, sessile, and superimposed (proliferating) knobs in their table of trapping organ types, but no adhesive columns. For more details about the different phylogenetic concepts of the genus see under series *Gamsylella*, p. 1610 ff.

No teleomorph is known for any of the anamorphic states here accepted in *Gamsylella*, with exception of '*Dactylella*' *alba*, described by Yu et al. (2009a) as anamorph of *O. alba* (Pl. 14: a). The authors misinterpreted the stalked adhesive knobs as a new type of spores similar to chlamydospores, and placed the species in *Dactylella*, although their phylogenetic analysis rather suggested placement in *Dactylellina*. In their elongate shape the heads of the adhesive knobs resemble those of '*Dactylellina*' *entomopaga* (Pl. 14: b) which, besides '*D.*' *ferox* (Pl. 14: c), deviates from all other species recognized in *Dactylellina* in a thick adhesive mucilage around the heads. Adhesive knobs with a thick mucilage represent an adaptation to the trapping of small arthropods. We observed this type of adhesive knob in two European collections referred to *O. alba*, and the presence of larger amounts of gel could also be demonstrated for the Chinese type of *Dactylella alba* (see p. 1615).

Gamsylella species have been collected in moist habitats like soil, decaying herbal material and wood, or on bryophytes. They are predatory by trapping nematodes as a rule; Drechsler observed once in *G. gephyropaga* also captured rhizopods. Abiko et al. (2005) reported mites and rotifers as additional prey of that species. Our new concept includes the capture of arthropods. *Gamsylella* species are probably worldwide distributed.

In the present study we reduce the genus *Gamsylella* with eight accepted species (Tabs 50 & S11) to a series of section *Arthrobotrys* and retain it as separate from series *Dactylellina*. The previous circumscription is changed, with *Dactylellina phymatopaga* (= *D. parvicollis*) and *Orbilia quercus* remaining in series *Dactylellina*, and with '*D.*' *entomopaga* and '*D.*' *ferox* newly included in series *Gamsylella*. This concept is, however, predominantly based on molecular results, which place also *O. alba* and *O. anigozanthi* (the latter without anamorph) in this clade. The arthropod-trapping taxa might deserve a separate series because of their special trapping organs.

Haptocara Drechsler – (Pl. 53)

The nematophagous genus *Haptocara* was erected by Drechsler (1975) with *H. latirostrum* as type species. The hitherto only described species is characterized by broad, 2–4-septate conidia with a hyphal, filiform, subapically emerging nonseptate appendage and a later developing subglobose adhesive knob at the apex (see Pl. 53: 3). Molecular data do not exist and a connection to a teleomorph is unknown. Drechsler (1975) demonstrated that not only the conidial knobs are able to capture

Table 50. Overview of the accepted species of *Gamsylella*.

Species	Conidial size [µm]	Number of septa	Conidial shape	Habitat	Reference
'*Dactylellina*' *ferox* (Onofri & Tosi) M. Scholler et al.	(13–)15–18(–24.5) × (5–)6–8(–9)	1	obovoidal to clavate	on mosses (*Bryum algens*, *Ceratodon purpureus*), continental Antarctica, predatory on springtails	Onofri & Tosi 1992
'*Dactylella*' *alba* Z.F. Yu & K.Q. Zhang (= *Orbilia alba*)	18–26(–34) × 5–7(–8)	1(–3)	cylindric (-ellipsoid)	on decaying bark of a broad-leaved tree, China, capturing springtails, flies, mites	Yu et al. 2009a, present study
'*Dactylellina*' *entomopaga* (Drechsler) M. Scholler et al.	15–28 × 4.5–5.5	1	cylindrical to clavate	decaying roots of *Polygonum pennsylvanicum*, USA, capturing springtails (and nematodes)	Drechsler 1944b
G. arcuata (Scheuer & J. Webster) M. Scholler et al. **Type species**	30–45 × 4.5–6	3	fusiform	decaying leaves of *Ammophila arenaria*, UK, nematophagous	Scheuer & Webster 1990
G. gephyropaga (Drechsler) M. Scholler et al.	27–46 × 16–21	(2–)3–4	top-shaped, fusiform	decaying leaves and wood, from soil, Germany, Sweden, Italy, Spain, UK, USA, nematodes, mites, rotifers, rhizopods	Drechsler 1937a, Rubner 1996, Abiko et al. 2005*
G. lobata (Dudd.) M. Scholler et al.	38–55 × 8–12	3	cylindrical to clavate	from *Dicranella heteromalla*, rabbit dung, Germany, UK, nematophagous	Duddington 1951b, Rubner 1996
G. cionopaga (Drechsler) Yang et al.	35–60 × 13–21	(2–)3–4(–6)	fusiform	decaying culms of *Triticum aestivum*, USA, nematophagous	Drechsler 1950a
G. robusta (J.S. McCulloch) M. Scholler et al.	68–85 × 20–30	3–5	fusiform	from soil, Australia, nematophagous	McCulloch 1977, Rubner 1996

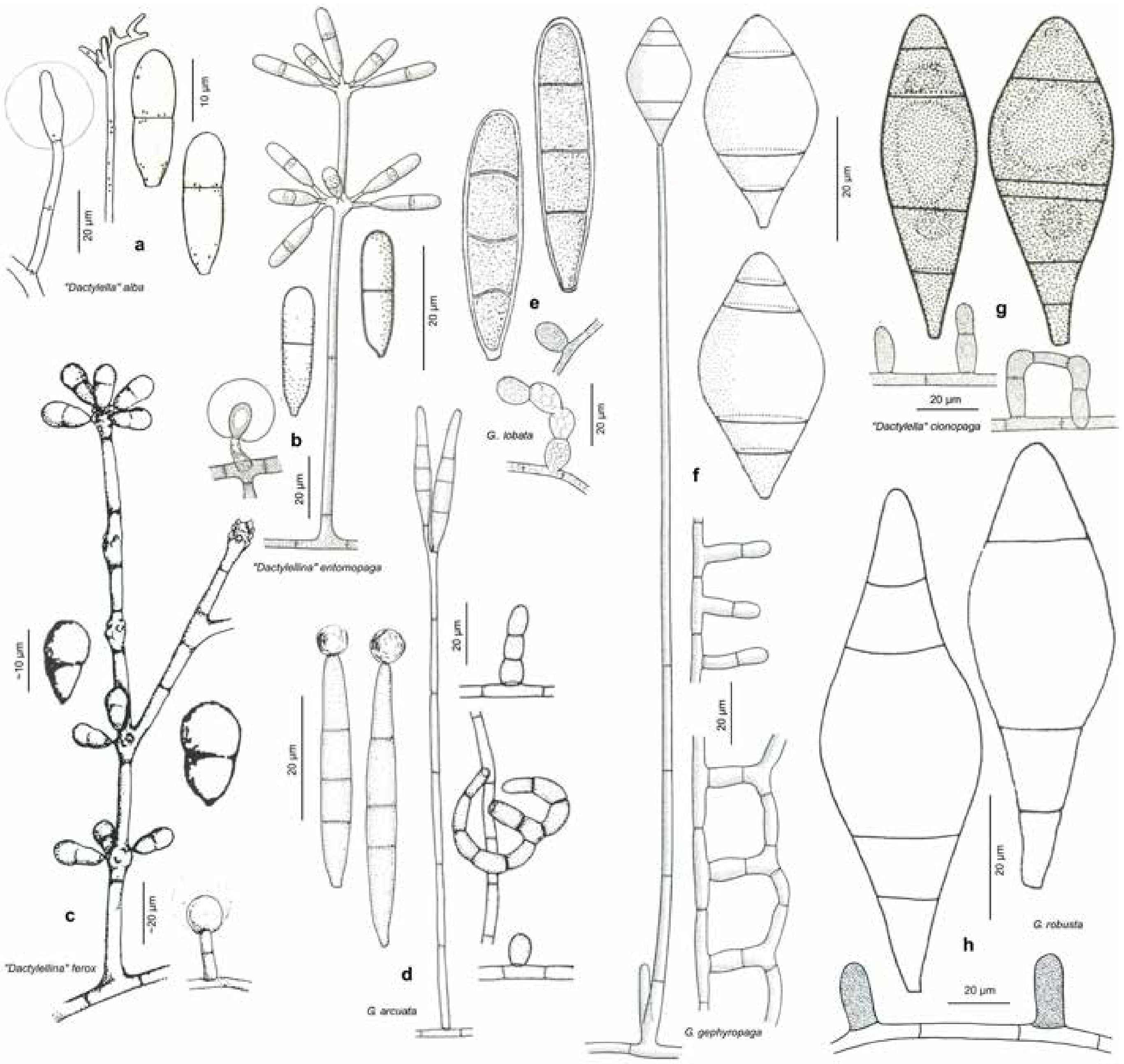


Plate 14. The accepted, hitherto known species of *Gamsylella* (conidiophores, conidia and trapping organs). — **a**. from Yu et al. (2009a) but adhesive knob from H.B. 9051a, **b**. from Drechsler (1944b), **c**. from Onofri & Tosi (1992), **d**. from Scheuer & Webster (1990), **e**. from Duddington (1951b), **f**. from Drechsler (1937a), **g**. from Drechsler (1950a), **h**. left conidium from Rubner (1996), right conidium and adhesive peg-like knobs from McCulloch (1977). The scale for conidia and conidiophores of *Dactylellina ferox* in Onofri & Tosi's (1992) illustration is modified by the factor ~1.45 in order to match the measurements given in their description.

nematodes with their adhesive surface, but also smaller knobs formed on short lateral branches of the mycelium.

In the present study, *Haptocara* is considered as probably orbiliaceous and closely related to *Lecophagus* based on very similar trapping organs and broad mycelial hyphae, also because of similar cubical bodies observed in an unnamed further member of *Haptocara* (see Pl. 53: 1–2).

Helicoon Morgan – (Pl. 15)

The genus was erected by Morgan (1892) with *H. sessile* Morgan as type species. The main characteristics of the genus in later circumscriptions are filiform, multiseptate, strongly coiled (helicosporous), barrel-shaped, hyaline to fuscous conidia, coiled more tightly towards the poles, produced on short to long, hyaline to brown conidiophores (Goos et al. 1986). Moore (1955) presented in his key to *Helicoon* nine and Goos et al. (l.c.) eight species. Among these, *H. sessile* and *H. farinosum* Linder deviate from the others in hyaline conidia and conidiophores.

Voglmayr (1994, 2000) found that the sense of rotation of the helicoid conidia in *Helicoon* represents a species-specific marker. As an exception, however, conidia of *H. sessile* were twisted either like a left-hand or a right-hand thread, and for a given strain this feature was consistent on the natural substrate as well as in culture (Pl. 15: b). Therefore, he assumed that two species are involved, according to the sense of rotation. Regrettably, molecular data could only be gained from a single strain which showed left-handed rotation. Reports in the older

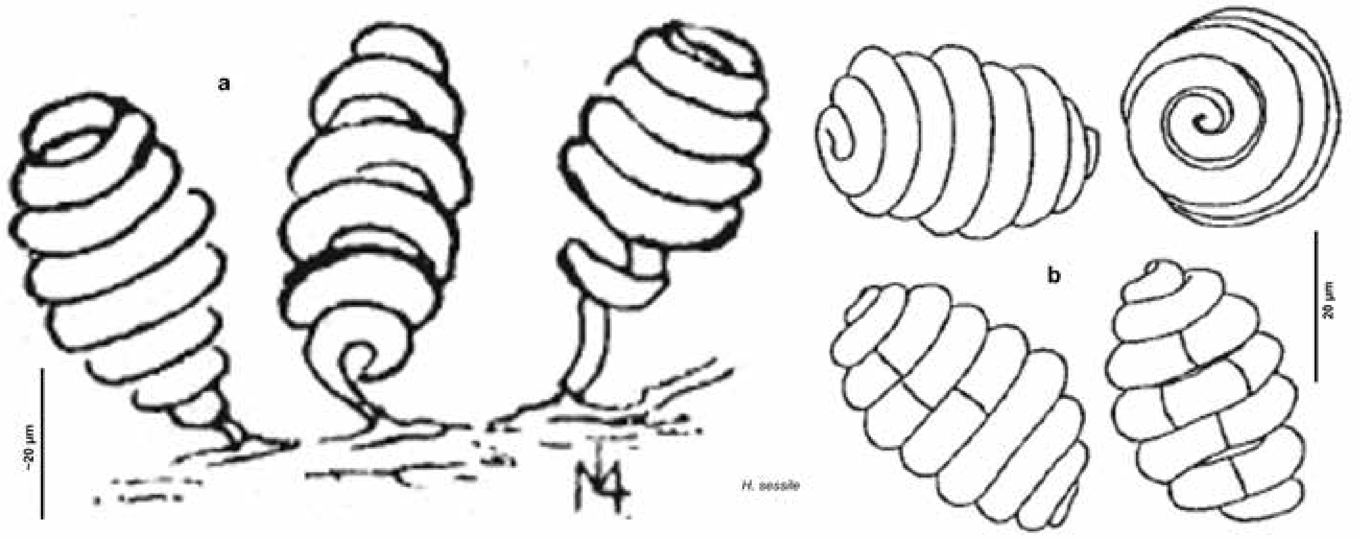


Plate 15. *Helicoon sessile* (conidia and conidiophores). — **a**. conidia twisted as right-handed helix (from Morgan 1892, type, but see in text), **b**. conidia from two different collections from the same geographic area, the above twisted left-handed, the below right-handed (from Voglmayr 2000).

literature usually do not stress this character, however, and illustrations may be misleading. For instance, Morgan (1892) figured the conidia of *H. sessile* as a right-handed helix but Voglmayr (1994) found them left-handed in the type material. Therefore, he assumed that the conidia in Morgan's sketch might have changed their chirality during reproduction.

Genera with similarly coiled conidia, such as *Helicoma* Corda, *Helicomyces* Link, and *Helicosporium* Nees, are anamorphs of *Tubeufia* Penz. & Sacc. and allied genera in the *Tubeufiaceae*, *Dothideomycetes* (Goos 1987). Most species of *Helicodendron* Peyronel so far sequenced belong to the *Leotiomycetes* (Tsui & Berbee 2006), although conidial morphology sometimes closely matches that of *Helicoon*, particularly *H. sessile*.

Tsui & Berbee (2006) found that *Helicoon* species, despite their distinctive, barrel-shaped conidia, have evolved polyphyletically in different ascomycete orders. They analysed three species and found in their phylogram *H. fuscosporum* Linder in a clade with *Botryosphaeria rhodina* Berk. & M.A. Curtis (*Dothideomycetes*), *H. gigantisporum* Goh & K.D. Hyde within the *Tubeufiaceae* (*Dothideomycetes*), and *H. richonis* (Boud.) Linder within the *Pleosporales*. *H. farinosum* was found to be the anamorph of *Ascotaiwania hughesii* Fallah, J.L. Crane & Shearer in the *Sordariomycetes* (Fallah et al. 1999). The type species *H. sessile* was not studied, however. Tsui & Berbee refer to Pfister (1997) who found *H. sessile* to be the anamorph of *Orbilia luteorubella*. However, Pfister's (1997) result was doubted by Hagedorn & Scholler (1999), because Pfister's sequences fall in the *Hypocreales*.

Helicoid conidia that form barrel-shaped bodies trap air in their interior which enables them to float on the water surface (aero-aquatic hyphomycetes). The mentioned molecular results show that such conidia, which represent an adaptation to dispersal in aquatic environments, arose convergently from very different classes in the *Ascomycota* (Tsui & Berbee l.c.).

In the present study, Pfister's finding of *H. sessile* as anamorph of *O. luteorubella* in North America is affirmed by our European and a Chinese ascospore isolate of *O. luteorubella* which also produced *H. sessile*. This indicates that Pfister's sequences belong to a hypocrealean contaminant (see p. 976). Among the known species of *Helicoon*, only the type species is connected to *Orbiliomycetes*, to the present knowledge, but a more simplified conidial type with just one turn occurs in the closely related *O. sarraziniana*. The conidia of *H. sessile* measure 30–59 × 17–30 µm, with 4–16 turns, and records are known from North America, Europe and Asia, on periodically submerged leaves and wood, mainly at standing water bodies.

The genus *Helicoon* is reduced here to a series of *Orbilia*, which belongs together with the closely related series *Pseudotripoconidium* to section *Helicoon*. Series *Helicoon* includes also closely related taxa with anguillospora-like anamorphs.

Lecophagus M.W. Dick – (Tab. 51, Pl. 16)

When investigating the systematic position of the rotifer-trapping *Zoophagus insidians* Sommerst. (*Zoopagales*), Dick (1990) stated that two distinct fungi were reported under this binomial. When studying an isolate deposited by H.C. Whisler

Table 51. Overview of the accepted species of *Lecophagus*.

Species	Conidial size [µm]	Number of septa	Habitat	Reference
L. navicularis (Tzean & G.L. Barron) M.W. Dick	28–34 × 6–9	(2–)3	from old manure, Ontario (Canada), predatory on bdelloid rotifers	Tzean & Barron 1983
L. muscicola (G.L. Barron et al.) Tanabe et al. (= *L. fasciculatus*) **Type species**	125–200 × 6.2–11 73–145 × 6–8 112.5–135 × 7.5–8.7	9–11 4–11 ~8	from organic debris or mossy soil in forests, water-filled tree-holes, New Zea-land, Japan, Hungary, capturing tardigrades and bdelloid or ploimoid rotifers	Barron et al. 1990 Dick 1990 (as *L. fasciculatus*) Magyar 2006
L. longisporus (G.L. Barron et al.) Tanabe et al.	125–228 × 8.5–10	(9–)10	from mossy soil, New Zealand, Ontario (Canada), capturing tardigrades and bdelloid rotifers	Barron et al. 1990
L. vermicola D. Magyar et al.	(45–)50–80(–86) × (8–)10.5–16.5(–18)	(3–)7(–8)	from xeric bark, Luxembourg, France, Hungary, capturing nematodes	Magyar et al. 2016

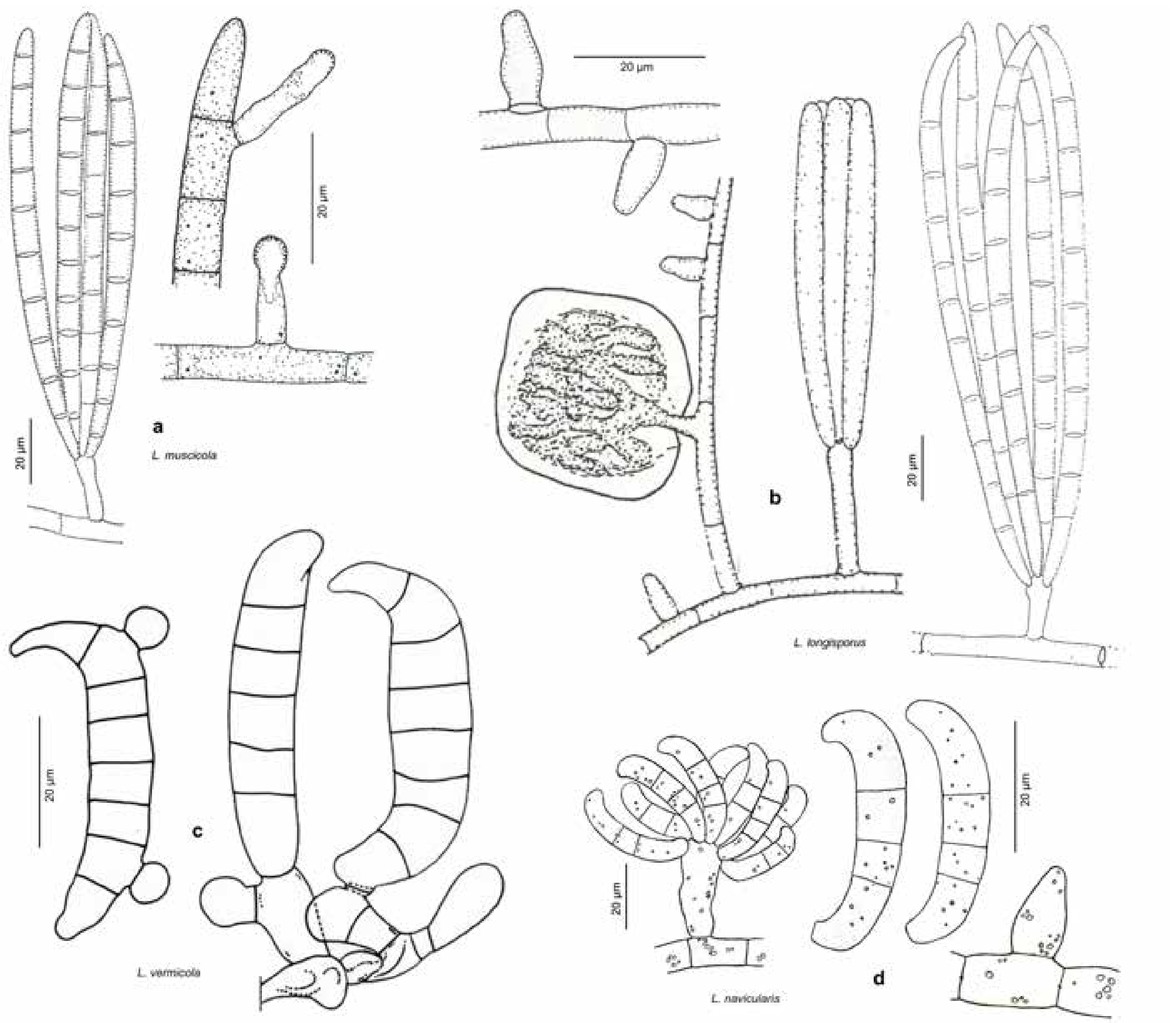


Plate 16. The accepted, hitherto known species of *Lecophagus* (conidiophores, conidia, and adhesive pegs). — **a**. from Barron et al. (1990), **b**. from Tzean & Barron (1983), **c**. from Magyar et al. (2016), **d**. from Barron et al. (1990).

as *Z. insidians* (APCC 9000), Dick found that this was not *Z. insidians* but an undescribed species, for which he proposed the new genus *Lecophagus* and the new species *L. fasciculatus* M.W. Dick. However, while Dick believed that APCC 9000 was the axenic culture which Whisler & Travland (1974) used for their ultrastructural studies (see also Morikawa et al. 1993), we assume that different strains were isolated by Whisler & Travland. Actually, their photographs show non-septate hyphae and cylindrical, basally non-septate pegs of varying length typical of *Z. insidians*.

Besides the new species *L. fasciculatus* (= *Z. insidians* s.auct.), Dick included *Cephaliophora navicularis* Tzean & G.L. Barron in the genus. The name of the new genus is derived from the rotifer genus *Lecane*, which Whisler & Travland 1974 used in their studies, and *phagus* (from Greek *phageín* = to eat), and indicates the ability to prey on rotifers. According to Dick, the main characteristics are: multinucleate mycelial cells, short lateral adhesive pegs of zoopagalean form, and blastic conidiogenesis on simple, short, lateral conidiogenous cells. Dick described the conidia as fusiform (although in the two included species they are drawn by him more cylindrical than fusoid), septate, slightly to strongly falcate. *L. fasciculatus* has very long conidia, whereas those of *L. navicularis* are much shorter and more canoe-shaped (claw-like). A possible relationship to the *Zoopagales* (earlier referred to the zygomycetes, today classified in *Zoopagomycotina*) was assumed.

In the same year, Barron et al. (1990) described two new species in *Cephaliophora* Thaxt. that produce large, slightly falcate conidia and capture rotifers and tardigrades, *C. muscicola* G.L. Barron et al. and *C. longispora* G.L. Barron et al. The genus *Cephaliophora* was erected by Thaxter (1903) with *C. tropica* Thaxt. as type species and *C. irregularis* Thaxt. (both isolated from animal dung, the latter preying on nematodes, see Barron et al. 1990). Based on morphological criteria, Morikawa et al. (1993) stated that *C. muscicola* and *L. fasciculatus* were conspecific. Because Barron et al.'s (1990) publication appeared one month earlier than that of Dick, *C. muscicola* has priority over *L. fasciculatus.* Morikawa et al. did not accept Dick's new genus *Lecophagus* but retained the species in *Cephaliophora*. They compared *Cephaliophora* with *Zoophagus insidians* and found by TEM that the central pore structure of hyphal and conidial septa of *C. muscicola* and *C. longispora* resembles those of ascomycetes rather than of zygomycetes which lack perforated septa and pore plug mechanisms. Further, *Cephaliophora* formed anastomoses between hyphae or conidia, a feature unknown in zygomycetes.

Tanabe et al. (1999) conducted molecular studies (18S rDNA) with four *Cephaliophora* species in comparison with nematophagous hyphomycetes. In their neighbour-joining tree *C. tropica* and *C. irregularis* are situated near *Ascodesmis sphaerospora* W. Obrist (*Pezizales*), whereas *C. muscicola* and *C. longispora* clustered in a monophyletic group with nematophagous hyphomycetes of the genera *Arthrobotrys*, *Monacrosporium*, and *Dactylella* (*L. navicularis* was not sequenced until now). Therefore, Tanabe et al. resurrected the genus *Lecophagus*, to which they transferred the two rotifer capturing species *C. muscicola* and *C. longispora.* This genus was emended by these authors in some points and transferred from the zygomycetes to the ascomycetes, with probable placement within the 'discomycetes'.

Three of the four species accepted in *Lecophagus* were collected in soil, moss, manure, treeholes and at shores of freshwater lakes in Canada, Japan, New Zealand, Europe, and Antarctica. They are predatory on rotifers and tardigrades. A fourth, recently described *Lecophagus* species, *L. vermicola* Magyar et al. (2016), is somewhat aberrant in growing on xeric branches and trunks, where it captures nematodes by sessile adhesive knobs formed on mycelial hyphae and on the large conidia (see Pl. 16: c and p. 300). Similar broad hyphae are described for *Haptocara* Drechsler, a nematophagous genus which, in our opinion, appears to be closely related to *Lecophagus*. *Haptocara* differs from *Lecophagus* mainly in morphology of conidia, showing a ± globose, sessile adhesive knob at their apex and a long, filiform hypha emerging laterally at their subapex (see Pl. 53). *L. vermicola* shares with *Haptocara* the nematophagy by means of sessile adhesive knobs, which are, however, formed in *L. vermicola* at the dorsal side of conidia.

McInnes (2003) described *L. antarcticus* from benthic cyanobacterial mats and sediments at the margin of lakes on maritime Antarctic Signy Island, capturing tardigrades and bdelloid rotifers. Apart from being invalid, the distinguishing features of this taxon against *L. muscicola* and *L. longisporus* are doubtful (see under *Lecophagus*, p. 297).

In the present study, *Lecophagus* is accepted as a separate genus within the *Orbiliaceae*. Teleomorphs of described anamorph taxa are unknown, but the connection between an undescribed anamorph and teleomorph exploiting dead rotifer bodies on xeric substrate is reported under the new name *L. ellipsoideus*. This connection was assumed based on strikingly similar, very broad mycelial hyphae containing extraordinary cubical bodies (see p. 94), and placement in *Lecophagus* was verified by molecular data gained from apothecia. The generic name *Lecophagus* is adopted here for the holomorph of these fungi. Some further observations support that the ecological range of *Lecophagus* encompasses also xeric substrate (see p. 290).

Microdochiella M. Hern.-Restr. & Crous – (Pl. 17)

Hernández-Restrepo et al. (2015) proposed this genus as different from *Microdochium* Syd. (*Sordariomycetes*) based on a single atypical species, *Microdochium fusarioides* D.C. Harris, growing on oospores of *Phytophthora syringae*. The three CBS cultures examined by these authors include the type strain. They remained sterile, therefore, the anamorph could not be redescribed. The gained sequences clustered in their phylogenetic analysis (LSU) highly supported as a sister clade of *Vermispora*.

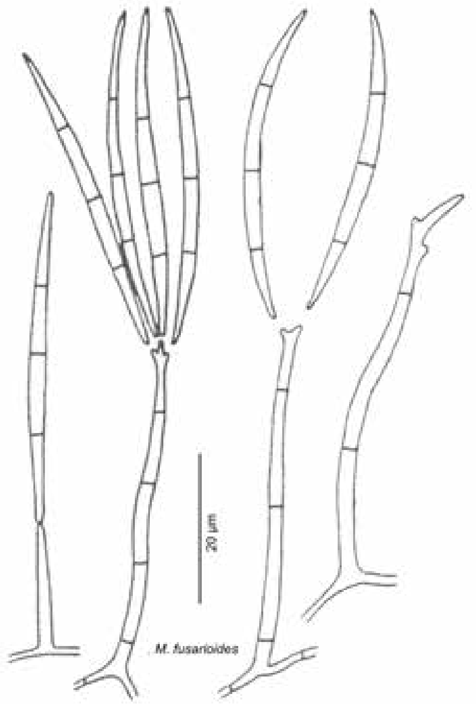


Plate 17. Conidiophores and conidia of *Microdochiella fusarioides* (from Harris 1985).

Morphologically, *Vermispora* and *Microdochiella* are very similar, and their main difference was thought to be an ecological one, parasitism on oospores in *Microdochiella* as reported by Harris (1985). However, spores of oomycetes are also invaded by *V. spermatophaga* (Drechsler 1938), and a strain of this species isolated from *Phytophthora megasperma* var. *sojae* (CBS 255.76) clustered in the *Vermispora* clade in the phylogenetic analyses of Chen et al. (2006a) and Hernández-Restrepo et al. (l.c.).

Microdochiella fusarioides (D.C. Harris) M. Hern.-Restr. & Crous was isolated during an experiment on the survival of *Phytophthora* oospores, which were buried for 8 months in soil of an apple orchard in Kent, U.K., together with the apple leaves which contained them. The species is characterized by narrowly fusiform, slightly curved (falcate), (1–)3(–5)-septate conidia of 30–60 × 2–3 µm, formed singly or in clusters of 2–3(–4) on short denticles at the tip (or sometimes at the sides or in whorls one above another) of very short to medium long, 0–7-septate conidiophores. From *Vermispora* it seems to differ merely in the rather narrow conidia with a drop of moisture at their mid-point, and presence of chlamydospores.

In the present study, *Microdochiella* is considered to be congeneric with *Vermispora* based on its close morphological and molecular similarity, but also *Vermispora* is included in *Hyalorbilia* despite a high molecular distance to the core clade of *Hyalorbilia* (see under *Vermispora*, p. 246–247).

Mycoceros D. Magyar & Z. Merényi – (Pl. 18)

Mycoceros was introduced by Magyar et al. (2017b) for a single species, *M. antennatissimus*. It is named after the shape of the conidia resembling horns with thin and often long branches, preying on wind-borne pollen grains which it apparently captures by erect hyphae. Its conidia resemble those of *Dwayaangam*

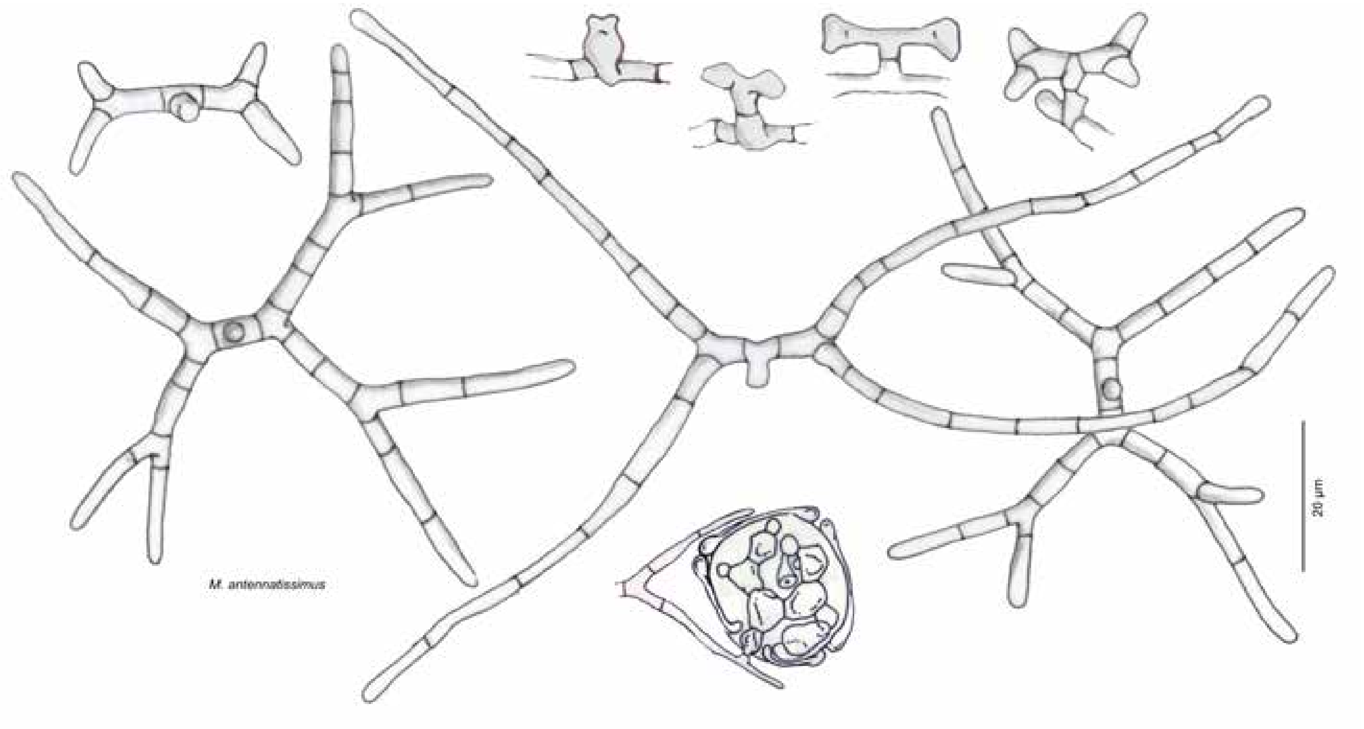


Plate 18. Conidiophores and conidia of *Mycoceros antennatissimus*, with infected pollen (from Magyar et al. 2017b).

but the primary arms are longer than the non-septate main axis, and the conidia are often three times dichotomously branched. No teleomorph is known. The similar pollen-capturing genus *Retiarius* differs by trinacrium-, curucispora-, or dwayaangam-like conidia, the latter with primary arms shorter than the septate main axis, but mainly by molecular data. In Magyar et al.'s (2017b) molecular phylogenetic analysis of different classes of ascomycetes, *Mycoceros* nested with high support as a sister clade to all the remaining *Orbiliomycetes*, nevertheless, it was considered to belong to this class.

M. antennatissimus was so far reported from xeric bark of *Elaeagnus angustifolia*, *Platanus* × *acerifolia*, and *Taxus baccata* in Budapest, Hungary, on which it parasitizes on pollen of *Pinaceae*.

In the present study, *Mycoceros* is accepted as a separate genus based on its isolated basal placement in phylogenetic analyses. Two samples possibly belonging to *M. antennatissimus* were observed by us on the natural substrate (see p. 287).

Pseudotripoconidium Z.F. Yu & K.Q. Zhang – (Pl. 19)

Yu et al. (2011) introduced the genus *Pseudotripoconidium* to accomodate an anamorph, *P. sinense* Z.F. Yu & K.Q. Zhang, which they obtained in four ascospore isolates from apothecia identified as *Orbilia* aff. *luteorubella* (= *O. sinensis*). The characters are: conidiophores 110–140 µm long, simple or occasionally branched, with prominent denticles near the apex, conidia non-septate, inversely pyramidal, slightly laterally compressed and with ± distinct nipple-shaped protuberances at their broad distal end, containing one or several large oil drops. The generic name refers to the conidial shape which resembles that in *Tripoconidium* (see p. 246).

Su et al. (2011c) reported and figured a *Pseudotripoconidium* anamorph from pure culture of *O. acicularis*, and H.Y. Su (pers. comm.) obtained such anamorphs in several further isolates here described as *O. fusiformis*, *O. jinguangsiensis*, and *O. tenuispora*. All these samples originate from montane, subtropical humid (winter-dry) southern China. They were isolated from ascospores from apothecia on decaying fallen branches. No trapping devices are known. A phylogenetic analysis of ITS rDNA by Yu et al. (l.c.) showed that the four investigated isolates clustered in a clade with two sequences in GenBank under the name *O.* cf. *luteorubella* (U72607 = D.H.P. 146, FJ719770). The former strain is a non-sporulating ascospore isolate from a temperate North American collection genetically connected to *Pseudotripoconidium* and described as *O. tenuispora* in the present monograph, the latter a Chinese isolate with a *Helicoon* anamorph falling in the scope of European *O. luteorubella*.

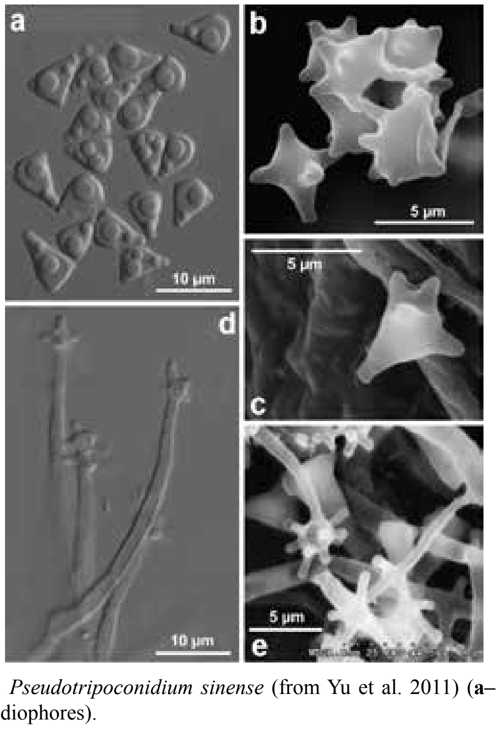


Plate 19. *Pseudotripoconidium sinense* (from Yu et al. 2011) (**a–c**. conidia, **d–e**. conidiophores).

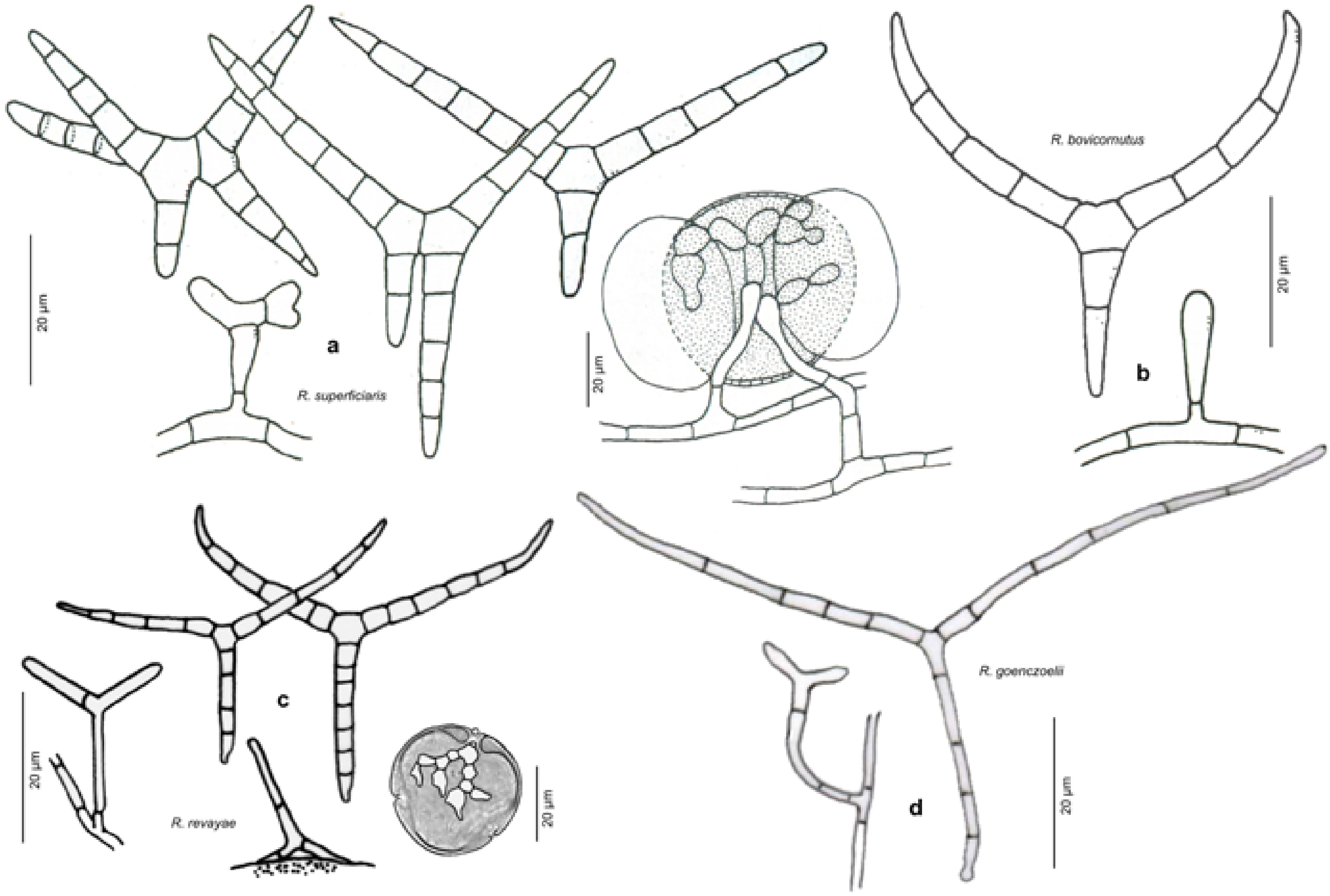


Plate 20. The accepted species of the genus *Retiarius* (conidiophores, conidia, and infected *Tilia* pollen). — **a** and **b**. from Olivier (1978), **c** and **d**. from Magyar et al. (2017a).

Similarly shaped conidia are found in the genus *Heliscella* Marvanová, but here conidiogenesis is phialidic. Conidia are also similar in *Clavatospora* Marvanová & Sv. Nilsson, *Clavariopsis* De Wild., *Heliscina* Marvanová, and *Coronospora* M.B. Ellis, but they differ in being septate and larger, and no oil drops are mentioned. In none of these genera conidiophores with denticulate apices occur.

In the present study, the genus *Pseudotripoconidium* is reduced to a series of *Orbilia* subgenus *Habrostictis* section *Helicoon* which comprises also series *Helicoon* with scolecosporous conidia currently referred to *Anguillospora* and *Helicoon* (see p. 214 and p. 236). Although we have never observed a pseudotripoconidium-like anamorph in European samples, there is a possibility for the occurrence of this series in Spain (*O.* cf. *sinensis*, Pl. 561: 5–6). The lack of both cultural and molecular data in most of the samples complicates recognition at the series level, because the teleomorphs hardly differ between the two series (see p. 953).

Retiarius D.L. Olivier **–** (Tab. 52, Pl. 20)

The genus *Retiarius*, named after a Roman gladiator armed with a cast net (which he threw over his rival), a trident, and a dagger, was introduced by Olivier (1978) for two species that capture wind-borne pollen grains of *Pinaceae* by means of erect hyphae (Pl. 20: a–b). The type species *R. superficiaris* has dwayaangam- to trinacrium- or curucispora-like conidia; Olivier compared it with the genus *Tripospermum*. The second included species, *R. bovicornutus*, was considered to belong to *Trinacrium* by Matsushima (1993: 30). Two further species with

Table 52. Overview of the accepted species of *Retiarius* (*total size, arm and stipe width evaluated from Olivier's and Magyar et al.'s drawings).

Species	Total size of conidia (height × width) * [µm]	Stipe [µm]	Arms [µm]	Conidial shape	Habitat	References
R. bovicornutus D.L. Olivier*	~47–50 × 45–55	(12–)15–20(–25) × 3.5–4.5(–5.5)	(25–)30–45(–50) × 4–5	Y-shaped	on leaves of *Brabejum stellatifolium*, South Africa, parasitic on pollen grains	Olivier 1978
R. superficiaris D.L. Olivier* **Type species**	~37–60 × 44–66	(8–)10–15 × 4–4.5(–5.5)	(20–)25–35(–45) × 4.5–6	dwayaangam-like, also Y or +-shaped	on leaves of *Eryobotrya japonica*, South Africa, parasitic on pollen grains	Olivier 1978
R. revayae D. Magyar & Z. Merényi	~26–40 × 32–48	†14–22 × 2–3.5	†22–30 × 2–3(–3.5)	Y-shaped	bark of *Taxus baccata*, Hungary, parasitic on pollen grains	Magyar et al. 2017a
R. goenczoelii D. Magyar	~37–70 × 100–150	†19–33 × 1.7–2.5(–3)	†42–90 × 2–2.5	Y/T-shaped	bark of *Platanus* × *acerifolia*, Hungary, parasitic on pollen grains	Magyar et al. 2017a

trinacrium-like conidia were added to the genus by Magyar et al. (2017a). No teleomorph is known.

Magyar et al. (2017a, b) gained rDNA sequences from the ex-type cultures of Olivier's two *Retiarius* species (IMI 223459, 223460) and *R. revayae*, which formed in their phylogenetic analysis a separate group within the clade containing *Lecophagus*.

Retiarius species were reported from South Africa, Europe, and Asia (Magyar et al. l.c., see also Tab. 52). Matsushima (1993: fig. 717, 2005: fig. F574, P508) figured a collection of *R. bovicornutus* from Peru, on palm petioles. Magyar et al. (l.c.) reported *Picea* pollen as nutrient source of their two species, but observed also infected *Tilia* pollen (Pl. 20: c). Olivier (l.c.) used *Pinus radiata* pollen to examine the parasitic behaviour of *Retiarius*.

In the present study, *Retiarius* is accepted as a different genus though very close to our new genus *Amphosoma*, Several samples referable to *Retiarius* were examined, most of them resembling *R. bovicornutus* or *R. revayae* (see p. 283–285).

Tridentaria Preuss – (Tab. 53, Pl. 21)

In the unillustrated protologue of *Tridentaria* Preuss (1852) and its single species *T. alba* Preuss, the hyaline 'spores' are oblong to clavate, and were formed in whitish acervuli on *Brassica oleracea*. The generic name refers to the tridentate shape which originates from the connection of several 'spores' to form a three-armed structure. A later included species, the aquatic hyphomycete *T. setigera* Grove, was combined into *Tetracladium* De Wild. by Ingold (1942) and belongs to the *Helotiales* based on available molecular data. Drechsler (1937b, 1940, 1962, 1964) described four new hyphomycetous, nematode- or rhizopod-trapping species in *Tridentaria*. In spite of the absence of conidiomata, he placed them in this genus because of the staurosporous, normally three-pronged (trident-like) conidia. For a similar reason, two further species were described in *Tridentaria*: *T. fertilis* by Castañeda Ruíz (1988) and *T. subuliphora* by Matsushima (1989, Pl. 21).

Like Drechsler (l.c.), Van der Aa & Van Oorschot (1985) regarded the genus *Tridentaria* as doubtful because 'the type specimen did not bear a fungus which agreed with the very brief original description'. According to the latter authors, similar genera like *Tricornispora* Bonar, *Fumagopsis* Speg., and *Kazulia* Nag Raj with sporodochia and holoblastic conidiogenesis, and *Eriosporella* Höhn. with acervuli and phialidic conidiogenesis, are properly typified and can be regarded as distinct from those taxa described by Drechsler. They concluded that 'the nematode-trapping hyphomycetes formerly placed in *Tridentaria* should be reclassified'.

Numerous genera of aquatic hyphomycetes with similar staurosporous conidia do exist. The tetraradiate form is seen as an adaptation to water dispersal and is a polyphyletic character (Belliveau & Bärlocher 2005). The genera *Alatospora* Ingold, *Articulospora* Ingold, *Flabellocladia* Nawawi, *Flabellospora* Alas., *Fontanospora* Dyko, *Geniculospora* Sv. Nilsson, *Isthmotricladia* Matsush. (with arms at the base strongly attenuated), *Lemonniera* De Wild., *Quadricladium* Nawawi & Kuthub., and *Tetrachaetum* Ingold are to be mentioned here. In *Alatospora* and *Lemonniera*, however, conidiogenesis is phialidic. In *Quadricladium* and *Lemonniera* conidia are attached to the conidiophore at their central cell (i.e., they have no stipe or main axis), while in the other genera, including *Tridentaria*, they insert at the base of a septate stipe. For *Articulospora tetracladia* Ingold and *Geniculospora grandis* (Greathead) Nolan a connection to teleomorphs of *Hymenoscyphus* (*Helotiales*) were found in pure culture (Abdullah et al. 1981, Descals et al. 1984), for *Lemonniera* a relation to the *Helotiales* was indicated by DNA-sequence analysis (Campbell et al. 2006, Baschien et al. 2006), and for *Alatospora* one with *Leotia* (*Leotiales*, Baschien et al. 2006), although sequences of *Alatospora* show also affinities with *Helotiales*. The type of *Flabellocladia*, *F. gigantea* Nawawi (1985b), possibly belongs to *Tridentaria* in the sense of Drechsler, as does *Articulospora foliicola* Matsush., based on a very similar morphology. *Flabellocladia* should be sequenced from the holotype to clarify its possible relationship with *Orbiliomycetes*.

Tridentaria species were isolated from decaying plant material, some were found to capture nematodes and rhizopods by means of sessile adhesive knobs, or parasitize oospores. They have been reported from Asia, Australia, South Africa, Europe, Northern, Middle, and South America (see Tab. 53). Up to now, no teleomorphs were reported in the form genus *Tridentaria*.

In the present study, *Tridentaria* is considered to be a nomen dubium. Tridentaria-like anamorphs developed in pure culture of *Orbilia quaestiformis*, *O. septispora*, and *O. quercus-ilicis* (section *Habrostictis*). In our phylogenetical analyses two non-authentic CBS strains of *T. implicans* and *T. subuliphora* clustered in the clade of series *Orbilia*. Since the identity of the type species of *Tridentaria*, *T. alba*, is doubtful and very probably not orbiliaceous, we use the term 'tridentaria-like' for describing conidia of a shape similar as in those taxa illustrated in Pl. 21.

Table 53. Overview of the accepted species of the form genus *Tridentaria* (the type species *T. alba* is of uncertain identity).

Species	Main axis/stipe [µm]	Arms [µm]	Habitat	Reference
T. tylota Drechsler	19–30 × 3–4.7	13–24 × 2.3–3.7	decaying bean stem, USA, capturing testaceous rhizopods, parasitic on *Pythium* oospores	Drechsler 1964
T. subuliphora Matsush.	12–24 × 3–5	22–35 × 2.8–3.8	decaying leaves, Australia	Matsushima 1989
T. implicans Drechsler	7–20 × 2.5–5	12–55 × 3.5–5.5	decaying leaves and stems, dead banana leaves, rotten wood, Japan, Peru, South Africa, USA, Taiwan, capturing nematodes	Drechsler 1940, Matsushima 1975, 1981, 1987, 1993, 1996
T. glossopaga Drechsler	12–15 × 2.8–3.5	21–45 × 2.2–3	leaf mould, USA, capturing testaceous rhizopods	Drechsler 1962
T. carnivora Drechsler	12–21 × 2.8–3.8	17–44 35–45 × 3–4	leaf mould, USA, capturing testaceous rhizopods, rotten *Acacia* leaves, Taiwan	Drechsler 1937b Matsushima 1987
T. fertilis R.F. Castañeda	3–8 × 2–3	7–20 × 2–3	dead *Poaceae* stem, Cuba	Castañeda Ruíz 1988

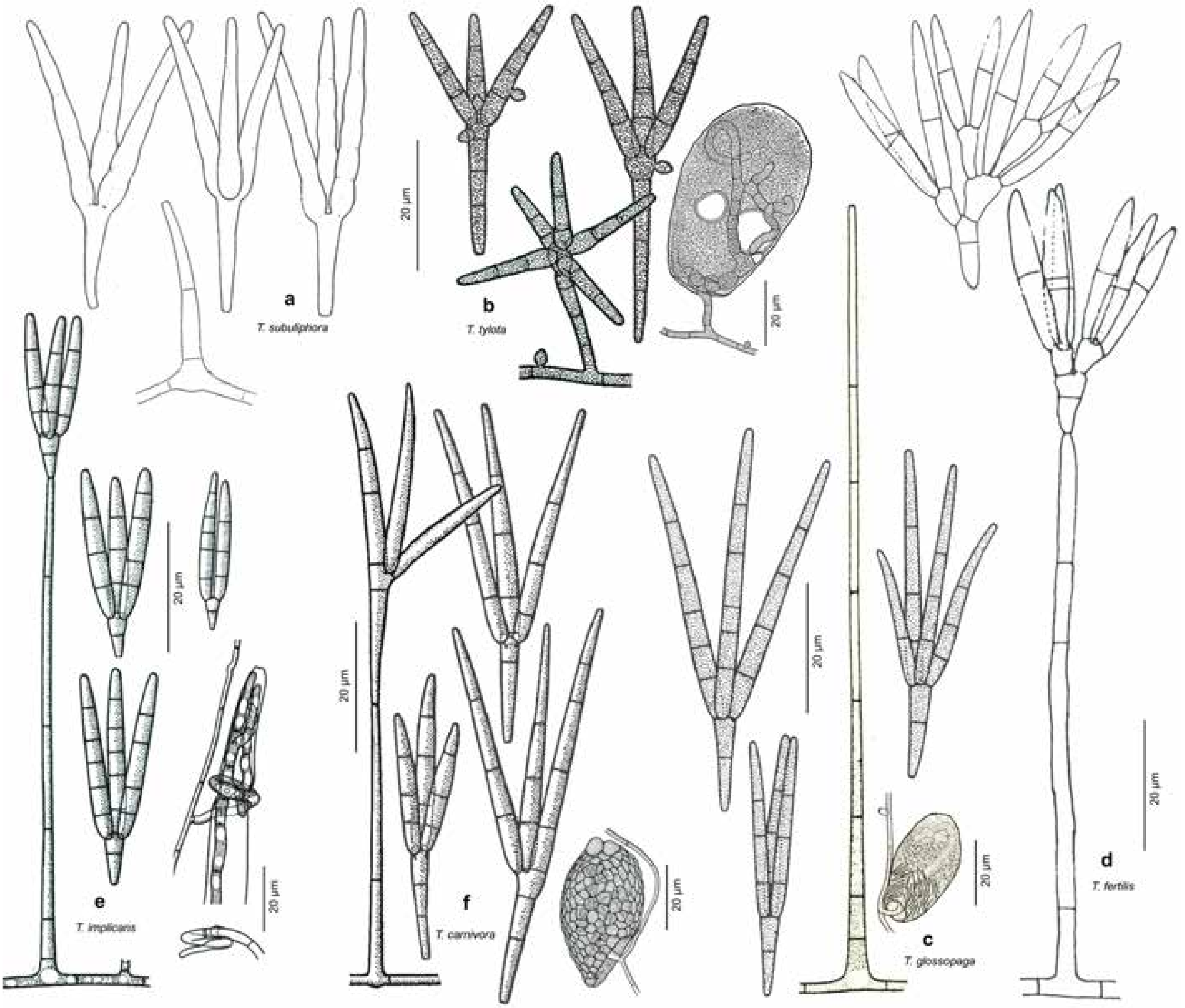


Plate 21. The accepted, hitherto known species of the form genus *Tridentaria* (conidiophores, conidia, and trapped rhizopods). — **a**. from Matsushima (1989), **b**. from Drechsler (1964), **c**. from Drechsler (1962), **d**. from Castañeda Ruíz (1988), **e**. from Drechsler (1940), **f**. from Drechsler (1937b).

Trinacrium Riess in Fresenius – (Tab. 54, Pl. 22)

The genus was erected in 1852 with the single species *Trinacrium subtile* Riess. The main characteristics are the triradiate (Y-shaped), hyaline conidia with one main axis and two divergent arms that arise by dichotomous branching (for the similar form genera *Dicranidion* and *Tridentaria* see there). The name *Trinacrium* refers to the fact that the two arms are hardly distinguishable from the main axis as soon as the conidia are detached. In some cases unbranched phragmoconidia, but also higher-branched conidia were reported to occur together with the typical triradiate conidia (*T. angamosense*, Matsushima 1995; *T. incurvum*, Matsushima 1993; *T. subtile*, Drechsler 1938, Ando 1992).

In the protologue of the type species, a slight uncertainty exists concerning the point of conidial attachment. The two conidia figured by Riess (in Fresenius 1852: pl. V figs 14 & 15) clearly show a scar-like protuberance at the tip of the main axis, reminiscent of *Trifurcospora* K. Ando & Tubaki (1987) where conidial attachment is indeed at the central cell. However, Riess reported and illustrated (l.c.: fig. 17) a very young conidium as being attached with the basal end of its short stipe to the short conidiophore (see Pl. 22: h).

Tzean & Chen (1989) gave an overview of six *Trinacrium* species. 16 species have to date been described, nine of which are listed and figured below (Tab. 54, Pl. 22), while another was transferred to *Arthrobotrys.* The remaining six species are only known from the short and mostly unillustrated type descriptions and are, therefore, doubtful. Three of them have triradiate conidia: *T. mycogenum* Tassi (conidial arms 15–20 × 4 µm, on *Nectria*, between *Fusarium*, Italy, Saccardo 1902), *T. torulosum* Sacc. & Malbr. (conidial arms 35–40 × 3–4 µm, on mycelium of *Sphaerulina boudieriana* on leaf of *Scabiosa sylvatica*, France, Saccardo 1886), and *T. minus* Speg. (conidial arms 20–25 × 2 µm, on *Fumago pannosa* on leaf of *Pernettya mucronata*, South America, Saccardo 1892). The other three taxa have 3–4- or 4-radiate conidia and, therefore, deviate from the form genus *Trinacrium* s.str.: *T. pulchellum* Speg., the presumed anamorph of *Paracapnodium pulchellum* Speg. (*Dothideomycetes*, with arms 10–15 × 2 µm, on leaf of *Ilex paraguariensis*, Java, Spegazzini 1909: 327, fig. 7), *T. subtropicale* Speg. (arms 30 × 5–6 µm, on 'subiculum' of *Symphaeophyma subtropicale* on leaf of *Lucuma neriifolia*, Argentina, Spegazzini 1912), and *T. tropicale* Speg.

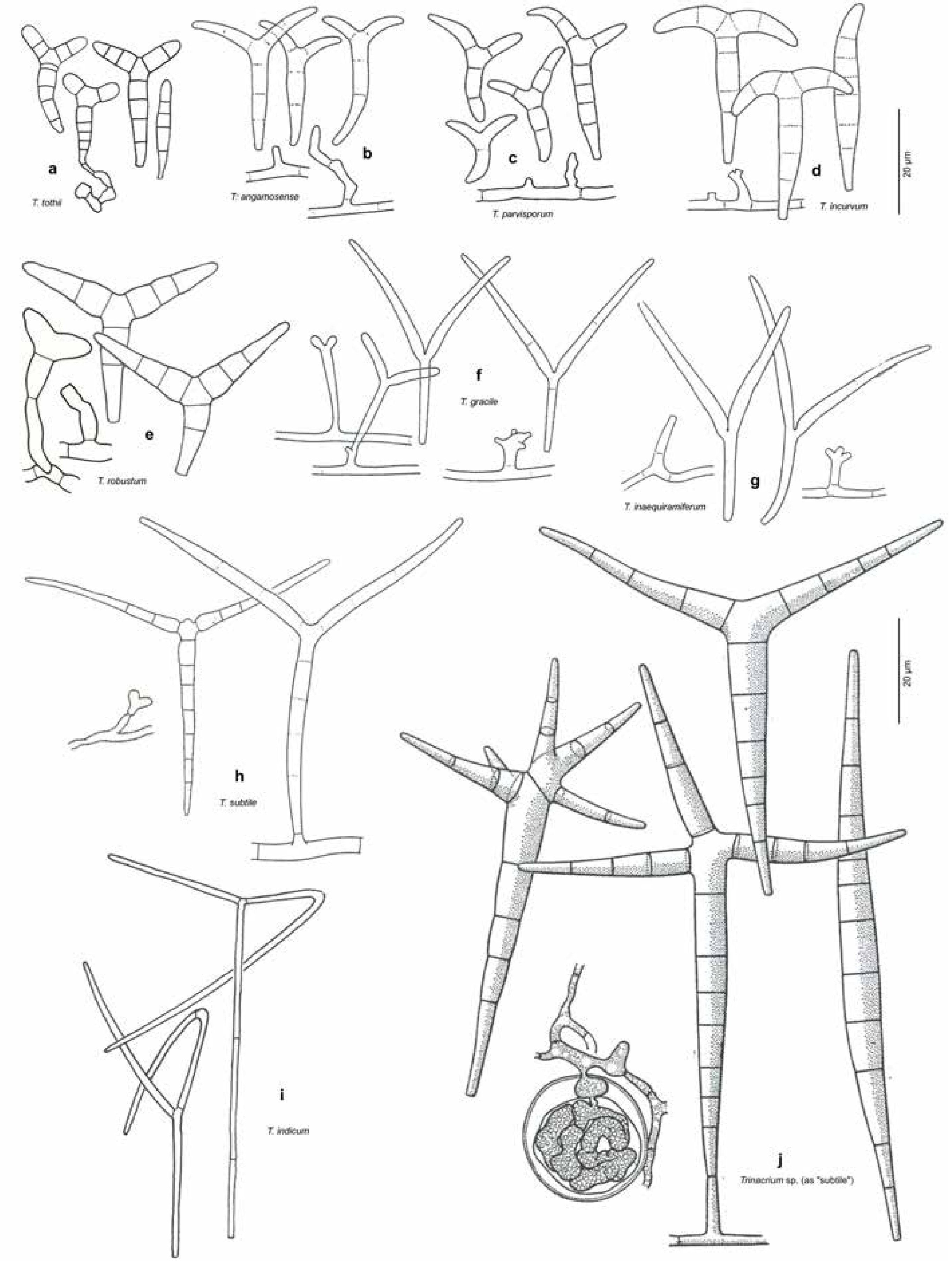


Plate 22. The accepted, hitherto known species of the form genus *Trinacrium* (conidiophores and conidia, **j**. invading a *Pythium* oospore). — **a**. from Magyar & Réval (2008), **b**. from Matsushima (1995), **c**. from Matsushima (1987), **d**. from Matsushima (1980), **e**. from Tzean & Chen (1989), **f**. from Matsushima (1975), **g**. from Matsushima (1989), **h**. from Fresenius (1852), right conidium: Matsushima (1975), **i**. from Soosamma et al. (2001), **j**. from Drechsler (1938).

Table 54. Overview of the accepted species of the form genus *Trinacrium*.

Species	Main axis/stipe [µm]	Arms [µm]	Habitat	Reference
T. tothii Magyar (= *Orbilia aprilis*)	14.5–22 × 2.7–3.6(–5)	2.5–7.5 × (2–)2.3–2.7(–4)	bark of *Elaeagnus angustifolia*, Hungary	Magyar & Révay 2008
T. angamosense Matsush.	11–18 × 2.5–3.5	(3–)5–10 × 2–2.5	palm petioles, Peru	Matsushima 1995
T. parvisporum Matsush.	8–20 × 2–4	4–16 × 2–3	basidiocarps of *Tremella foliacea*, stems of *Bambus*, Japan, Taiwan	Matsushima 1987
T. incurvum Matsush.	18–36 × 3.5–6	6–14 × 3–5.5	plant material, decaying leaves and bark, Peru, Taiwan	Matsushima 1980, 1993, Tzean & Chen 1989
T. robustum Tzean & J.L. Chen	15–20 × 3.8–6.3	9.6–25 × 4.6–6.3	decaying stem, Taiwan	Tzean & Chen 1989
T. gracile Matsush.	13–18 × 1.6–2	18–30 × 1.8–2.2	decaying leaf, Japan, Peru	Matsushima 1975, 1993
T. inaequiramiferum Matsush.	13–20	23–36 × 1.8–2.8	decaying leaves, leaf litter, Australia, Japan	Matsushima 1989, 1995
T. subtile Riess **Type species**	30–47 × 2–3.5	20–46 × 3.5–4	on *Stilbospora*, insect eggs, on *Chloridium brunneum* on *Tilia*, *Berberis* twigs, *Fagus sylvatica* bark, decaying *Quercus* wood, Austria, Germany, Italy, Japan	Fresenius 1852, Saccardo 1886, Lindau 1907, Matsushima 1975
T. indicum Soosamma et al. (as *T. indica*)	28–56 × 1.2–2.5	23–35 / 46–65 × 1.2–2.5 (short / long arm)	on decaying *Coffea* leaves, India	Soosamma et al. 2001
Trinacrium sp. (as *T. subtile*)	52–65 × 6,7–8	21–42 × 3.3–7.5	decaying plant material of *Spinacia oleracea*, parasitizing oospores of *Pythium butleri* and rhizopods, USA	Drechsler 1938

(arms 15–20 × 3–4 µm, on various mycelia on leaves of various plants, Costa Rica, Spegazzini 1918). Another unillustrated taxon, *T. subtile* var. *tjibodense* Penz. & Sacc. (on rotten branch, associated with *Stictis pallidula*, Java), differs from *T. subtile* in the arms being curved upwards and with thicker bases (Saccardo & Saccardo 1906). *T. indicum* Soosamma et al. (2001), with the two slender arms differing in length and only one of them being curved, does not fit well in *Trinacrium*. *T. iridis* Ts. Watan. from *Iris* roots in Japan was described by Watanabe (1992) and, after several transfers, was later called *Arthrobotrys iridis* (Ts. Watan.) M. Scholler et al. (1999) because of its capability of trapping nematodes by means of adhesive networks.

Drechsler (1938) reported and figured an isolate identified as *T. subtile*, which parasitizes oospores of *Pythium* (Pl. 22: j) but also testaceous rhizopods. This isolate shows a high variability in conidial shape: with typical trinacrium- and descalsia-like (┼-shaped) conidia in majority, but also with unbranched and higher-branched ones. Because of a greater width of the conidial main axis we consider Drechsler's isolate as not conspecific with *T. subtile.* Drechsler's species is also figured in Carmichael et al. (1980) and Seifert et al. (2011) as *T. subtile*. Similarly, Ando (1992) reported six different conidial types in a Japanese isolate named *T. subtile*. Here a majority of conidia (97%) were two-armed, trinacrium-like and fit quite well typical *T. subtile*, the remaining being unbranched or higher-branched. According to Tzean & Chen's (1989) protologue, curucispora/descalsia-like or dwayaangam-like conidia with 3–4 arms rarely occurred in *T. robustum* in addition to triradiate conidia.

The two-armed *Trinacrium inaequiramiferum* has one or two arms basally constricted, and this is apparently why the species was considered to be congeneric with the three-armed *Tridentaria carnivora* Drechsler (Matsushima 1989). Matsushima (1987) considered the genus *Retiarius* (Pl. 20) as a possible synonym of *Trinacrium*. Three of the four included species have trinacrium-like conidia, whereas the type species *R. superficiaris* shows more resemblance to *Dwayaangam* (see there).

In five cases a proved connection to an orbiliaceous teleomorph has been reported: in a culture of an unidentified *Trinacrium*, Matsushima (1995) obtained apothecia referable to *Hyalorbilia erythrostigma* s.l. (as *Orbilia trinacriifera* Matsush., but see p. 421); Liu (2006) reported in an ascospore isolate of '*O. brasiliensis*' (= *O.* aff. *pilifera*) an anamorph identified as *Trinacrium incurvum*; Guo et al. (2013) obtained the trinacrium-like anamorph of a not mentioned *Orbilia* here referred to as *O.* aff. *bannaensis* based on unpublished photos; Ren et al. (2014b) obtained the trinacrium-like anamorph of *O. corculispora*, and Shao et al. (2018) that of *O. occulta*.

Besides *Dicranidion*, *Dwayaangam*, and *Tridentaria*, similar trinacrium-like staurosporous conidia were described in *Trifurcospora* (see above), *Ypsilinia* Descals et al. (1999) with an additional phialidic microconidial state (Marvanová & Bärlocher 2001), and *Lambdasporium* Matsush. (1971). Within the genus *Tripospermum* Speg. similar conidial forms occur, but here the conidia are more or less pigmented.

Most of the known *Trinacrium* species were isolated from decaying plant material, whereas some collections originate from fungal substrates. Gönczöl & Révay (2006) found seven species in rainwater collected from different trees. *Trinacrium* species have been reported from Asia, South Africa, Europe, North and South America.

In the present study we treat *Trinacrium* as a synonym of *Orbilia* and, at the series level, as a possible synonym of series *Hemiorbilia* of section *Hemiorbilia*. We frequently observed trinacrium-like anamorphs, particularly in *Orbilia* but also in *Hyalorbilia* and *Amphosoma*, often in pure culture. Within *Orbilia*, mainly sections *Habrostictis* and *Hemiorbilia*, but also *Lentiformes*, *Aurantiorubrae* (series *Albovinosae* and *Piliferae*), and *Orbilia* (series *Microsomates*) are connected to trinacrium-like anamorphs. Among the described *Trinacrium* species only *T. tothii* can be assigned with high probability to a teleomorph (*O. aprilis*). Anamorphs referable to *T. robustum* were observed in about 30 *Orbilia* species of sections *Habrostictis* and *Hemiorbilia*, while for the teleomorph of *T. incurvum* members of series *Piliferae*, but also of section *Lentiformes* come into question, and several members of series *Hemiorbilia* form conidia similar to those of *T. subtile*. Without molecular data gained from a holo- or epitype, reliable assignments of these anamorph names to a teleomorph are impossible.

Tripoconidium Subram. – (Pl. 23)

The genus was erected in 1978 with a single species, *Tripoconidium aphanopagum* (Drechsler) Subram. It is mainly characterized by hyaline, septate, twice dichotomously branched conidia formed on long conidiophores. The conidia consist of a large triangular central cell, a short obconical stipe, and four short conical arms.

Drechsler (1937a, 1962) described two species in *Triposporina* Höhn., *T. aphanopaga* and *T. quadridens*. However, the type species of that genus, *T. uredinicola*, differs in the annellidic mode of conidiogenesis (see under *Dwayaangam*, p. 233). Therefore, Subramanian (l.c.) proposed new genera for Drechsler's species: *Tripoconidium* for *Triposporina aphanopaga*, and *Dwayaangam* for *Triposporina quadridens*. The name *Triposporina* was derived from the Greek 'tripos' or 'tripodo' = tripod (referring to conidial shape), after which Subramanian named his genus *Tripoconidium*. Drechsler mentioned the similarity of conidia of *Triposporina aphanopaga* with those of the broadly fusiform type found in *Drechslerella bembicodes* (as *Dactylella*), 'modified by two successive bifurcations'.

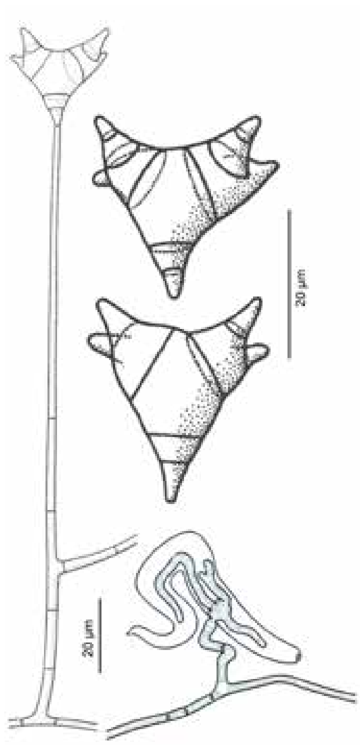


Plate 23. *Tripoconidium aphanopagum* (conidiophore, conidia, and captured nematode). From Drechsler (1937a).

Tripoconidium aphanopagum was isolated from leaf mould from North America. It is weakly predacious on nematodes but does not form conspicuously differentiated trapping organs (Drechsler 1937a: 534).

In the present study we did not observe anamorphs of this type of conidia. Yet, judging from the morphology of conidia and conidiophores, this species seems to belong to *Orbilia* section *Arthrobotrys*.

Vermispora Deighton & Piroz. – (Tab. 55, Pl. 24)

Vermispora was erected in 1972 with the single species *Vermispora grandispora* Deighton & Piroz., and five species were later added to the genus. According to Chen et al. (2007a, c) the genus is characterized by hyaline, simple, short to long conidiophores with sympodial conidiogenesis, slightly geniculate above the older conidiogenous scars, and conidia elongate (cylindric-)fusoid to fusiform, slightly curved and usually slightly sigmoid (possibly slightly helicoid). The name *Vermispora* is derived from the worm-shaped conidia. Chen et al. obtained in their molecular analysis of several isolates of *Brachyphoris*, *Dactylella*, and *Vermispora* a well-supported clade (*Vermispora* group) comprising *V. leguminacea*, *V. fusarina*, and *V. spermatophaga* (≡ *Dactylella spermatophaga*). The authors accepted five species in *Vermispora* (see Tab. 55), and excluded *V. obclavata* V. Rao & de Hoog, which was added to the genus in 1986, by morphology (e. g., faintly pigmented conidiophores). No teleomorphs are reported for any of these five accepted species. The phylogenetic analysis by Chen et al. (l.c.) suggests that the three included species are members of *Orbiliomycetes*.

However, no sequence data were available for the type species of *Vermispora*, *V. grandispora*, which was not taken into culture (Burghouts & Gams 1989), and *V. cauveriana*. The latter deviates from the remaining species in having the longest conidiophores (up to 170 µm) and the largest conidia which produce microconidia on long and thin germ tubes emerging from the macroconidia (Pl. 24: f). Rajashekhar et al. (1991) compared *V. cauveriana* with nematophagous orbiliaceous taxa but did not mention to have tested their cultures with nematodes. A relation to *Arthrobotrys* or *Drechslerella*, in which microconidia are frequent, cannot be excluded.

The genus *Microdochiella* is very similar to *Vermispora* (see p. 239), and also *Lecophagus* resembles *Vermispora* in conidial shape, but differs in conidiophore shape, very broad mycelial hyphae containing cubical bodies, and in the capture of invertebrates by adhesive pegs. Anamorphs in *Brachyphoris* mainly differ in ± straight conidia.

Similar phragmosporous conidia with holoblastic conidiogenesis can be found in *Dactylaria* Sacc., with mostly straight conidia and brownish conidiophores, or in *Neta* Shearer & Crane where conidiogenous cells develop in an arachnoid mat of setose (thick-walled), brown, dichotomously branched hyphae, and the conidia may contain very large lipid bodies. The type species of *Dactylaria*, *D. purpurella* (Sacc.) Sacc., was described from Italy with a pale purple pigmentation of conidia and lower part of conidiophores, whereas other species

Table 55. Overview of the accepted species of the form genus *Vermispora*.

Species	Conidial size [µm]	Septa	Conidial shape	Habitat	References
V. leguminacea Juan Chen et al.	20–34 × 4–5	(1–)3(–5)	cylindric-fusoid	soil, China, Fujian	Chen et al. 2007a, c
V. fusarina Burghouts & W. Gams	30–50(–55) × (3.5–)4–4.5(–5)	(2–)3(–4)	elongate fusiform	on eggs of *Globodera pallida*, Netherlands	Burghouts & Gams 1989, Chen et al. 2007a, c
V. spermatophaga (Drechsler) Juan Chen et al.	35–65 × 3.8–5.2	(2–)3(–4)	elongate fusiform	in soil and decaying plants, parasitic on oospores etc. of oomycetes, eastern USA	Drechsler 1938, Chen et al. 2007a, c
V. grandispora Deighton & Piroz. **Type species**	73–96 × 4.5–5	5–8	cylindric-fusiform	hyperparasite of *Irenopsis aciculosa*, on leaves of *Sida urens*, Sierra Leone (western Africa)	Deighton & Pirozynski 1972, Chen et al. 2007c
V. cauveriana Rajash et al.	160–180 × 10–22	6–9	elongate fusiform	decaying leaves of *Ficus religiosa*, India	Rajashekhar et al. 1991

of *Dactylaria* section *Dactylaria* have hyaline or pale brown pigmented conidiophores (De Hoog 1985). With its denticulate sympodial conidiophores, *Dactylaria* resembles orbiliaceous anamorphs in the genera *Brachyphoris* and *Vermispora*. However, a molecular study by Bhilabutra (2009) shows that a Japanese strain of *D. purpurella* and strains of some other species of *Dactylaria* show affinities with *Herpotrichiellaceae* (*Chaetothyriales*).

For *Aquaphila albicans* Goh et al. (1998) with similar conidia, Tsui et al. (2007) reported *Tubeufia asiana* Sivichai & K. M. Tsui (*Pleosporales*) as teleomorph. The genus *Trichoconis* Clem. (e.g., *T. sigmoidea* Deighton & Piroz.) is somewhat similar to *Vermispora*, but here conidial secession is rhexolytic: the denticles on which the conidia are produced are narrow tubular separating cells cut off from both conidiophore and conidium by a septum. A BLAST search based on a sequence of *T. echinophila* (C. Massal.) de Hoog & Oorschot in GenBank did not show any relation to *Orbiliomycetes*. In the genus *Sigmoidea* J.L. Crane the teleomorph is said to be *Corollospora* Werderm. (*Halosphaeriales*, Jones et al. 2009). However, *S. aurantiaca* Descals (in Descals & Webster 1982) shows similarities to anamorphs of *Orbilia*. *Chionomyces* Deighton & Piroz. (*Pezizomycotina* incertae sedis) deviates in more or less thick-walled conidiophores with a percurrent proliferation. Yet, the later added *C. ponapensis* (Matsushima 1983, as '*Chinomyces*') is very probably an anamorph of *Orbilia*, judging from its conidial morphology (conidia 17–32 × 3–4 µm, 3–6-septate, cylindric-fusoid, on decaying bark, Micronesia; Pl. 24: e) which especially resembles that reported here in *Orbilia* section *Aurantiorubrae*. Finally, the phragmoconidia of *Fusarium* Link and *Cylindrocarpon* Wollenw. resemble *Vermispora* but originate from phialides, their teleomorphs belonging to *Nectriaceae* (*Hypocreales*).

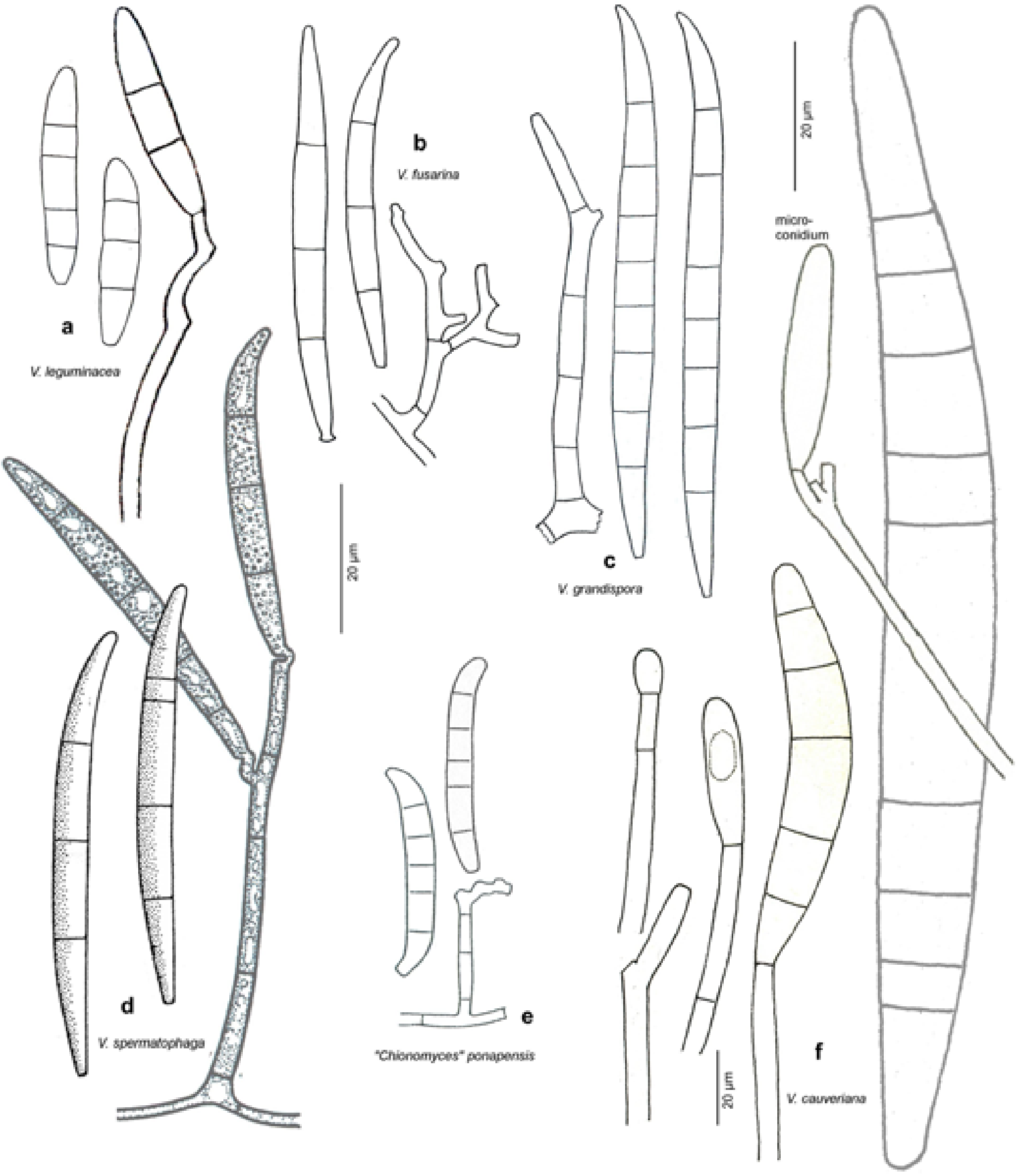


Plate 24. The accepted, hitherto known species of *Vermispora*, and '*Chionomyces*' *ponapensis*, a potential anamorph of *Orbilia* with a similar conidial shape (conidiophores and conidia). — **a**. from Chen et al. (2007a, c), **b**. from Burghouts & Gams (1989), **c**. from Deighton & Pirozynski (1972), **d**. from Drechsler (1938), **e**. from Matsushima (1983), **f**. from Rajashekhar et al. (1991).

The five *Vermispora* species were isolated from decaying herbal material, from living leaves overgrown with *Irenopsis* (*Meliolaceae*), from soil, and from nematode eggs. They have been collected in Asia, Oceania, Africa, North America, and Europe.

In the present study, *Vermispora* is tentatively considered as a synonym of *Hyalorbilia*. *Vermispora fusarina*, *V. leguminacea*, and *V. spermatophaga* are regarded as unquestionable members of *Hyalorbilia*, based on a sequence gained from apothecia of *H. rotifera* with the typical morphology of a *Hyalorbilia*, which formed together with the three *Vermispora* species and *Microdochiella fusarioides* a strongly supported clade. Because of lacking molecular data for *V. grandispora*, the synonymy of *Vermispora* remains at present uncertain. In our combined analysis of rDNA (Phyl. 2), *Hyalorbilia* formed a weakly supported clade distant from *Orbilia* and other orbiliaceous genera. Because slightly to strongly curved phragmoconidia reminiscent of *Vermispora* occur in most sections of *Orbilia*, particularly in section *Aurantiorubrae*, we refer to such anamorphs as 'vermispora-like'.

TAXONOMIC PART

Orbiliomycetes O.E. Erikss. & Baral, in Eriksson et al., Myconet 9: 96 (2003) – Type: *Orbilia* Fr. (series *Orbilia*)

1 order: ***Orbiliales*** Baral, O.E. Erikss., G. Marson & E. Weber, in Eriksson et al., Myconet 9: 96 (2003)

1 family: ***Orbiliaceae*** Nannf., Nova Acta Regiae Soc. Sci. Ups., ser. 4, 8: 250 (1932) [= *Orbiliaceae* Velen., Monogr. Discom. Bohem.: 90 (1934), nom. illegit., ICN Art. 52.1 (nomenclaturally superfluous)]

= *Trinacriaceae* Nann., Repert. mic. uomo: 473 (1934) – Type: *Trinacrium* Riess [= *Orbilia* (?series *Hemiorbilia*)]

= *Monacrosporiaceae* Locq., Mycol. gén. struct. (Paris): 207 (1984), nom. inval., ICN Art. 39.1 (Latin diagnosis missing) – Type: *Monacrosporium* Oudem. [= *Orbilia* (series *Arthrobotrys*)]

= *Helicoonaceae* Locq., Mycol. gén. struct. (Paris): 201 (1984), nom. inval., ICN Art. 39.1 – Type: *Helicoon* Morgan [= *Orbilia* (series *Helicoon*)]

Description of the class, **order and family**: — **TELEOMORPH**: **Apothecia** round to undulating, cupulate to flat or convex, sessile or sometimes distinctly stalked (stalk rarely and only a bit longer than wide), with a gymnohymenial, sometimes cleistohymenial development, superficial to erumpent, not or sometimes medium gelatinous, hyaline to bright, rarely dark-coloured, exterior smooth or with short to long prolongations being frequently agglutinated as teeth, rarely with protruding teeth-like excipular tissue. **Asci** ± cylindrical in the region of the pars sporifera, apex of dead asci either hemispherical to subconical (irrespective of the viewing direction), or ± saddle-shaped (± truncate or hemispherical depending on the viewing direction), thin- or thick-walled, never with a ring structure in the apical wall, 8–128-spored, usually some of the spores inversely oriented (if spores heteropolar), at maturity spores generally glued together to form a compact body being ejected as a single entity, arising from croziers or simple septa (then base often furcate). **Ascospores** hyaline at all development stages, almost always non-septate when mature but sometimes septate prior to germination, thin-walled, smooth or rarely warted by minute cell wall protrusions, never with sheaths or appendages, sporoplasm at maturity generally containing one or several variously shaped refractive **spore bodies** (**SBs**, visible only in living state) and a few small **lipid bodies** (LBs), rarely also **glycogen bodies**. **Paraphyses** septate, apically inflated or not, with anastomoses at the base, branched below or also above. **Excipulum** sharply or indistinctly divided into a compact ectal tissue of angular to prismatic cells and a dense or loose medullary tissue of usually a mixture of slender hyphae and inflated cells. Cortical cells at margin and flanks sometimes terminated in short to very long, solid prolongations (**glassy processes**) or septate **hairs**. Cells of paraphyses and ectal excipulum often containing globose or elongate **vacuolar bodies** (VBs), globose or crystalloid **cytoplasmic bodies** (SCBs), or globose **lipid bodies** (LBs), the former two visible only in living state, the latter often containing **carotenoids**; exterior of apothecium usually covered by a granular to cloddy, hyaline to yellowish (rarely dark-coloured) **exudate**. — **ANAMORPH**: **Mycelium** hyaline, septate, smooth, very slow- to moderately fast-growing. **Conidiophores** hyaline, thin-walled, smooth, unbranched or branched, mononematous or reduced, rarely synnematous, with holoblastic conidiogenesis, never included in a peridium. **Conidiogenous cells** monoblastic or sympodial, rarely synchronous; conidial secession schizolytic. **Conidia** hyaline, smooth, thin-walled, either unbranched (amero-, didymo-, phragmo- or scolecosporous), straight or curved (falcate to canoe-shaped, rarely helicoid), sometimes with protuberances, or variously branched (staurosporous), with straight or curved arms, 2- or 3-dimensional, lipid content low to sometimes high. **Trapping organs** known in some groups: adhesive pegs capturing rotifers in *Lecophagus*, peg-like knobs capturing rhizopods in *Hyalorbilia*, or various, mainly nematode-trapping organs (adhesive knobs, columns or networks, constricting and non-constricting rings) in 4 of the 5 series of *Orbilia* section *Arthrobotrys* (*Arthrobotrys*, *Dactylellina*, *Gamsylella*, *Drechslerella*). — **Chemical characteristics**: **IKI/MLZ**: apical and lateral ascus wall consistently inamyloid (with or without KOH-pretreatment), rarely the thickened apical endoascal wall faintly dextrinoid; glassy processes always unstained; carotenoids staining blue-green. $\mathrm{CR}_{\mathrm{SDS}}$: ascus apical thickenings and glassy processes stain rose-red, ectotunica negative. **CRB**: a very thin or sometimes thick gel layer over the walls of all kinds of cells (except ascospores) staining lilac; light-coloured exudate staining bright turquoise-blue; SBs and VBs selectively staining turquoise-blue or blue-violet, SCBs unstained. **KOH**: SBs, VBs and SCBs irreversibly disappearing; LBs, glassy processes and exudate unaltered.

Habitat: saprobiontic on various plant and fungal substrates, often invading pollen, some species preying on spores of oomycetes, eggs of nematodes, or capturing various invertebrates. **Desiccation tolerance**: hygro- to xerobiotic. **Distribution**: worldwide.

Recognized genera: *Amphosoma*, *Bryorbilia*, *Hyalorbilia* (incl. *Microdochiella* and *Vermispora*), *Lecophagus* (?incl. *Haptocara*), *Liladisca*, *Lilapila*, *Mycoceros*, *Orbilia*, *Pseudorbilia*, and *Retiarius*. with 470 recognized species plus 8 provisional names and ~83 unnamed species. For a survey on the various aspects of the class see Pfister (2015).

Characteristics of the teleomorph. Among taxa with a known teleomorph, about 470 species have been accepted in the class *Orbiliomycetes* in the present monograph, 331 of which being here described as new species. Circa 90 more or less distinctive further taxa are at present without a valid name. For ca. 50 of these roughly 560 taxa no vital characters are known because they have never been studied and documented in the living state.

Besides ascus inamyloidity, three previously frequently overlooked and therefore rarely reported features are emphasized here as most diagnostic of the class: (1) the transient spore bodies within the ascospores (being typical of all eight genera with a known teleomorph as recognized here), (2) the inverse orientation of some of the spores within the asci (typical of three of these eight genera – the other five genera lack the prerequisite for this: elongate spores with one polar spore body), and (3) the existence of unique transient plasmatic inclusions (crystalloid SCBs) in the vegetative cells (present in about 25 % of the species).

Among the teleomorph characteristics of *Orbiliomycetes*, the spore body (SB), a refractive organelle that is usually clearly visible in living spores but often undiscernible in dead spores, represents the most important key character, as it is unknown from any other group of ascomycetes. Further remarkable though not consistent characteristics of the class are: a saddle-shaped (shouldered) type of ascus apex (dead state), present in *Pseudorbilia* and in many species of *Orbilia*, and a simple-septate ascus base that is often furcate with two legs, a feature occurring throughout *Orbilia*, but also in *Amphosoma* and *Bryorbilia*.

Although the group was often characterized as having exceptionally small asci and ascospores, the at present known species diversity comprises also comparatively large asci and/or ascospores. Polyspory of asci at four different levels (16- up to 128-spored) was observed in about 34 % of *Orbiliomycetes* (ca. 140 species), although being previously only known in one species (*O. polyspora*). Large spores and/or polysporous asci are exclusively observed in desiccation-tolerant species (with exception of *Bryorbilia* which has rather large spores in 8-spored asci), whereas small spores and 8-spored asci are not only found in desiccation-sensitive species. A considerable number of desiccation-tolerant taxa have asci with an apical thickening with apical chamber, a feature completely unknown to the whole group until reported by Baral (1994). Likewise, croziers were previously not reported although consistently present in the genus *Hyalorbilia*. The inverse spore orientation is characteristic of almost all taxa in which elongate spores are heteropolar in regard to their sporoplasm (presence of a single SB near the spore apex). The morphological spectrum of characters within the *Orbiliomycetes* is enlarged to include also some species with dark-coloured, blackish-olivaceous or dark purple-lilac apothecia.

None of the many species of *Orbiliomycetes* tested with IKI showed an amyloid (eu- or hemiamyloid) reaction of the ascal walls, with or without KOH-pretreatment. This is astonishing because members of most other classes of ascomycetes, e. g., *Pezizomycetes*, *Leotiomycetes*, *Lecanoromycetes*, *Arthoniomycetes*, *Sordariomycetes*, and even *Neolectomycetes*, possess an amyloid ascus wall and/or amyloid apical ring in some or many of its members. Also the vegetative elements of *Orbiliomycetes* (paraphyses, excipular cells, hairs, anchoring hyphae) never displayed an amyloid or dextrinoid reaction of the cell wall or its gelatinous sheath. Only in a few species of subgenus *Hemiorbilia* a faint dextrinoid reaction of the internal thickenings of the ascus apical wall could be noted. Remarkable ecological characters include the frequent desiccation tolerance of both teleomorphs and anamorphs, and the ability of some groups to prey on invertebrates by means of various types of trapping organs.

Confusion with other classes. Although the *Orbiliomycetes* appear to form a natural group with sharp limits against other classes of *Ascomycota*, cases of confusion, mainly against *Leotiomycetes*, quite often happened, particularly in the older literature. Authors have included helotialean species in the family *Orbiliaceae* because of characters such as translucent, waxy-gelatinous apothecia, or capitate paraphyses, but were usually unaware of the characteristic vital characters of the class, and included even species with amyloid asci.

Spore bodies provide the most convincing morphological trait to accept *Liladisca*, *Lilapila*, *Lecophagus*, *Pseudorbilia*, and *Amphosoma* as phylogenetically related to *Orbilia* and *Hyalorbilia*. For example, *Lilapila* possesses a lens-shaped spore body very similar to that in *Orbilia* series *Lentiformes*. The prominent hair vesture of *Lilapila* recalls hairy members of the *Helotiales*, such as *Perrotia* Boud., in which genus a herbarium taxonomist would have placed this species, but thick-walled hairs similar to *Lilapila*, though hyaline, also occur in a few *Orbilia* species (e.g., *O. phragmotricha*, *O. pilosa*). Teleomorphs here referred to the genus *Lecophagus* are recognizable as orbiliaceous mainly on account of a distinct spore body and asci with inversely oriented spores. *Hyalorbilia erythrostigma* was transferred by Baral & Marson (2001) from *Pithyella* (*Helotiales*) to the *Orbiliomycetes* based on the presence of a spore body and a trinacrium-like anamorph.

Spore bodies are usually only visible in living material, therefore, studying dead herbarium specimens of such teleomorphs hardly allows to recognize the class. As an exception, SBs could be discerned in, e.g., *Liladisca acicola*, which is only known from the old type specimen. Without living spores, a member of *Lecophagus* may easily be mistaken as belonging to *Leotiomycetes*, e.g., to *Gelatinopsis* Rambold & Triebel or *Parorbiliopsis* Spooner & Dennis (= *Hyaloscypha* Boud.), and in the older literature it might have been described in genera such as *Pezizella* Fuckel or *Helotium* Pers.

Because of capitate paraphyses, Nannfeldt (1932) treated the dark-coloured *Patinella hyalophaea*, the type species of *Patinella* Sacc., in the *Orbiliaceae*. This taxon was correctly excluded from the family by Spooner (1987, see p. 208). Nevertheless, six here described orbiliaceous species with black apothecia may easily be mistaken as belonging in the *Leotiomycetes*, e.g., in *Patinella*, *Durella* Tul. & C. Tul., or *Claussenomyces* s.auct. regarding both macro- and microscopy, though only when studied in the dead state by overlooking the spore bodies and the inverse spore orientation. Only the bifurcate ascus bases would argue for a relationship with the *Orbiliomycetes*.

Our molecular data support the high diagnostic value of spore bodies as a morphological marker to place a species in the *Orbiliomycetes*. Available sequences from taxa with dark apothecia (*Lilapila* spp., *Amphosoma atroolivaceum*, *Orbilia patellarioides*) confirm their relationship within the class. Likewise, molecular data of *Hyalorbilia erythrostigma* confirm placement in *Hyalorbilia*. *Bryorbilia* strongly resembles *Orbiliomycetes* in having a bifurcate ascus base and globose SCBs in the inflated paraphysis apices, and molecular data confirmed its relationship with the class (the presence of SBs is not fully assured). Genera which lack SBs, such as *Claussenomyces* s.auct. and *Gelatinopsis*, or *Deltopyxis* clustered in the *Leotiomycetes* or *Lecanoromycetes*, respectively (Phyl. 1).

Characteristics of the anamorph. Although our monograph concentrated over a long time on the teleomorph and largely relies on the classical morphological method based on light microscopy, cultural work was later carried out on a fairly large number of species. During this study, roughly 120 species were taken into culture.

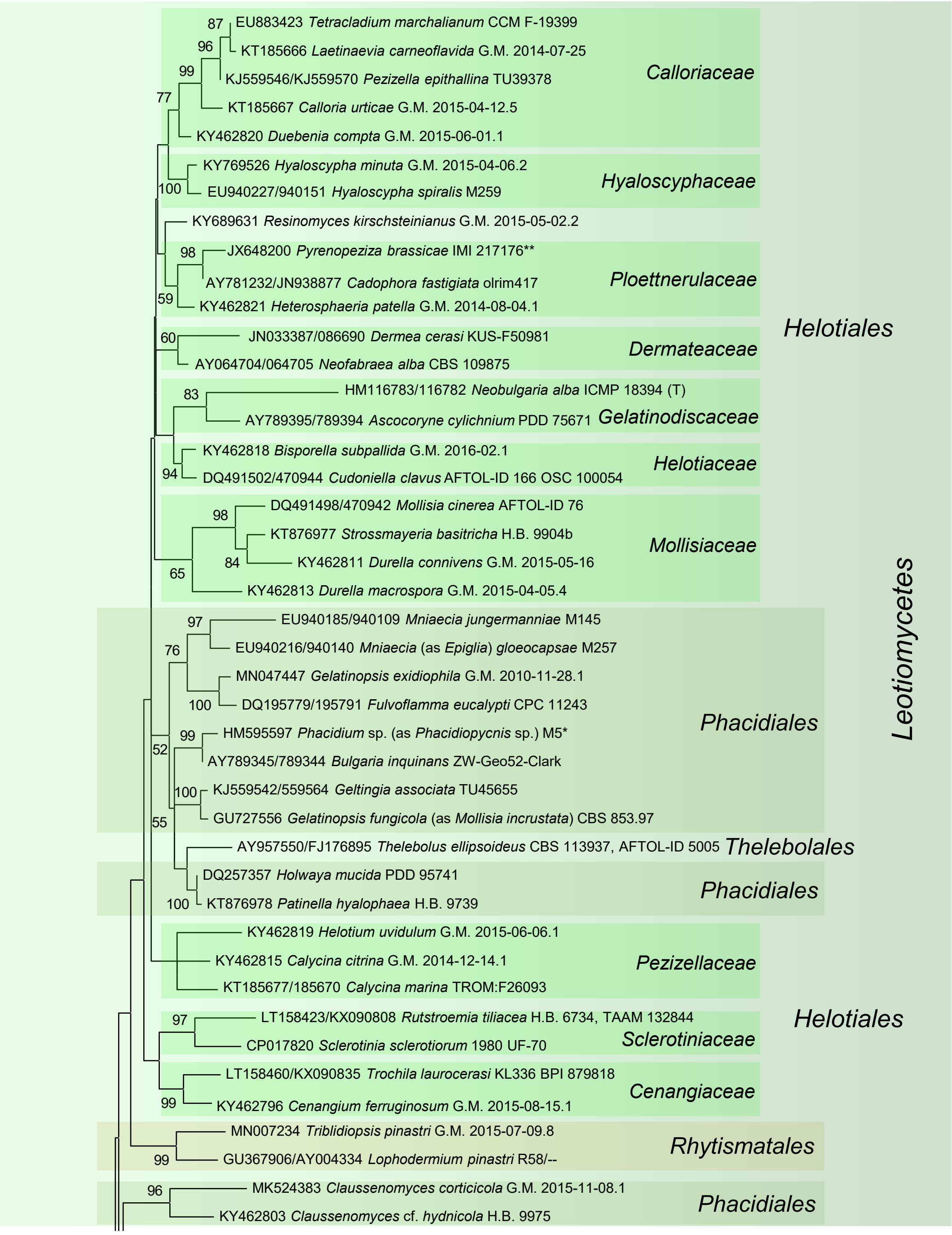
Anamorphs exist in probably all species of *Orbiliomycetes*. They exhibit a high diversity in conidial morphology, including so-called Ingoldian fungi with variously branched multicellular conidia. Such stauroconidia, though previously believed to represent an adaptation to an aquatic environment, belong to the life cycle of many desiccation-tolerant species, which occur with a vast species diversity in a largely unexplored ecological niche: substrate exposed to dry air. Despite growing under xeric conditions, often far from watercourses or lakes, their conidia are adapted to a periodically aquatic environment during rainy periods.

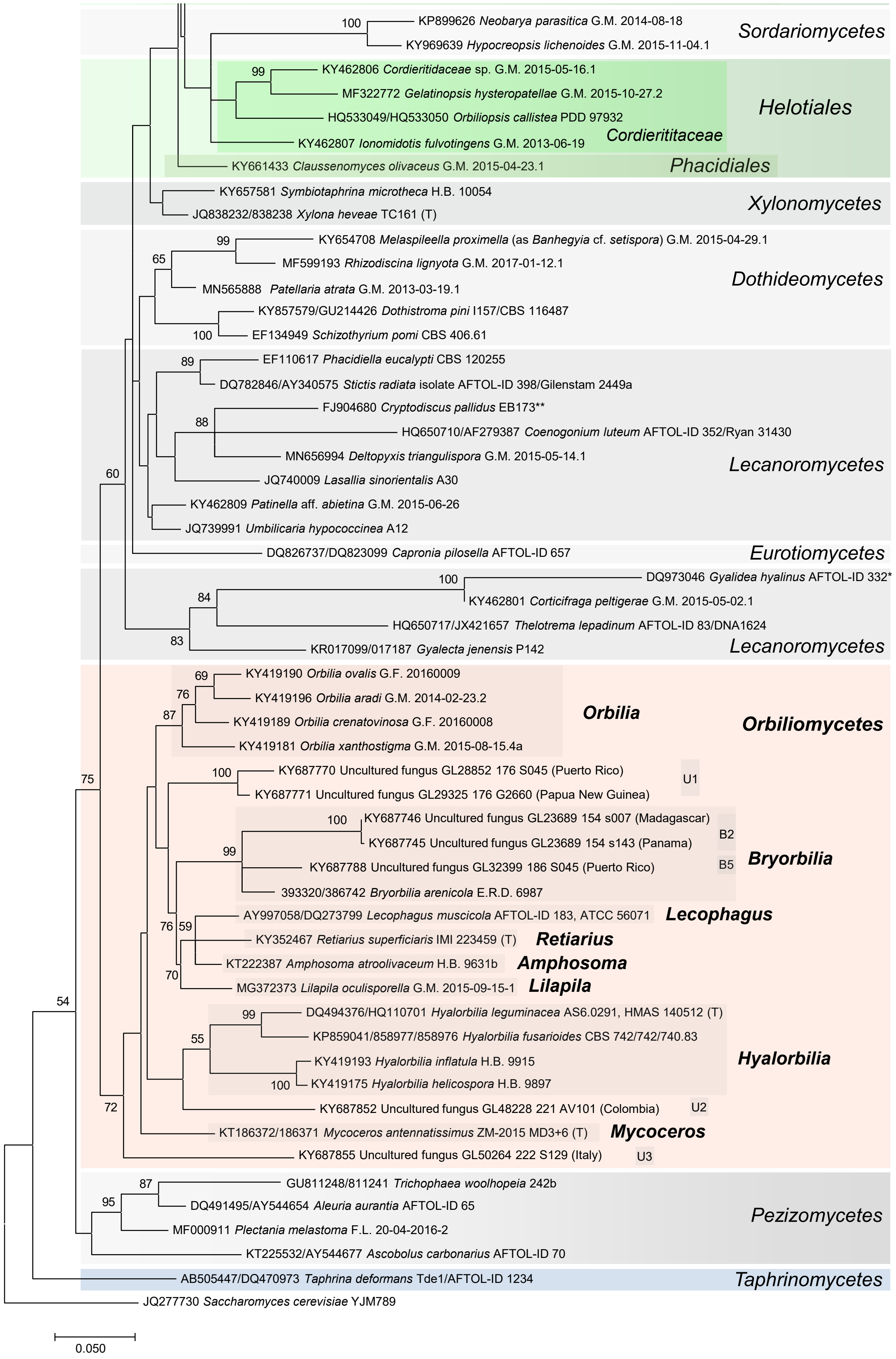
Up to the present, the connection between anamorph and teleomorph is known with certainty in 4 of the 10 recognized genera: *Lecophagus*, *Hyalorbilia*, *Amphosoma*, and *Orbilia*. Anamorphs are unknown in *Bryorbilia*, *Liladisca*, *Lilapila*, and *Pseudorbilia*, whereas *Mycoceros* and *Retiarius* are only known from their anamorph. Numerous species of orbiliaceous anamorphs have previously been recognized in about 20 genera (see p. 214 ff.), but for many of them a connection to a teleomorph is still unknown. Judging from their morphological and molecular data, a majority of them (~100 species) belong to *Orbilia* section *Arthrobotrys*, and particularly to series *Arthrobotrys* (~50 species). In the present monograph, within section *Arthrobotrys* the number of taxa with both teleomorphs and known or presumed anamorphs is comparatively low (~48), for about 14 only the teleomorph is known. It could be speculated that those taxa without a known teleomorph have lost the ability for sexual reproduction, but we suspect that their teleomorphs still remain to be discovered (see also p. 40). Out of the here accepted ca. 470 species of *Orbiliomycetes* with a known teleomorph, only ca. 140 are so far with a verified anamorph, but we report presumed anamorphs for further ~90 species (see also p. 108, Formation of conidial state).

Some orbiliaceous anamorphs are morphologically difficult to distinguish from those of other classes. This particularly concerns the anamorph-typified genera *Anguillospora* and *Helicoon*. These genera turned out to be highly polyphyletic in their current usage and include also members of *Leotiomycetes* and *Dothideomycetes*. Similarly, species today assigned to *Lecophagus* were previously merged with *Zoophagus* (*Zygomycota*) and *Cephaliophora* (*Pezizomycetes*). Conidia of the genus *Fusarium* (*Hypocreales*) closely resemble those of vermispora-like orbiliaceous anamorphs but differ in being formed from phialides.

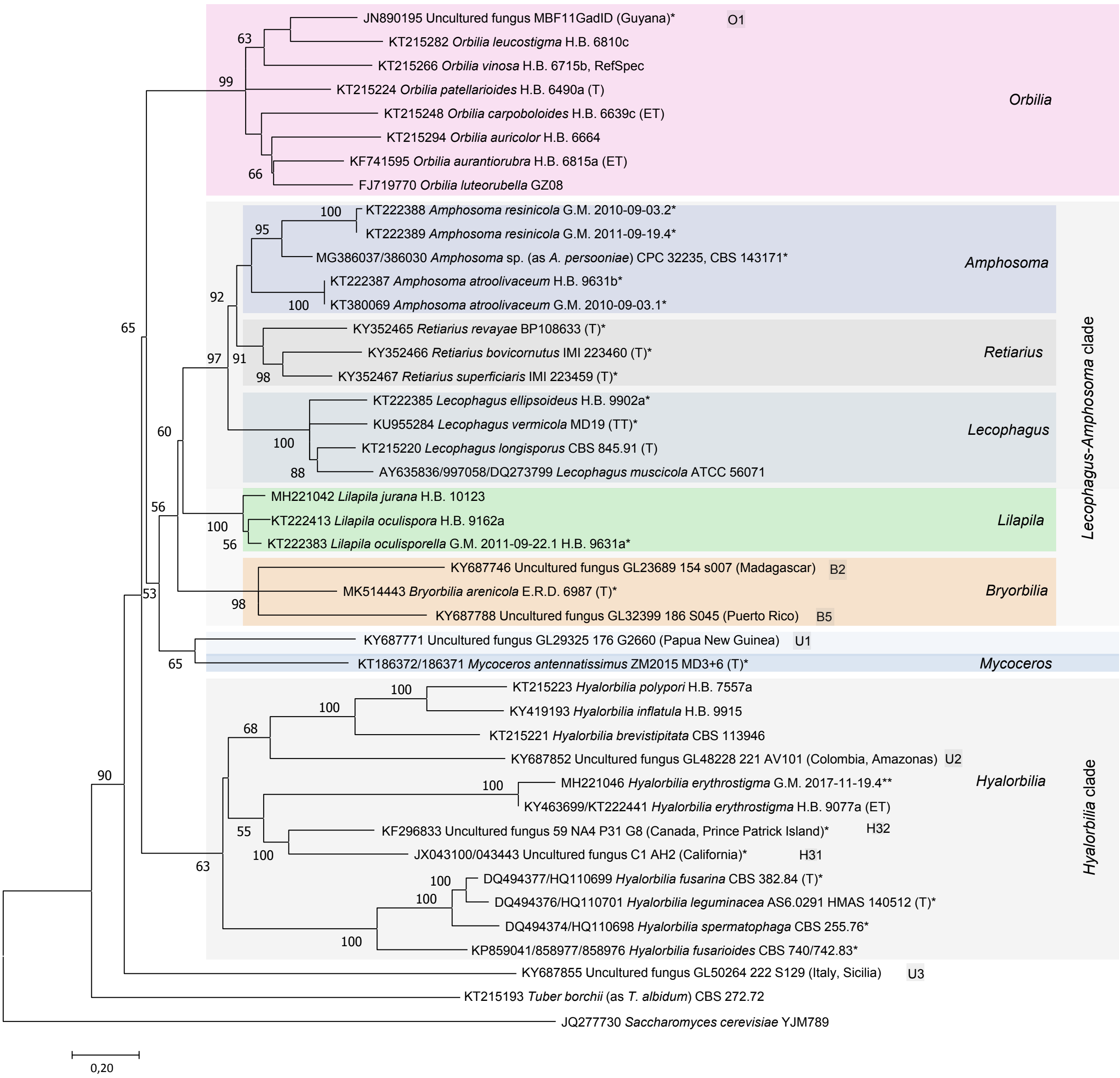
Convergent evolution is also observed in anamorphs with staurosporous conidia. For instance, dwayaangam-like conidia also occur in the *Helotiales* (*Dwayaangam colodena*). Various genera with pigmented conidia remarkably resemble orbiliaceous anamorphs in conidial shape. For instance, conidia of *Ceratosporium aequatoriale* Matsush. closely resemble *Trinacrium robustum* but have finely warted, pale brown cells. In fact, truly warted ascospores or conidia have never been observed in *Orbiliomycetes*, and also cell walls with melanin-like pigments never occurred, which suggests that the whole class is incapable to produce such pigments.

Members of *Leotiomycetes* are frequently associated with phialidic anamorphs, whereas *Orbiliomycetes* are known to produce solely holoblastic, sympodulosporous anamorphs, in which they concur with the *Pezizomycetes*. An interesting difference between the two groups lies also in the fact that polyspory of asci in *Leotiomycetes* is generally achieved by small phialoconidia formed on germinating ascospores, whereas in *Orbiliomycetes* and *Pezizomycetes* polyspory originates from multiple nuclear divisions after meiosis.





Phylogenetic analysis 1. Phylogram of *Ascomycota* inferred from combined ML analysis of 5.8S+LSU (D1–D6) rDNA dataset (97 sequences, 1686 positions, aligned with MUSCLE) using the TN+I model in MEGA7 (500 replicates), showing placement of 10 out of 12 here recognized genera of *Orbiliomycetes* within the *Ascomycota* (no sequences were available for *Pseudorbilia* and *Liladisca*). Some environmental sequences are included to indicate their affiliation in the class (B2, B5 = *Bryorbilia* spp., U1–U3 = species of unidentified genus of *Orbiliomycetes*). The tree is rooted with *Saccharomyces cerevisiae* and *Taphrina deformans*. T = type, * = without 5.8S, ** = only LSU (D1–D2); about half of the sequences without LSU (D4–D6).



Phylogenetic analysis 2. Phylogram of *Orbiliomycetes* inferred from combined ML analysis of SSU (V8–V9)+ITS1-5.8S-ITS2+LSU (D1–D2) rDNA dataset (43 sequences, 1920 positions, aligned with MUSCLE) using the GTR+G+I model in MEGA7 (500 replicates). Four main clades are recognized (*Hyalorbilia* clade, *Mycoceros*, *Lecophagus-Amphosoma* clade, *Orbilia*), whereby *Lilapila* and *Bryorbilia* are tentatively included in the *Lecophagus-Amphosoma* clade. Some selected environmental strains are included to indicate their affiliation in *Orbiliomycetes* (B2, B5 = *Bryorbilia* spp., H31, H32 = *Hyalorbilia* sp., O1 = *Orbilia* sp., U1–U3 = species of unidentified genus). The tree is rooted with *Saccharomyces cerevisiae* and *Tuber borchii*. T = type, ET = epitype, TT = topotype, * = without SSU, ** = without LSU (D2).

Phylogeny within *Orbiliomycetes*. Prior to this monograph, the subdivision of *Orbiliaceae* into genera was based on a few traits of the teleomorph, such as presence of glassy processes (*Hyalinia*) or septate hairs (*Orbiliaster*) and their absence (*Orbilia*), paraphysis apices being uninflated (*Hyalinia*), capitate (*Orbilia*), or beaked (*Habrostictis*), and apothecia being erumpent (*Habrostictis*) or superficial (remaining genera). Within *Orbilia*, infrageneric groupings followed mainly a sporological system. The present study provides evidence that all these traits have a polyphyletic origin within the class. A survey of the new system of *Orbiliomycetes* with eight included genera is given in Jaklitsch et al. (2016). At that time the genus *Retiarius* was of unclear relationship, and *Mycoceros* and *Bryorbilia* were as yet unknown.

The here presented phylogenetic trees are based on SSU, ITS, and LSU rDNA, and the S1506 intron at the 3'-end of SSU, or a combination of them. In the course of our study, rDNA sequences were taken from ca. 550 samples representing about 200 species, either from ascospore isolates or from apothecia, exceptionally from conidial isolates. A total of ca. 1400 samples with a sequence are listed in Tab. S5 as being treated in this monograph, representing ca. 320 species with a name, about 240 of them with a known teleomorph. About 225 sequences in GenBank belonging to 108 unidentified orbiliaceous species are only known from DNA isolates (abbreviated in the phylotrees as H1–37 for members of *Hyalorbilia*, O1–27 for those of *Orbilia*, etc.). On the whole, rDNA data exist for about 50% of the species treated in this monograph.

The results of our phylogenetic analyses have influenced the present classification in various ways. In many cases they confirmed conclusions gained by our morphological approach, but also provided unexpected information, particularly about the infrageneric classification of the genus *Orbilia*. The future inclusion of protein-coding genes will undoubtedly throw more light on the backbone phylogeny of the class but, irrespective of this lack of molecular data, we believe that morphological markers should be given equal attention in circumscribing taxonomic units, and even priority whenever this appears to be more logical. As a consequence, our system of classifying members of the class into genera, subgenera, sections, and series arose as a synthesis of morphological and molecular data. In the case when morphologically well-defined groups do not form monophyletic clades as, for example, series *Lentiformes* and *Phanosomates* of section *Lentiformes*, we preferred to rely more on morphology, because applying strict monophyly would inevitably result in heterogeneous assemblages, besides the impossibility to classify similar taxa for which sequences are lacking at present. We herein follow authors who accept paraphyletic taxonomic entities as a natural consequence of evolution, for instance, Brummit (2002), Davydov et al. (2010), and Gams et al. (2012b: 503).

In a recently performed Bayesian analysis of ITS-LSU rDNA by Magyar et al. (2017b), one medium and two strongly supported monophyletic main lineages could be recognized within the class: (1) the *Lecophagus* clade, which includes *Amphosoma*, *Retiarius*, *Lecophagus*, and *Lilapila*; (2) the *Hyalorbilia* clade, which includes *Hyalorbilia* s.str., *H. latispora*, the *erythrostigma-orbiliicola* clade, and the anamorph-typified genera *Vermispora* and *Microdochiella* which are considered here as congeneric with *Hyalorbilia*; (3) the large genus *Orbilia*. The two branching nodes leading to these three main lineages did not receive high support, however: the *Lecophagus* clade formed without support a sister clade to the weakly supported branch that includes *Hyalorbilia* and *Orbilia*. Magyar et al. (l.c.) described a new anamorph-typified genus and species (*Mycoceros antennatissimus*), which resembles *Retiarius* but nested very basally as a sister taxon ('*Mycoceros* clade') to all remaining *Orbiliomycetes*. That it belongs to this class is evident from the phylogenetic analysis and an evaluation of specific molecular motifs in comparison with other classes.

Sequences of *Mycoceros* and *Retiarius* were not yet available when the maximum likelihood analysis of SSU+ITS+LSU rDNA in Baral et al. (2017b) was made (erroneously as 'SSU+5.8S+LSU'). This analysis resulted in the same backbone tree topology as that of Magyar et al. (2017b), but with lacking support also at the branching node leading to *Hyalorbilia* and *Orbilia*. Magyar et al.'s Bayesian analysis included 20 species of *Orbilia*, whereas the ML analysis in Baral et al. comprised ~100 *Orbilia* species and, therefore, resolved a higher number of supported clades within the genus. Like in the entire class, the backbone phylogeny of *Orbilia* remained unresolved and the question unanswered which subgenus or section represents the ancestral one within the genus.

The present maximum likelihood analysis (Phyl. 2) additionally includes the genus *Bryorbilia*. The genus *Orbilia* formed a strongly supported clade, while the *Hyalorbilia* clade received low support. Within the *Lecophagus-Amphosoma* clade, only the genera *Amphosoma*, *Lecophagus*, and *Retiarius* clustered in a strongly supported clade. When tentatively including *Lilapila* and *Bryorbilia*, the *Lecophagus-Amphosoma* clade received only low support. Contrary to Magyar et al. (2017b), *Mycoceros* stands with low support sister to the *Lecophagus-Amphosoma*. The *Hyalorbilia* clade branches off as a sister group to all other clades, though unsupported. In Baral et al.'s (2017b) and the present ML analysis of LSU (Phyl. 4) the morphologically homogeneous genus *Amphosoma* appears paraphyletic, whereas in the Bayesian analyses of ITS+LSU by Magyar et al. (2017a, b) and our remaining ML analyses it came out as a monophyletic clade (SSU+ITS+LSU, unsupported, Phyl. 2; ITS, strongly supported (Phyl. 3).

To prove their relationship with *Orbiliomycetes* we included various environmental strains from GenBank, which were predominantly isolated from soil and clustered with *Amphosoma*, *Bryorbilia*, *Hyalorbilia*, *Lecophagus*, *Mycoceros*, *Orbilia*, *Retiarius* or unresolved in clades of their own. In cases when strains could not be assigned to a known species, we abbreviated their clades according to the first letter of the genus to which they clustered, as A1–A6, B1–B5, H1–H37, L1–L5, M1, O1–O36, R1–R4, U1–U11, and V1–V16 (U = unidentified genus of *Orbiliomycetes*, V = *Vermispora* clade of *Hyalorbilia*). For example, in our combined analysis of SSU+ITS+LSU (Phyl. 2), eight selected environmental strains which comprise more than one gene region are included. They clustered in seven different groups: three with high support (in *Orbilia* [O1] and *Bryorbilia* [B2 and B5]), four with low support (in *Mycoceros* [U1] and the *Hyalorbilia* clade [H31–H32, U2], see also Phyls 5–6), whereas the strain from Italy (U3) consistently remained unresolved. This Italy strain and that from Colombia (U2) in the *Hyalorbilia* clade show a peculiarity in the SSU V8–V9 (pos. 109 & 126) by which they concur with adhesive trap formers of *Orbilia* section *Arthrobotrys* and members of *Hyalorbilia* (see Tab. 60 and 76).

Multigene analyses are required to obtain a better supported backbone of the phylogeny of *Orbiliomycetes*. Various characteristic nucleotide positions could be detected in the available rDNA that correlate with the class or enable distinction among genera (see p. 123–129).

From a morphological point of view, the closest relatives of the large genus *Orbilia* could be sought in the small genera *Bryorbilia* and *Amphosoma*. These three genera represent all those *Orbiliomycetes* with a simple-septate, bifurcate ascus base. *Bryorbilia* and *Amphosoma* differ from *Orbilia* in ascospores with a bipolar SB arrangement and could herein resemble the common ancestor of *Orbilia*, considering also their predominant occurrence on phylogenetically old hosts (bryophytes and conifers). *Orbilia* might have descended from one of these genera by maintaining a simple-septate, bifurcate ascus base. The also small and in part conifericolous genera *Lecophagus*, *Lilapila*, and *Liladisca* share ascospores with unipolar SBs and an ascus base arising from croziers or sometimes from simple septa but never of a bifurcate shape. The genus *Liladisca* is assumed to be closely related to *Lilapila*, despite its deviating morphology regarding asci, spores, and paraphyses. The closest relative of the comparatively large genus *Hyalorbilia* should undoubtedly be sought in the small genus *Pseudorbilia*. Both have asci with croziers but differ in a hemispherical vs. truncate ascus apex. Members of the *Hyalorbilia* clade combine homopolar ascospores with mainly bipolar SBs. With this combination of characters, the *Hyalorbilia* clade possesses three plesiomorphic traits and would, therefore, most closely resemble the common ancestor of the *Orbiliomycetes*.

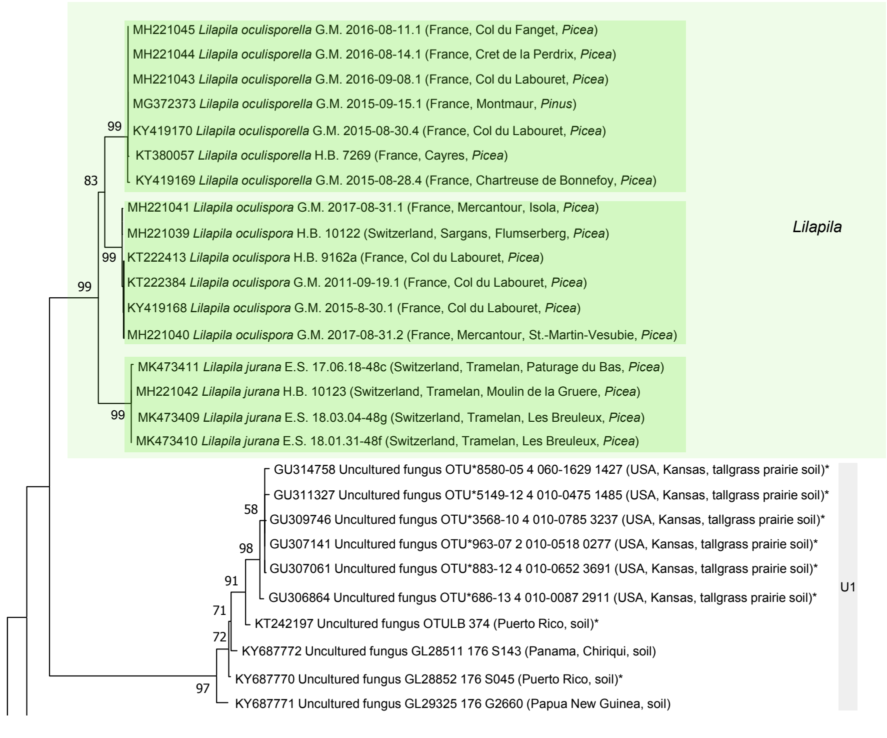
Plesiomorphic characters in *Orbiliomycetes*. We have developed hypotheses on the evolution of various morphological traits of both ana- and teleomorph within the class *Orbiliomycetes* (see the two chapters on teleomorph and anamorph morphology). Based on the combination of these traits and comparison with the situation in other classes, we present arguments about which of them might be the primary, plesiomorphic and which the secondary, apomorphic character states. Examples of characters of the teleomorph which we believe to be plesiomorphic are: desiccation tolerance of apothecia, dark pigments, equally septate, apically uninflated paraphyses, presence of croziers, hemispherical and/or thick-walled ascus apices, octospory, homopolar, globose to ellipsoid ascospores, and globose spore bodies attached by a short filum, and a bipolar arrangement of SBs.

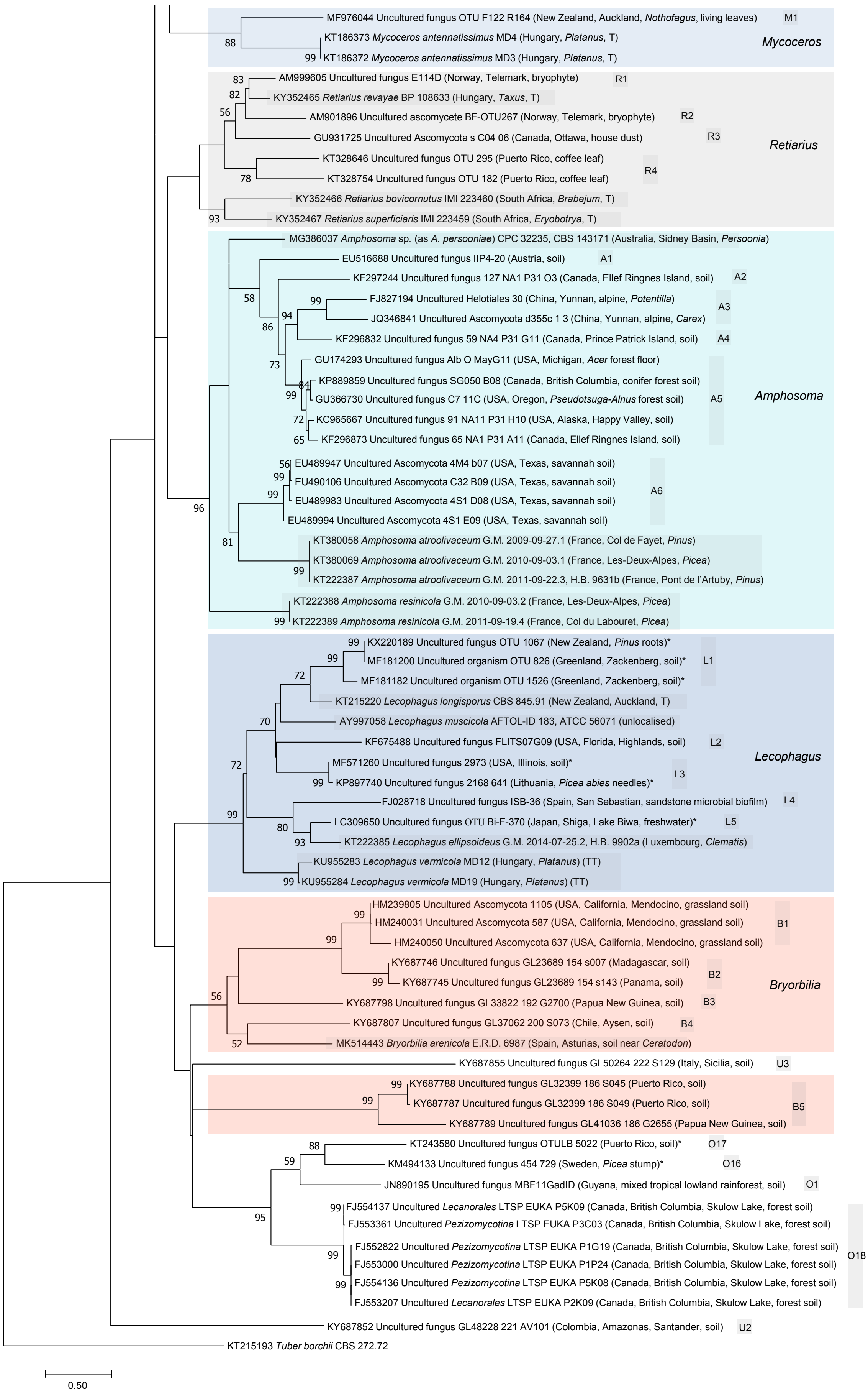
Whether crystalloid SCBs and glassy processes or hairs are plesio- or apomorphic remained unclear, but a secondary loss of these features undoubtedly occurred. Crystalloid SCBs are largely absent in *Hyalorbilia* and *Orbilia* section *Lentiformes*, which supports the hypothesis of apomorphy, but they occur as an exception in *Hyalorbilia ulicicola* and in *Orbilia cercidicola* of section *Lentiformes*, which suggests an ancient origin of these organelles. An ectal excipulum of horizontal textura prismatica, typical of *Hyalorbilia*, might have developed from a vertical t. angularis, typical of *Lilapila* and most members of *Orbilia*, but also the reverse case is imaginable, or a scenario in which both types of excipulum emerged from an intermediate case with oblique or ambiguous orientation which is found in *Amphosoma*, *Bryorbilia*, and *Lecophagus*. Plesiomorphic characters of the anamorph may include: short conidiophores, unbranched, straight conidia, and adhesive pegs as trapping device. A survey of selected characters is shown in Tab. 56.

Our hypotheses on plesiomorphic characters within *Orbiliomycetes* is supported to some extent by our molecular analyses, which confirm that *Amphosoma*, *Bryorbilia*, *Hyalorbilia*, *Lecophagus*, and *Lilapila* represent the ancestral group of the class (no DNA data exist for *Liladisca* and *Pseudorbilia*). Within *Orbilia* it is subgenus *Hemiorbilia* which complies best with this set of morphological criteria, and within that subgenus it is series *Vibrioides* of section *Hemiorbilia* and a majority of section *Lentiformes* which appear to form the phylogenetically older part, whereas a majority of section *Hemiorbilia* and a small minority of section *Lentiformes* (series *Ovales* and *Cercidicola*) might represent younger parts of the group. Also section *Ovoideae* of subgenus *Orbilia* complies with the above criteria to a certain degree, except that the ascus apices are predominantly thin-walled and truncate, the paraphyses often apically inflated, and glassy processes and crystalloid SCBs present in some species. Croziers occur in *Bryorbilia*, *Hyalorbilia*, *Lecophagus*, *Liladisca*, *Lilapila*, and *Pseudorbilia*, but in combination with a thick-walled ascus apex they occur only in *Lecophagus*.

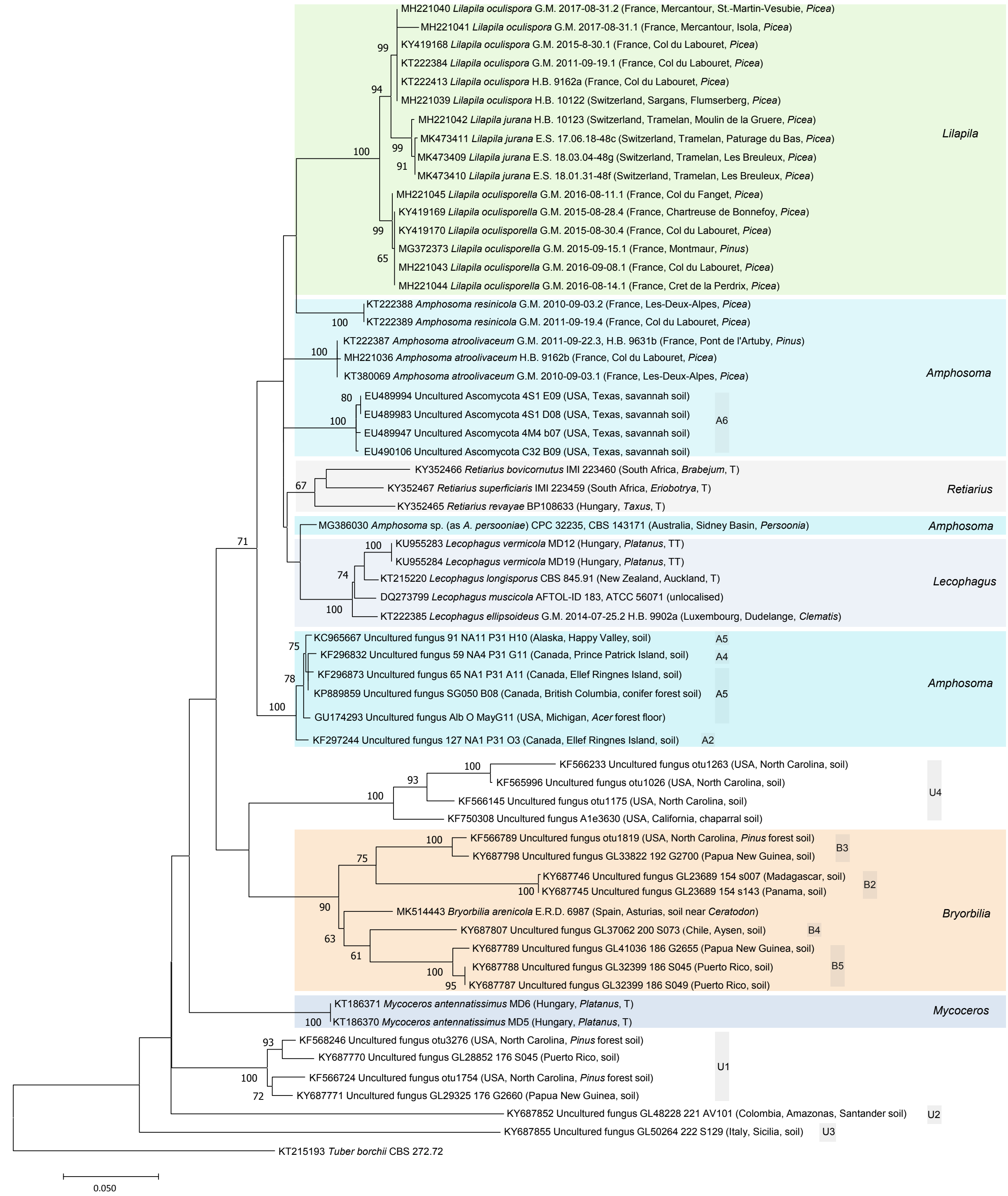
Whether the lens- or the lantern-shaped type of SBs represents the more plesiomorphic spore body type is difficult to determine. Besides series *Lentiformes*, lens-shaped SBs are characteristic of *Lilapila*, *Pseudorbilia*, and *Amphosoma*. They also occur in *O. microlentiformis* (series *Microsomates* of subgenus *Orbilia*) and inconsistently in *O. multicreosoteris* and *O. yuccae* (section *Ovoideae*). A tendency to lens-shaped SBs is observed in *Hyalorbilia multiguttulata*, in which globose SBs may get flattened at the attachment to the wall. More or less lantern-shaped SBs with a rather long filum are typical of series *Phanosomates*. The lantern-shaped type much more resembles the here postulated ancient type of SB which is globose and attached by a short, visible or invisible filum. This hypothesis would be in concordance with the general ontogeny of vacuoles as globose vesicles with a short and narrow attachment to the plasmalemma. Globose SBs attached by a short filum occur in *Lecophagus* but also in various groups of *Orbilia*. Also in *Hyalorbilia* roundish SBs with a filiform attachment appear to be typical but this attachment is usually below the resolution of the light microscope.

The bipolar arrangement of SBs is characteristic of *Amphosoma*, *Pseudorbilia*, and *Hyalorbilia* p.p.maj., and was observed in the large genus *Orbilia* only in abnormal spores as an exceptional case of regression. The reduction from bipolar to unipolar and also the migration of the SB attachment from apical to lateral appears to have occurred polyphyletically in different lineages. Within *Hyalorbilia* *H. erythrostigma* and *H. orbiliicola* (with unipolar SBs) clustered in a clade distant from the majority of taxa, all of





Phylogenetic analysis 3. Phylogram of *Lecophagus-Amphosoma* clade (see Phyl. 2) and *Mycoceros* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (94 sequences, 1187 positions, aligned with MUSCLE) using the GTR+G+I model in MEGA7 (500 replicates). The genera *Amphosoma*, *Bryorbilia*, *Lecophagus*, *Lilapila*, *Mycoceros*, and *Retiarius* are well resolved, but their relationship among each other remained unsupported. Environmental strains from GenBank clustered in supported clades with species of known genera (A1–A6 = *Amphosoma* spp., B1–B5 = *Bryorbilia* spp., L1–L5 = *Lecophagus* spp., M1 = *Mycoceros* sp., R1–R4 = *Retiarius* spp.) or formed clades with unresolved relationship (U = unidentified genus). The tree is rooted with *Tuber borchii*. T = type, TT = topotype, * = without ITS1 and partial 5.8S.



Phylogenetic analysis 4. Phylogram of *Lecophagus-Amphosoma* clade (see Phyl. 2) and *Mycoceros* inferred from ML analysis of LSU (D1–D3) rDNA dataset (63 sequences, 945 positions, aligned with MUSCLE) using the GTR+G+I model in MEGA7 (500 replicates). Except for *Amphosoma*, the recognized genera are well resolved, but their relationship among each other remained unresolved. Environmental sequences assigned in Phyl. 3 to *Amphosoma* (A1–A6) likewise clustered in clades with unresolved relationship. U = unknown genus of *Orbiliomycetes*. The tree is rooted with *Tuber borchii*. T = type, TT = topotype; without LSU (D3) in some sequences.

which being characterized by bipolar SB arrangement (Phyls 2, 7); whether the common ancestor possessed bipolar SBs is unclear since teleomorphs in several basal anamorph genera are unknown and our sequence of *H. latispora* (with bipolar SBs and isolated position) needs confirmation.

Ecology. Species of *Orbiliomycetes* form their apothecia as saprobionts on usually strongly decayed bark and wood, also herbaceous stems, sometimes basidiomycetes or pyrenomycetes, exceptionally dung or other residues of animals, and soil. Some species are adapted to rather undecayed bark and wood, or occur on more or less decayed resin of conifers. *Orbiliomycetes* inhabit a wide range of climatic regions, extending from humid to arid vegetation types. A more or less pronounced desiccation tolerance of the apothecia (xerobiotic species) applies to ~80% of *Orbiliomycetes* (455 out of a total of ca. 575 species treated in our study, unnamed

Key to genera of *Orbiliomycetes* based on characters of the teleomorph

(including easily confusable discomycetous genera with hyaline ascospores belonging to *Leotiomycetes*, *Lecanoromycetes*, *Pezizomycetes*, or apothecioid *Dothideomycetes*)

1. Asci amyloid[1] (apical ring and/or entire outer ascus wall); living mature ascospores eguttulate or containing globose refractive inclusions ('guttules') in a generally symmetrical arrangement, guttules KOH-resistant (LBs[2]), rarely KOH-sensitive (VBs[3]).......[certain genera of ***Helotiales*** (e. g., ***Laetinaevia***), ***Pezizales*** (e. g., ***Iodophanus***), ***Ostropales*** (e. g., ***Coenogonium***), ***Lecanorales*** (e. g., ***Scutula***), ***Agyriales*** (e. g., ***Agyrium***) etc.]

1. Asci inamyloid, when KOH-pretreated without any trace of a blue iodine reaction 2

2. Asci 8-spored, frequently producing small phialoconidia directly from the spores (often as ascoconidia formed already inside living asci); living ascospores never containing SBs[4] (or VBs[2]); apex of dead asci never truncate, apical or rarely lateral wall slightly to strongly thickened; hymenial parasite in apothecia of *Orbilia* spp. (if apothecia dark-coloured compare members of *Tympanidaceae*)...... .... ***Helicogonium*** (?***Phacidiales***)[5]

2. Asci 8- or multispored (by multiple mitoses), spores not producing small phialoconidia; living ascospores usually containing SBs (one or more per spore); apex of dead asci hemispherical to conical or truncate, with or without apical thickening 3

3. Apothecia macroscopically black, under transmitted light appearing bright purplish or olivaceous 4

3. Apothecia macroscopically white, yellow, ochre, rose, orange, red, rarely greyish-brownish-vinaceous, under transmitted light appearing hyaline or pale yellow, rose-orange, or ochraceous 9

4. Tissue deep purple-lilac under transmitted light; asci arising from croziers 5

4. Tissue dark olivaceous, blue-green, or grey-brown under transmitted light 6

5. Apothecia 0.3–0.4 mm diam., with a crenulate, hairless margin; spores narrowly fusoid-clavate, †7–11.5 × 1.5–1.8 µm, with a single tear-shaped SB at upper end (faintly visible in dead state); apices of paraphyses capitate, covered by deep purple caps of exudate; medullary excipulum hardly different from ectal excipulum; fallen needles of *Pinus*, temperate .... ***Liladisca***, p. 259

5. Apothecia 0.4–2(–4) mm diam., covered with dark purple-lilac, thick-walled, septate, finely warted hairs 50–200 × 6–9 µm; spores (sub) globose, *3–4.8 × 2.5–4.7 µm, with a single, broadly attached, lens-shaped SB; paraphyses not apically inflated, purple exudate between them but not on top; medullary excipulum sharply differentiated from ectal excipulum; resinous wounds of xeric branches or trunks of conifers, orotemperate to suprasubmediterranean .... ***Lilapila***, p. 262

6. Asci usually bitunicate: in dead state both apical and lateral wall often strongly thickened, 8- or multispored, usually arising from croziers; living spores without SBs, lipid content high or low .... ***Patellaria*** (*Dothideomycetes*), ***Symbiotaphrina*** (*Xylonomycetes*), ***Deltopyxis*** (*Lecanoromycetes*)

6. Asci unitunicate: in dead state laterally thin-walled, 8- or 16-spored, arising from simple septa (ascus bases ± bifurcate); living spores containing ± distinct SBs, lipid content ± low 7

7. Exudate light to dark grey-brown; spores *4.2–7.5 × 1–1.4 µm, SBs very small, ± eccentric; margin with glassy processes; hygric angiosperm wood, temperate .... ***Orbilia polybrocha*** (**series *Drechslerella***), p. 1631

7. Exudate dark olivaceous to blue-green; spores *5–17 × 2.3–4.2 µm; apothecia with ± smooth margin without glassy processes; xeric wood and bark, boreal or mesomediterranean 8

8. Living spores with 2 SBs (one at each end); living paraphyses and marginal excipulum containing globose, strongly refractive VBs .... ***Amphosoma***, p. 271

8. Living spores with a single apical SB; living paraphyses and marginal excipular cells without VBs .... **series *Lentiformes*** (**subgenus *Hemiorbilia***), p. 459, and ***Orbilia olivacea*** (**section *Ovoideae***), p. 1290

9. Anchoring hyphae *(5–)6–13(–17) µm wide, each cell usually containing one or a few cubical refractive bodies (SCBs[6]) 0.4–2 µm diam. in their centre; dead asci with a hemispherical to indistinctly mammiform apex with a small lens-shaped apical thickening; apothecia white, 0.08–0.25 mm diam.; spores subglobose to ellipsoid, *3.8–8 × 3–4.6 µm, with a single globose SB shortly connected to the spore apex; xeric wood & bark, parasitic on rotifers etc., subarctic to submediterranean .... ***Lecophagus***, p. 287

9. Anchoring hyphae *1.5–6 µm wide (only exceptionally wider), without central cubical bodies; dead asci with a hemispherical or truncate (partly saddle-shaped) apex, apical thickening absent or present (then almost as broad as ascus) 10

10. Living spores without SBs, with low to high lipid content, ellipsoid to oblong; ascus base never distinctly furcate .... ***Calloria***, ***Calloriopsis***, ***Gelatinopsis***, ***Laetinaevia*** etc. (***Helotiales***), ***Thelebolus*** (***Thelebolales***)[7]

10. Living spores mostly with one or several SBs, lipid content mostly low 11

11. Spores with a single SB in each spore [if SBs absent then ascus apex (†) distinctly truncate in front view], variously shaped; asci 8–128-spored; hymenial elements not firmly conglutinated in gel; plurivorous, from subarctic to temperate and tropical. ***Orbilia***, p. 444
If asci with croziers compare also *Hyalorbilia erythrostigma* (p. 417) and *H. orbiliicola* (p. 424).

11. Spores consistently with two or more SBs, situated near both ends or in both halves of the spore [if no SBs present then ascus apex (†) ± hemispherical]; asci 8(–16)-spored 12

12. Asci arising from simple septa, ascus base ± furcate or T- to L-shaped (exceptionally a few perforated croziers may occur among the simple-septate ascus bases); apex (†) with or without internal wall thickening; paraphyses multiguttulate or without VBs 13

12. Asci consistently arising from croziers (sometimes perforated, looking bifurcate); apex (†) without internal wall thickening; paraphyses and marginal excipulum usually with globose to often elongate, low- to medium refractive, hyaline to pale chlorinaceous VBs 14

13. Asci (†) often with internal wall thickening at apex, laterally always thin-walled; terminal cell of paraphyses containing a few large or many small, always globose and strongly refractive, hyaline VBs, without SCBs; spores with one SB at each end; xeric bark, wood & resin, temperate to subtropical .... ***Amphosoma***, p. 271

13. Asci (†) apically always thin-walled but laterally thick-walled when immature; terminal cell of paraphyses containing one globose refractive SCB, without VBs; spores with various small and large SBs; soil among moss, suprasubmediterranean ...... ***Bryorbilia***, p. 302

14. Hymenial elements non-gelatinized, easily separable; ectal excipulum at flanks of textura angularis; ascus apex (†) hemispherical (to conical) or strongly truncate depending on viewing direction; spores with one lens-shaped SB at each end; anchoring hyphae 1.2–2.5 µm wide, not radiating; apothecia white, 0.09–0.35 mm diam.; wood or bryophytes, subboreal to subtropical .... ***Pseudorbilia***, p. 305

14. Hymenial elements usually strongly gelatinized and conglutinate; ectal excipulum at flanks of horizontal t. prismatica (sometimes short-celled); ascus apex (†) hemispherical to conical or subtruncate irrespective of viewing direction; spores with 1–6 SBs towards each end; anchoring hyphae (1.3–)2–5(–10) µm wide, often radiating to form a hairy apothecial base; apothecia whitish to chlorinaceous or yellow, rarely reddish, 0.05–5 mm diam.; plurivorous, boreal to tropical .... ***Hyalorbilia***, p. 307

[1]) amyloid = parts of the ascus wall stain faintly to strongly blue (euamyloid) or red (hemiamyloid) when applying IKI directly, or consistently blue in IKI or MLZ when KOH-pretreated.

[2]) LBs = lipid bodies (oil drops). LBs represent a storage organelle for energy reserves. They are consistently globose inside living cells, but tend to fuse to irregular aggregations in damaged cells.

[3]) VBs = refractive vacuolar bodies. VBs are usually only visible in the living state; they disappear in KOH and selectively stain turquoise in CRB when applied to living cells. Usually they occur in the cells of paraphyses and marginal excipulum, but in some species in ascospores or conidia. They are either small and globose (multiguttulate) or large and globose to ellipsoid or very elongate.

[4]) SBs = spore bodies. SBs are a special type of refractive vacuolar bodies (VBs) inside the ascospores that are only known to occur in the *Orbiliomycetes*. Like vacuoles they are formed by invagination of the plasmalemma and stain with basic dyes; yet, they remain attached to the plasmalemma, either broadly or by a narrow point or filum (when very narrow the filum is invisible under the light microscope).

[5]) Members of *Helicogonium* do not produce ascomata but grow as intrahymenial parasites in ascomata of discomycetes (*Orbiliomycetes*, *Helotiales* and other orders) by forming asci among the paraphyses of the host, and often completely suppressing the asci of the host. Three species are known to occur in apothecia of *Orbilia*: *H. fusisporum* with fusoid ascospores with large LBs (conidia unknown), *H. orbiliarum* and *H. hyphodisci* with ellipsoid to subglobose, almost eguttulate ascospores, the former budding off ellipsoid ascoconidia, the latter cashew-shaped ascoconidia.

[6]) SCBs = KOH-sensitive ('soluble') cytoplasmic bodies. SCBs are ± refractive, variously shaped organelles which are only visible in the living state. They disappear in KOH and, contrary to VBs, do not stain in CRB.

[7]) Compare also couplet 13 (a few species of *Orbilia* and *Hyalorbilia* are without SBs; *Hyalorbilia* is then difficult to separate from *Gelatinopsis*, even on the basis of living material).

taxa included), whereas ± desiccation-sensitive apothecia (hygrobiotic species) were observed in ~20 % (ca. 120 species; see also Tab. 5).

Predatory capabilities, mainly of the anamorph, are so far observed with certainty in *Hyalorbilia* (testaceous rhizopods, nematode eggs), *Lecophagus* (rotifers and nematodes), and *Orbilia* (nematodes, copepodes, arthropods). Utilization of pollen as additional nutrient source is observed in many taxa but is especially typical of *Mycoceros* and *Retiarius*, and utilization of oospores occurs in *Hyalorbilia*.

Table 56. Synoptic table of genera of *Orbiliomycetes* with known teleomorph (presumed plesiomorphic features are highlighted in bold; for a more detailed treatise see Tab. S3). Explanation: **Apothecial pigment**: hyal = ± hyaline/white, red = yellow/orange/rose/lilaceous, oliv = black-olivaceous/blue-green. **Ascus apex**: con = conical, hem = hemispherical, trc = truncate, thin = thin-walled, lent = lens-shaped thickening, thick = broad thickening (often with apical chamber); **ascus base**: + = croziers, – = predominantly simple septate. **Ascospore shape**: g = (sub)globose, e = ellipsoid, c = cylindrical, f = fusoid/fusiform, t = with a tail; **ascospore curvature**: – = not curved, + = slightly to strongly curved; **number of spore bodies**: 1 = one SB per spore (usually apically), 2+ = two or more SBs per spore; **spore body shape**: g = ± globose, l = lens- (to plug-)shaped, t = tear-shaped, v = vermiform/filiform. **Paraphysis apex**: 0 = not inflated, 4 = very strongly inflated; **exudate over paraphyses**: -/+ = absent/present. **Ectal excipulum** at lower flanks: │ = vertical textura angularis or t. prismatica (70–90°), ⁄ = obliquely oriented t. prismatica (20–70°), — = horizontal t. (angularis-)prismatica(-porrecta) (0–20°). **Hairs**: – = without hairs, s = septate hairs, g = glassy processes. **Cell inclusions in paraphyses and excipular cells (or sometimes in conidia)**: **VBs**: g = with strongly refractive, globose guttules, e = with low- to medium refractive, soon elongate vacuoles; **SCBs**: a = small angular (cubical) central bodies, g = globose, hyaline, low-refractive bodies, c = crystalloid, partly pigmented, refractive bodies. **Anchoring hyphae**: n = narrow (< 5 µm), w = wide (> 5 µm). **Desiccation tolerance of apothecia**: t = desiccation-tolerant, s = desiccation-sensitive. **Anamorph**: bra = brachyphoris-like, cur = curucispora-like, dwa = dwayaangam-like, lec = lecophagus-like, tri = trinacrium-like, ver. = vermispora-like, var. = anguillospora-, arthrobotrys-, curucispora-, dactylella-, dactylellina-, descalsia-, dicranidion-, drechslerella-, dwayaangam-, helicoon-, tridentaria-, trinacrium-, and vermispora-like.

	Pigment	Ascus apex	Ascus apical wall	Croziers	Spore number	Spore shape	Spore curvature	Spore bodies		Paraphyses	Exudate	Ectal excipulum	Hairs	VBs	SCBs	Anchoring hyphae	Desiccation tolerance	Anamorph
Liladisca	**dark lilac**	**con**	**thick**	+	**8**	f	–	1	t	2–3	+	⁄—	–	?	?	n	**t?**	?
Lilapila	**dark lilac**	**hem**	thin	+	**8**	g	–	1	l	**0**	–	│	s	(g)	–	n	**t**	?
Lecophagus	hyal	**hem**	**thick**	+/–	**8**	**e**g	–	1	**g**	**0**–1	–	(—)	–	–	a	w	**t**	lec
Pseudorbilia	hyal	trc	thin	+	**8**	**c**	–	**2**	l	1	(–)	(│)	–	e	–	n	s	?
Hyalorbilia	hyal	**hem**	thin	+	**8**–16	**ce**gf	–/+	1–**12**	**g**	**0**–2	+	—	–/(g)	e	-/a/(c)	n/(w)	**t**/s	bra/cur/ dwa/ tri/ver
Amphosoma	hyal	**hem**	**thick**	–	**8**	**ce**f	–	**2**	**g**l	**0**–2	+	│⁄—	–	g	–	n	**t**	tri
Bryorbilia	hyal	**con**-trc	thin	–	**8**	**e**	–	**~2–10**	**g**	**0**–2	+	⁄	–	–	g	n	s	?
Orbilia	hyal/red/ **dark olive**	**hem** /trc	**thick** /thin	–	**8**–128	**ce**gft	–/+	1	**g**ltv	**0**–4	+/–	│(—)	–/s/g	–/e	g/c/–	n	**t**/s	var.

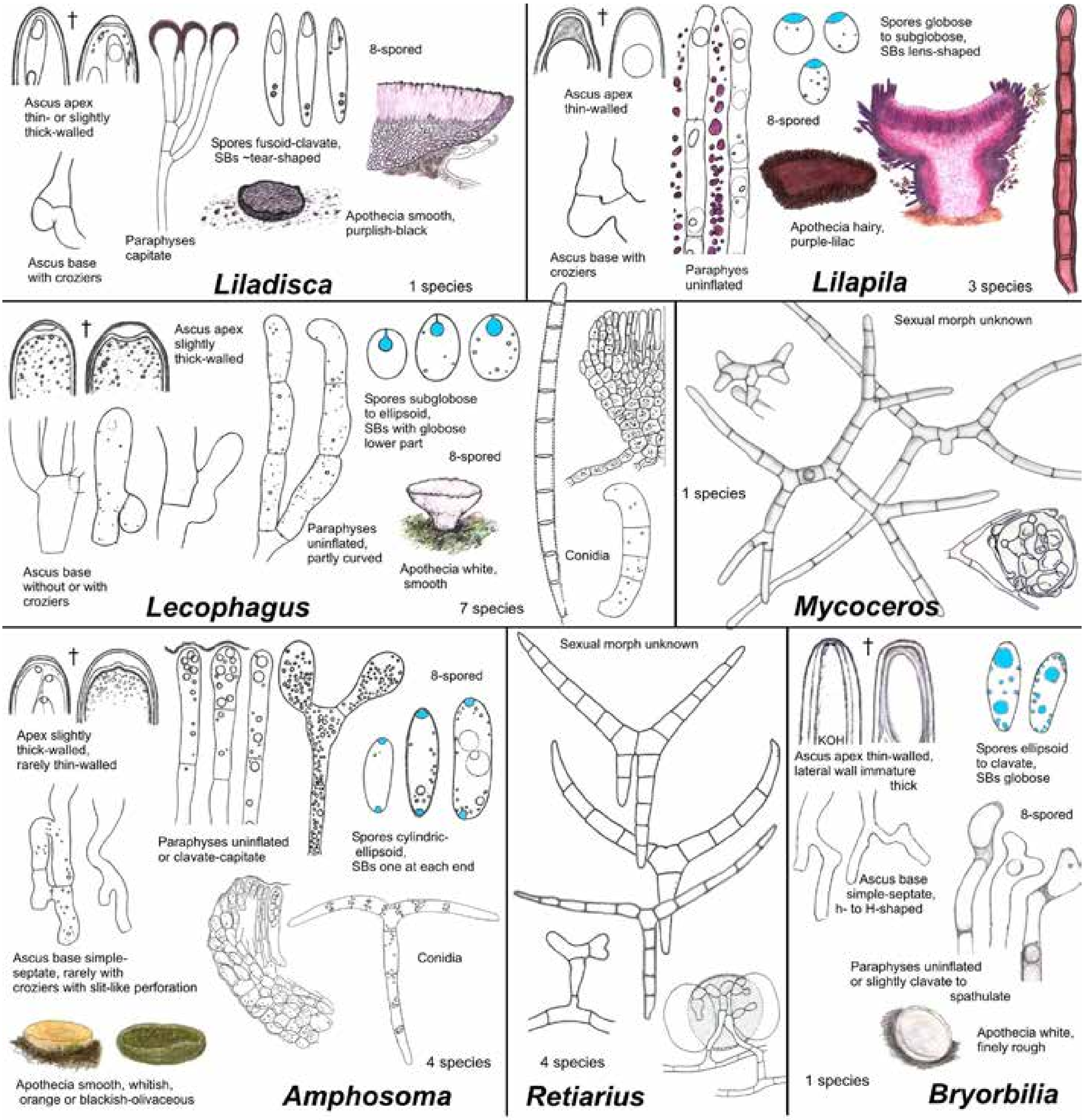


Plate 25. Overview of the genera of *Orbiliomycetes* I.

Liladisca Baral, **gen. nov.**, MB 812647

Type species: *Tympanis acicola* Fuckel

Etymology: referring to the deep purple-lilac colour of the apothecia when seen under transmitted light.

Latin diagnosis: *Apothecia in statu rehydratato 0.2–0.4 mm diam., orbicularia, sessilia, erumpentia, tota obscure purpureo-lilacea vel atra, hymenio plano vel convexo, margine irregulariter minute crenulato. Asci clavati, apice obtuso vel conico, tunica in statu emortuo tenui vel minute incrassata, non amyloidei (IKI), octospori, stipitati, ex uncis nati. Ascosporae distichae in asco emortuo, oblonge fusiformes-clavatae, aseptatae, hyalinae, in statu emortuo prope apicem corpusculum non refringens, ellipsoideum vel lacrimiformem continentes. Paraphyses ad apicem capitatae, exsudato crasso et fortiter purpureo-lilaceo tectae, non cohaerentes, ramosae. Excipulum ectale e textura prismatica(-angulari) crassitunicata, exsudato intercellulari fortiter purpureo-lilaceo, excipulum medullare e textura prismatica similiter compositum. Habitat ad acus putridos dejectos* Pini sylvestris.

Recognized species: *L. acicola*.

Liladisca acicola (Fuckel) Baral, **comb. nov.**, MB 812648 — Pls 27–28

Basionym: *Tympanis acicola* Fuckel, Fungi Rhen. Exs., suppl. fasc. V, no. 1965 (1867)

≡ *Pezicula aterrima* Fuckel, Jahrb. Nassau. Ver. Naturkd. 23–24: 278 (1870), nom. illegit., ICN Art. 30.8, 52.1

≡ *Phacidium aterrimum* (Fuckel) Sacc., Syll. Fung. 8: 713 (1889)

≡ *Patinella aterrima* (Fuckel) Rehm, Rabenh. Krypt.-Fl., 1.3: 312 (1889)

Etymology: *acicola*: referring to the habitat (needles of *Pinus*); *aterrima*: according to the black apothecial colour in external view.

Typification: Germany, Rheinland-Pfalz, Ingelheim, needles of *Pinus sylvestris*, undated (autumn), L. Fuckel (Fungi Rhen. Exs. 1965, M-0206556, lectotype, designated here, MBT382100).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.4 mm diam., 0.11–0.12 mm high (receptacle 0.07–0.09 mm), purplish-black, non-translucent, round, slightly gelatinous, scattered or gregarious in

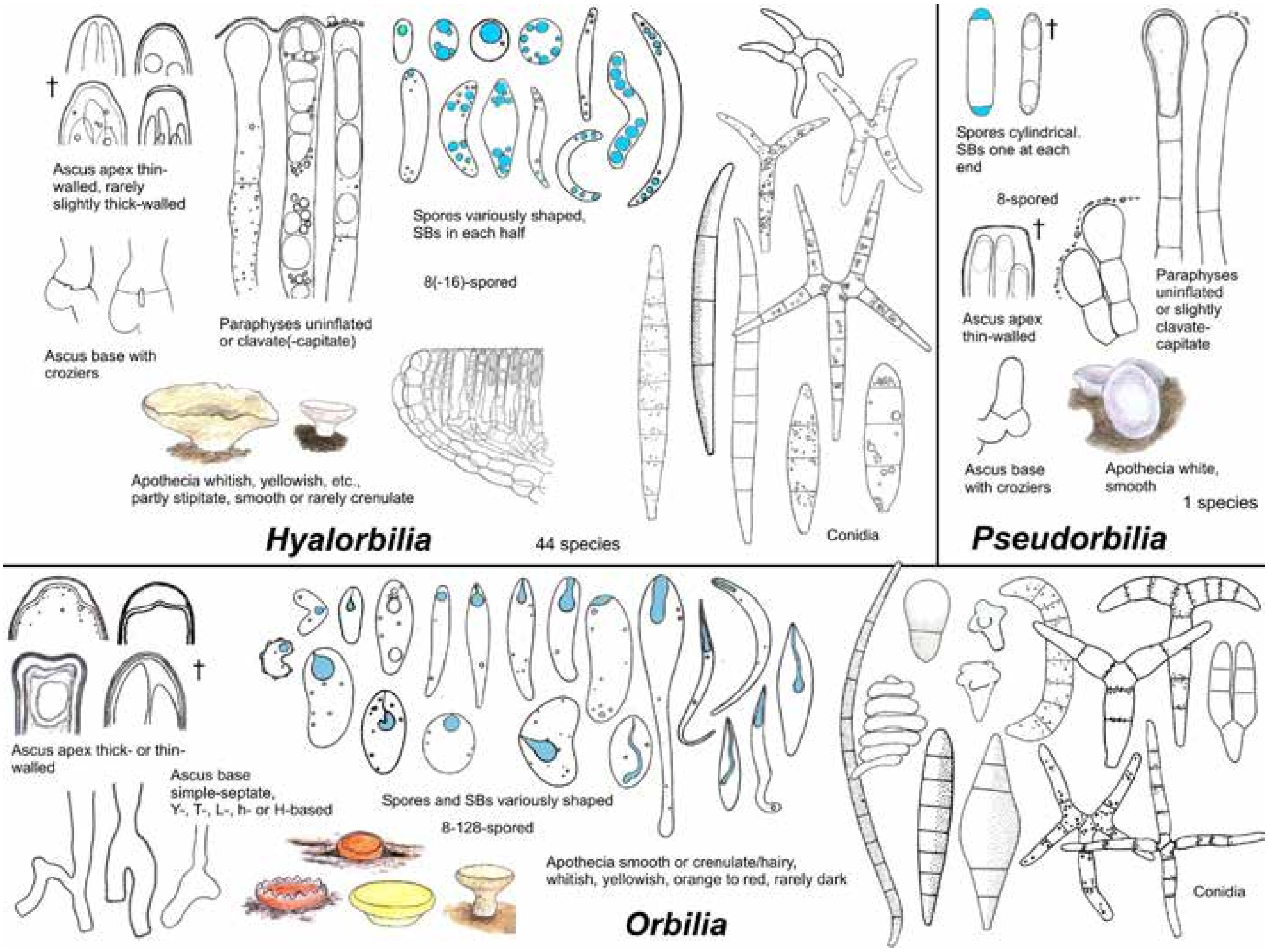


Plate 26. Overview of the genera of *Orbiliomycetes* II.

small groups; disc flat to slightly concave, margin distinct, irregularly crenulate by small protruding warts; broadly sessile, erumpent from beneath epidermis; dry black. **Asci** †40–62 × 4–6 µm, 8-spored, spores biseriate, lower spores inverted, pars sporifera †20–30 µm long; **apex** (†) obtuse to conical irrespective of the viewing direction, with or without minute dome ~0.7 µm thick, without apical chamber; **base** with short to medium long and thick, often flexuous stalk, arising from croziers (without perforation). **Ascospores** †7–10.5(–11.5) × 1.5–1.8 µm, non-septate, smooth, narrowly fusoid-clavate, apex obtuse (to subacute), base slightly to strongly attenuated, straight to very slightly curved; **SBs** †1.7–2.2 × 0.8–1.2 µm, tear-shaped to ellipsoid, seen as a transparent area in KOH, attachment to wall unclear, perhaps by a small point. **Paraphyses** apically medium to strongly capitate, terminal cells †12–23 × 2.5–4.3 µm, lower cells †4.5–15 × 1.2–1.8 µm; frequently branched in upper half, not immersed in gel, therefore separable by pressure, hymenium in H_2O pale to bright (apically dark) purple-lilac. **Medullary excipulum** in H_2O deep purple-lilac to wine-red, ~35 µm thick, of strongly gelatinized textura prismatica-angularis (common walls ~0.5–2.5 µm thick), upwards oriented in centre, horizontally at flanks, indistinctly delimited from ectal excipulum. **Ectal excipulum** in H_2O deep purple-lilac, of strongly gelatinized t. prismatica(-angularis) (common walls ~0.5–3 µm thick), 15–20 µm thick from base to margin, oriented at a 10–50° angle to the surface, cells at flanks †4–10 × 2.8–5 µm, marginal cortical cells not clearly seen; **glassy processes** and **hairs** absent. **Anchoring hyphae** medium abundant, hyaline, †2–2.8 µm wide, walls 0.3 µm thick, smooth. **SCBs** no data available. **Exudate** in ectal and medullary excipulum intercellular, homogeneously pigmented, in H_2O dark purple-lilac or wine-red; over paraphyses forming 1–3 µm thick, individual, firmly attached caps, over margin and flanks 1–3 µm thick. **Chemical reactions**: purple-lilac pigment in alkali (KOH) turning darker and more greyish-lilac-violet, purplish-violet-brown, or blackish-brown, in acids (PVA) deep (fox-) orange- to red-brown. **— ANAMORPH**: unknown.

Habitat: on rather strongly decayed needles of *Pinus sylvestris* fallen to ground, on both sides of the needles, green algae not seen. **Associated**: *Lophodermium pinastri*. **Desiccation tolerance**: probably desiccation-tolerant, according to the associated *Lophodermium*. **Altitude**: 85 m a.s.l. **Geology**: Devonian Taunus quartzite. **Phenology**: autumn.

Taxonomic remarks. *Liladisca acicola* is easily recognized by its deep purple-lilac pigment of the intercellular gel-like exudate in the entire excipulum when viewing under transmitted light in a water mount. The species differs from *Lilapila* in the absence of hairs, narrower anchoring hyphae with a thin, smooth wall, an ectal excipulum of textura prismatica oriented at a low to oblique angle at the flanks, a medullary excipulum being hardly differentiated from the ectal excipulum, narrowly fusoid-clavate ascospores with ± tear-shaped SBs, a conical ascus apex which is often provided with a small apical thickening, and capitate paraphyses covered by thick, deep purplish caps of exudate. These differences support distinction at the generic level, although admittedly similar amounts of differences occur within the large genus *Orbilia* as circumscribed at present.

The purple-lilac or wine-red pigment appears to be very similar to that found in *Lilapila*. However, when mounted in KOH or PVA the pigment exhibits colours different from

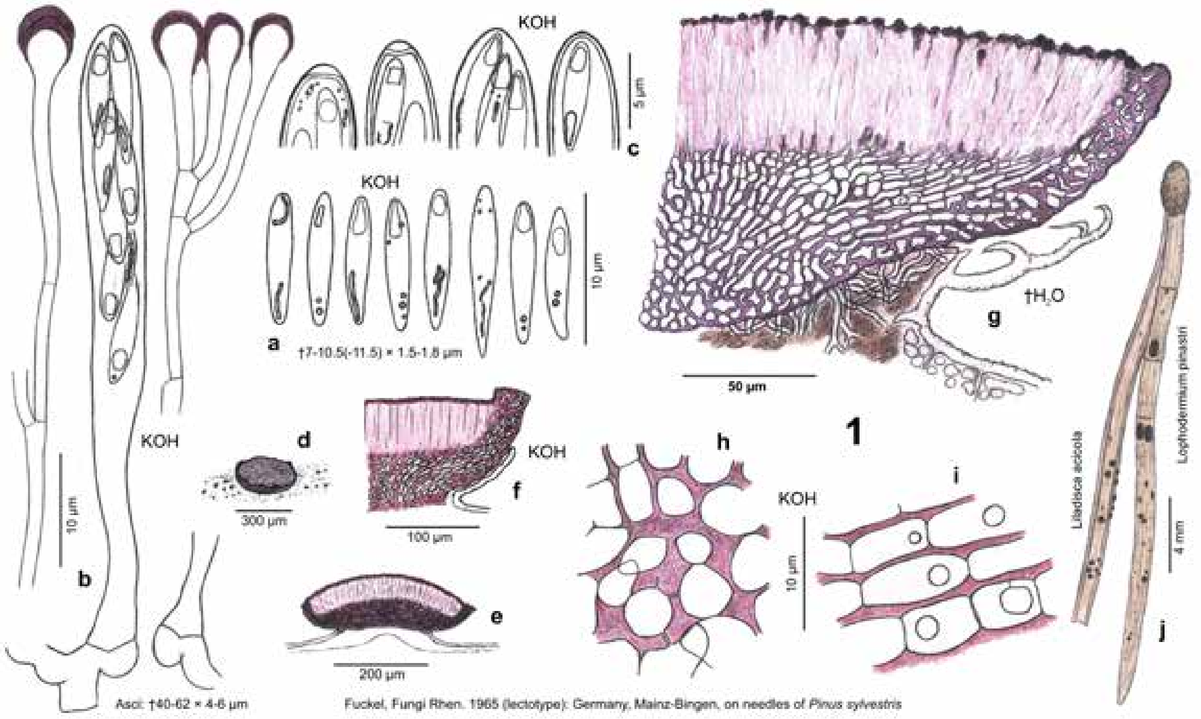


Plate 27. **1**: *Liladisca acicola*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium (rehydrated); **e–g**. apothecia in median section; **h**. id., central part of medullary excipulum; **i**. id., lateral part of medullary excipulum at mid flanks, near ectal excipulum; **j**. needles of *Pinus sylvestris*.

Lilapila. In KOH it keeps the purplish-violet shade whereas that in *Lilapila* changes to an olivaceous colour. In PVA *Liladisca* turns orange-brown whereas *Lilapila* keeps the purple-lilac pigment. In both media the exudate is not dissolved in either of the two genera.

Rehm (1889) described the pigment over the paraphyses and in the excipular tissue as 'brown-red'. Fuckel (1867, 1870) reported the apices of paraphyses as uniguttulate, fuscous, 5 µm wide, but he did not mention the pigmentation of the excipular tissue under transmitted light. The spores were described by Fuckel and Rehm as cylindrical although they are actually more fusoid-clavate.

The single species here recognized in *Liladisca* is only known from the old type collection made by L. Fuckel in or before 1867. It undoubtedly belongs to the *Orbiliomycetes* on account of the presence of a spore body in the ascospore apex, and because of the inverse orientation of the lower spores within the asci, characters which were overlooked by Fuckel and also by Rehm who examined a syntype specimen. The SBs are now rather inconspicuous (Pl. 27: 1a), but have probably been refractive and perhaps more slender in the living state. There are also irregular, strongly refractive, filiform artifactual structures to be found in the dead sporoplasm which probably originate from fusion of small LBs.

Because of inamyloid asci and a pigmented medullary excipulum, Rehm (1889) doubted a relation to *Pezicula* and *Phacidium*, but believed that the species belonged to the *Patellariaceae*. Without personal studies, DiCosmo et al. (1984: 172) excluded it from *Phacidium*, and Verkley (1999: 141) suggested affinities with the tribe *Mollisieae* s. Korf (*Helotiales*).

Nomenclature and type studies. Fuckel introduced two different names for the same collection. On the printed herbarium label of the excsiccatum distributed in 1867 (Fungi Rhen. Exs. 1965) he named the species *Tympanis acicola* and provided a Latin diagnosis. An almost exactly concurring diagnosis was later published in his 'Symbolae Mycologicae'. Here Fuckel (1870) changed the name to *Pezicula aterrima* by referring to the older name *Tympanis acicola*. According to Art. 30.8 (Turland et al. 2018), printed matter accompanying exsiccatae must be considered as effectively published. Hence '*acicola*' becomes the correct epithet (see also Pfister 1985: 49) and '*aterrima*' is nomenclaturally superfluous (Art. 52.1, Turland et al. 2018).

The specimen in M consists of about 40 well-preserved apothecia and fully concurs with the protologue. Rehm (1889) appears to be the only author who ever published a reexamination of the fungus. Saccardo (1889) copied Fuckel's description, and Migula (1913: 890) copied that of Rehm. Syntype specimens exist

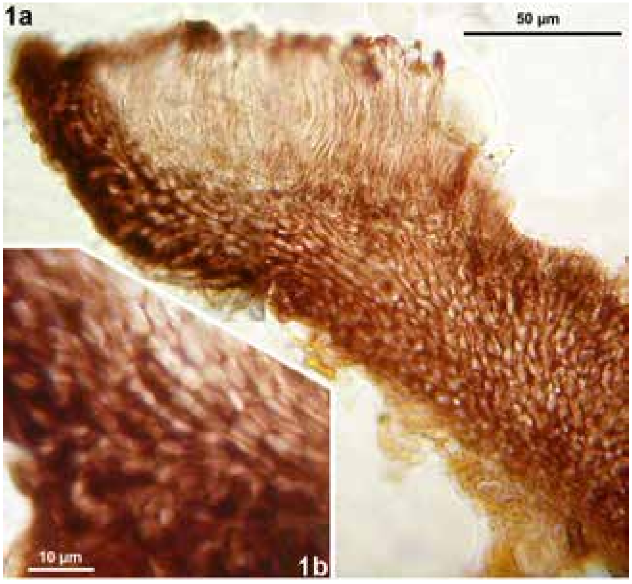


Plate 28. **1**: *Liladisca acicola*. – **1a**. apothecium in median section; **1b**. id., closeup of ectal and medullary excipulum at mid flanks. – Dead state (permanent slide, in PVA). — **1a–b**. Fungi Rhen. Exs. 1965 (H.B. 5045): Germany, Ingelheim, on *Pinus*.

also in other herbaria (e.g., S-F90272), but were not requested in the present study. In order to fix the new genus on a specimen, we here designate M-0206556 as **lectotype** of *Tympanis acicola*.

Ecology. *Liladisca acicola* grew on fallen, rather rotten needles of *Pinus sylvestris* probably in a pine forest, near the Rhine river, in cold-temperate humid, subcontinental central Europe. This remarkable fungus was considered to be 'very rare' by Fuckel, and indeed no further collections came to our notice.

Specimens included. **GERMANY**: **Rheinland-Pfalz**, Rheingau between Mainz and Bingen, NW of Ingelheim, near Frei-Weinheim, 85 m, on needles of *Pinus sylvestris*, undated (autumn), L. Fuckel, Fungi Rhen. Exs. 1965 (M-0206556, **lectotype**, H.B. 5045 ø).

Lilapila Baral & G. Marson, **gen. nov.**, MB 813441

Type species: *Lilapila oculispora* Baral & G. Marson

Etymology: named according to the deep purple-lilac colour of the apothecial tissue and hairs when seen under transmitted light.

Latin diagnosis: *Apothecia in statu rehydratato subsessilia, superficialia, hymenio obscure purpureo-lilaceo vel atro, pilis longis lilaceo-nigris dense confertis. Asci cylindrici, apice in statu emortuo rotundati, tunica tenui, non amyloidei (IKI), octospori, ad basim uncinati. Ascosporae monostichae in ascis vivis, globosae vel subglobosae, intus corpusculo refringente lentiforme ad tunicam appresso. Paraphyses deorsum ramosae, ad apicem non inflatae, non cohaerentes. Pili cylindrici, plerumque 50–150 µm longi, crassitunicati, 3–7 septati, in toto intense lilaceo-purpurei, tunica dense minute granulosa, apice rotundato. Excipulum ectale e textura prismatica-angulari, cellulis hyalinis, extus crassitunicatis, exsudato brunneo-lilaceo tectis, excipulum medullare in parte inferiore textura oblita leniter vel valde gelatinosa. Inter cellulis hymenii, subhymenii et excipuli medullaris exsudatum abundans e multis granulis lilaceo-rubris compositum. Habitat in ramis vulneratis siccis* Piceae *et* Pini, *vivis vel leniter putridis, in corona arborum, ad corticem vel plerumque resinam nigram, in Alpibus meridio-occidentalibus.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated dark purple-lilac-blackish, round, somewhat elliptical or irregular if large, slightly to medium gelatinous, scattered to gregarious in small groups; disc medium concave to flat, margin and exterior densely covered by fascicles of blackish-purple hairs; sessile or mostly with a ± abrupt stipe, stipe sometimes also with scattered purple-brown hairs and completely immersed in blackish layer of associated hyphomycetes; dry black, contracted, sometimes ± hysterioid, disc completely covered by the converging hairs. **Asci** *(43–)50–80(–84) × (4.5–)5–10.3(–11.5) µm, †(44–)49–65(–70) × (4–)4.3–5.8(–6.7) µm, 8-spored (rarely 1–2 spores aborted), spores (*) uniseriate, sometimes subbiseriate, orientation irregular but SBs preferably pointing sideways; **apex** (†) hemispherical to very slightly truncate or conical (irrespective of the viewing direction), apical wall only slightly thickened [†0.3–0.4(–0.5) µm {3}], without internal wall thickening, wall CR–; **base** with a medium long, thick, slightly flexuous stalk, arising from croziers of variable shape, mostly with a 1–3 µm long, ± slit-like perforation (up to 6 µm in ascogenous hyphae). **Ascospores** *(3–)3.3–4.5(–5.5) × (2.5–)2.8–4.5(–5.5) µm, †2.8–4.2 × 2.3–4 µm, smooth, globose to subglobose, slightly flattened (e.g., 4 × 3.7 × 2.8 µm, distinctly subglobose only in profile view); **SBs** (0.3–)0.4–0.8(–1) × 1.4–3.3 µm, strongly refractive, lens- to calotte-shaped, circular in front view, very broadly attached to wall where flattened spore is broadest (simulating terminal attachment, Pls 31: 1a, 2a, 3a; 32: 4b); with 1–7 minute LBs; germination by germ tubes once seen in an old apothecium. **Paraphyses** apically uninflated or only slightly inflated or attenuated, *(1.7–)2–3(–3.7) µm wide, ± equalling the living asci (protruding 0–5 µm over dead asci), ± equidistantly septate, branched only near base, here sometimes with anastomoses, paraphyses and asci ± easily separable, hymenium bright purple-lilac by numerous exudate granules. **Medullary excipulum** 50–200 µm thick, hyaline but young with dense, later scattered patches of purple-lilac granules, especially in the perihymenial region and towards the ectal excipulum, granules embedded in an invisible gel matrix; 2-layered: **upper part** non- or medium gelatinized, ~40–150 µm thick, of medium dense to dense, horizontally or ± upwards oriented textura intricata, hyphae *1.8–2.5 µm wide, intermingled with many inflated, globose to ellipsoid, catenate cells *5–15(–20) × 5–10(–15) µm; **lower part** of slightly to strongly gelatinized t. intricata-porrecta-oblita, 10–100 µm thick, irregularly oriented or at 0–50° towards the very sharply delimited ectal excipulum, individual cells *17–30 × 1.7–3(–5) µm, †1.2–3 µm wide, if strongly gelatinized then with slightly refractive gelatinous sheath ~1 µm thick. **Ectal excipulum** hyaline to pale yellowish-ochraceous, near base with bright to dark ochre-brown to purple-lilac intercellular exudate, of vertically oriented t. angularis-prismatica from base to mid flanks, cells *(7–)9–19(–22) × (5–)7–10(–14) µm, (†) strongly gelatinized (wall swelling in dead state to 1.5–3 µm), outer wall of cortical cells *1.5–2 µm thick, lateral wall *0.5–1.5 µm, glassy; marginal cortical cells more elongated, oriented at a 20–30° angle to the surface. **Hairs** covering the whole exterior but sometimes lacking at base and flanks, inserted on cortical cells, free or in converging, agglutinated fascicles, at margin and flanks (30–)80–150(–200) × 5–9(–11) µm, cylindrical, straight to slightly flexuous, with (1–)3–8(–11) refractive septa (0.3–1.3 µm thick), apex rounded, whole surface densely covered by low but distinct warts, wall surface and warts dark purple-lilac in H_2O, sometimes ochre-brown when dead, marginal hairs ± paler towards apex (upper 5–20 µm or more), sometimes almost smooth; lateral wall */†1–2.5 µm thick {3}, 2-layered, warts 0.1–0.3 µm high, 0.2–0.8 µm wide, sometimes almost confluent, **glassy processes** absent. **Anchoring hyphae** sparse to very abundant, restricted to base, subhyaline to pale yellowish-cream, (3.5–)4–5.5(–6.5) µm wide, walls *(0.2–)0.5–1.3 µm thick [†(0.2–)1–1.5(–2) µm], surface finely or mostly roughly and densely warted, rarely some hyphae smooth. **SCBs** in terminal cells of paraphyses absent or globose to ellipsoid, sparse, very slightly or medium refractive; in cells of medullary excipulum regularly present, 1.5–4 µm diam., strongly refractive, ± globose or often ring-shaped, unstained in CRB_A; **VBs** sometimes present inside vacuoles of asci, paraphyses and medullary excipulum: one or a few strongly refractive, globose, hyaline, trembling bodies 0.3–1 µm diam., staining tardily blue in CRB_A, disappearing in KOH; **LBs** never containing carotenoids. **Exudate**: bright to deep purple-lilac granules or clods 0.3–1.5 µm diam., abundant in hymenium and medullary excipulum, between paraphyses from base to apex or subapex, not covering the tips, in ectal excipulum abundant between the cells, also covering the entire hair wall as a thin film; exterior covered by a ± continuous reddish-brown layer, in stipe pale yellowish-ochraceous; anchoring hyphae warted by a hyaline exudate. **Chemical reactions**: purple-lilac exudate in 5% **KOH** turning light to dark dirty grey- to olive-brown, warts on hairs not dissolved; adding strong acids to the KOH-mount fully recovers the purple-lilac colour. **CRB** stains the warted exudate on the anchoring hyphae (turquoise-)blue and a thin gel layer beneath lilac and the medullary excipular gel faintly lilac. — **ANAMORPH**: **Colonies** whitish to pale yellowish, slow-growing (see below). **Conidiophores** and **conidia** unknown (but see under *L. oculispora*).

Habitat: on resinous, usually blackened wounds of corticated, living or recently dead, still-attached branches or standing trunks of conifers, never directly on wood, wounds either with small to large, resinous decorticated areas or completely overgrown by bark, apothecia often only on bark that borders the decorticated wound, preferably growing in the niche between bark and wood; often also on the decorticated resinous area but then on a ± thick layer of resin covered by a black layer of dark brown hyphomycetes, green algae sparse or lacking. Growing in association with various resinicolous ascomycetes.

Recognized species: *L. jurana*, *L. oculispora*, *L. oculisporella*, *L. gallica* nom. prov.

Taxonomic remarks. The genus *Lilapila* is quite extraordinary by it purplish-black apothecia covered with large, deep purple, septate, thick-walled, finely warted hairs and by (sub)globose ascospores with a single, broad and thin, lens-shaped spore body. Further characteristics are: asci arising from croziers, with rounded, thin-walled apex, paraphyses simple, non-inflated at apex, with purple-lilac exudate between, ectal excipulum of thick-walled, angular to prismatic, vertically oriented cells, medullary excipulum sharply delimited, of gelatinized textura intricata.

Some variation was noted in the rate of gelatinization of the outer medullary excipulum, but this seems to depend on the development stage: in younger apothecia the gel was more refractive and therefore more obvious. The purple-lilac pigment of *Lilapila* belongs to the most spectacular characteristics of the genus. It is best seen under transmitted light in a water mount, but also in acidic solutions. Unlike *Liladisca*, the pigment turns greyish-olivaceous in alcali, moreover, it is granular in the inner regions of the apothecium, and only on the surface of the hairs it forms a continuous layer. In aged but still-living apothecia the lilac pigment on the hairs may change to red-brown in water without application of alkali. Thus, the hairs at the flanks may appear brownish while the younger marginal hairs are still bright lilac.

Species delimitation. Although the four taxa within *Lilapila* are morphologically very similar, we have separated them based on strong molecular evidence. However, a correlation of molecular data with differences in ascus and ascospore measurements was noted between some of them. This variation was observed when sequences were not yet available, and was considered as quite unusual within the species level.

Cultural characteristics and anamorph. Ascospores of *L. oculispora* and *L. oculisporella* tardily germinated when shot on agar (CMA:5), and the whitish to very pale yellowish mycelium was very slow-growing. No conidiophores and conidia could be obtained in culture under different CMA concentrations.

Phylogeny. Sequences from 28 samples of *Lilapila* spp. were obtained, comprising ITS and LSU (D1–D2, often also D3–D4 and D5–D6; 2 sequences only ITS), 10 also SSU (V7–V9). Two sequences (*L. oculispora* H.B. 10122, *L. jurana* H.B. 10123) include SSU V1–V9, LSU D1–D12, *L. oculispora* also IGS. Sequence similarity and phylogenetic analysis support affiliation of the genus in *Orbiliomycetes*. BLAST search for SSU (V7–V9) yields *Lecophagus* spp. as closest hit (distance 2%). When analysing 5.8S+LSU or SSU+ITS+LSU, *Lilapila* clustered in a clade with *Amphosoma*, *Bryorbilia*, *Lecophagus*, and *Retiarius* with medium or low support, respectively (Phyls 1, 2). However, a high distance to these and other genera is observed, ranging in the LSU (D1–D2) at 6.2–7.5% (*Amphosoma*), 8.3–10% (*Bryorbilia*), 8.7–10.5% (*Lecophagus*), 9–10.7% (*Retiarius*), 10–12% (*Mycoceros*), and 13–19% (*Hyalorbilia*).

Nucleotide positions specific for the genus. A few motifs occur in the more frequently sequenced rDNA regions that characterize *Lilapila*. In the SSU V9 at pos. 287 *Lilapila* has AGT**A**AGT (*L. oculispora*, *L. oculisporella*) or AGT**G**AGT (*L. jurana*, *L. gallica*), whereas other *Orbiliomycetes* have **T** (mostly AGT**T**GGT). In the LSU D1 domain pos. 226 is unique (GTT**G**ACGGC or in *L. oculisporella* GTC**G**TCGGC; in all other *Orbiliomycetes* mainly **C**, sometimes **T** or **A** but never **G**), and also pos. 300 and 311 are unique (**A**GGTAAATTTC**T**), except for *O. pilifera* which has likewise A + T. In a few more variable regions of the LSU D2 domain the following motifs are almost unique for *Lilapila*: TCGGTGCAATG (pos. 561–571) also occurs in *Retiarius bovicornutus*, and CGCGATCGAG (pos. 580–589) in section *Lentiformes* p.p. (*O. foliicola*, *O. cucumispora*, *O.pluristomachia*). In the D3 domain the motifs AGGTGGGAGCCGC (pos. 717–729) and adjacent AAGGTGCACCATCG (pos. 730–743) each were otherwise only observed in *O. crenatofalcata*.

In the region of the three '*Orbiliales*-specific' primers (Smith & Jaffee 2009, see Tabs 18–19), *Lilapila* concurs with different other genera of *Orbiliomycetes*. For primer Orb5.8s1F this is *Amphosoma*, *Bryorbilia*, *Lecophagus*, *Retiarius*, and the *Vermispora* clade of *Hyalorbilia*, whereas for Orb5.8s3F it is *Mycoceros* and *Orbilia* p.p.maj. *Lilapila* is variable in the primer region Orb28s2R: *L. oculispora* concurs here mainly with *Mycoceros*, *L. oculisporella* with *Retiarius*, *Amphosoma*, and *Lecophagus*, and *L. jurana*/*L. gallica* show a further variant which is so far unique within *Orbiliomycetes*. However, especially in Orb28s2R various non-orbiliaceous ascomycetes concur with *Lilapila*. Congruence of *Lilapila* with *Mycoceros* and *Hyalorbilia* p.p. is observed in stem-loop B8 near the 3'-end of 5.8S (Tab. S4).

Nucleotide positions specific for the recognized species. Despite their close morphological similarity, a high distance is observed between the three validly described species, although the infraspecific variability is negligibly low (Tab. 57, Phyl. 3). In the ITS region more than 50 nt and 9 gaps consistently differ between *L. oculispora* and *L. oculisporella*, which easily permits recognition of the species from the alignment, and an even higher distance is noted between those and *L. jurana*. In the LSU D1–D2 domain, 14 nt differ between *L. oculispora* and *L. oculisporella* (mainly in D2). The number of deviating D1–D2 nucleotides in *L. jurana* is lower in comparison with *L. oculispora* (10) than with *L. oculisporella* (18–19).

The S1506 intron is absent in all sequences of the four recognized species. The S943 intron is present in *L. oculispora* (380 nt) but absent in *L. oculisporella* and *L. jurana*. This enables recognition of *L. oculispora* already from the PCR product on gel without sequencing, using the primer SR5 which binds upstream of the S943 intron. Also L2449 and L2563 introns are present in *L. oculispora* but not in *L. jurana* (this region so far is not covered in *L. oculisporella*). Deviations in the SSU region occur at 2 positions in the V9 region: at pos. 238 and 241 *L. oculispora* has CT**C**TC**G**G, *L. jurana* and *L. gallica* CT**T**TC**G**G, and *L. oculisporella* CT**C**TC**A**G (other *Orbiliomycetes* have **T**+**G**); in addition, *L. jurana* and *L. gallica* deviate from the other two at pos. 287 by **A** vs. **G** (see above). All this supports the existence of three four different species.

Ecology. Members of *Lilapila* were so far only detected in montane to subalpine, orotemperate to orosub- or rarely suprasubmediterranean, humid to slightly semihumid, often pure conifer forests of Southern French Alps (Rhône-Alpes and Provence-Alpes-Côte d'Azur) and Massif central (Auvergne) in southern Europe, from orotemperate humid Northern and Central Alps and High Tatras, and from (alti)montane, orotemperate humid French and Swiss Jura. The forests are often on steep north-, east-, or south-exposed slopes, but also on the top of high plateaus. The geology was almost always calcareous, but in the samples from Central Alps and High Tatras it was acidic bedrock. Apothecia were exclusively found on black resinous wounds of still-attached, xeric branches or trunks of *Picea* and *Pinus*, which were often still viable by carrying green needles at their ends. The wounds have been injured some years ago, perhaps as a result of avalanches and snowslides or other influences of snow and frost during winter, or by rockfall, also by passing forestry machines.

Apothecia of all species usually grow in a black mould of dark brown hyphae of some dematiaceous hyphomycetes that

Table 57. Distances in the rDNA among the three described species of *Lilapila*.

rDNA	*oculispora-oculisporella*	*oculispora-jurana*	*oculisporella-jurana*
ITS (505–513 nt)	10–10.8%	13–13.5%	13.5%
ITS1 (199–205)	16.5–18%	21.7–22.6%	25.5–26%
ITS2 (149–153 nt)	12.1–12.8%	14.7–15.3%	10.8–11.5%
LSU D1–D2 (643 nt)	2.2%	1.7%	2.8–3%
SSU V8–V9 (360 nt)	0.3%	0.6%	0.8%

abundantly cover the resin. The dry contracted apothecia appear blackish and can hardly be detected when growing in black mould, but even after rehydration the lilac pigment appears blackish in external view (similar as in *Liladisca*). Although the apothecia are comparatively large and occur in numbers of dozens on a given branch, the genus appears to have escaped notice on account of its camouflage, xeric habitat, and ecological restriction.

The currently known phenology of the genus *Lilapila* (mainly summer and autumn) is certainly only accidental. It results from the difficulty during winter and spring to travel and collect in mountainous areas rich in snow. The detection by E. Stöckli (pers. comm.) of mature apothecia of *L. jurana* in late January and early March proved our assumption. A striking correlation is observed in the distribution area of samples on *Picea* and *Pinus* in the Southern French Alps. Those on *Picea* are more in the north (*L. oculispora*, *L. oculisporella*) and those on *Pinus* more in the south (*L. oculisporella*). Together with an altitude of sometimes below 1000 m in the *Pinus* samples, it appears that *L. oculisporella* is adapted to a warmer, strictly orosub- or rarely suprasubmediterranean climate. Because *L. oculisporella* occurred at about equal frequency on *Picea* and *Pinus* and was recorded even at the type locality of *L. oculispora* (Col du Labouret) on *Picea*, a sharp geographical or host specificity limit cannot be recognized. Therefore, a number of older collections remained undetermined due to the lack of ascus or spore measurements, voucher specimens, or DNA data.

Lilapila oculispora Baral & G. Marson, **sp. nov**.,
MB 813442 — Pls 29–30, Map 1

Etymology: referring to the living ascospores with their spore body resembling the transection of an eye.

Typification: France, Alpes-de-Haute-Provence, Col du Labouret, resinous branch of *Picea abies*, 24.X.1992, G. Marson, (ex H.B. 4822, M-0276610, holotype).

Latin diagnosis: *Apothecia in statu rehydratato 0.4–2.5 mm diam., subsessilia. Asci *43–84 × 5.8–11.5 µm. Ascosporae *3.8–5.3 × 3.7–5.3 µm, corpusculo refringente 2.4–3.3 µm lato. Pili cylindrici, plerumque 6–9 µm lati, 5–8-septati. Habitat in ramis vulneratis siccis* Piceae, *vivis vel leniter putridis, ad corticem vel plerumque resinam nigram, in zona orotemperata et orosubmediterranea praealpium et alpium Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–1.5(–2.5) mm diam. (including hairs), 0.27–0.35 mm high (receptacle 0.12–0.23 mm), subsessile with indistinct, broad stipe or with ± abrupt stipe 0.08–0.17 × 0.25–0.3 mm. **Asci** *(43–)60–77(–84) {3} × 5.8–7.2 {2} or (7–)7.5–9(–11.5) µm {3}, †(49–)53–65(–70) × 5–7 µm {5}, pars sporifera *(22–)26–33 µm long, †(30–)40–53 µm; **base** arising from croziers {4}. **Ascospores** *(3.8–)4–4.7(–5.3) × (3.5–)3.7–4.5(–5.3) µm {9}, †3–4.2 × (2.5–)3–4 µm {4}, globose to subglobose (slightly flattened in side view); **SBs** 0.4–1 × 2.2–3.3 µm {6}. **Paraphyses** terminal cells *14–27 × 2.5–3.5 µm {1}, lower cells *7–21 × 2–3(–3.5) µm {2}. **Ectal excipulum** 30–50 µm thick near base, cells *11–21 × 5–9.5 µm {1}; 25–35 µm thick at lower flanks. **Hairs** */†100–150(–200) × (5–)6–9(–10) µm {3}, at flanks 40–70 µm long, (1–)5–8(–11)-septate, terminal cells 8–25 µm long {1}. **Anchoring hyphae** †(3.5–)4–5.5(–6.5) µm wide, walls †0.2–0.4 up to 1–1.5 µm thick {2}. — **ANAMORPH**: unknown (but see below).

Habitat: collected 1–2.5(–5) m above the ground, on small or mostly large, strongly resinous, (8–)15–43 mm thick wounds of corticated, completely undecayed (often living), still-attached branches of *Picea abies* {13}, on not or slightly decayed bark {2} or on blackened layer of resin {13}. **Associated**: *Amphosoma atroolivaceum* {3}, *A. resinicola* {2}, *Capronia* sp. {1}, *Chrysodisca peziculoides* {1}, *Ciliolarina* sp. {1}, *Claussenomyces olivaceus* {1}, *Lachnellula resinaria* {1}, *Lilapila oculisporella* {1}, *Melaspileella proximella* {1}, *Orbilia flagellispora* {1}, *Parmelia* sp. {1}, *Resinomyces griseus* {1}, *R. kirschsteinianus* {1}, *Sarea difformis* {3}, *Tryblidiopsis pinastri* {1}, crustose and foliose lichens. **Desiccation tolerance**: fully tolerant for at least 2 months, after 6 months many spores, paraphyses, and excipular cells still viable. **Altitude**: 1002–1820 m a.s.l. **Geology**: France: Middle & Upper Jurassic lime- & marlstone, rarely alluvial gravel (migmatite); Switzerland: peat over Permian mud- & sandstone, alluvial gravel (amphibolite, migmatite). **Phenology**: VI–X (but probably throughout the year).

Taxonomic remarks. *Lilapila oculispora* is distinguished from *L. oculisporella* merely by larger, especially wider asci, larger ascospores, and wider SBs. Because all remaining traits are virtually the same, the observed differences were previously thought to originate from variation. Yet, available rDNA-data show a high distance between small- and large-spored populations and a very low genetic variation within each group, therefore, a split into two different species seemed necessary.

Variation. Ascus size varied from *60–80 × 7–8.3(–8.8) µm (H.B. 4822, 9162a, Col du Labouret) to *61–84 × 8.5–10.3(–11.5) µm (6.X.1993, Col St.-Jean), and ascospore size from *3.7–4.5 × 3.5–4 µm to 4.2–5.2 × 4–4.8 µm. The largest spores (up to *5.3–5.5 × 5.2–5.3 µm) were measured in samples from Col du Labouret. SBs varied between 2.2–2.6 µm and 3–3.3 µm in diam. and between 0.5 µm and 1 µm in height. That this range of variation is not due to confusion is confirmed by the high molecular similarity among the six samples with available sequences and morphological data.

Key to species of *Lilapila*

(unequivocal species identification only possible by molecular methods)

1. Orotemperate humid Swiss and French Jura, Carpathians, on *Picea*; SBs 1.8–2.9 µm wide 2
1. Orotemperate to orosub- or suprasubmediterranean humid Massif central, Jura, Alps, on *Picea* and *Pinus* 3

2. Asci mainly *50–70 × 6–8 µm; spores *3.7–4.3 × 3.3–4 µm; 1003–1408 m .... ***L. jurana***, p. 269
2. Asci *69–74 × 7–8.2 µm; spores *4.1–4.7 × 3.5–4.5 µm; 888–912 m .... ***L. gallica*** nom. prov., p. 271

2. Asci mainly *60–77 × 7.5–9 µm; spores *4–4.7 × 3.7–4.5 µm, SBs 2.2–3.3 µm wide; on *Picea*, 1002–1820 m .... ***L. oculispora***, p. 264
2. Asci mainly *50–65 × 5–6.5 µm; spores *3.3–4 × 2.5–3.5 µm, SBs 1.4–2.3 µm wide; on *Picea* & *Pinus*, 800–1445 m........ ***L. oculisporella***, p. 267

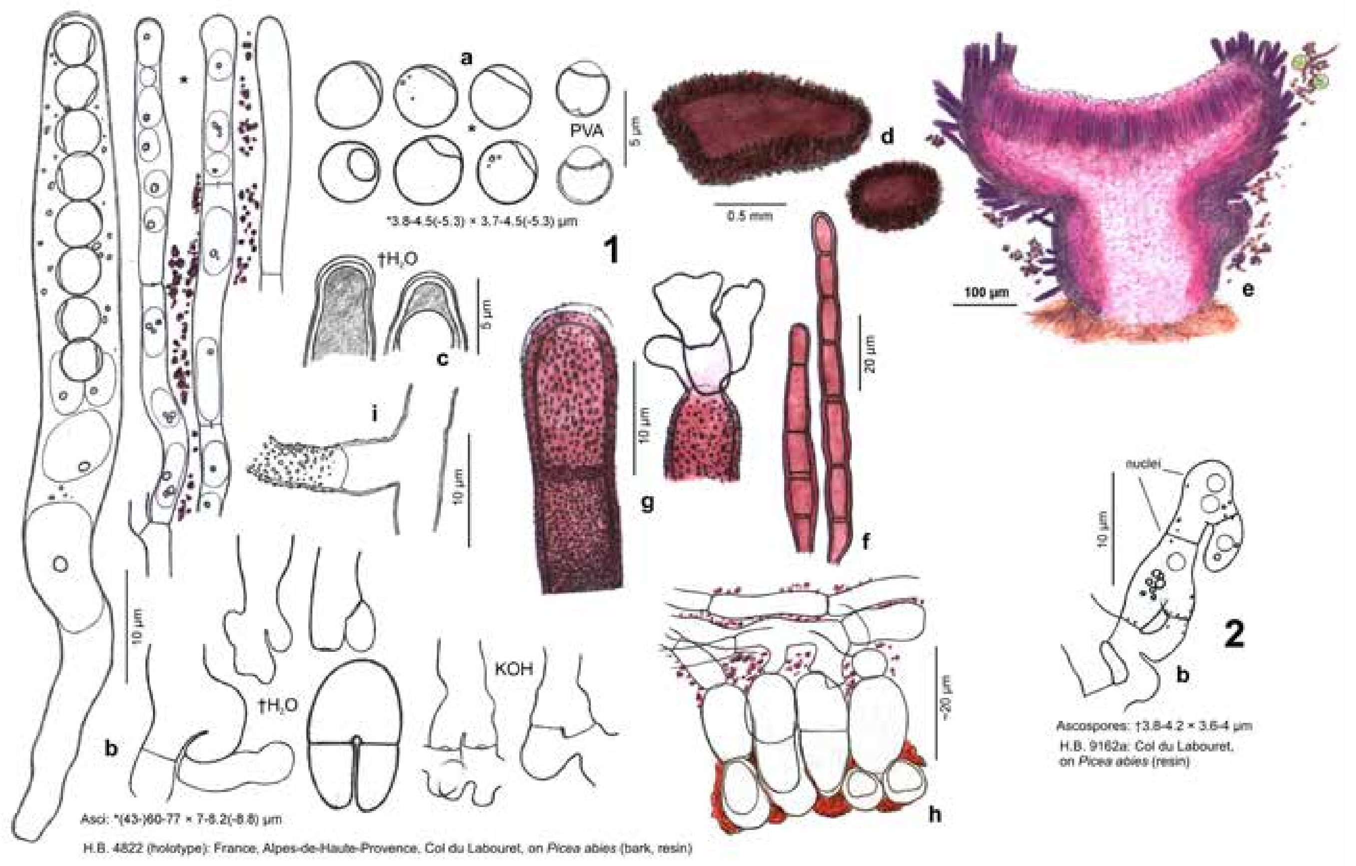


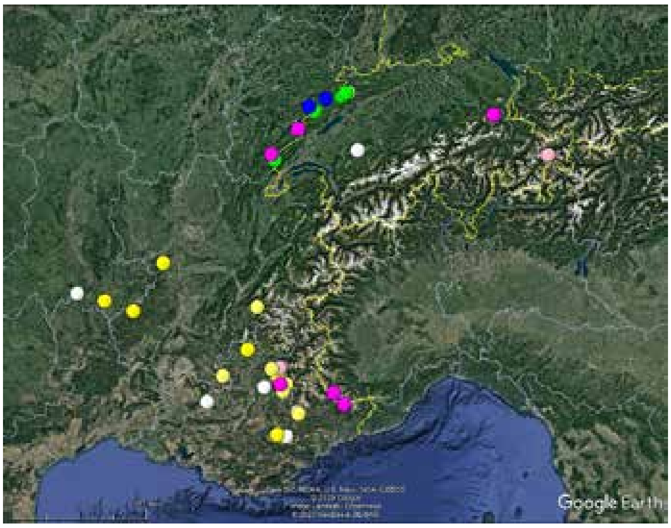
Plate 29. **1–2**: *Lilapila oculispora*. – **a**. ascospores; **b**. asci and paraphyses (vacuoles of paraphyses often containing small VB-guttules, sometimes with SCBs near the apex), ascus bases (**2b** with dikaryon); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. hairs; **g**. details of hairs (hairs rarely with hyaline apical outgrowths); **h**. ectal and medullary excipulum (lower flanks, median section); **i**. anchoring hypha.

Cultural characteristics and anamorph. A pure culture was obtained from ascospores of G.M. 2015-08-30.1. The mycelium grew very slowly (~2.5–3 mm radius per week on CMA:5), and conidia were not observed. Curved, vermispora-like conidia were seen on the natural substrate in two collections: Col du Labouret: *(26–)32–37(–41) × 4–4.6(–4.9) µm (in situ, ~35–42 µm actual length), (1–)2–3–5(–6)-septate (Pl. 30: 1u); Flumserberg: *17–22 × 2.4–2.8 µm (in situ, ~25–29 µm actual length), 6–7-septate (IVV: H.B. 10122). Similar conidia were also twice observed near apothecia of *Amphosoma atroolivaceum* on *Pinus sylvestris* (IVV: 6.VIII.1999 and H.B. 7248, without apothecia of *Lilapila*), with a size close to the former sample and a septal number more as in the latter.

Phylogeny. Sequences of *L. oculispora* were taken from eight collections, seven from apothecia and one from pure culture, comprising ITS+LSU (D1–D3), in some also SSU (V7–V9) or complete SSU and LSU. In the ITS region they vary by 0–1.4%, even within a collection (G.M. 2015-08-30.1/.3, 0.8%). In the LSU (D1–D2) all eight collections are identical. For the interspecific distances see Tab. 57.

DNA data were not available for the type collection, but sequences were taken from three later collections at the type locality. Since ascus and spore size differences were shown to be correlated with DNA data, we conclude that the holotype should also fall in the clade.

Ecology. *Lilapila oculispora* is so far only known with certainty from eight collection sites in altimontane humid conifer forests. Four are in orosubmediterranean or once orotemperate (Isola, 1820 m) Southern French Alps, two in orotemperate French Jura, and two in orotemperate Northern and Central Swiss Alps (Map 1). The geology is mainly calcareous, whereas the sample on acidic soil from Zernez in the Central Alps needs molecular confirmation. The apothecia occurred on old resinous wounds of attached, corticated, often living branches of *Picea abies*. The species was repeatedly recorded from the type locality, but there also *L. oculisporella* was three times found (on *Picea*). At present, the available collections suggest a restriction of *L. oculispora* to *Picea*.



Map 1. Known distribution of *Lilapila* spp. in southeastern France and Switzerland: magenta = *L. oculispora*, yellow = *L. oculisporella*, green = *L. jurana*, blue = *L. gallica*. Pale colours indicate unsequenced samples; white = *Lilapila* sp. (without both measurements and DNA data).

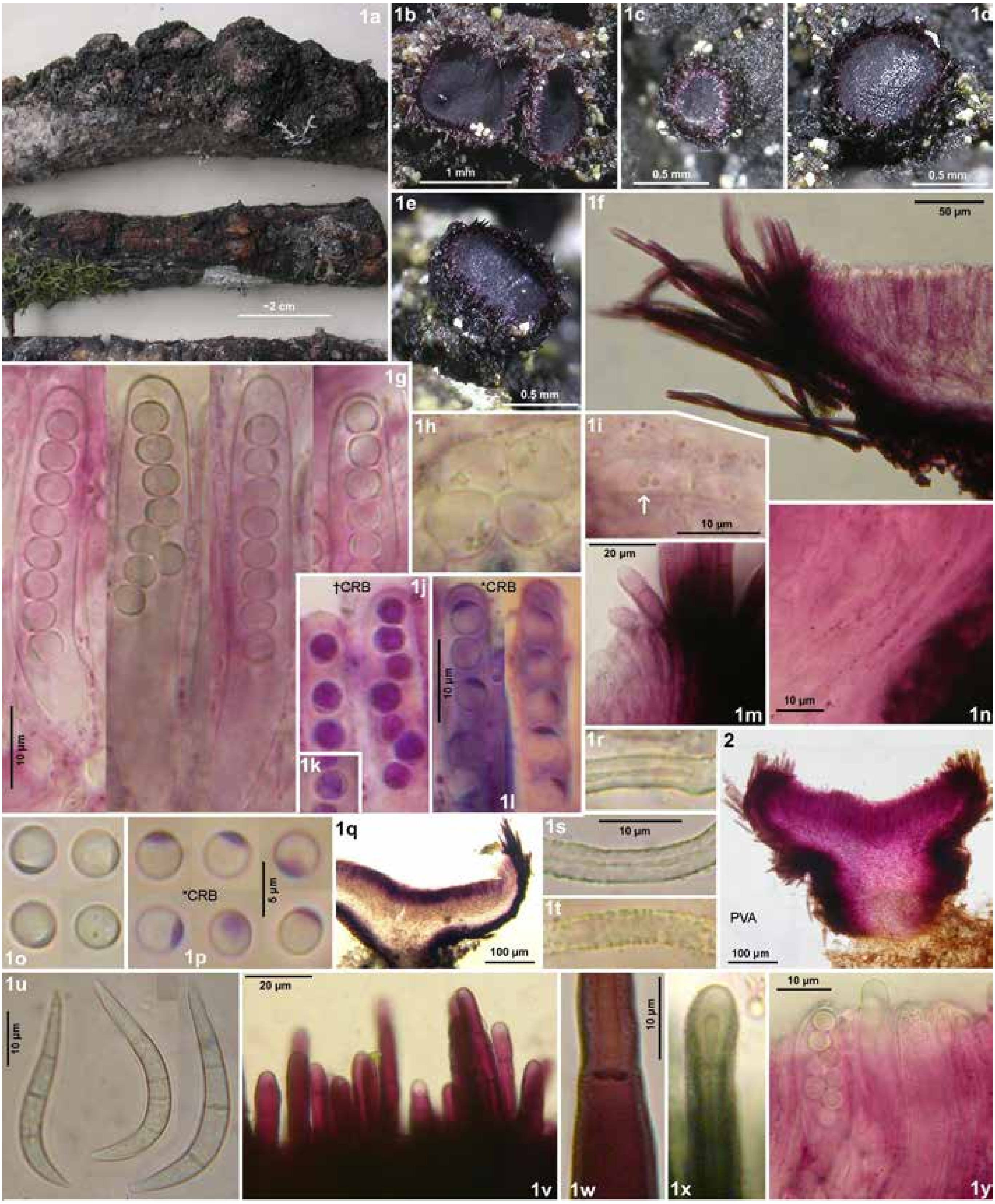


Plate 30. **1–2**: *Lilapila oculispora*. – **1a**. branches of *Picea abies* with blackened resinous wounds; **1b–e**. rehydrated apothecia; **1q**, **2**. apothecia in median section; **1f**, m. id., marginal region; **1v–x**. hairs; **1n**. gelatinized medullary excipulum at flanks (median section); **1h–i**. SCBs in inflated cells of medullary excipulum; **1r–t**. anchoring hyphae; **1g**. mature asci; **1y**. asci (mature and immature) and paraphyses; **1j–l**. ascospores in asci; **1o–p**. free ascospores; **1u**. conidia from substrate. – Living state (**1l** & **p**: SBs selectively stained violet in CRB), except for **1r–s** (in H_2O); **1x** (in KOH); **1j–k** (KOH+CRB, the sporoplasm is stained excluding the SBs); asci in **1l**. — **1a–y**. H.B. 9162a: France, Digne-les-Bains, Col du Labouret, on *Picea*; **2**. H.B. 4822: ibid.

Specimens included (all on resin). **SWITZERLAND**: **St**. **Gallen**, 13 km WNW of Sargans, 3.5 km SE of Quarten, Flumserberg, Gamperdon, 1465 m, branch of *P. abies*, 14.VI.2017, U. Graf (U.G. 1406-17UG1, H.B. 10122; sq.: MH221039). – **Graubünden**, 1.3 km ESE of Zernez, Selva Dadaint, 1570 m, branch of *Picea abies*, 23.VI.2018, B. Senn-Irlet (B.S.I. 18/75, doc. vid.). — **FRANCE**: **Franche-Comté**, **Doubs**, 8 km SSE of Pontarlier, 1.5 km W of Les Fourgs, 1075 m, trunk of *P. abies*, 23.VI.2019, G. Marson (G.M. 2019-06-23.6, sq.: MT367533). – **Jura**, 4.3 km ESE of St.-Laurent-en-Grandvaux, NW of Les Marais, 1002 m, branch of *P. abies*, 19.IX.2019, G. Marson (G.M. 2019-09-19.11, sq.: MT367530). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-**

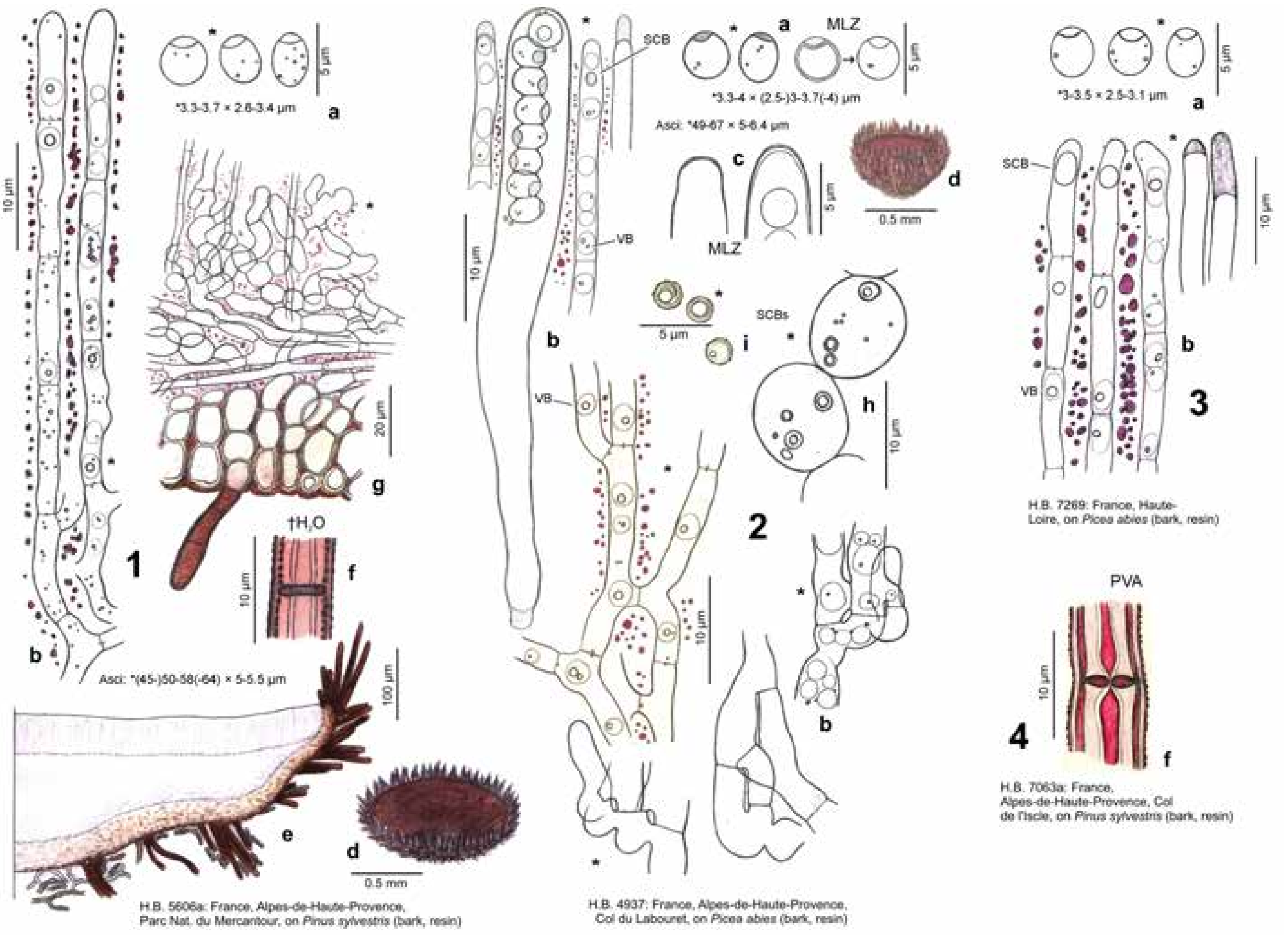


Plate 31. **1–4**: *Lilapila oculisporella*. – **a**. ascospores (**2a** showing plasmolysis at the moment when adding MLZ, a few seconds later cytoplasm getting invisible while SB remaining faintly visible); **b**. asci and paraphyses, ascus bases (vacuoles of paraphyses often containing small VBs, sometimes SCBs near apex); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. detail of hairs; **g**. ectal and medullary excipulum (lower flanks, median section); **h**. inflated catenate cells of medullary excipulum, with SCBs; **i**. closeup of SCBs.

Provence, 2.5 km NE of Montclar, 0.6 km N of St.-Jean, Col St.-Jean, 1335 m, branch of *P. abies*, 6.X.1993, G. Marson (ø). – 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *P. abies*, on bark & resin, 24.X.1992, G. Marson (ex H.B. 4822, M-0276610, **holotype**, G.M. 4923 **isotype**). – ibid., branches of *P. abies*, 6.X.1993, G. Marson (H.B. 5007a). – ibid., branches of *P. abies*, on resin & bark, 17.VII.1994, G. Marson (H.B. 7399a ø). – ibid., branches of *P. abies*, 14.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9162a; sq.: KT222413). – ibid., branch of *P. abies*, 19.IX.2011, G. Marson (G.M. 2011-09-19.1; sq.: KT222384). – ibid., 1.3 km NNE of Le Labouret, 1300 m, branches of *P. abies*, 30.VIII.2015, G. Marson (G.M. 2015-08-30.1; sq.: KY419168). – **Alpes Maritimes**, Mercantour, 18 km ESE of St.-Étienne-de-Tinée, 6.4 km E of Isola, 2.5 km WNW of Isola 2000 ski resort, 1820 m, branch of *Picea abies*, 31.VIII.2017, G. Marson (G.M. 2017-08-31.1; sq.: MH221041). – 8 km N of Roquebillière, 3 km NE of St.-Martin-Vésubie, 1333 m, branch of *Picea abies*, 31.VIII.2017, G. Marson (G.M. 2017-08-31.2; sq.: MH221040).

Lilapila oculisporella G. Marson, Baral & E. Weber, **sp. nov.**, MB 825639 — Pls 31–32, Map 1

Etymology: named after the similar but larger-spored *L. oculispora*.

Typification: France, Alpes-de-Haute-Provence, Seyne-les-Alpes, branches of *Pinus sylvestris*, 24.VIII.1996, G. Marson (M-0281047, holotype).

Latin diagnosis: Lilapilae oculisporae *similis, sed asci angustiores (*45–70 × 4.5–7.5 µm), ascosporae minores (*3–4.8 × 2.5–4 µm), corpusculo refringente minore (1.4–2.2 µm lato), pili leniter minores (plerumque 5–7.5 µm lati, 3–7-septati), sequentia nucleotidium valde distincta. Habitat in ramis vel truncis vulneratis siccis* Piceae *et* Pini, *vivis vel leniter putridis, ad corticem vel plerumque resinam nigram, in zona orotemperata ad orosub-, raro suprasubmediterranea praealpium Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.5–)0.7–1.5(–2.2) mm diam. (including hairs), 0.2–0.3(–0.4) mm high (receptacle 0.12–0.28 mm), subsessile with indistinct or mostly ± abrupt broad stipe 0.06–0.25 × 0.1–0.25 mm. **Asci** *(45–)50–65(–70) × (4.5–)5–6.5(–7.5) µm {8}, †(44–)48–60(–70) × (4–)4.3–5.5 µm {4}, pars sporifera *23–28 → 19–22 µm long, †(25–)28–32 µm; **base** arising from croziers {4}. **Ascospores** *(3–)3.3–4(–4.8) × (2.5–)2.8–3.5(–4) {12}, †2.8–3.5 × 2.3–3.3(–3.5) µm {3}, globose to subglobose (slightly flattened in side view); **SBs** (0.3–)0.5–0.8(–1) × 1.4–2.3 µm {6}. **Paraphyses** terminal cells *8–19(–28) × (1.7–)2–2.8(–3.7) µm {4}, lower cells *8–15 × 1.7–2.5(–2.8) µm {2}. **Ectal excipulum** 30–40 µm thick near base, cells *(7–)10–19(–22) × (6.5–)8–10(–14) µm {2}, 20–35 µm thick at lower flanks, cells †10–15 × 6–9 µm, 15 µm at mid flanks and margin. **Hairs** */†80–150(–200) × 5–7.5(–9) µm {4}, at flanks ~30–80 µm long, (1–)3–7(–9)-septate, terminal cells 7–27 µm long {2}. **Anchoring hyphae** †(3.5–)4–5(–6.5) µm wide, walls †1–2 µm thick {4}. **— ANAMORPH**: unknown.

Habitat: collected 1–5 m above the ground, on small or mostly large, strongly resinous, 10–60 mm thick wounds of corticated, completely undecayed, often living, still-attached branches, also on resinous knotholes of thick trunks, of *Picea abies* {8}, *Pinus sylvestris* {7}, on on usually blackened layer of resin {15} or on not or slightly to medium decayed bark {7}. **Associated**: *Amphosoma atroolivaceum* {5}, *Capronia* sp. {1}, *Ciliolarina* sp. {1}, *C. pinicola* {1}, *Cistella* sp. {1}, *Claussenomyces olivaceus* {1}, *Crumenulopsis pinicola* {1}, *Hysterium angustatum* {1}, *Lachnellula resinaria* {3},

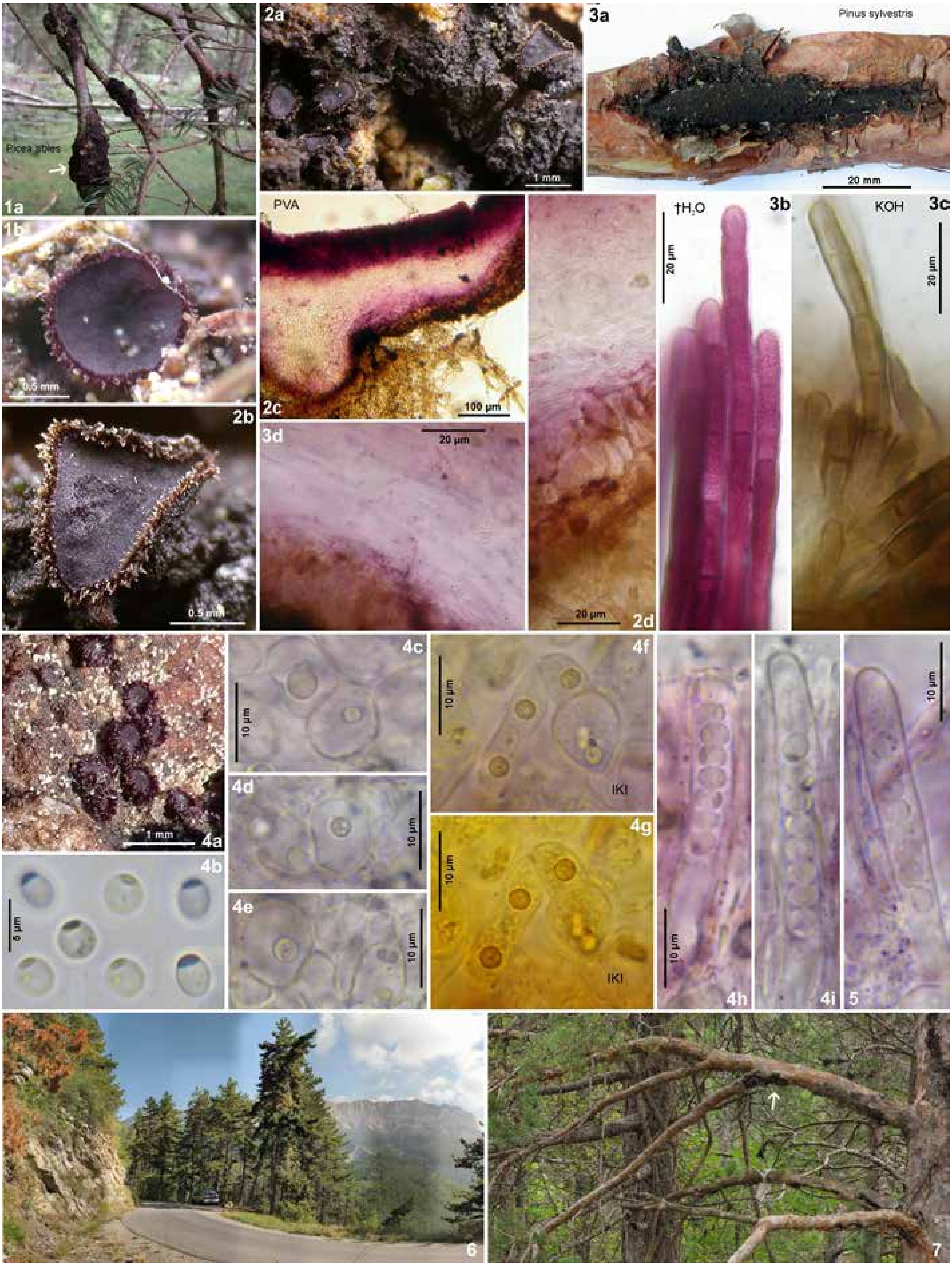


Plate 32. **2–5**: *Lilapila oculisporella*; **1**, **6**, **7**: *L.* cf. *oculisporella*. – **6**. south-exposed orosubmediterranean pine forest in Préalpes de Digne; **7**. living *Pinus sylvestris* trunk and branches with blackened resin; **1a**. living *Picea abies* branches with swollen blackened resinous wounds; **3a**. cut piece of *Pinus sylvestris* branch with blackened resinous wound; **1b**, **2a–b**, **4a**. rehydrated apothecia (**4a**: in situ, **1b**: after 10 days, **2a–b**: after 4.5 years); **2c**. apothecium in median section; **3b–c**. marginal hairs in different media; **2d**. ectal and medullary excipulum at lower flanks, with anchoring hyphae (median section); **3d**. (ectal and) gelatinized medullary excipulum at flanks (median section); **4b**. ascospres; **4h–i**, **5**. asci; **4c–g**. SCBs in inflated catenate cells of medullary excipulum. – Living

Lecophagus pini {1}, *Lilapila oculispora* {1}, *Orbilia eucalypti* {1}, *O. flagellispora* {1/1}, *O. ?graminis* {2}, *O. sphaerospora* {2}, *Pragmopora amphibola* {1}, *Propolis betulae* {1}, *Resinomyces griseus* {5}, *R. kirschsteinianus* {6}, *Sarea difformis* {7}, *S. resinae* {2}. **Desiccation tolerance**: fully tolerant for at least 3.5 months. **Altitude**: 800–1445 m. **Geology**: French Alps: Middle & Upper Jurassic and Cretaceous lime- & marlstone and clay; Massif central: basalt, gneiss. **Phenology**: VI–X (but probably throughout the year).

Taxonomic remarks. *Lilapila oculisporella* is distinguished from *L. oculispora* by narrower asci and smaller ascospores, but measurements overlap in the two species. Another clear distinguishing character appears to be the diameter of the spore bodies. Separation into two species is mainly based on strongly deviating DNA data.

Variation. Ascus size varied between *50–65 × (4.5–)5–5.5 and *55–70 × 5.5–6.5(–7.5) µm, spore size between *3–3.5 × 2.5–3 and 3.5–4(–4.8) × 3–3.5(–4) µm, and SBs between 1.4–2 and 1.8–2.2 µm in diam. and between 0.3 and 1 µm in thickness. This variation was observed on both host tree genera and is confirmed by molecular data.

Not included collections. In five older samples on *Pinus* from Southern French Alps {4} and *Picea* from Auvergne {1} neither measurements were taken nor a voucher specimen retained nor DNA data gained. Since we have so far never collected *L. oculispora* with certainty on *Pinus*, we assume that the *Pinus* samples belong to *L. oculisporella*, and also that on *Picea* might belong here because only *L. oculisporella* was so far recorded from Auvergne.

Cultural characteristics. A pure culture was obtained from ascospores of G.M. 2015-08-30.4. The mycelium grew very slowly (~2.5–3 mm radius per week on CMA:5). Conidia were not observed, neither in culture nor on the natural substrate.

Phylogeny. Sequences from eight samples were taken, six on *Picea* and two on *Pinus*, seven from apothecia and one from pure culture, comprising ITS+LSU (in H.B. 7269 only ITS), four of them also SSU (V7–V9). In the ITS region, strain G.M. 2015-08-28.4 differs by 1 nt (A vs. G) in the ITS1 and 3 nt (A vs. G, T vs. C, C vs. T) in the ITS2, and strain H.B. 7269 by 2 nt (T vs. C) in the ITS1 from the other six samples which show full identity. In the LSU (D1–D2) the seven strains are identical, except for one (G.M. 2016-08-11.1) which deviates at pos. 445 from the typical character of *L. oculisporella* (C) by concurring with *L. oculispora* (T). For the interspecific distances Tab. 57.

DNA data were not available for the type collection. However, in all eight sequenced samples of *L. oculisporella*, which derive from seven remote sites, small asci and spores similar to the holotype were documented.

Ecology. Collections of *Lilapila oculisporella* on *Picea* derive from orotemperate to orosubmediterranean humid Southern French Alps and Massif central, whereas those on *Pinus* are from orosub- or rarely suprasubmediterranean, humid or slightly semihumid Southern French Alps. The geology comprises calcareous bedrock from different epochs.

Specimens included. **FRANCE** (all on resin): **Auvergne**, **Haute-Loire**, Massif central, 15.5 km ESE of St.-Étienne, 4 km ENE of Le Bessat, Mont Pilat, Crêt de la Perdrix, 1370 m, branch of *Picea abies*, 14.VIII.2016, G. Marson (G.M. 2016-08-14.1; sq.: MH221044). – 15 km SSW of Le-Puy-en-Velay, 4 km WNW of Cayres, 1365 m, branch of *Picea abies*, on bark & resin, 5.X.2002, G. Marson (H.B. 7269; sq.: KT380057). – **Rhône-Alpes**, **Drôme**, 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branch of *Pinus sylvestris*, on bark & resin, 23.VIII.1996, G. Marson (H.B. 5624a). –**Isère**, 27 km SE of Grenoble, 1.7 km N of Les Siauds, Col d' Ornon, 1380 m, *Picea abies* trunk, 7.IX.2010, G. Marson (ø). – **Ardèche**, 31 km SE of Le Puy-en-Velay, 1.5 km ESE of Chartreuse de Bonnefoy, *P. abies* branches, 28.VIII.2015, G. Marson (G.M. 2015-08-28.4; sq.: KY419169). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 3 km SW of Seyne, N of Col du Fanget, 1445 m, branch of *Picea abies*, 11.VIII.2016, G. Marson (G.M. 2016-08-11.1; sq.: MH221045). – 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branches of *P. abies*, on bark & resin, 16.VIII.1993, G. Marson (H.B. 4937a, G.M. 5011). – ibid., 1.3 km NNE of Le Labouret, 1300 m, *P. abies* branches, 30.VIII.2015, G. Marson (G.M. 2015-08-30.4; sq.: KY419170). – ibid., 8.IX.2016 (G.M. 2016-09-08.1; sq.: MH221043). – Mercantour, 13.5 km SE of Seyne-les-Alpes, 5.5 km SW of Tête de l'Estrop, SE of Vière, 1350 m, branches of *Pinus sylvestris*, on bark & resin, 24.VIII.1996, G. Marson (M-0281047, **holotype**, **isotype** in H.B. 5606a). – 18 km NE of Digne-les-Bains, 5 km SSW of Prads-Haute-Bléone, Blégier, 970 m, branch of *P. sylvestris*, on bark & resin, 24.VIII.1996, G. Marson (H.B. 5628a). – 12 km E of St.-André-les-Alpes, 1 km SW of Annot, ENE of Col de l'Iscle, 855 m, branches of *P. sylvestris*, on bark & resin, 16.VIII.2001, G. Marson (H.B. 7063a). – **Hautes-Alpes**, 16 km W of Gap, N of Montmaur, 1020 m, trunk of *P. sylvestris*, 15.IX.2015, G. Marson (G.M. 2015-09-15.1, sq.: MG372373). – 24 km SE of Gap, 5 km E of Turriers, 0.6 km SW of Col des Garcinets, 1147 m, branches of *P. sylvestris*, on bark & resin, 25.VIII.1996, G. Marson (H.B. 5621a). – **Var**, 11 km WNW of Comps-sur-Artuby, 6.3 km SW of Trigance, WNW of Pont de l'Artuby, 800 m, branches of *P. sylvestris*, 22.IX.2011, G. Marson (G.M. 2011-09-22.1; sq.: KT222383; H.B. 9631a ø).

Not included (all on resin). **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 14.5 km NW of Digne-les-Bains, 3.8 km SE of Authon, Col de Font-Belle, 1310 m, *Pinus sylvestris*, 23.IX.2009, G. Marson (ø) – 2.8 km NW of Annot, 3.5 km NNE of Col de l'Iscle, 1050 m, *P. sylvestris*, 26.IX.2009, G. Marson (ø) – **Vaucluse**, Plateau de Vaucluse, 19 km S of Mont Ventoux, 26 km ESE of Carpentras, 10 km SSW of Sault, Forêt de Javon, 745 m, branches of *P. sylvestris*, 10.X.2002, G. Marson (ø). – **Var**, E of Gorges du Verdon, 1.6 km NNW of Comps-sur-Artuby, 2.3 km S of Jabron, 910 m, branch of *P. sylvestris*, 27.IX.2009, G. Marson (ø). – **Auvergne**, **Haute-Loire**, Massif central, 21 km ESE of St.-Flour, 6 km E of Clavières, Forêt d'Auvers (W of Mt. Mouchet), 1346 m, branch of *Picea abies*, on bark & resin, 26.VIII.2004, G. Marson (ø).

Lilapila jurana Stöckli, G. Marson, Baral, U. Graf, Gilgen, Wergen & E. Weber, **sp. nov.**, MB 825647 — Pl. 33, Map 1

Etymology: referring to the occurrence in the Swiss Jura.

Typification: Switzerland, Jura, Tramelan, Moulin de la Gruère, resinous branch of *Picea abies*, 4.VI.2017, J. Gilgen & U. Graf (ex U.G. 0406-17UG1 & ex H.B. 10123, M-0291754, **holotype**; sq.: MH221042)

Latin diagnosis: Lilapilae oculisporae *morphologia persimilis, sed sequentia nucleotidium valde distincta. Habitat ad resinam nigram in ramis siccis, vulneratis, vivis vel leniter putridis* Piceae abietis *in zona orotemperata jurassicae et carpathicae Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.8–2(–3) mm diam. (including hairs), receptacle 0.15–0.25 mm thick, sessile or with a stalk 0.2 × 0.28 mm. **Asci** *(44–)50–70(–80) × (5.5–)6–8(–10) µm {7} [type: *57–70 × 6.2–7.2 µm], spores uniseriate or sometimes 4 spores biseriate, SBs mainly laterally oriented, pars sporifera *25–30 µm long; **base** arising from croziers {4}. **Ascospores** *(3.3–)3.7–4.3(–4.7) × (3–)3.3–4(–4.5) µm {9} [type: *3.7–4.2(–4.5) × (3–)3.3–3.7(–4.2) µm], globose to subglobose (very slightly flattened in side view); **SBs** (0.3–)0.6–0.9(–1.1) × 1.8–2.8 µm {8}. **Paraphyses** terminal cells *13–20 × 2.8–3.5(–4) µm {1}, lower cells *12–18 × 2–3 µm {1}. **Ectal excipulum** 40 µm thick near base and lower flanks, cells *8–19 × 6–11 µm {1}. **Hairs** at margin */†(40–)80–160 × (5–)6–7(–7.5) µm {3}, (3–)6–7(–9)-septate, upper cell 10–20(–35) µm long. **— ANAMORPH**: unknown.

Habitat: collected 1–6 m above the ground, on small to often large, strongly resinous, often swollen wounds of corticated, completely undecayed, still-attached, mostly living, 1.5–10 cm thick branches

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state: **4a–e**, **h–i**, **5**; dead state: **2c** in PVA; **2d**, **3b**, **d** in H_2O; **3c** in KOH, **4f–g** in IKI. — **1a–b**. 26.VIII.2004: France, Massif central, Mt. Mouchet, on *Picea*; **2a–d**. H.B. 7063a: Annot, Col de l'Iscle, on *Pinus*; **3a–d**. H.B. 5606a: ibid., Mercantour, Vière, on *Pinus* (**holotype**); **4a–i**. H.B. 9631a: Var, Trigance, on *Pinus*; **5**. 7.IX.2010: Isère, Col d'Ornon, on *Picea*; **6**. 23.IX.2009: Authon, Col de Font-Belle, on *Pinus*; **7**. 26.IX.2009: Annot, Col de l'Iscle, on *Pinus*.

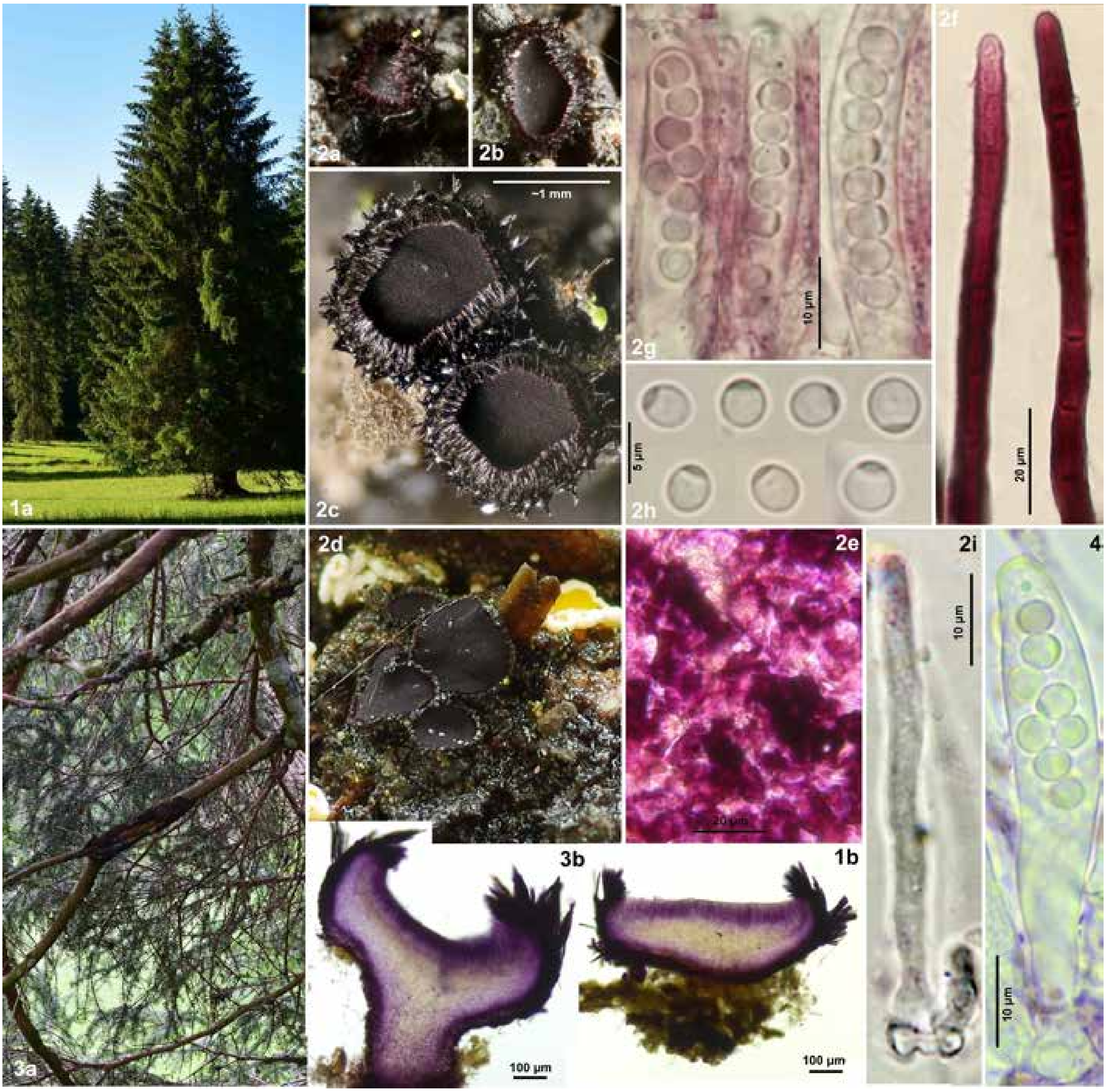


Plate 33. **1–4**: *Lilapila jurana* (all on *Picea*). – **1a**. altimontane (orotemperate) conifer forest, adjacent pasture with free-standing *Picea* trees; **3a**. living basal branches of free-standing *Picea* tree, one with resinous wound; **2a–d**. rehydrated apothecia on blackened resin; **1b**, **3b**. apothecia in median section; **2e**. external view of ectal excipulum at flanks; **2f**. marginal hairs; **2g**, **4**. mature asci; **2i** young ascus with basal crozier; **2h**. ascospres. – Living state (except for upper hair cells in **2f** and ascus in **2i**), all in H_2O. – **1**, **3**: phot. E. Stöckli, **2a–c**, **2f–i**: phot. B. Wergen, **2d**: phot. U. Graf. — **1a–b**. E.S. 17.06.18-48c: Switzerland, Jura, Tramelan, Pâturage du Bas; **2a–i**. H.B. 10123 (holotype): ibid., Moulin de la Gruère, on *Picea*; **3a–b**. E.S. 17.06.05-48b: ibid., Les Breuleux, Pâturage communal; **4**. E.S. 17.08.27-48e: ibid.

or rarely 35–40 cm thick trunks of *Picea abies* {17}, always on blackened layer of resin. **Associated**: *Amphosoma atroolivaceum* {1}, *Claussenomyces olivaceus* {1}, *Colpoma crispum* {~3}, *Eustilbum aureum* {1}, *Lachnellula resinaria* {3}, *Lepraria* sp. {1}, *Sarea difformis* {~10}, *S. resinae* {1}. **Desiccation tolerance**: after 6.5–7 months many cells of medullary excipulum and spores still viable. **Altitude**: 1003–1408 m a.s.l. **Geology**: French & Swiss Jura: Upper Jurassic limestone, micrite & marl, decalcified clay, peat; Slovakia: granite, granodiorite. **Phenology**: I, III–IX (throughout the year).

Taxonomic remarks. Morphologically, *Lilapila jurana* appears to be intermediate between *L. oculispora* and *L. oculisporella*. We here recognize it as a separate species because of its strongly deviating DNA data, which was obtained in eight of the 17 included samples. All those without DNA data were tentatively included in the description because they derive from the same substrate, vegetation type, and geographical region in the Swiss Jura on calcareous soil. Four of them are unpreserved and without documentation. Remarkable is the disjunct record from the Slovakian Carpathians on acidic soil. Co-occurrence of different species within a mountain range could be demonstrated by molecular methods; for instance, *L. jurana*, *L. gallica*, and *L. oculispora* are shown to occur in the French Jura (Map. 1).

Variation. Ascus size varied among the collections between *53–75 × 5.3–6.5 and *34–70 × 7–10 µm. This variation was correlated with an infrequent partial biseriate spore arrangement rather than differences in spore size. But also ascospore size varied from *3.3–4 × 3–3.6 to 4–4.7 × 3.6–4.5 µm, though sometimes due to a small amount of oversized spores in 6–7-spored asci. Two collections from the acidic Carpathian Mountains concur well in their asci (*70–75 × (5.5–)6–6.5 µm) and spores (*3.7–4.3 × 3.4–4.2 µm).

Not included collections. The sample from Fribourg is not included because it was not from the Jura region and no documentation or voucher exists. Some recent collections from French Jura sufficiently differ in their rDNA to be treated here as a separate species, ***Lilapila gallica*** G. Marson, Baral & E. Weber nom. prov., which morphologically does not noticeably differ from the other species of the genus: the apothecia measured 0.6–1.25 mm diam., the spores *4.1–4.7 × 3.5–4.5 µm, and the SBs 1.9–2.9 × 0.3–0.7 µm (see IVV).

Phylogeny. Sequences were taken from apothecia of the holotype and three paratypes from Switzerland (ITS, LSU D1–D2, in the holotype also SSU V7–V9), two French samples (SSU V9, ITS, LSU D1–D4), and one from Slovakia (ITS). Six of them coincide in the ITS region, including the holotype and the French and Slovakian samples (the latter three not shown in Phyl. 3), except for an inserted nucleotide at the 5'-end of ITS1 in two of them. One sample (from Pâturage du Bas) deviates by 3 nt in the ITS. In the LSU three positions are variable: pos. 243 and 297 are either C or T, and pos. 136 deviates in the sample from Pâturage du Bas (T) from all other *Lilapila* sequences which have C. All these deviations are unequivocal in the chromatograms. For the interspecific distances see Tab. 57.

L. gallica has the lowest distances to *L. jurana* (ITS/LSU D1–D2: 7–8/1.1–2 %) and clusters with it in a strongly supported clade in NJ or ML analyses of ITS (not shown). In comparison, *L. oculispora* differs from *L. gallica* by 11–13/2.2–2.6 % and *L. oculisporella* by 14–15.3/2.7–3.1 %. The five *L. gallica* samples belong to two genotypes (A/B) which deviate by 1.2–1.4/0.6 %.

Ecology. *Lilapila jurana* is so far mainly known from the orotemperate (altimontane) Swiss and French Jura, where it was collected on blackened resinous wounds of the lowermost living or sometimes recently dead branches of *Picea abies*. It always occurred at sites with a long-lasting snow cover and frequent wafts of mist over the ground. The area of the Swiss Jura is a high plateau with many bogs of which only some remainders exist, because the region is used as a wood pasture for horses and cows, being also manured with slurry. *Picea abies* is the main tree, but also *Abies alba* and different deciduous trees occur. Many collection sites are located close to ± boggy places. The inhabited branches belong to large and old trees that stand free under high sun-exposure and, therefore, have projecting living branches extending down to the ground (Pl. 33: 1). The soil was mainly calcareous (Upper Jurassic) but in Slovakia acidic. Low temperatures all over the year are typical (in winter down to –35 °C), and also high precipitation throughout the year and frequent winds characterize the area. Since *L. jurana* also occurs during winter, the apothecia resist the cold, which could be shown in January 2018 when they survived -22 °C (E. Stöckli pers. comm.). The collection sites in the Slovakian Carpathians are characterized by a similar climate but, in contrast, a strongly acidic bedrock. *L. gallica* from French Jura (on Upper Jurassic limestone, in one case covered by a peat bog) also grew on wounds of *Picea* branches and, like *L. jurana* from French Jura, often in association with *Eustilbum aureum*, but at lower altitudes.

Specimens included (all on resin of *Picea abies*). **SWITZERLAND**: **Jura**, Swiss Jura, 18 km NW of Biel, 2.3 km N of Tramelan, 3 km SW of Les Genevez, La Tourbière du Pâturage du Bas, 1035 m, branch of *P. abies*, 5.VI.2017, J. Gilgen (ø, non vid.). – ibid., 2 km N of Tramelan, La Tourbière du Pâturage du Bas, 1035 m, branch of *P. abies*, 18.VI.2017, E. Stöckli (E.S. 17.06.18-48c, H.B. 10193, doc. vid.; sq.: MK473411). – 3.8 km WNW of Tramelan, 1.3 km SE of La Theurre, Moulin de la Gruère, 1020 m, branch of *P. abies*, 4.VI.2017, J. Gilgen, U. Graf, vid. B. Wergen & E. Stöckli (ex U.G. 0406-17UG1, ex H.B. 10123, M-0291754, **holotype**; sq.: MH221042). – ibid., 1.5 km ESE of La Theurre, 1017 m, branch of *P. abies*, 17.I.2020, E. Stöckli (ø, non vid.). – ibid., 1.6 km ESE of La Theurre, 1003 m, branch of *P. abies*, 30.IV.2018, E. Stöckli (ø, non vid.). – 8 km WSW of Tramelan, 1 km SSW of Les Breuleux, Pâturage communal, 1027 m, branch of *P. abies*, 5.VI.2017, E. Stöckli (E.S. 17.06.05-48b, doc. vid.). – ibid., branches and trunk of *P. abies*, 14.VI.2018, E. Stöckli, H.O. Baral, K. Pätzold, R. Dougoud et al. (H.B. 10149a, J.G. et al.). – ibid., 1 km S of Les Breuleux, 1035 m, branch of *P. abies*, 5.VI.2017, J. Gilgen (ø, non vid.). – ibid., branches of *P. abies*, 1020 m, 4.III.2018, E. Stöckli (E.S. 18.03.04-48g, H.B. 10186, doc. vid.; sq.: MK473409). – ibid., 1 km SE of Les Breuleux, 1032 m, branch of *P. abies*, 3.IX.2017, E. Stöckli, vid. M. Hairaud (M.H. 90917, doc. vid.). – ibid., 1 km SSE of Les Breuleux, 1015 m, branch of *P. abies*, 31.I.2018, E. Stöckli (E.S. 18.01.31-48f, H.B. 10192, doc. vid. sq.: MK473410). – ibid., 2.3 km SW of Les Breuleux, 1047 m, branch of *P. abies*, 27.VIII.2017, E. Stöckli (E.S. 17.08.27-48e, doc. vid.). – 3.3 km SW of Les Breuleux, Muriaux Ju, 1038 m, branch of *P. abies*, 29.IV.2018, E. Stöckli (ø, non vid.). — **FRANCE**: **Franche-Comté**, **Doubs**, French Jura, 23.5 km NW of Pontarlier, 1.5 km S of Montlebon, Mont Gaudichot, 1010 m, branch of *P. abies*, 30.VII.2019, G. Marson (G.M. 2019-07-30.4, sq.: MT367525). – **Jura**, 11.5 km SE of St.-Laurent-en-Grandvaux, 2.8 km NNE of Les Rousses, 1253 m, branch of *P. abies*, 19.IX.2019, G. Marson (G.M. 2019-09-19.8, sq.: MT367528). — **SLOVAKIA**, **Prešov**, Carpathian Mts., Vysoké Tatry, 8.7 km SSW of Tatranská Javorina, Bielovodská valley, 1310 m, branch of *P. abies*, 12.VII.2018, A. Polhorský (A.P. 18/68, doc. vid.; sq.: MK028715). – 9.5 km SSW of Tatranská Javorina, 1408 m, trunk of *P. abies*, 30.VII.2018, A. Polhorský (A.P. 18/84, doc. vid.).

Not included (all on resin of *Picea abies* branches). ***Lilapila* sp.**: **SWITZERLAND**: **Fribourg**, 18.5 km SSE of Fribourg, 9 km S of Plaffeien, Seeweid, SW of Lac Noir, 1055 m, 8.VI.2017, J. Gilgen (ø, non vid.). — ***L. gallica***: **FRANCE**: **Franche-Comté**, **Doubs**, 10.3 km SSW of Maîche, 3.4 km E of Le Russey, Le Grand Bois, 912 m, 30.VII.2019, G. Marson (G.M. 2019-07-30.5, genotype A, sq.: MT367523). – ibid., 2.9 km E of Le Russey, 888 m, 7.VII.2019, G. Marson (G.M. 2019-07-07.3, genotype B, sq.: MT367532). – ibid., 2.8 km E of Le Russey, 886 m, 7.VII.2019, G. Marson (G.M. 2019.07-07.7, genotype A, sq.: MT367526). – ibid., 1.7 km E of Le Russey, 890 m, 7.VII.2019, G. Marson (G.M. 2019-07-07.9, genotype B, sq.: MT367527). – 22.5 km NNE of Pontarlier, 7 km WNW of Morteau, 900 m, 29.VII.2019, G. Marson (G.M. 2019-07-29.5, genotype A, sq.: MT367524).

Amphosoma Baral, **gen. nov.**, MB 813478

Type species: *Amphosoma resinicola* Baral & G. Marson

Etymology: referring to the presence of a spore body at both ends of ascospores.

Latin diagnosis: *Apothecia rehydratata 0.1–0.5 mm diam., alba, roseo-aurantiaca vel atro-olivacea, sessilia vel breviter stipitata, superficialia vel immersa. Asci apice rotundati, tunica in statu emortuo plerumque incrassata, non amyloidei (IKI), octospori, in basi non uncinati, bifurcati. Ascosporae di- vel tristichae in ascis vivis, cylindrico-ellipsoideae vel fusoideo-clavatae, rectae, intus ad polis in statu vivo cum corpusculo lentiformi ad globoso, refringenti. Paraphyses ad apicem non vel valde inflatae, exsudato continuo vel granuloso tectae, cohaerentes vel non cohaerentes. Cellulae excipuli marginalis et paraphysium in statu vivo vacuolas globosas refringentes continentes. Habitat ad corticem, lignum et resinam, in ramis arborum plerumque coniferarum, in aere prominentibus.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.5 mm diam., whitish to rose-orange or dark blackish-olivaceous, translucent when light-coloured, sessile to short-stalked, superficial to immersed. **Asci** *26–120 × 5.5–11 µm, protruding 1–3 µm beyond exudate when turgescent, 8-spored, spores 2–3-seriate inside living asci; **apex** hemispherical to conical or slightly truncate, with distinct apical thickening (rarely without); **base** simple septate, T-, L-, Y-, h- (or H-) shaped, exceptionally with true croziers with long slit-like perforation. **Ascospores** *(3.3–)5–15(–17.5) × (1.7–)2–4(–5) µm, cylindric-ellipsoid, also fusoid, usually homopolar in shape but some distinctly clavate (then some spores inversely oriented), straight, overmature sometimes becoming 1(–3)-septate, **SBs** *(0.2–)0.3–1(–1.2) × 0.5–1.3 µm, strongly refractive, lens- to plug-shaped or (sub)globose, ± broadly attached to wall at both spore ends. **Paraphyses** apically not or only slightly inflated, rarely strongly clavate-capitate or sublanceolate, *1.8–6 µm wide, terminal cells about as long as lower cells. **Medullary excipulum** of dense textura angularis(-intricata), indistinctly to medium sharply delimited. **Ectal excipulum** hyaline or with yellowish or olivaceous exudate, near base of t. angularis, at flanks and margin of t. angularis to t. prismatica oriented at a high or low angle, (†) slightly to medium gelatinized (common walls 1–1.5 µm thick), cells near base *5–12(–16) × 4–8(–11) µm; **glassy processes** and **hairs** absent. **Anchoring hyphae** *1.8–6 µm wide, wall 0.2–0.5 µm thick, sometimes covered by a thick gel sheath. **SCBs** not observed; **VBs** present in both paraphysis and ectal excipular cells (living state), scattered to abundant, consistently globose and strongly refractive, hyaline, 0.2–2 µm diam., staining bright turquoise in CRB, dead plasma showing a light copper-amber pigmentation due to oxidation of VBs; **LBs** with carotenoids sometimes present. **Exudate** 0.2–0.5 µm thick, continuous, externally smooth or warted to granular, hymenial elements conglutinated or ± easily separable by pressure, **gel** staining distinctly lilac in CRB. — **ANAMORPH**: trinacrium-like. **Colonies** whitish to pale salmon-coloured, slow growing (CMA:2, MEA 2%; *A. resinicola*). **Conidiophores** not observed. **Conidia** 2-armed (T-shaped), total size */†16–41.5 × 11–44 µm, stipe 1–6-septate, arms bent downwards, 0–5-septate.

Habitat: on dead, ± undecayed bark and wood of coniferous branches (usually associated with blackened resin), rarely on angiosperm bark. **Desiccation tolerance**: mature asci tolerating ~0.5–2 years. **Distribution**: Europe, North America, South Africa, (oro)temperate to (sub)tropical, humid to semi- or subhumid.

Recognized species: *A. atroolivaceum*, *A. macrosporum*, *A. natalense*, *A. resinicola*, *A.* aff. *resinicola.*

Taxonomy and relationship. The genus *Amphosoma* forms a small, undoubtedly natural group of species with desiccation-tolerant apothecia, which are predominantly conifer-inhabiting and associated with slightly decayed, blackened resinous wounds. Two characteristics are only visible in the living state, but serve as consistent key characteristics of the genus: (1) small, lens- to plug-shaped SBs occur at both ends of the ascospores; (2) refractive, globose VBs are regularly found inside the terminal cells of paraphyses and marginal ectal excipulum. When only dead specimens are studied, the genus *Amphosoma* may easily be misclassified in the *Helotiales*.

The bipolar arrangement of SBs and the preference for gymnosperms appear to argue for a phylogenetically old group within the *Orbiliomycetes* (see Phylogeny). *Amphosoma* seems to represent a connecting link between *Hyalorbilia* and *Orbilia* by sharing characteristics of both genera. *Amphosoma* resembles *Hyalorbilia* mainly in sporological features: the ascospores are more or less homopolar in shape, and the SBs bipolar-symmetrically arranged. For instance, *Hyalorbilia subfusispora* closely resembles *Amphosoma* in spore shape and bipolar SBs. Also the thin continuous exudate over the paraphyses of *A. resinicola* is reminiscent of a *Hyalorbilia*. However, *Hyalorbilia* differs in a number of traits, especially concerning ascus apex and base, orientation of the ectal excipulum at flanks, length of terminal cells of paraphyses in relation to lower cells, and type of VBs (see also Tab. 56).

The ascospores in the large genus *Orbilia* possess, in contrast to *Amphosoma*, only 1 SB per spore (usually at the upper end, rarely ± laterally), and the spores are often ± heteropolar in shape. As a rare exception, a few aberrant spores of *Orbilia* may contain two SBs, one at each end, reminiscent of *Amphosoma*. What underlines proximity of *Amphosoma* to *Orbilia* is that their asci have a bifurcate, generally simple-septate base and a more or less pronounced apical dome, sometimes with an apical chamber, reminiscent of subgenus *Hemiorbilia*. *Amphosoma* appears to represent the common ancestor of the large genus *Orbilia*, when assuming that in this genus the bifurcate ascus base lacking croziers evolved for the first time within the *Orbiliomycetes*.

The hymenial elements of *Amphosoma* are usually easily separable because the gel on the walls forms an only thin layer, which can be visualized by a deep lilac stain in CRB. The living paraphyses and marginal excipular cells contain strongly refractive, hyaline, globose VBs. This striking guttular pattern provides a characteristic being never observed in *Hyalorbilia* or *Orbilia.* The VBs are consistently globose and usually show no or only slight Brownian motion, apparently because the vacuoles in which they occur are rather small. However, in *A. macrosporum* strong Brownian motion was noted. In *Hyalorbilia* a similar guttular pattern inside the paraphyses and cortical cells may be seen in submature apothecia, but the VBs are larger and only slightly to medium refractive, sometimes pale chlorinaceous, and at progressed maturity they tend to fuse by forming large elongate bodies of a width corresponding to that of the cell lumen. No such fusion of VBs has been seen in *Amphosoma*.

The molecular closeness of *Amphosoma* and *Retiarius* (see below) raises the question whether it is justified to distinguish these two genera. The morphology of the teleomorph of *Retiarius* is unknown, and an adaptation to pollen as nutrient source was so far not determined in *Amphosoma*.

Species delimitation and confusion. The four recognized species are quite easily distinguished. Only in the rare case of albinism in *A. atroolivaceum*, delimitation against the shorter-spored *A. resinicola* was difficult.

Amphosoma persooniae Crous was proposed by Crous (2017) for a pycnidial fungus on stem canker of *Persoonia* sp. from southeastern Australia. It was placed in *Amphosoma* solely based on molecular data which clearly point to that genus (see below). We have doubts, however, that the described fungus is orbiliaceous. The species formed minute, globose, dark brown pycnidia which contain hyaline phialidic conidiogenous cells with prominent periclinal thickening that form 4.5–7 × 2–3 µm large, hyaline, smooth, subcylindrical conidia. For the time being we consider *Amphosoma persooniae* as non-orbiliaceous and the associated molecular data as belonging to an unknown species of *Amphosoma*. Besides, the taxon is invalid because the generic name was only proposed as a nomen provisorium in Baral et al. (2017b) (ICN Art. 35.1).

Anamorph. In three of the *Amphosoma* species a trinacrium-like anamorph was recorded in which the arms of the slender, Y- or T-shaped conidia are consistently bent downwards. This anamorph strongly resembles that found in *Hyalorbilia erythrostigma* and *H. orbiliicola*. Similar but more robust conidia with downwards curved arms resemble *Trinacrium incurvum* and occur in *Orbilia* in series *Lentiformes*, *Piliferae*, and *Hesperideae* (*O. corculispora*).

Phylogeny. Molecular data were available for three species, *A. atroolivaceum*, *A. resinicola*, *A.* aff. *resinicola* (G.M. 2015-09-15.2), and the dubious *A. persooniae*, comprising ITS and LSU. A deviating sequence of *A. atroolivaceum* (G.M. 2017-11-05.1) includes also SSU V6–V9. The S1506 intron is absent in all of them. Our phylogenetic analyses of 5.8S+LSU or SSU+ITS+LSU (Phyls 1–2) support the position of *Amphosoma* near *Lecophagus*, *Retiarius*, and *Lilapila* by showing a higher distance to the morphologically similar genus *Hyalorbilia.* However, the distance to all these genera is very high, and even between *A. atroolivaceum* and *A. resinicola* it is 21% in the ITS. In the combined analysis of SSU+ITS+LSU in Baral et al. (2017b), the genus appeared paraphyletic by forming together with *Lecophagus* and *Lilapila* a strongly supported clade, distant from the *Hyalorbilia* clade and *Orbilia*. In the present combined analysis of all orbiliaceous genera with DNA data (Phyl. 2), *Amphosoma* appeared as an unsupported monophyletic clade which formed a strongly supported clade only under inclusion of *Retiarius* (and *Lecophagus*). This result is astonishing, considering the high morphological similarity between *Amphosoma* and *Hyalorbilia*, particularly regarding the bipolar SB arrangement in the ascospores.

When analysing ITS (Phyl. 3), *Amphosoma* formed a strongly supported monophyletic clade, whereas when analysing LSU (Phyl. 4) its species clustered unresolved among the other genera. Based on these analyses we feel affirmed in recognizing *Amphosoma* and *Retiarius* as two different genera, which is supported by a number of distinctive nucleotides in the ITS and LSU (Tab. 58). In Magyar et al.'s (2017a, b) Bayesian analyses of ITS+LSU the two genera formed strongly supported monophyletic clades in an unsupported sister position. The two genera include also various environmental sequences of different taxa from GenBank (A1–A6, R1–R4 in Phyl. 3; A5–A6, R1–R4 in Magyar et al. l.c.). It seems interesting that in the SSU V8–V9 *Amphosoma* and *Lecophagus* concur at some informative positions (Pl. 56) at which other genera differ (no SSU was available for the genus *Retiarius*).

A. persooniae shows a 10.5% ITS distance to *A.* aff. *resinicola*, 14.5% to *A. resinicola*, and 19% to *A. atroolivaceum*. In our analysis of SSU+ITS+LSU (Phyl. 2), it clustered strongly supported with *A. resinicola* in a clade, but when including *A.* aff. *resinicola* (not shown) it clustered strongly supported with this species (NJ) or unresolved with *A. resinicola* s.l. (ML). The morphological similarity between *A.* aff. *resinicola* and *A. natalense*, including a very similar spore size, might indicate that the *A. persooniae* sequence belongs to a teleomorph that closely resembles *A. natalense*. Both originate from angiosperm hosts and the present phylogeny suggests that angiosperm inhabiting species of *Amphosoma* developed from the so far predominant conifericolous taxa. The phylogeny of the angiosperm inhabiting sister genus *Retiarius* appears to have taken place in a separate lineage.

Specific nucleotide positions. In the entire 5.8S region *Amphosoma atroolivaceum*, *A.* aff. *resinicola*, and '*A. persooniae*' concur with *Retiarius revayae* and *R. superficiaris*, whereas *A. resinicola* differs by 1 nt and *R. bovicornutus* by 2 nt (3 nt between the latter two). Because of this similarity, *Amphosoma* concurs with *Retiarius* in the region of the '*Orbiliales*-specific' primers Orb5.8s1F and Orb5.8s3F (Smith & Jaffee 2009), except that *A. resinicola* deviates in Orb5.8s3F by concurring with *Lecophagus* (Tab. 18). In the primer Orb28s2R, *A. atroolivaceum* and '*A. persooniae*' concur with *R. bovicornutus* and *R. superficiaris*, but also with *Lecophagus*, *Lilapila* p.p., and some *Orbilia* spp., whereas *A. resinicola* and *R. revayae* deviate by the same nucleotide, and *A.* aff. *resinicola* shows another variant (Tab. 19). In the LSU D3 domain, 2 positions are unique for *Amphosoma* (including the strains from Texas): at pos. 748 and 770 the genus has GACCG**G**TCCTG and GGAT**C**TGAG, respectively, in contrast to all other *Orbiliomycetes* (including *Retiarius*) which have GACCG**A**TCCTG (very rarely other variants) and GGAT**T**TGAG. Another motif (pos. 726–730) is characteristic for *Amphosoma* (including the strains from Texas) and *Retiarius revayae* (AGGTGGGAG**CCCGC**AAG), in contrast to various other variants of this motif in the remaining *Orbiliomycetes*. However, *A.* aff. *resinicola* has here AGGTGGGAGCCCG**T**AAG similar as *Bryorbilia* sp. (B2, AGGTGGGAGCCCG**T**AG). Members of the *Vermispora* clade of *Hyalorbilia* have a similar motif here, deviating only at pos. 722: AGGTG**A**GAG**CCCGC**AAG.

Ecology. The two European members of *Amphosoma* occur in the same habitats as those of *Lilapila*, i.e., resinous, xeric, undecayed coniferous bark or sometimes wood in montane to subalpine, orotemperate to orosubmediterranean, humid (mixed) conifer forests. *A. atroolivaceum* also occurs in temperate colline regions of central Europe. The single record of the North American *A. macrosporum* was on xeric, rotten, non-resinous bark of *Pinus* in the cold-temperate subhumid southwest, and that from South African *A. natalense* on xeric, medium decayed bark of a legume tree in a subtropical humid (winter-dry) coastal forest.

Key to species of *Amphosoma*

1. Asci *80–120 × 10.5–11 µm; spores *11–15(–17.5) × 3.5–4.5(–5) µm, SBs 1.1–1.3 µm wide; paraphyses apically *3–6 µm wide; anchoring hyphae *4–6 µm wide; apothecia whitish to pale rose; bark of *Pinus edulis*, cold-temperate subhumid western North America .... ***A. macrosporum***, p. 281

1. Asci *26–70 × 5.5–11 µm; spores *4–10.5 × 1.7–3 µm, SBs 0.5–1 µm wide; paraphyses apically *1.8–4.3 µm wide; anchoring hyphae *1.8–3.5 µm wide 2

2. Apothecia dark blue-green-olivaceous to almost black, exceptionally some apothecia light blue-green or whitish; spores *(5.5–)6.5–9.5(–10.5) × (2.2–)2.5–3 µm, ellipsoid to clavate; blackened resinous cankers of various gymnosperms, (oro)temperate to (oro) submediterranean humid Europe .... ***A. atroolivaceum***, p. 278

2. Apothecia whitish to light cream-reddish; spores *(3.3–)4–6.5(–8) µm long 3

3. Spores *(3.3–)4–6.5(–8) × (1.8–)2–2.7(–3) µm, ellipsoid, rarely subclavate; asci *32–63 µm long; resinous cankers of various gymnosperms, orotemperate to orosub- or suprasubmediterranean humid southern Europe, boreal western North America .... ***A. resinicola***, p. 274

3. Spores *(4.8–)5.5–6.5(–7) × 1.7–2.1 µm 4

4. Asci *36–40 µm long; spores ellipsoid-fusoid to subclavate; resinous canker of *Pinus*, orosubmediterranean humid southern Europe .... ***A.* aff. *resinicola***, p. 275

4. Asci *~ 24–33 µm long; spores fusoid to clavate; bark of angiosperm (?*Pterocarpus*), subtropical humid southeastern Africa .... ***A. natalense***, p. 277

Amphosoma resinicola Baral & G. Marson, **sp. nov.**, MB 813479 — Pls 34–35, Map 2

Etymology: referring to the growth on resinous wounds of gymnosperms.

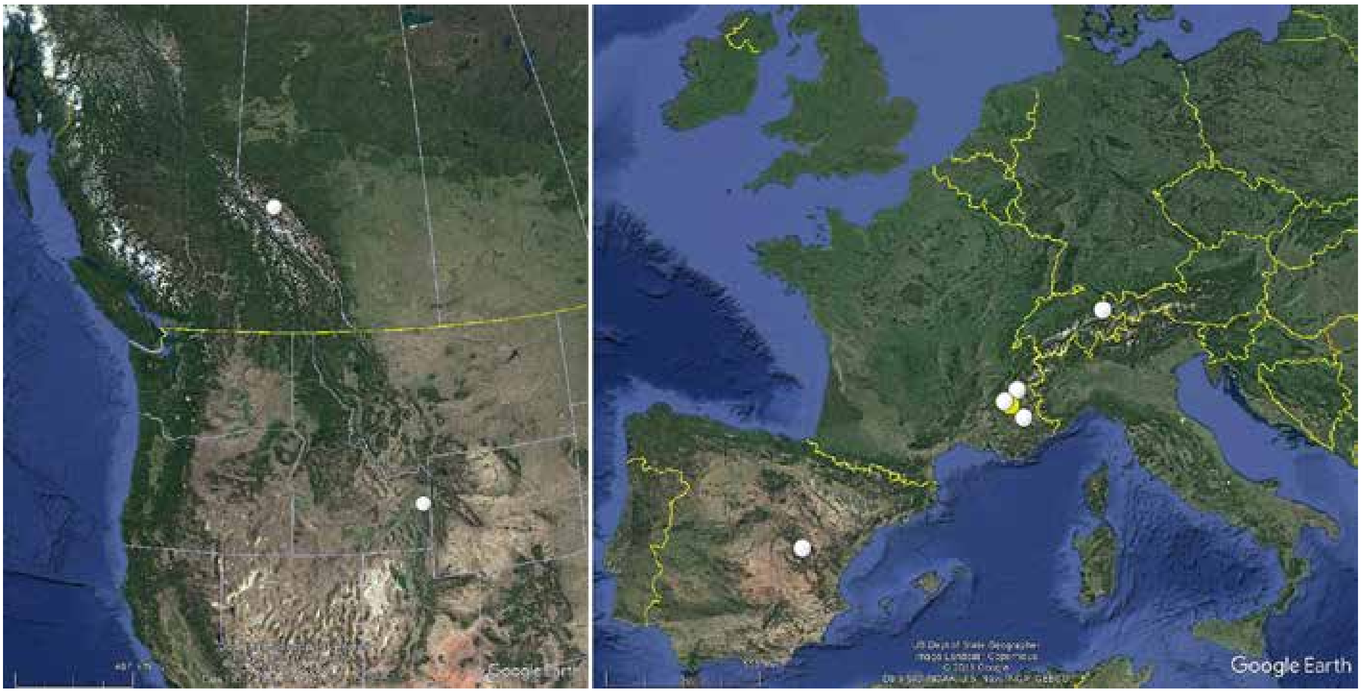
Typification: Spain, Teruel, Frías de Albarracín, branch of *Pinus sylvestris*, 26.IX.1999, G. Marson (ex H.B. 6491, M-0276404, holotype).

Latin diagnosis: *Apothecia in statu rehydratato tota alba, luteo-ochracea vel roseo-aurantiaca, lentiformia, margine glabro. Ascosporae *4–6.5 × 2–2.8 µm, (clavato-)ellipsoideae. Habitat in ramis vulneratis siccis coniferarum, leniter putridis, in aere prominentibus, plerumque ad resinam nigram, in zona orotemperata et orosubmediterranea Europae meridionalis et zona boreale Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.35(–0.5) mm diam., 0.1–0.14(–0.21) mm thick (receptacle 0.07–0.08 mm), whitish-greyish or usually pale to light (or bright) (cream-)rose, yellowish-ochraceous, or amber-orange, translucent, round, scattered to subgregarious in small groups; disc flat to slightly convex, margin thin, 0–5 µm rising above disc, exterior glabrous; sessile on an obconical base, also with an obconical stipe 0.05–0.14 × 0.15–0.25 mm sometimes immersed in biofilm; dry deeper orange-reddish. **Asci** *(32–)36–52(–63) × (4.5–)5.5–7 {8} → 7–8 µm, †33–48(–61) × (4.3–)5–5.8(–7) µm {3}, 8-spored (rarely 1–4 spores aborted), spores 2–3-seriate, sometimes 1–3 spores inverted if distinctly heteropolar, pars sporifera *15–24 → 15 µm long; **apex** (†) hemispherical to slightly truncate, dome *0.6–0.8 µm thick {2}, immature †0.7–1.2(–1.8) µm, mature †0.6–1.2 µm thick {5}, rarely with a distinct annular protrusion and apical chamber, sometimes only */†0.3–0.8 µm thick {2} thick; **base** with medium long, thick, slightly flexuous stalk, L-, Y- or h-shaped, croziers only exceptionally present (with slit-like perforation). **Ascospores** *(3.3–)4–6.5(–8) × (1.8–)2–2.7(–3) µm {8}, †4–5.5 × 1.8–2.4 µm {1}, (subcylindric–)ellipsoid, sometimes slightly to distinctly clavate, ends rounded (rarely obtuse), straight to somewhat inequilateral; **SBs** *(0.2–)0.4–0.8 × 0.5–1 µm {8}, lens- to plug-shaped, broadly attached to wall at both spore ends; **LBs** very sparse, small; rarely some overmature 1-septate spores observed. **Paraphyses** apically uninflated to medium clavate-capitate, terminal cells *5–16 × (1.8–)2.2–3.7(–4.3) µm {4}, lower cells *6–13.5 × 1.5–2.7(–3.5) µm {4}, frequently branched near base, rarely at upper septum. **Medullary excipulum** 20–60 µm thick, of dense textura angularis-intricata, indistinctly to medium sharply delimited. **Ectal excipulum** hyaline, of (†) slightly to medium gelatinized (common walls 1–1.5 µm thick), indistinctly oriented t. angularis(-prismatica) from base to mid flanks, 20–30(–130) µm thick near base, cells *7–12(–16) × 6–10(–11) µm {3}, cells at flanks *5–8 µm wide; near margin of 10–15 µm thick t. prismatica-globulosa oriented at a 0–45° angle to the surface, marginal cortical cells *(4.5–)6–11 × 3–4(–4.5) µm {3}. **Anchoring hyphae** sparse, */†1.8–2.5 µm wide, walls 0.2–0.4 µm thick {2}. **VBs** present in paraphyses [upper 1–2(–3) cells] and uppermost margin {5}, globose, 0.2–0.6(–1.3) µm diam., strongly refractive, hyaline, medium abundant (multiguttulate); **LBs** in paraphyses scattered, small, also in ectal excipulum, excipular cells at base and flanks each with 1–2 LBs 1.5–2 µm diam. {1}. **Exudate** over paraphyses and entire excipulum 0.2–0.5 µm thick {6}, hyaline, strongly refractive, continuous, smooth or finely warted. **— ANAMORPH**: trinacrium-like (from ascospore isolate {1} and natural substrate {2}). **Conidiophores** not observed. **Conidia** 2-armed (T-shaped), total size *25–41.5 × 24–44 µm {2}, stipe *22–34.5 × 2.5–3 µm, (1–)2–6-septate, arms not or slightly tapering, bent downwards, *11.5–22 × 2.5–3.5 µm in situ (actual length ~ 12–23 µm), (0–)1-5-septate.

Habitat: on still-attached (0.8–2.5 m above the ground), living or recently dead, corticated, 6–35 mm thick branches, also 10–15 cm thick trunks, of *Abies alba* {1}, *Picea* sp. {1}, *P. abies* {5}, *Pinus sylvestris* {1}, *Pseudotsuga menziesii* {1}, always in or close to ± swollen wounds, mainly on medium to strongly blackened resin {9}, or on bulging bark along decorticated wound, on slightly to sometimes medium decayed bark {5} and wood {1}, green algae sparse to abundant. **Associated**: *Amphosoma atroolivaceum* {3}, *Capronia ?mansonii* {1}, *Ciliolarina* sp. {1}, *C. ?laricina* {1}, *C. pinicola* {1}, *Claussenomyces olivaceus* {1}, *Eustilbum aureum* {1}, *Durandiella gallica* {1}, *Evernia prunastri* {1}, *Hypogymnia physodes* {1}, *H. vittata* {1}, *Lachnellula abietis* {1}, *L. resinaria* {2}, *Lilapila oculisporella* {2}, *Orbilia alpigena* {1}, *O. aristata* {2}, *O. flagellispora* {3}, *O. vinosa* {1}, *?Pragmopora* sp. {1}, *Pseudohelotium sordidulum* {1}, *Resinomyces griseus* {2}, *Sarea difformis* {4/1}, *Stictis* sp. {1}, *Usnea* sp. {1}. **Desiccation tolerance**: fully tolerant for at least 5.5 months, some mature asci, ascospores and conidia still viable after 2 years. **Altitude**: 1165–1780 m a.s.l. **Geology**: USA: Cambrian-Ordovician & Devonian-Carboniferous sedimentary rock, basalt; Europe: Lower to Upper Jurassic marl- & limestone, dolomite. **Phenology**: VI–IX (possibly throughout the year?).

Taxonomic remarks. *Amphosoma resinicola* is characterized by rather small, ± ellipsoid ascospores containing two small polar SBs, and light-coloured apothecia. *A. macrosporum* differs in much



Map 2. Known distribution of *A. resinicola* in North America and Europe (yellow = genetically deviating collection).

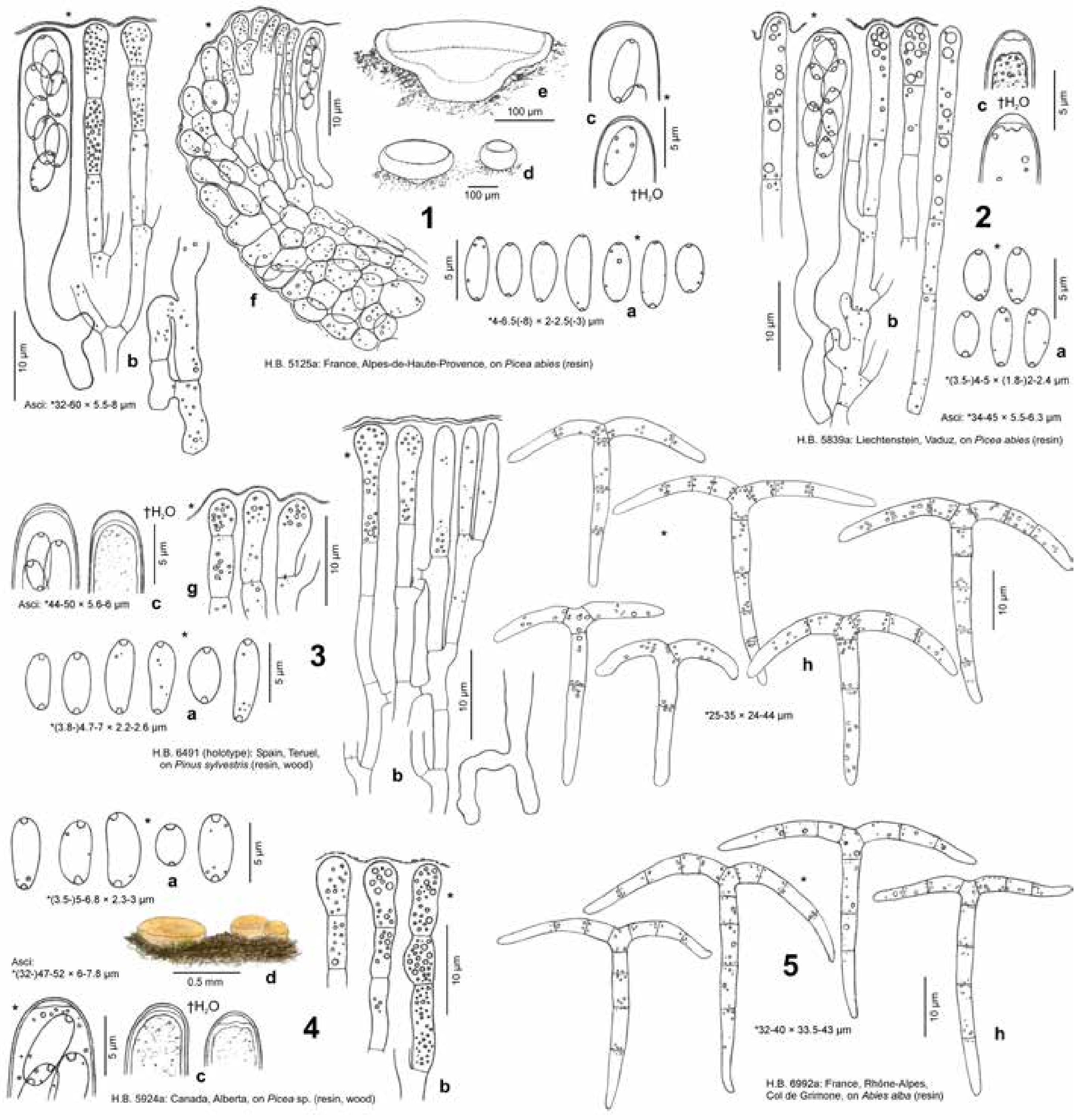


Plate 34. **1–5**: *Amphosoma resinicola*. – **a**. ascospores; **b**. asci and paraphyses (containing VBs); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., ectal excipulum at margin and flanks; **g**. external view on marginal cells; **h**. conidia (from substrate).

larger asci and spores. For confusion with the similar but usually dark-coloured *A. atroolivaceum* see under that species (p. 278).

Variation. A certain degree of variation was noted in ascus and spore size. In the North American collections the width of asci, ascospores and paraphyses was at the upper end of the range of the species, but in their morphology they fit well European populations. The asci are usually provided with a distinct apical thickening, but in two collections from Col du Labouret (H.B. 5125a, 9136d/9162e) the apices were almost thin-walled, without an internal wall thickening in the dead state. Remarkable is the occasional formation of croziers at the ascus base.

Not included collection. A sample with slightly longer and especially narrower spores (*5.7–6.7 × 1.7–2 µm) is genetically quite distant and represents a species of its own, though occurring like *A. resinicola* on coniferous resin in orosubmediterranean Europe (IVV: 15.IX.2015). In spore size it approaches the African *A. natalense* on angiosperm bark, but its spores are less fusoid-clavate and its asci longer (*36–40 × 5.2–5.8 µm).

Anamorph. In our agar cultures of the holotype of *A. resinicola* (CMA:2, MEA, WA) no conidia were produced. However, when an agar block was flooded with water, a few trinacrium-like conidia were seen after about a week which fully coincided with those observed on the natural substrate.

Phylogeny. Sequences were taken from apothecia of three samples (G.M. 2010-09-03.2, Isère, *Picea*; G.M. 2011-09-19.4, Alpes-de-Haute-Provence, *Picea*; G.M. 2015-09-15.5, Hautes

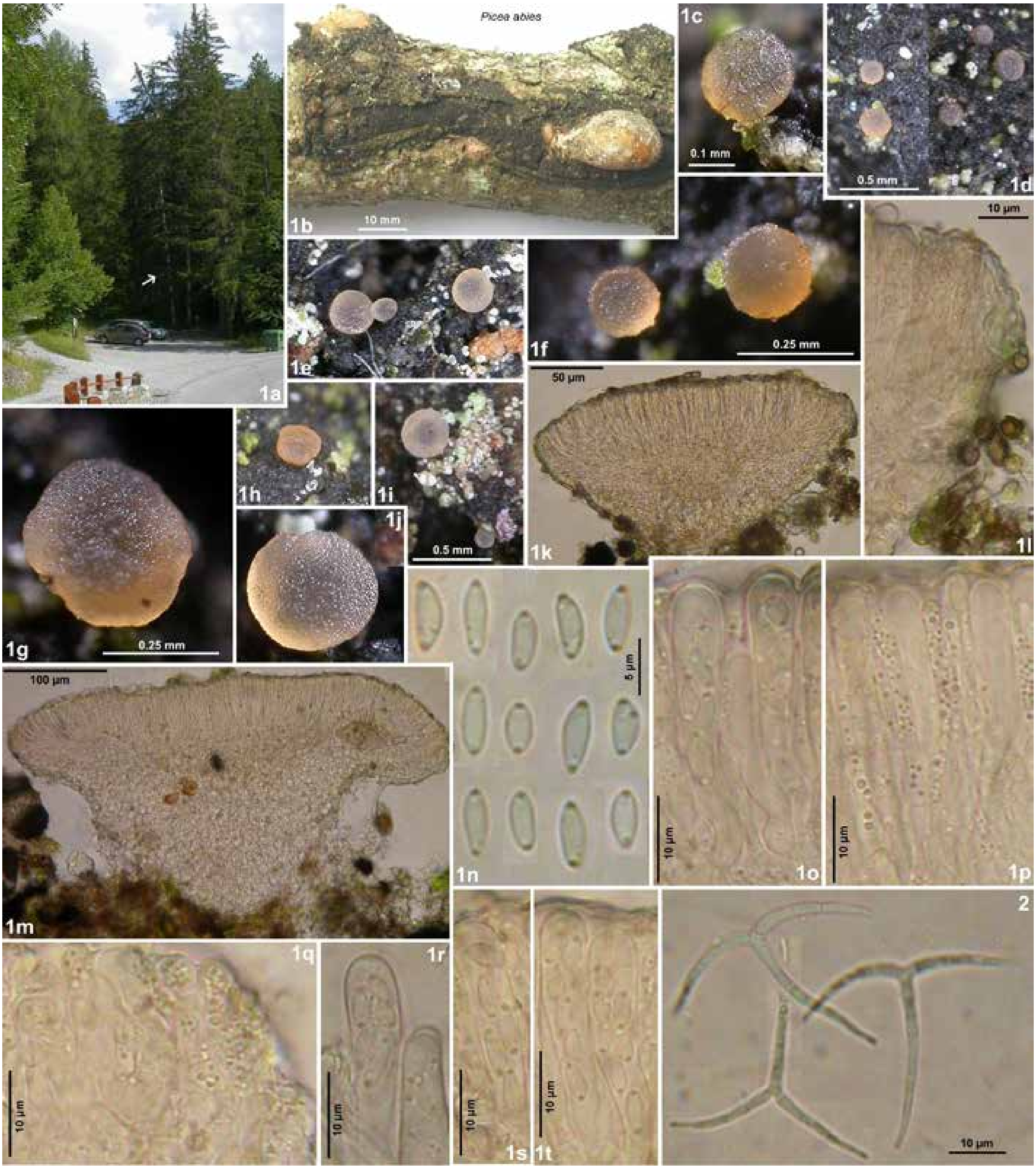


Plate 35. **1–2**: *Amphosoma resinicola*. – **1a**. orosubmediterranean *Picea* forest (Massif des Trois-Évêchés); **1b**. living *Picea* branch with blackened resinous wound; **1c–j**. rehydrated apothecia; **1k**, m. apothecia in median section; **1l**. id., ectal excipulum at flanks and margin; **1q**. id., marginal excipular cells containing VBs; **1o**, **r–t**. mature asci; **1p**. paraphyses (containing VBs); **1n**. ascospores; **2**. conidia from substrate. – Living state, except for **2** (in H_2O), **1o** (right ascus) — **1a–t**. H.B. 9162e: France, Col du Labouret, on *Picea*; **2**. H.B. 6992a: France, Col de Grimone, on *Abies*.

Alpes, *Pinus*), comprising ITS and LSU. In all the S1506 intron is absent. In the ITS region the two on *Picea* are 100 % identical. The distance to *A. atroolivaceum* lies at ~21 % in the ITS and at 5.5 % in the LSU (D1–D3).

The *Pinus* sample surprisingly differs in the ITS from both *A. resinicola* and *A. atroolivaceum* by 19 % and from *A. persooniae*, with which it clustered in a supported clade in our analysis (not shown), by 10.5 %. Because of its whitish apothecia and resinicolous habitat it is named *A.* aff. *resinicola* here.

Ecology. *Amphosoma resinicola* appears to be restricted to resinous wounds of still-living or recently dead xeric branches and trunks of gymnosperms. The apothecia grew mainly on resin covered by black hyphomycetes. The species is apparently not rare in subcontinental, altimontane to subalpine, orotemperate to orosubmediterranean, sometimes almost suprasubmediterranean, humid (to slightly semihumid), mixed or pure conifer forests of the Northern Calcareous and Southern French Alps and the Sistema Ibérico in Spain on Jurassic soil (the not included sample on Oligocene marl & molasse). *A. resinicola* in western North America was found in the boreal humid Douglas fir mixed forest of the Canadian and Northern Rocky Mountains on Paleozoic soil.

Specimens included. **LIECHTENSTEIN**: 5 km SE of Vaduz, S of Steg, Saminatal, Im Grund, 1310 m, branch of *Picea abies*, on resin, 7.VII.1997, H.O. Baral (H.B. 5839a). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 55 km S of Grenoble, 5 km NW of Lus-la-Croix-Haute, Col de Grimone, 1330 m, branch of *Abies alba*, on resinous bark, 3.VIII.1999, G. Marson (H.B. 6992a, anam. substr.). – **Isère**, 38 km SE of Grenoble, 1.5 km SSE of Les-Deux-Alpes, 1780 m, trunk of *Picea abies*, on resinous bark, 3.IX.2010, G. Marson (G.M. 2010-09-03.2; sq.: KT222388). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branches of *P. abies*, on resin, 17.VII.1994, G. Marson (H.B. 5125a, G.M. 5205). – ibid., branches of *P. abies*, on resin & bark, 14.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9136d, 9162e). – ibid., branch of *P. abies*, 19.IX.2011, G. Marson (G.M. 2011-09-19.4; sq.: KT222389). — **SPAIN**: **Aragón**, **Teruel**, Sierra de Albarracín, 49 km W of Teruel, 5.8 km WSW of Frías de Albarracín, 1615 m, branch of *Pinus sylvestris*, on bark & resin, 26.IX.1999, G. Marson (ex H.B. 6491, M-0276404, **holotype**; anam. substr., anam. cult.). — **CANADA**: **Alberta**, 7 km NE of Jasper, Maligne Canyon, 1165 m, branch of *Picea* sp., on wood & resin, 17.VIII.1997, G. Marson (H.B. 5924a). — **USA**: **Idaho**, Columbia Plateau, base of Rocky Mountains, 60 km E of Idaho Falls, 47 km W of Jackson, Swan Valley, 1750 m, branch of *Pseudotsuga menziesii*, on bark & resin, 5.VI.1996, G. Marson (H.B. 5603).

Not included. **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 16 km W of Gap, NNE of Montmaur, 1020 m, branch of *Pinus sylvestris*, on resin, 15.IX.2015, G. Marson (G.M. 2015-09-15.2, sq.: MN151404).

Amphosoma natalense Baral, **sp. nov.**, MB 813480 — Pls 36–37

Etymology: named after the geographical origin, KwaZulu-Natal (South Africa).
Typification: South Africa, KwaZulu-Natal, Santa Lucia, branch of indet. angiosperm (?*Pterocarpus*), 25.II.2006, V. Kummer (ex H.B. 8086a, M-0276403, holotype).

Latin diagnosis: Amphosomati resinicolae *similis, sed asci breviores, ascosporae angustiores, magis fusoideae. Habitat ad corticem putridum rami sicci arboris ?*Pterocarpi *in zona subtropica humida Africae australis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2 mm diam., whitish-cream, round, scattered; disc flat, margin smooth; with a short and broad stipe, superficial. **Asci** *26 × 5.6 µm, †22–30 × 4.7–5.1 µm, 8-spored, spores *3-seriate, ~4 lower spores inverted, pars sporifera *14.5 µm long; **apex** (†) hemispherical to slightly truncate-conical, dome †0.7 → 0.2–0.5 µm thick, without apical chamber; **base** with short to medium long, flexuous stalk, Y- to h-shaped. **Ascospores** *(4.8–)5.5–6.5(–7) × (1.7–)1.8–2(–2.1) µm, fusoid-ellipsoid to fusoid-clavate or clavate, ends obtuse to subacute, sometimes rounded, straight to slightly inequilateral; **SBs** *0.5–0.9 × 0.5–0.8 µm, globose to somewhat plug-shaped, ± broadly attached to wall at both spore ends; often with some small and medium-sized LBs. **Paraphyses** apically uninflated to slightly clavate-capitate, terminal cells *1.8–2 wide. **Medullary excipulum** not studied. **Ectal excipulum** of slightly gelatinized textura angularis(-prismatica) from base to margin, cells at flanks *5–7 × 4–5 µm, oriented at a high angle to the surface, marginal cortical cells *5–9 × 3–4.7 µm; **glassy processes** absent. **Anchoring hyphae** not seen. **VBs** in paraphyses not seen, in marginal ectal excipulum globose, strongly refractive, hyaline, 1.3–2 µm diam. **Exudate** over paraphyses and margin 0.2–0.3 µm thick, hyaline, continuous, ± smooth. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {1}). **Conidiophores** not observed. **Conidia** 2-armed (Y/T-shaped), total size */†20–23 × 24–27 µm {1}, stipe */†16–18 × 3–4 µm, 2–4-septate, arms gradually tapering, mostly distinctly bent downwards, */†11.5–14.5 × 2.7–3.2 µm, (1–)2-septate.

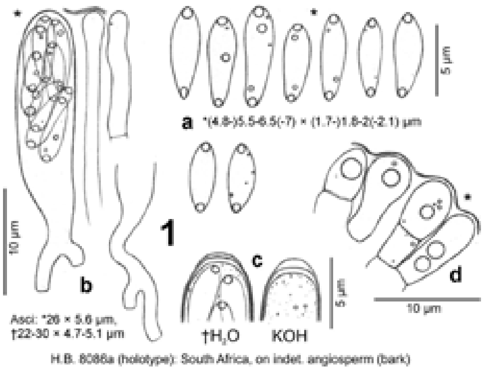


Plate 36. **1**: *Amphosoma natalense*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal excipular cells (containing VBs).

Habitat: collected ~4 m above the ground, medium sun-exposed, corticated, 20 mm thick branch of indet. angiosperm (?*Pterocarpus*), recently dead, on medium decayed bast in transversal cleft of bark. **Associated**: *Helicoma muelleri*, *Tremella* sp., various lichens (fruticose, foliose, crustose). **Desiccation tolerance**: fully tolerant for at least 3 weeks. **Altitude**: 10 m a.s.l. **Phenology**: II (southern hemisphere).

Taxonomic remarks. *Amphosoma natalense* differs from *A. resinicola* in shorter asci and narrower, more fusoid ascospores, and especially in growing on bark of an angiosperm.

Anamorph. A few conidia similar to *Trinacrium angamosense* (?= *Hyalorbilia erythrostigma*) were found on the natural substrate (Pl. 37: 1d). Among them was also one with 3 arms that formed the shape of a K (curucispora-like), and one reminiscent of *Retiarius revayae*.

Phylogeny. No sequence was available, but based on habitat, angiosperm bark, *A. natalense* might be related to '*A. persooniae*' (see p. 272).

Ecology. *Amphosoma natalense* was collected on a xeric branch of a free-standing broad-leaved tree of an unidentified member of *Fabaceae*. Only a single apothecium could be discovered on medium decayed bast in a transversal cleft of bark. The area belongs to a subtropical humid (winter-dry savannah) oceanic coastal dune and swamp forest in southeastern Africa.

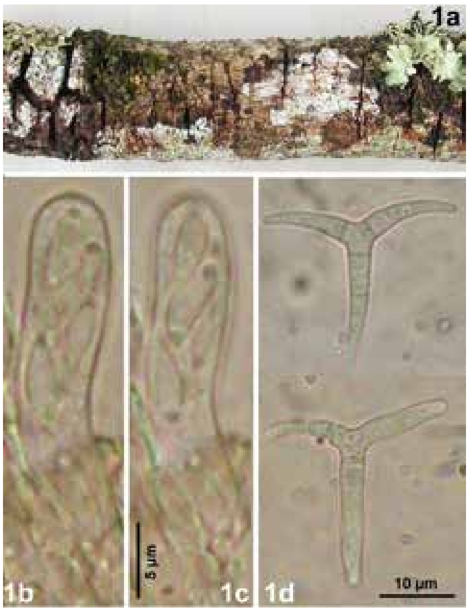


Plate 37. **1**: *Amphosoma natalense*. – **1a**. dead corticated branch with transversal clefts and foliose and fruticose lichens; **1b–c**. ascus with ascospores; **1d**. conidia (from substrate). – Living state (except for left arm of lower conidium). — **1a–d**. H.B. 8086a (holotype): South Africa, on indet. angiosperm (?*Pterocarpus*).

Specimens included. **SOUTH AFRICA**: **KwaZulu-Natal**, 210 km NE of Durban, 55 km NE of Richards Bay, 1 km SE of Santa Lucia, St. Lucia Estuary, Sugarloaf Rest Camp, 10 m, branch of indet. *Fabaceae* (?*Pterocarpus*), on bark, 25.II.2006, V. Kummer (ex H.B. 8086a, M-0276403, **holotype**, anam. substr.).

Amphosoma atroolivaceum Baral & G. Marson, **sp. nov.**, MB 813481 — Pls 38–39, Map 3

Etymology: named after the dark-coloured, blackish-olivaceous apothecia.

Typification: France, Vaucluse, Mont Ventoux, branch of *P. sylvestris*, 14.VIII.2009, H.O. Baral & G. Marson (ex H.B. 9143b, M-0276401, holotype).

Latin diagnosis: *Ab* Amphosomate resinicola *apotheciis atroolivaceis, ascosporis longioribus differt. Habitat in ramis vel truncis vulneratis siccis coniferarum, leniter putridis, in aere prominentibus, plerumque ad resinam nigram, in zona (oro)temperata ad (oro)submediterranea Europae centralis et meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.15–0.35(–0.5) mm diam., 0.11–0.18 mm thick (receptacle 0.07–0.1 mm), dark blue-green-olivaceous to black (exceptionally light blue-green or whitish-cream), shining, round, rarely irregular by mutual pressure, scattered to gregarious; disc slightly concave to slightly convex, margin distinct, only young slightly rising above disc, even, externally glabrous; sessile on a narrowed base, often with a pale stalk ~0.05–0.09 × 0.06–0.15 mm completely immersed in layer of dark hyphomycetes; dry black, invisible. **Asci** *(32–)40–61(–68) × (6.3–)7–8.5(–11) µm {7}, †28–40 {1} or 40–67 {2} × 5.5–7.3 {3} µm, 8-spored (rarely only 6 spores developed), spores *2–3-seriate, 1–4 lower (exceptionally upper) spores inversely oriented (if heteropolar) {5}, pars sporifera *18–33 µm long; **apex** (†) hemispherical to slightly truncate, dome *1 µm thick, †0.8–1.5(–1.8) µm {5}, sometimes with apical chamber, surface often covered by a thin olivaceous cap; **base** with or without short to medium long, thick, ± flexuous stalk, H-, h-, U-, T- or L-shaped, simple-septate, exceptionally forming a crozier with slit-like, 12 µm long perforation. **Ascospores** *(5.5–)6.5–9.5(–10.5)((–12.5)) × (2.2–)2.5–3((3.5)) µm {20}, †5.5–9.2 × 2.3–2.8 µm {2}, (subcylindric-)ellipsoid, sometimes distinctly (fusoid-)clavate, ends rounded or obtuse, straight, rarely medium curved near base; rarely some free spores 1-septate {2}; **SBs** *0.3–0.8 × 0.7–1.1 µm {7}, lens- or plug-shaped, broadly attached to wall at both spore ends {23}; usually with 1–2 large **LBs** 0.4–1(–1.3) µm diam. and a few or many small ones. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, sometimes sublanceolate, terminal cells *7–14(–19) × 1.8–3(–3.6) µm {5}, lower cells *7–15 × 1.7–2.3 µm {5}; rarely branched near apex. **Medullary excipulum** hyaline to pale olivaceous-brownish, 30–50 µm thick, of dense irregular textura angularis, cells *4–11(–13) × 4–8 µm, distinctly delimited from ectal excipulum by a thin, olivaceous t. porrecta. **Ectal excipulum** with a pale to bright olive-brown intercellular exudate (but hyaline at base of stipe), slightly to medium gelatinized, near base of t. angularis(-prismatica) oriented at a 70–90° angle to the surface, 20–35 µm thick, cells *6–9 × 4–6(–7) µm {2}; at flanks and margin of t. angularis-prismatica or t. porrecta, 15–25 µm thick at lower flanks, oriented at 10–45°; 5–15 µm thick near margin, oriented at 10°, marginal cortical cells *5–12 × 2–4 µm {4}. **VBs** present in terminal cells of paraphyses (sometimes also in 1–2 lower cells) and in marginal cortical cells {18}, 0.3–1.5 µm diam., globose, strongly refractive, hyaline, sparse to abundant (multiguttulate); 1–2 faintly yellow **LBs** (carotenoids) in cells of basal ectal excipulum, ~1–2 µm diam. **Exudate** over paraphyses ~1–4 µm thick, granular, dark olivaceous-green(-brownish), extending ± far down between the paraphyses, sometimes attached to lateral wall, individual granules 0.2–0.5(–1) µm diam., KOH-resistant (turning light reddish-brown-brass to ochraceous-olive), in PVA or other acids bright dirty blue-green to green, externally covered by a hyaline, refractive, continuous, 0.2–0.3 µm thick layer; over margin and flanks granular to continuous, ~0.5–2 µm thick (more cloddy near base); in hyaline apothecia only a thin hyaline layer present. **Anchoring hyphae** sparse to abundant, hyaline, *2–3.5 µm wide, walls 0.2–0.3 µm thick {3}, sometimes covered by a 0.7–1.5 µm thick gel sheath. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {4}). **Conidiophores** not observed. **Conidia** 2-armed (T-shaped), total size */†16–22 × (11–)15–25(–29) µm {4}, stipe */†15–19 × 2–3 µm, 2-septate, arms slightly to strongly tapering, bent downwards, */†9–15 × 2.3–3.2 µm, (0–)1–2-septate.

Habitat: on living trees or on fallen or cut trees or canopy parts, collected 1–4 m above the ground, recently dead (sometimes still-living), corticated, 8–80 mm thick branches, also 10–15 cm thick trunks, of *Larix decidua* {5}, *Larix* sp. {1}, *Picea abies* {14/1}, *P. ?sitchensis* {1}, *Pinus nigra* {1}, *P. sylvestris* {18}, in small or mostly large, sometimes very long, often strongly swollen canker-like wounds, on upperside or laterally, sometimes fully sun-exposed, on ± undecayed, rarely medium to strongly decayed, naked bark {14} and wood {3}, mostly on resin {> 38}, e.g., on central area of wound covered by abundant brown to black hyphomycetes (sometimes with green algae). **Associated**: *Amphosoma resinicola* {3}, *Capronia* sp. {2}, *Chrysodisca peziculoides* {1}, *Ciliolarina* sp. {3}, *C. pinicola* {6}, *Claussenomyces* sp. {1}, *C. olivaceus* {3}, *Crumenulopsis pinicola* {2}, *Diplolaeviopsis* sp. {1}, *Echinula resinicola* {2}, *Eustilbum aureum* {1}, *Evernia prunastri* {1}, *Hypogymnia physodes* {2}, *H. vittata* {1}, *Hysterium angustatum* {1}, *Lachnellula abietis* {1}, *L. occidentalis* {3}, *L. resinaria* {4}, *Lecophagus pini* {2}, *Lilapila oculispora* {3}, *L. oculisporella* {5}, *L. jurana* {1}, *Melaspileella proximella* {1}, *Mollisia lividofusca* {1}, *Mytilinidion gemmigenum* {1}, *Orbilia aristata* {1}, *O. cylindrospora* {1}, *O. eucalypti* {1}, *O. flagellispora* {2}, *O. ?graminis* {2}, *O. olivacea* {2}, *O. sphaerospora* {3}, *O. vinosa* {1}, *O. subvinosa* {1}, *Pragmopora* sp. {1}, *P. amphibola* {2}, *Propolis betulae* {1}, *Pseudohelotium sordidulum* {2}, *Resinomyces griseus* {6}, *R. kirschsteinianus* {16}, *Sarea difformis* {16}, *S. resinae* {4}, *Stictis* sp. {1}, *Tryblidiopsis pinastri* {1}, *Usnea* sp. {1}. **Desiccation tolerance**: fully tolerant for at least 6 weeks, after 2 months paraphyses and ectal excipulum still alive. **Altitude**: 350–1310 m a.s.l. (central Europe) or 743–1780 m (southern Europe). **Geology**: Lower to Upper Jurassic and Cretaceous sand-, lime- & marlstone, Pleistocene loess & silt, decalcified clay; granite, granodiorite, migmatite, mica schist, gneiss. **Phenology**: throughout the year (long-lived).

Phenology of *A. atroolivaceum*

Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2	1	1	4	0	0	3	11	9	7	3	1

Taxonomic remarks. *Amphosoma atroolivaceum* is readily distinguished from *A. resinicola* by its dark pigmentation. However, in one of the many collections studied, some apothecia were less strongly pigmented or sometimes completely whitish. The microscopic characters of these two species are quite similar, but the distinctly longer and more often clavate ascospores of *A. atroolivaceum* provide sufficient evidence that *A. resinicola* is not merely an albinotic form of *A. atroolivaceum*. The two species illustrate the comparatively low taxonomic value of pigmentation at higher levels.

Dry apothecia of *A. atroolivaceum* are impossible to detect under the dissecting microscope among the blackish-brown mould covering the resin. When rewetted they can be recognized by their shining, dark blue-green hymenium. The characteristic colour is more distinct when studying sections under transmitted light under the microscope.

Variation. *A. atroolivaceum* seems to be quite constant in its micromorphological characteristics, with little variation in ascus and spore size. As in *A. resinicola*, croziers were occasionally observed at the ascus base. In the collection from Gérardmer, one apothecium was pale blue-green and three whitish, while only three apothecia showed the typical dark pigmentation.

Anamorph. The observed trinacrium-like conidia are similar to those of *A. resinicola* but smaller. Since *A. resinicola* likewise inhabits resinous wounds of conifers and grew a single time in assocation with *A. atroolivaceum*, it cannot be excluded

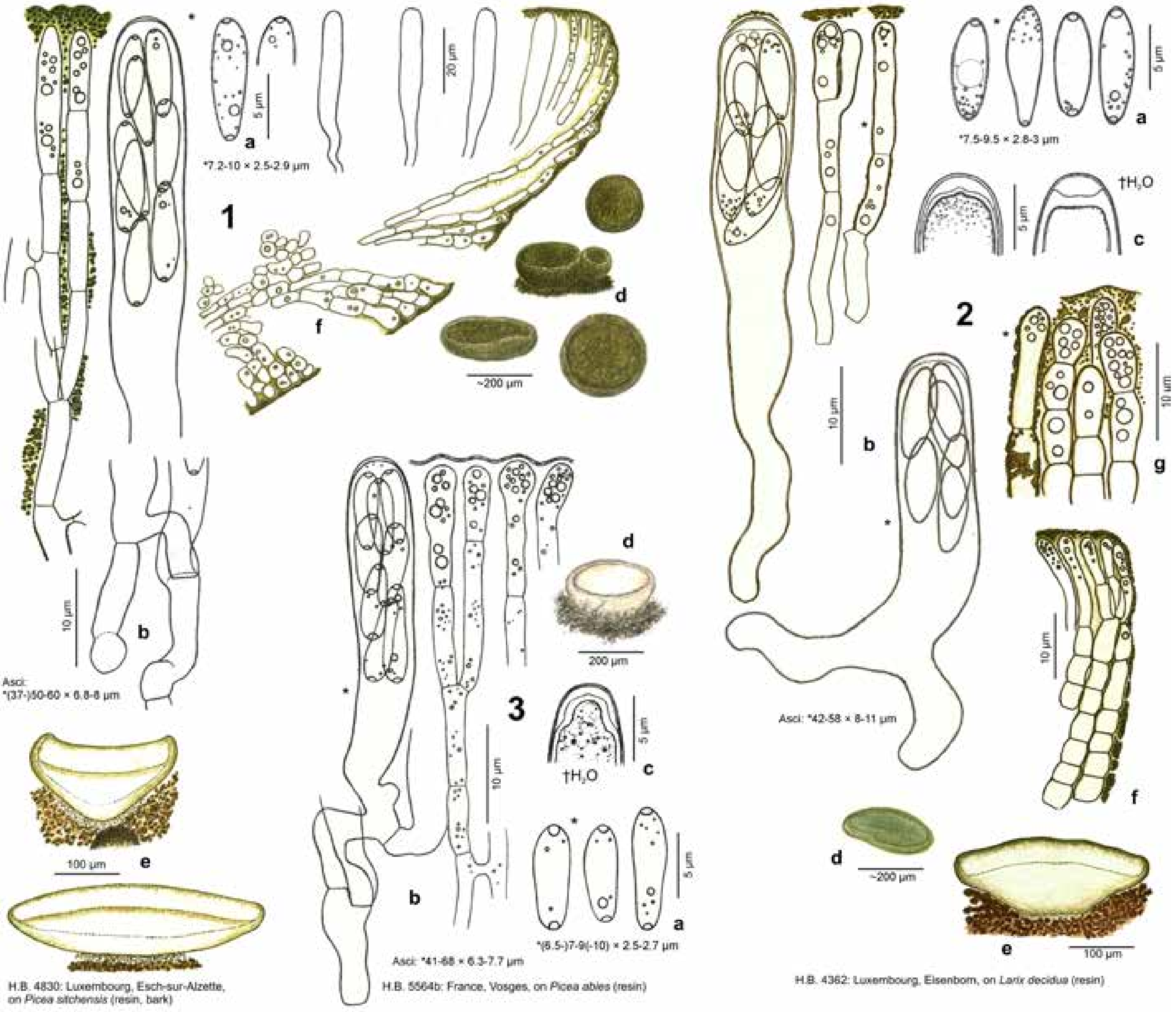


Plate 38. **1–3**: *Amphosoma atroolivaceum*. – **a**. ascospores; **b**. asci and paraphyses (containing VBs); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. median section of ectal excipulum and hymenium (lower flanks up to margin); g. ectal excipulum (margin, surface view), cells containing VBs.

that the observed conidia belong to that species. However, two of the four collections of *A. atroolivaceum* in which conidia were found originate from Luxembourg, whereas *A. resinicola* was so far recorded within central Europe only from the region of the Alps.

Phylogeny. Sequences were taken from apothecia of five specimens, four from the Southern French Alps (ITS: G.M. 2009-09-27.1; ITS+LSU: G.M. 2010-09-03.1, H.B. 9162b, 9631b), one from Vosges (SSU+ITS+LSU: G.M. 2017-11-05.1). Four of them (including Vosges) cover enough of the 3'-end of SSU, in which the S1506 intron is always absent. Those from the Alps are fully identical in the ITS and LSU (H.B. 9162b consists only of fragments of ITS and LSU and appears to be uncertain at the few deviating positions in the ITS1 and LSU). The sample from Vosges deviates by 15 nt (3.2 %) in the ITS and 2 nt (0.3 %) in the LSU D1–D2. Regrettably no morphological data were available for this sample. If it represents the northern genotype of the species aggregate, then morphological differences appear to be absent, similar as in *Lilapila*. For the distance to *A. resinicola* see p. 276.

Ecology. Like *Amphosoma resinicola*, *A. atroolivaceum* was exclusively found on resinous wounds of dead or living, undecayed xeric branches and trunks of gymnosperms, on which it grew especially on old resin blackened by hyphomycetes. No preference among the coniferous host trees was noted. *A. atroolivaceum* was collected in submontane to subalpine mixed conifer forests in cold- to orotemperate subcontinental humid central Europe (Eifel, Luxembourg, Vosges, Schwarzwald, Central Sudetes, High Tatras) and orotemperate to orosubmediterranean humid or sometimes suprasubmediterranean semihumid southern Europe (Southern French Alps, Massif central).

Specimens included. **POLAND**: **Lower Silesia**, Central Sudetes, 9 km SSW of Stronie Śląskie, 0.9 km NNE of Śnieżnik, 1125 m, branch of *Picea abies*, on resin, 9.IX.2009, P. Perz (P.P. 20090909-3, doc. vid.). — **SLOVAKIA**: **Prešov**, Carpathian Mts., Vysoké Tatry, 8.7 km SSW of Tatranská Javorina, Bielovodská valley, 1310 m, branch of *P. abies*, on resin, 12.VII.2018, A. Polhorský (A.P. 18/96, doc. vid.). — **LUXEMBOURG**: **Gutland**, **Mersch**, 6 km SW of Mersch, 1.2 km NE of Lorentzweiler, Haereboesch, 380 m, branch of *Larix decidua*, on bark & resin, 24.XI.1990, G. Marson (H.B. 4342, G.M. 4381). – 8 km NE of Mersch, 1 km E of Nommern, W of Kéngertsbësch,

Plate 39. **1–6**: *Amphosoma atroolivaceum*. – **1a**, **3a**, **4a**. living branches and trunk, with blackened resinous wounds; **1b–d**, **2a–b**, **3b–d**. rehydrated apothecia. **4d**. apothecium in median section; **2c**. ectal excipulum in surface view; **3e–f**. id., **e**: living cells containing VBs, **f**: small clods of olivaceous exudate over cells; **2e**, **3g**, **4e**. ascospores; **2d**, **4b**. asci; **4c**. hymenium in median section; **1e**, **4f**, **5**, **6**. conidia (from substrate). – Living state, except for **1e** (right), **5**, **6** (in H_2O). — **1a–e**. H.B. 8069a: France, Col de Perty, on *Pinus*; **2a–e**. H.B. 9143b (holotype): France, Mont Ventoux, on *Pinus*; **3a–g**. H.B. 9162b: France, Col du Labouret, on *Picea*; **4a–f**. H.B. 8057: Luxembourg, on *Larix*; **5**. H.B. 4268: France, Lavillatte, on *Pinus*; **6**. H.B. 7248: France, Javon, on *Pinus*.

400 m, branch of *L. decidua*, on resin, 23.IV.1994, G. Marson & H.O. Baral (ø). – ibid., ~1.8 km NW of Larochette, Kéngertsbësch, ~370 m, on resin of *L. decidua*, 4.IV.1994, G. Marson (H.B. 6282, dried culture). – **Luxembourg**, 6.5 km NNE of Luxembourg, 1.5 km ESE of Heisdorf, Mägrond, 380 m, branch of *Pinus nigra* subsp. *nigra*, on resin, 6.XI.1990, G. Marson (H.B. 4307, G.M. 4342). – 7 km NE of Luxembourg, 3 km S of Eisenborn, NW of Waldhaff, 350 m, branch of *Larix decidua*, on resin, 12.III.1991, G. Marson (H.B. 4362, G.M. 4496). – ibid., SE of Waldhaff, Gréngewald, 417 m, trunk of *L. decidua*, on resin, 12.II.2006, G. Marson (H.B. 8057 ø, anam. substr.). – **Esch-sur-Alzette**, 2.2 km S of Esch-sur-Alzette, 1.5 km ENE of Audun-le-Tiche, Ellergronn, 350 m, branch of *Picea ?sitchensis*, on bark & resin, 16.XII.1992, G. Marson (H.B. 4830, G.M. 4928). – 3.5 km WSW of Pétange, 1 km S of Rodange, Le Haut de Saulnes, 360 m, branch of *Larix*, on resin, 2.IV.1999, G. Marson (ø). — **GERMANY**: **Rheinland-Pfalz**, 6 km SE of

Map 3. Known distribution of *A. atroolivaceum* in Europe

Daun, 1.9 km SSE of Schalkenmehren, Sangweiher, 405 m, branch of *Picea abies*, on resin, 17.IV.1993, G. Marson (H.B. 4865a). – **Baden-Württemberg**, 6.5 km SSW of St. Blasien, 1 km NW of Wolpadingen, 930 m, branch of *P. abies*, on resin, 7.X.1992, G. Marson (ø). — **SWITZERLAND**: **Jura**, 3.6 km WNW of Tramelan, 1.5 km ESE of La Theurre, Moulin de la Gruère, 1017 m, branch of *Picea abies*, on resin, 17.I.2020, E. Stöckli (doc. vid.). — **FRANCE**: **Lorraine**, **Vosges**, 5 km NNE of Gérardmer, *P. abies*, 5.XI.2017, G. Marson (G.M. 2017-11-05.1, non vid., sq.: MN151403). – 3.5 km ESE of Gérardmer, les Vazenées, le Cerceneux Marion, 990 m, branch of *P. abies*, on resin, 2.IX.1996, H.O. Baral (H.B. 5564b). – 1 km S of les Vazenées, la Chaume-Francis, NW of Tête de Grouvelin, 1100 m, branch of *P. abies*, on resin, 8.IX.1998, H.O. Baral & J. Deny (ø). – **Franche-Comté**, **Doubs**, 25 km SSW of Pontarlier, W of Mouthe, branch of *P. abies*, on resin, 1016 m, 19.I.2020, A. Mombert (doc. vid.). – **Rhône-Alpes**, **Drôme**, 4.5 km S of Rémuzat, Col de Soubeyrand, 1005 m, branch of *Pinus sylvestris*, on bark & resin, 10.X.2002, G. Marson (ø). – 7.5 km NNE of Séderon, 2 km S of Col de Perty, 1120 m, branch of *P. sylvestris*, on resin & bark, 7.VIII.2003, G. Marson (H.B. 8069a, anam. substr.). – 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branch of *P. sylvestris*, on bark & resin, 23.VIII.1996, G. Marson (ø). – ibid., branch of *P. sylvestris*, on resin, 6.VIII.1999, G. Marson (unpreserved) – **Savoie**, 19 km ENE of Albertville, 4.5 km ESE of Beaufort, ~1350 m, (?)*Picea abies*, 4.VIII.1995, G. Marson (ø). – **Ardèche**, 8.5 km ESE of Pradelles, 3 km ENE of Lavillatte, parking spot, 1250 m, branch of *Pinus sylvestris*, on bark, 21.IX.1990, G. Marson (H.B. 4268, anam. substr.). – **Isère**, 38 km SE of Grenoble, 1.5 km SSE of Les-Deux-Alpes, 1780 m, trunk of *Picea abies*, on resin, 3.IX.2010, G. Marson (G.M. 2010-09-03.1; sq.: KT380069). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 24 km SE of Gap, 5 km E of Turriers, 0.6 km SW of Col des Garcinets, 1147 m, branch of *Pinus sylvestris*, on wood, bark & resin, 25.VIII.1996, G. Marson (H.B. 5621f). – **Vaucluse**, 26 km ESE of Carpentras, 19 km S of Mont Ventoux, Forêt de Javon, 743 m, branch of *P. sylvestris*, on bark & resin, 10.X.2002, G. Marson (H.B. 7248, anam. substr.). – 10.5 km SE of Mont Ventoux, 3.5 km NW of Sault, 870 m, branch of *P. sylvestris*, on resin, 14.VIII.2009, H.O. Baral & G. Marson (ex H.B. 9143b, M-0276401, **holotype**). – **Alpes-de-Haute-Provence**, 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *Picea abies*, on resin, 6.X.1993, G. Marson (H.B. 5007e). – ibid., branch of *P. abies*, on bark & resin, 17.VII.1994, G. Marson (ø). – ibid., branch of *P. abies*, on resin, 14.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9162b, sq.: MH221036; H.B. 9136c). – ibid., branch of *P. abies*, on resin, 19.IX.2011, G. Marson (G.M. 2011-09-19.2). – ibid., branch of *Pinus sylvestris*, on resin & wood, 24.X.1992, G. Marson (ø). – 8 km SE of St.-Julien-du-Verdon, 3 km NW of Soleilhas, Vauplane, 1600 m, branch of *P. sylvestris*, on bark & resin, 16.VII.1994, G. Marson (H.B. 5137a). – 18 km NE of Digne-les-Bains, 5 km SSW of Prads-Haute-Bléone, Blégier, 970 m, branch of *P. sylvestris*, on bark & resin, 24.VIII.1996, G. Marson (H.B. 5628f). – Mercantour, 13.5 km SE of Seyne-les-Alpes, 5.5 km SW of Tête de l'Estrop, Vière, 1350 m, branch of *P. sylvestris*, on bark & resin, 24.VIII.1996, G. Marson (ø). – 12 km E of St.-André-les-Alpes, 1 km SW of Annot, E of Col de l'Iscle, 855 m, branch of *P. sylvestris*, on bark, resin & wood, 16.VIII.2001, G. Marson (ø). – **Var**, Grand Canyon du Verdon, 6.8 km NW of Comps-sur-Artuby, 2.8 km SSW of Trigance, 980 m, branch of *P. sylvestris*, on bark & resin, 23.X.1992, G. Marson (H.B. 4831a, G.M. 4919). – 11 km WNW of Comps-sur-Artuby, 6.3 km SW of Trigance, 0.8 km WNW of Pont de l'Artuby, 800 m, branches of *P. sylvestris*, on resin, 22.IX.2011, G. Marson (H.B. 9631b ø, G.M. 2011-09-22.3; sq.: KT222387). – 6.7 km WSW of Trigance, Col de Fayet, 870 m, branches of *P. sylvestris*, on resin, 27.IX.2009, G. Marson (G.M. 2009-09-27.1; sq.: KT380058). – 1.6 km NNW of Comps-sur-Artuby, 2.3 km S of Jabron, 910 m, branch of *P. sylvestris*, on resin, 27.IX.2009, G. Marson (ø). — **Alpes Maritimes**, Préalpes de Grasse, 19 km NNE of Grasse, 4 km NNE of Gréolières, Gréolières les Neiges, 1400 m, branch of *P. sylvestris*, on resin, 1.X.1993, G. Marson (ø).

Amphosoma macrosporum Baral & G. Marson, **sp. nov.**, MB 813482 — Pl. 40

Etymology: according to the comparatively large ascospores.
Typification: USA, Utah, Cedar City, branch of *Pinus edulis*, 24.VIII.1994, G. Marson (ex H.B. 5181b, M-0276402, holotype).

Latin diagnosis: *Differt ab* Amphosomate resinicola *ascis et sporis multo majoribus. Habitat ad corticem putridum rami sicci* Pini edulis *in zona temperata subhumida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.12–0.35 mm diam., up to 0.23 mm thick (receptacle 0.13 mm), whitish to pure pale rose, also pale yellowish-cream, round; disc flat, margin even; with a distinct stipe 0.1 × 0.16 mm, superficial. **Asci** *81–90 × 10.5–11 µm, †75–95(–115) × (7.5–)8–9 µm, 8-spored (often only 5–7 spores developed), spores biseriate; **apex** (†) ± hemispherical, dome †1.8–2.3 → 1.2 µm thick (complete wall deep lilac-violet in CRB), with slight apical chamber; **base** with thick, flexuous stalk, unbranched or h- to H-shaped. **Ascospores** *11–15(–17.5) × 3.5–4.5(–5) µm, †10.3–14.5 × 3.3–4.5 µm; (sub)cylindrical, homopolar, ends rounded or very slightly papillate, straight or very slightly curved, overmature with 1, rarely 3 transverse septa, up to 5.5–7 µm wide; **SBs** *(0.7–)0.9–1.2 × 1.1–1.3 µm, plug-shaped, broadly attached to wall at both ends; with several small to medium-sized LBs (up to 1.7 µm). **Paraphyses** apically slightly to strongly clavate-capitate, terminal cells *6.5–15 × 3–6 µm, lower cells *6–15 × 1.8–2.2 µm (near base –2.6 µm); frequently di- or trichotomously branched at apex. **Medullary excipulum** not examined. **Ectal excipulum** hyaline, at base of irregular textura angularis 40 µm thick, at lower and mid flanks 15–20 µm thick, of (?)thin-walled, horizontal t. prismatica; at margin 15 µm thick. **Anchoring hyphae** sparse, *4–6 µm wide, walls *0.2–0.5 µm thick. **VBs** present in paraphyses (in all cells but a little more dense in upper cells) and in marginal cortical cells, globose, 0.2–0.5(–1) µm diam., strongly refractive, abundant (multiguttulate), often trembling. **Exudate** over paraphyses absent; at flanks continuous, yellowish-brass-coloured. **— ANAMORPH**: unknown.

Habitat: ~0.5 m above the ground, on corticated, 9 mm thick branch of *Pinus edulis*, on strongly decayed bark (periderm), greyed, covered by green algae, not associated with resin. **Associated**: ?*Venturia* sp., remotely with *Orbilia macroasca*. **Desiccation tolerance**: fully tolerant for at least 2.5 months. **Altitude**: 1815 m. **Geology**: Upper Cretaceous sedimentary rock. **Phenology**: VIII.

Taxonomic remarks. *Amphosoma macrosporum* is closely related to *A. resinicola*, from which it differs in much larger asci and ascospores, and in the latter being more cylindrical and becoming 1–3-septate when overmature.

Ecology. The species is only known from the holotype collection. It grew on rotten bark of a dead xeric branch of *Pinus edulis*. Unlike the other two conifericolous species, *A. macrosporum* was not associated with resin. It was found in a dry riverbed in the cold-temperate subhumid pinyon-juniper woodland of the Dixie Forest (Utah Mountains, western North America).

Specimens included. **USA**: **Utah**, Utah Mts., Dixie Forest, ~1.5 km ESE of Cedar City, 1815 m, branch of *Pinus edulis*, on bark, 24.VIII.1994, G. Marson (ex H.B. 5181b; M-0276402, **holotype**).

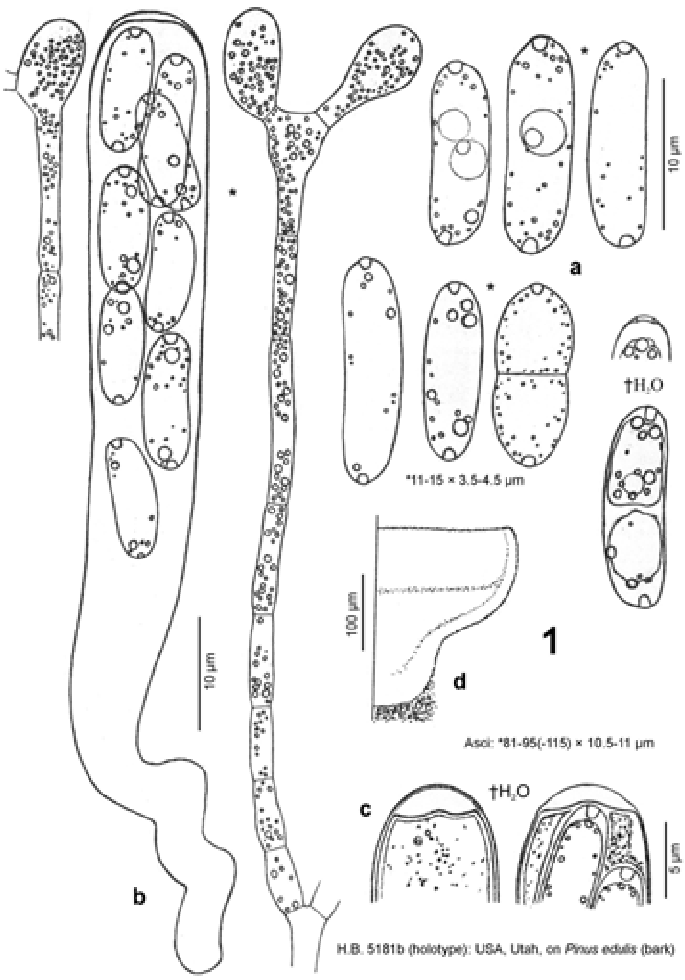


Plate 40. **1**: *Amphosoma macrosporum*. – **1a**. ascospores (lower right: spore bodies persistent in dead state, or spores with a polar pore); **1b**. ascus and paraphyses (containing VBs); 1c. ascus apices; **1d**. apothecium in median section.

Retiarius D.L. Olivier, Trans. Br. Mycol. Soc. 71: 193 (1978)

Type species: *R. superficiaris* D.L. Olivier (see p. 241)

Etymology: named after a Roman gladiator armed with a cast net (referring to the ability of the fungus to capture pollen).

Description (according to Olivier 1978 and Magyar et al. 2017a): — **TELEOMORPH**: unknown. — **ANAMORPH**: **Mycelial hyphae** †1.5–4 µm wide, hyaline. **Colonies** salmon or flesh-coloured, slow-growing (oatmeal agar, *R. superficiaris*, *R. bovicornutus*). **Conidiophores** integrated, reduced or sympodial, †1.5–5 up to 9–14 × 1.5–2.5 µm, conidia developing singly or also on lateral scars. **Conidia** multicellular, staurosporous, dichotomously branched, main axis (10–)13–30(–36) µm long [stipe (8–)10–27(–33) µm], 1–3-septate, either with consistently two arms (trinacrium-like), or with predominantly 3–4 arms (dwayaangam- or tripospermum-like), arms straight or slightly to medium curved upwards, 20–90 µm long. **Trapping hyphae**: capturing pollen grains by erect, attenuated, 12–35 µm long hyphae and by conidial arms.

Habitat: forming small colonies on adaxial surfaces of living leaves or on xeric bark of living branches and trunks of trees, parasitic on pollen grains of both gymno- and angiosperms.

Recognized species: *R. bovicornutus*, *R.* aff. *bovicornutus*, *R. goenczoelii*, *R. revayae*, *R.* aff. *revayae*, *R. superficiaris* (all without known teleomorph).

Taxonomic and ecological remarks. Olivier (1978) described the genus based on two species (*R. superficiaris* and *R. bovicornutus*) from South Africa growing on living leaves of *Eryobotrya japonica* and *Brabejum stellatifolium* on which they trap pollen. In her experiments, Olivier worked with pollen of *Pinus radiata*, but she did not mention whether pollen captured in the field was also from conifers. Magyar et al. (2017a) added two species from Hungary to the genus (*R. goenczoelii*, *R. revayae*), which grew on bark of living trees of *Platanus* and *Taxus* where they parasitize pollen grains of *Picea*, unidentified *Pinaceae*, but also *Tilia*.

Cultivation on artificial media was unsuccessful in *R. revayae* and *R. goenczoelii* (Magyar et al. 2017a). Olivier's two species (*R. superficiaris* and *R. bovicornutus*) were cultivated on oatmeal agar (OA).

During the present study, conidia similar to *R. bovicornutus* or *R. revayae* were found on different trees at several occasions, sometimes in association with pollen grains (Pl. 41–43, see also IVV).

Phylogeny. Magyar et al. (2017a, b) gained sequences (ITS, LSU) from Olivier's two ex-type cultures and from *R. revayae*. The S1506 intron region is not fully covered because the ITS1 primer was used (not the ITS1F as stated by Magyar et al.), but in the reverse direction the position of the intron is just reached in *R. bovicornutus* and *R. superficiaris*, and it seems that here the intron is present, unlike any other related taxon. In Magyar et al.'s Bayesian analyses of ITS+LSU the genus formed a strongly supported group that nested in the *Lilapila-Lecophagus-Amphosoma* clade sister to *Amphosoma*. In our ML analyses of SSU+ITS+LSU, ITS, and LSU (Phyls 2–4), the three species always clustered in a monophyletic clade, with high (SSU+ITS+LSU), low (LSU), or lacking support (ITS). *Retiarius* always nested in the *Lecophagus-Amphosoma* clade (see p. 253). The distance to *Lilapila* ranges around 20–26 % in the ITS region and 7.5–8.3 % in the LSU (D1–D3), but also within *Retiarius* it lies at 16.5–17.5 % in the ITS and 6–6.3 % in the LSU.

Specific nucleotide positions. *Retiarius* shows specific nucleotides in the region of the '*Orbiliales*-specific' primers (Smith & Jaffee 2009) (Tabs 18–19). In the primer Orb5.8s1F it concurs with *Lilapila*, *Amphosoma*, *Lecophagus*, *Vermispora* clade of *Hyalorbilia* etc., and in the primer Orb5.8s3F only with some of them. In the entire 5.8S region *R. bovicornutus* concurs with various environmental samples, including some which cluster in analyses of ITS or ITS+LSU in the *Amphosoma* clade (A1–A5). Two variants are observed in the primer Orb28s2R: *Retiarius* concurs here with various non-orbiliaceous ascomycetes, *R. superficiaris* and *R. bovicornutus* also with *Lecophagus* and some other orbiliaceous taxa, and *R. revayae* with *Amphosoma resinicola*. However, this primer region is badly sequenced in *Retiarius* and leaves some doubts about the correct motifs. In stem-loop B8 at 3'-end of 5.8S *R. superficiaris* and *R. revayae* concur with *Amphosoma* spp., whereas *R. bovicornutus* concurs with various uncultured clones related to *Amphosoma* (A1–A5) and deviates from the former by 2 nt. Some nucleotide positions in the LSU D3 domain separate *Retiarius* from *Amphosoma* (see p. 273).

Retiarius superficiaris D.L. Olivier, Trans. Br. mycol. Soc. 71: 194 (1978) — Pl. 20: a

Etymology: probably according to the superficial, epiphyllous growth.

Description of holotype (Olivier 1978, modified): Conidia 37–60 × 44–66 µm, (2–)3(–4)-armed; stipe (8–)10–15 × 4–4.5(–5.5) µm, tapering towards base, 1–2(–3)-septate; arms (20–)25–35(–45) × 4.5–6 µm, straight, tapering towards the ends, 4–7-septate.

Key to species of *Retiarius* (only anamorph known)

1. Conidia predominantly 3-armed, tripospermum-like, also 2- and 4-armed, arms straight, 20–45 × 4.5–6 µm, 4–7-septate; South Africa, on *Eriobotrya* leaves .... ***R. superficiaris***, p. 282
1. Conidia consistently 2-armed, trinacrium-like 2

2. Arms straight to flexuous, †42–90 × 2–2.5 µm, 5–8-septate, stipe 19–33 µm long; Hungary, on *Platanus* bark ..... ***R. goenczoelii***, p. 286
2. Arms curved upwards, up to 40–55 µm long 3

3. Arms (25–)30–45(–50) × 4–5.5 µm, stipe 12–25 × 3.5–5.5 µm, (1–)2–3-septate; South Africa, on *Brabejum* leaves (± similar records from Peru, Japan, and Europe on bark and leaves of angiosperms) .... ***R. bovicornutus***, p. 283
3. Arms and stipe narrower, 2–3.5(–4) µm wide 4

4. Arms †22–30 × 2–3(–3.5) µm, stipe †14–22 × 2–3.5 µm, 3–5(–7)-septate; Hungary, on *Taxus* bark (similar records from South Africa on bark of *Fabaceae*) .... ***R. revayae***, p. 285
4. Arms *33–70 × 3–3.5 µm, stipe * 20–24 × 3–4 µm, 2-septate; Luxembourg, on *Cytisus* and *Sambucus* .... ***R.* aff. *revayae***, p. 285

The 3-armed conidia resemble those of *Tripospermum*, the 4-armed conidia those of *Dwayaangam*, and the 2-armed conidia those of *Trinacrium*.

Specimens included. **SOUTH AFRICA**: **Western Cape**, 47 km S of Cape Town, 58 km SW of Stellenbosch, Cape of Good Hope, leaves of *Eriobotrya japonica*, parasitic on pollen, 15.IX.1974, D.L. Olivier (IMI 223459, **holotype**, doc. vid., sq.: KY352467).

Retiarius bovicornutus D.L. Olivier, Trans. Br. mycol. Soc. 71: 195 (1978) (Pls 20: b; 41–42; 43: 5)

Etymology: after the conidial arms resembling horns of cows.

Description of holotype (Olivier 1978, modified): Conidia 47–50 × 45–55 µm, 2-armed; stipe (12–)15–20(–25) × 3.5–4.5(–5.5) µm (in situ), tapering towards base, (1–)2–3-septate; arms (25–)30–45(–50) × 4–5 µm, curved upwards, tapering towards ends, (2–)4–5-septate.

Taxonomic remarks. The conidia of *R. bovicornutus* resemble those of *Trinacrium*, but deviate from typical members of that genus in the two arms being curved upwards. We have seen several records of conidia with upwards curved arms which appear to belong in the relationship of *R. bovicornutus*: one from Germany on wood of *Salix* (Pl. 43: 5) shows a strong resemblance in conidial shape (arms *30–32 × 5–5.5 µm, total size *38 × 43 µm) and appears to be conspecific.

Not included collections. A British sample on living leaves of *Rhododendron* with infected *Pinaceae* pollen (Pl. 42: 1) deviates from the type mainly in slightly longer arms (*45–55 × 5–6 µm, total size *52–60 × 65–86 µm) and a narrower, more cylindrical stipe. Also two samples from Luxembourg on branches of *Clematis* (Pl. 42: 2) and *Salix* (Pl. 41: 1) are very similar to *R. bovicornutus* but resemble the British sample in the stipe. The latter sample consisted of only one incomplete conidium having captured a pollen grain of probably *Salix*. Two samples from France on branches of *Pinus* deviate among another: in Pl. 42: 3 conidia are similiar to *R. bovicornutus* but insufficiently documented, whereas in Pl. 41: 2 they concur rather well, including a basally tapered stipe. A sample from Luxembourg on *Robinia* bark (Pl. 43: 4) showed distinctly smaller conidia (total size *27–31 × 27–29 µm, arms *15–17 × 4–4.5 µm) which, however, closely concur with *R. bovicornutus* in shape.

Ando & Tubaki (1984c, 2005) described a collection under the name *R. bovicornutus* from Japan (in rainwater draining from *Pinus*, total size 36–44 × 27–56 µm, arms 20–33.5 × 3.5–5.2 µm), and Matsushima (1993) one from Peru (on decaying palm petioles, total size 19–35 × 25–50 µm, arms 12–27 × 4–5 µm). Particularly in the latter sample the conidial arms are reported distinctly shorter than in the type.

Specimens included. **SOUTH AFRICA**: **Western Cape**, 47 km S of Cape Town, 58 km SW of Stellenbosch, Cape of Good Hope, leaves of *Brabejum stellatifolium*, parasitic on pollen, 30.VIII.1976, D.L. Olivier (IMI 223460, **holotype**, doc. vid., sq.: KY352466). — **GERMANY**: **Bayern**, **Oberbayern**, Kocheler Berge, 6.5 km WSW of Lenggries, NW of Latschenkopfhütte, S of Vorderer Kirchstein, 1600 m, branch of *Salix caprea*, on wood, 21.VI.2005, P. Karasch & B. Fellmann (H.B. 7830b ø, anam. only).

Not included. ***Retiarius* cf. *bovicornutus***: **GREAT BRITAIN**: **Yorkshire**, **South Yorkshire**, Barnsley, Wentworth Castle, *Rhododendron* leaves, on *Pinus* pollen, 175 m, 26.VI.2016, C. Yeates (CSVY/F/2698, anam. only). — **LUXEMBOURG**: unlocalized, branch of *Clematis vitalba*, 4.I.2014, G. Marson (ø, anam. only). – **Gutland**, 1.5 km SW of Cessange, Bois de Cessange, 305 m,

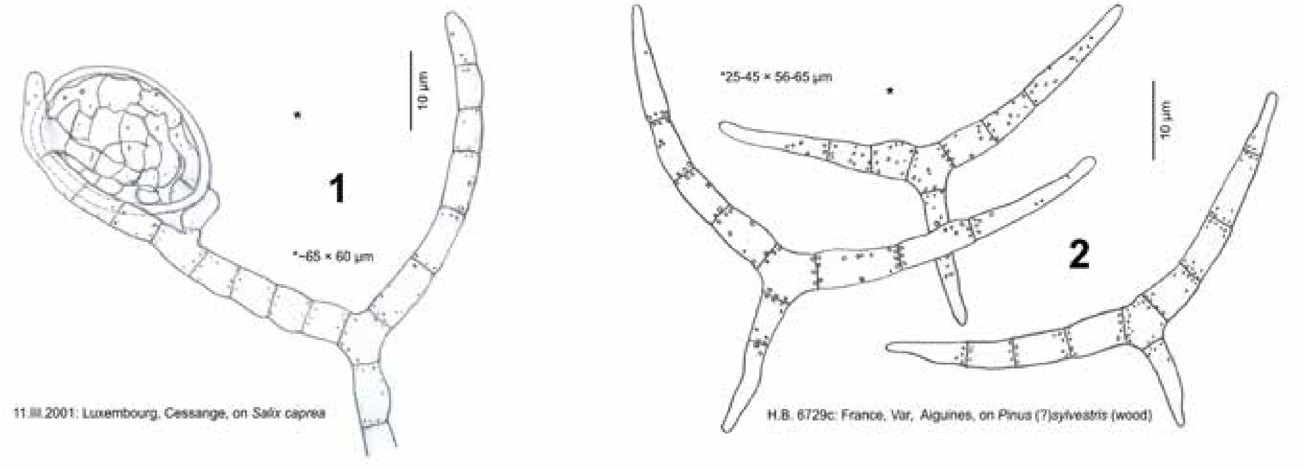


Plate 41. **1–2**: *Retiarius* cf. *bovicornutus*. – Conidia from natural substrate.

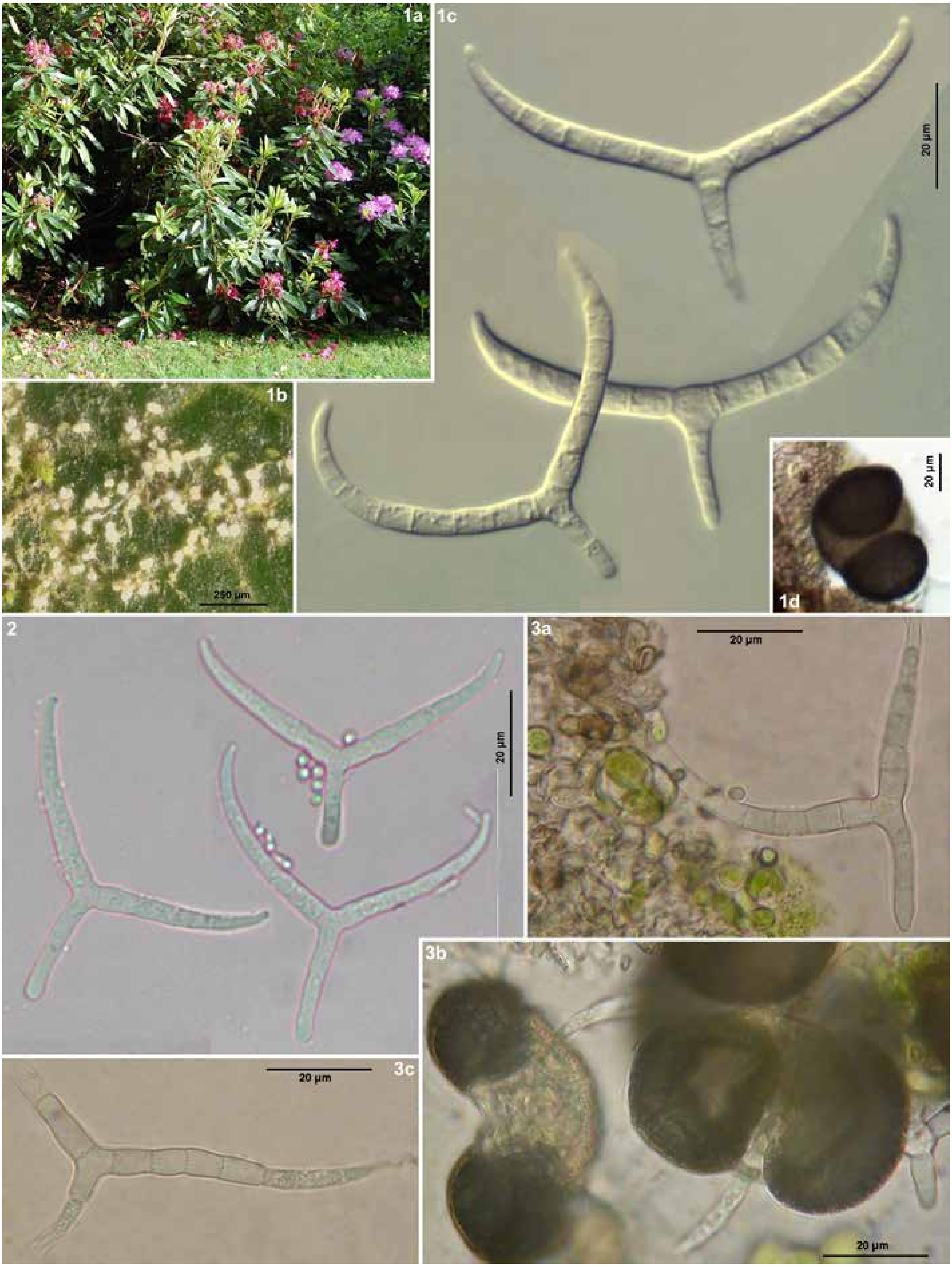


Plate 42. **1–3**: *Retiarius* cf. *bovicornutus*. – **1a**. *Rhododendron* shrubs in a park; **1b**, **d**. *Pinus* pollen grains in fungal mesh on the upper side of a *Rhododendron* leaf; **3b**. *Pinus* pollen grains with *Retiarius* conidia; **1c**, **2**, **3a–c**: conidia from natural substrate. Living state. – **1a–d**: phot. C. Yeates. — **1a–d**. 26.VI.2016: Great Britain, Barnsley, on *Rhododendron*; **2**. 4.I.2014: Luxembourg, on *Clematis*; **3a–c**. H.B. 9173: France, Bedoin, on *Pinus*.

branch of *Salix caprea*, on ?*Salix* pollen, 11.III.2001, G. Marson (ø, anam. only). — **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Var**, Aiguines, branch of *Pinus sylvestris*, 5.VIII.1999, G. Marson (H.B. 6729c ø, anam. only). – **Vaucluse**, 9.5 km NE of Bedoin, 1.5 km NW of Mt. Ventoux summit, Mt. Serein, 1385 m, branches of *P. sylvestris*, on wood and *Pinus* pollen, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (mixtum in *Orbilia subvinosa* H.B. 9173b, anam. only). ***Retiarius* aff. *bovicornutus***: **LUXEMBOURG**: **Gutland**, 0.5 km W of Echternach, Troosknеppchen, 220 m, trunk of *Robinia pseudoacacia*, on bark, 6.VI.2004, G. Marson (ø, anam. only). — **PERU**: **Madre de Dios**, Tambopata, petioles of a palm, V.1989, T. Matsushima (MFC-9P086). — **JAPAN**: **Honshu**, **Ibaraki**, campus of University of Tsukuba, rainwater draining from *Pinus densiflora*, 27.X.1983, K. Ando (TKB-C-1298).

Retiarius revayae D. Magyar & Z. Merényi, Nova Hedwigia 105(3–4): 413 (2017) — Pl. 20: c, Pl. 43: 2–3

Etymology: in honour of Ágnes Révay, Hungarian mycologist on staurosporous fungi.

Description of holotype (Magyar et al. 2017a, modified): Conidia †26–40 × 32–48 µm (in situ), 2-armed; stipe †14–22 × 2–3.5 µm, cylindrical, tapered only at very base, 3–5(–7)-septate; arms †22–30 × 2–3(–3.5) µm, curved upwards, tapering towards ends, (3–)4–7-septate.

Taxonomic remarks. The conidia of *R. revayae* resemble those of *R. bovicornutus* but differ in narrower arms and in longer stipes with more septa, a combination which does not fit any of our samples, except for two from South Africa, each with only one observed conidium (Pl. 43: 2–3).

Not included collections. The two South African samples have rather long and narrow, ~3-septate stipes of 15–30 × 3 µm and could be conspecific with *R. revayae*. Magyar et al. (2017a) gave the arms as 22–38 × 2–4 µm, but the figured conidia do not attain that size, even when including the curvature.

Gönczöl & Révay (2004: fig. 11, Révay & Gönczöl (2010: figs 2–4, 2011: figs 1–8) reported conidia under the name *R. bovicornutus* which they observed in 85 % of the bark samples of twigs attached to various living trees in Hungary and Sweden. In Magyar et al.'s (2017a, pers. comm.) opinion, however, figs 3–4 in Révay & Gönczöl (2010) and figs 3–4 in Révay & Gönczöl (2011) belong to *R. revayae* and the fourth conidium from left in Gönczöl & Révay (2004) represents typical *R. revayae*, whereas, e. g., the third conidium from left seems to be of uncertain identity because of much too wide arms (~5 µm), and Révay & Gönczöl (2011: fig. 1) concerns *R. goenczoelii*.

An unlocalized sample on *Cytisus* (Pl. 43: 1) deviates in distinctly narrower arms and stipes and resemble *R. revayae* except for the short, 2-septate stipes which are more reminiscent of *R. bovicornutus*. In their total size (*50–75 × 50–76 µm, arms *33–70 × 3–3.5 µm) these conidia exceed the types of *R. bovicornutus* and *R. revayae*.

Specimens included. **HUNGARY**: **Pest**, Budapest, 110 m, trunk of *Taxus baccata*, on bark, parasitic on pollen of *Pinaceae* and *Tilia*, 7.I.2014, D. Magyar (BP 108633, **holotype**, doc. vid., sq.: KY352465). – ibid., 23.I.2014 (KMD174/5).

Not included. ***Retiarius* cf. *revayae***: **SOUTH AFRICA**: **KwaZulu-Natal**, 210 km NE of Durban, 55 km NE of Richards Bay, 1 km SE of Santa Lucia, St. Lucia Estuary, Sugarloaf Rest Camp, 10 m, branch of indet. angiosperm (?*Pterocarpus*), on bark, 25.II.2006, V. Kummer (mixture with *Amphosoma natalense*, ex H.B.

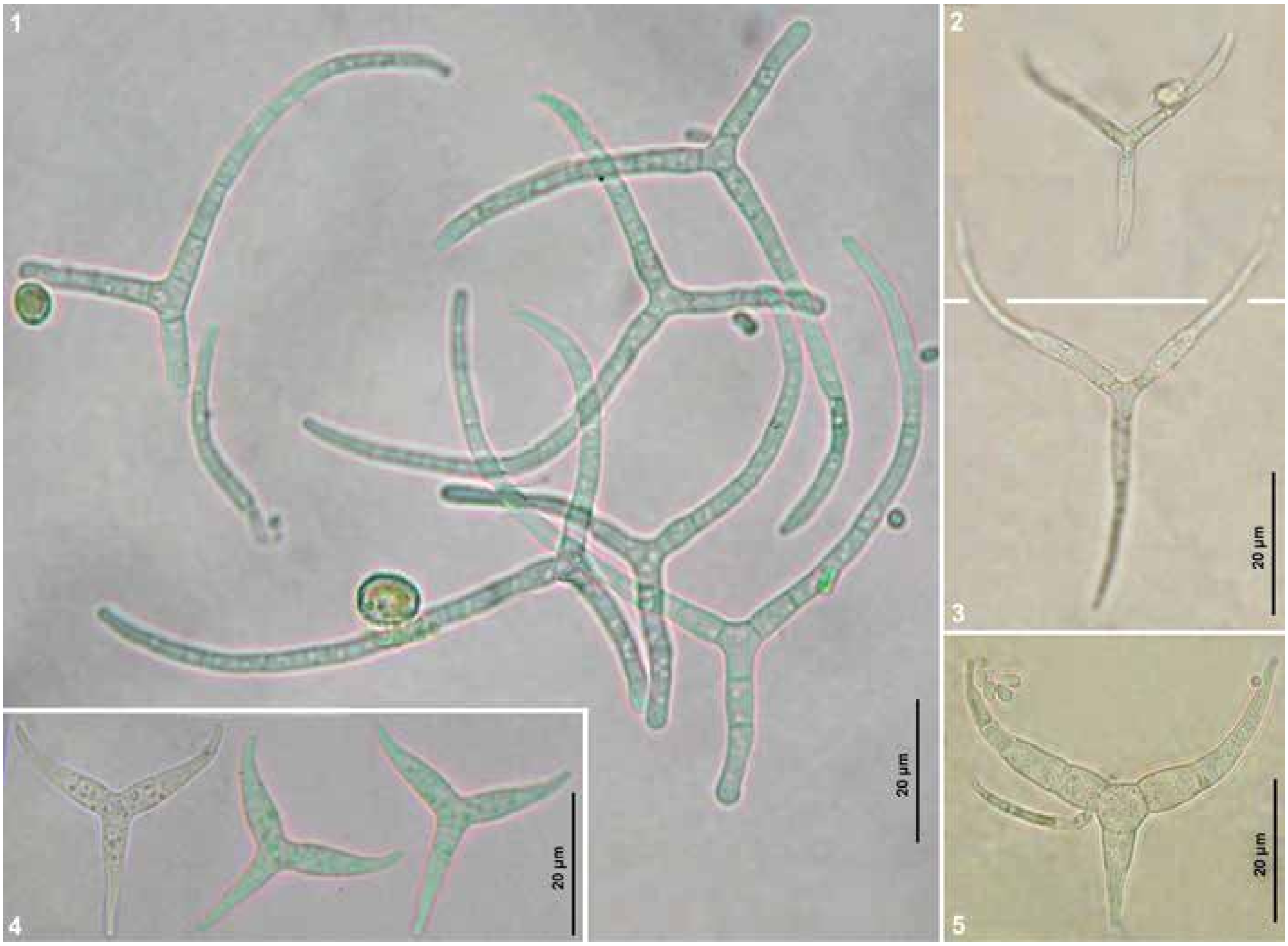


Plate 43. **1**: *Retiarius* aff. *revayae*; **2–3**: *R.* cf. *revayae*; **4**. *R.* aff. *bovicornutus*; **5**. *R. bovicornutus*. – Conidia from natural substrate. Living state but conidia in **3** and **5** with some dead cells, **2** in dead state. — **1**. Luxembourg, on *Cytisus*; **2**. H.B. 8086: South Africa, KwaZulu-Natal, St. Lucia, on ?*Pterocarpus*; **3**. H.B. 8087: South Africa, Mpumalanga, Drakensberg, on ?*Vachellia*; **4**. 6.VI.2004: Luxembourg, on *Robinia*; **5**. H.B. 7830b: Germany, Bayern, Lenggries, on *Salix*.

8086a, M-0276403, anam. only). – **Mpumalanga**, Drakensberg Mts., 12 km SSE of Mbombela (Nelspruit), NE of Umhloti Lodge, 1106 m, branch of ?*Vachellia*, on bark, 16.II.2006, V. Kummer (H.B. 8087 ø, anam. only).

Retiarius* aff. *revayae: **LUXEMBOURG**: unlocalized, branch of *Cytisus scoparius*, ?V.2002, G. Marson (ø, anam. only). – unlocalized, branch of *Sambucus nigra*, ?XII.2002, G. Marson (ø, anam. only)

Retiarius goenczoelii D. Magyar, in Magyar et al., Nova Hedwigia 105(3–4): 416 (2017) — Pl. 20: d

Etymology: in honour of János Gönczöl, Hungarian researcher on canopy fungi.

Description of holotype (Magyar et al. 2017a, modified): Conidia †37–70 × 100–150 µm, 2-armed; stipe †19–33 × 1.7–2.5(–3) µm, cylindrical, often constricted at base, (2–)3(–5)-septate; arms †42–90 × 2–2.5 µm, straight to ± flexuous, slightly tapering towards ends, 5–7(–8)-septate.

The conidia of *R. goenczoelii* have long and thin, straight to ± flexuous arms, and the stipe has a foot-like basal swelling due to a subbasal constriction. Unfortunately, this species is without sequence data, therefore, its affiliation in *Retiarius* is not assured.

Specimens included. **HUNGARY**: **Pest**, Budapest, 110 m, trunk of *Platanus* × *acerifolia*, on bark, parasitic on pollen of *Pinaceae* etc., 14.V.2014, D. Magyar (BP 105173, **holotype**, doc. vid.). – ibid., 23.I.2014 (KMD07/36).

Mycoceros D. Magyar & Merényi, in Magyar et al., Mycol. Prog. 17(1–2): 36 (2017),

Type species: *Mycoceros antennatissimus*

Etymology: referring to the shape of the conidia resembling horns.

Recognized species: *M. antennatissimus* (without known teleomorph).

Mycoceros antennatissimus D. Magyar, in Magyar et al., Mycol. Progr. 17(1–2): 37 (2017) — see p. 239–240 and Pl. 44

Etymology: referring to the multibranched shape of the conidia.

Description of genus and species (according to Magyar et al. 2017b): — **TELEOMORPH**: unknown. **— ANAMORPH**: **Mycelial hyphae** †1.2–2.5 µm wide, hyaline. **Cultivation** on artificial media unsuccessful. **Conidiophores** integrated, reduced, †~2 × 2 µm. **Conidia** multicellular, staurosporous by repeated dichotomous branching, ~55–90 × 70–190 µm, stipe †2–4(–8.5) × 2–3 µm, non-septate, primary arms 1(–3)-septate, straight, secondary arms 1–4-septate or sometimes higher-septate when without tertiary arms, tertiary arms 1–6-septate, secondary and tertiary arms straight, or flexuous when getting longer. **Trapping organs**: capturing pollen grains by erect, attenuated, 20–135 µm long hyphae or conidial arms (assumed).

Habitat: forming small colonies on bark of living trees, parasitizing pollen grains.

Taxonomic remarks. Magyar et al. (2017b) proposed the new genus for a single species from Hungary. In its staurosporous conidia and mode of life, *Mycoceros* (Pl. 18) resembles the genus *Retiarius* (Pl. 20). However, trinacrium-like conidia were not observed, and those lacking tertiary arms recall the genus *Dwayaangam*, e.g. the presumed anamorph of *Orbilia arachnovinosa* (Pl. 269), from which they differ in the relative length of the conidial main axis and its branches: in *Mycoceros* the main axis is much shorter than the primary branches, whereas in dwayaangam-like conidia of *Retiarius* and *Orbilia* the primary branches are much shorter than the main axis. Moreover, the conidia of *Mycoceros* are 3-dimensional regarding their secondary and tertiary arms.

The protologue gives the conidial stipes as 0(–2)-septate, but all illustrated conidia have no septa, including that of 8.5 µm length (Magyar et al. 2017b: fig. 2g).

Phylogeny. The genus *Mycoceros* was mainly erected for molecular reasons. Magyar et al. (2017b) gained four sequences from four individual conidia, ITS from two and LSU from two (the S1506 intron is absent). In their phylogenetic analysis, *Mycoceros* clustered with support within the *Orbiliomycetes* as a basal sister clade to all other genera. In our combined ML analysis, however, *Mycoceros* nested with low support as a sister group to the *Lecophagus*-*Amphosoma* clade (Phyl. 2). The genus shows a high distance to any other taxon, the lowest in the ITS region being 23–26 % to *Lilapila* (LSU D1–D3: 9.3–9.8 %) and 27–31 % to *Retiarius* (LSU D1–D3: 10.8–11 %).

Specific nucleotide positions. *Mycoceros* concurs in the region of the '*Orbiliales*-specific' primers (Smith & Jaffee 2009) with some other orbiliaceous taxa: in Orb**5.8s**3F with *Lilapila* and the majority of *Orbilia* (Tab. 18), and in Orb**28s**2R with

Plate 44. **1**: *Mycoceros antennatissimus*. – Conidia from natural substrate, living state. – Unlocalized (Europe), host unknown

Lilapila oculispora and two species of *Orbilia* (Tab. 19). In the primer Orb**5.8s**1F, however, *Mycoceros* deviates at one position (pos. 56, T vs. C) from all other orbiliaceous taxa, except for one uncultured basal *Orbiliomycetes* (KY687855, U3). In comparison with non-orbiliaceous fungi, *Mycoceros* concurs in two of these primers (Orb**5.8s**1F, Orb**28s**2R) with various other ascomycetes, in Orb**5.8s**1F also with basidiomycetes, whereas in Orb**5.8s**3F only a few ascomycetous yeasts and basidiomycetes concur (Tab. 18). In stem-loop B8 of 5.8S (pos. 117–138) *Mycoceros* matches *Lilapila* and some *Hyalorbilia* spp. (Tab. 18). A remarkable deviation is observed at the border between SSU and ITS1: in *Mycoceros* it is **ATCATT–**GAAA, whereas in *Retiarius* it is **ATCATTA**GAAA and in *Lilapila* and *Amphosoma* p.p. **ATCATTA**AAAA. Characteristic positions occur in the LSU: for instance, in the D1 domain pos. 80 is TTGCC**C**CAGTA, whereas all other *Orbiliomycetes* have **T**, and pos. 332 and 346 are **G**GAGACCGATAGCG**A** vs. **A**GAGACCGATAGCG**C** or **G**GAGACCGATAGCG**C** in any other *Orbiliomycetes*.

Ecology. *M. antennatissimus* was detected on xeric bark of living *Elaeagnus*, *Platanus*, and *Taxus* where it parasitizes *Pinaceae* pollen grains. During the present study, young 4–6-armed conidia of *Mycoceros* cf. *antennatissimus* formed on hyphae emerging from conifer and other pollen were found in a sample from cold-temperate, semiarid western USA (IVV: 15.VI.1996). Similar mature 4-armed conidia were observed in a European sample without known location (?Luxembourg), substrate, or association with pollen, which morphologically fits *M. antennatissimus* (Pl. 44).

Specimens included (all parasitic on pollen of *Pinaceae*): **HUNGARY**: **Pest**, Budapest, 110 m, trunk of *Platanus* × *acerifolia*, on bark, 6.V.2014, D. Magyar (BP 105172, **holotype**, doc. vid.). – ibid., 9.V.2011 (KMD07/4). – ibid., 12.V.2011 (KMD07/5). – ibid., 6.V.2016 (KMD07/7b). – ibid., trunk of *Elaeagnus angustifolia*, on bark, 10.IV.2007 (KMD07/2). – ibid., *Taxus baccata*, on bark, V.2010, D. Magyar (ø). – ibid., 29.II.2016, D. Magyar (ø). – **?Luxembourg**: unlocalized, substrate not noted, ?V.–VI.2002, G Marson.

Not included. **USA**: **Colorado**, ~5 km S of Great Sand Dunes, ~2430 m, branches of *Fallugia paradoxa*, on bark and wood, 15.VI.1996, G. Marson.

Lecophagus M.W. Dick, Mycol. Res. 94: 351 (1990),

Type species: *L. fasciculatus* M.W. Dick [= *L. muscicola* (G.L. Barron et al.) Tanabe et al.]

Etymology: referring to the capture of rotifers of the genus *Lecane*.

Emended diagnosis: **TELEOMORPH**: **Apothecia** minute, white, sessile to short-stipitate, margin smooth. **Asci** arising from croziers or simple septa, never furcate, apex hemispherical with a small lens-shaped wall thickening, 8-spored. **Ascospores** ellipsoid to subglobose, with a globose to broadly tear-shaped spore body attached to the spore apex by a short, thin or thick connecting part. **Paraphyses** simple, not or slightly inflated above, straight or sometimes curved. **Ectal excipulum** of indistinctly horizontally oriented textura angularis, cells near base *8–35 × 7–28 µm. **Anchoring hyphae** *5–17 µm wide. **Exudate** absent. — **ANAMORPH**: **Conidiophores** short and thick, unbranched. **Conidia** formed synchronously and terminally in a fascicle, large, slightly to strongly curved (C-shaped), multiseptate. **Trapping organs**: adhesive pegs for capturing rotifers and tardigrades, also adhesive knobs for capturing nematodes. — **SCBs**: All types of vegetative cells of both teleomorph and anamorph containing small, refractive, globose to cubical (crystalloid) bodies in their centre.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.08–0.25 mm diam., 0.07–0.16 mm thick, white throughout, glassy translucent, non-gelatinous; disc flat, margin thin, not protruding, exterior glabrous; subsessile or often with a short stipe, superficial. **Asci** *29–68 × 6.5–9.5 µm, †26–48 × 5.5–8 µm, turgescent asci ± equalling the paraphyses, 8-spored, spores uni- to biseriate inside living asci, some of the spores usually inversely oriented (often oblique or in lateral direction); **apex** (†) ± hemispherical to slightly mammiform irrespective of the viewing direction, with distinct, small, lens-shaped dome 0.8–1.4 µm thick, without apical chamber; **base** with ± short and thick stalk, arising from croziers (some with small perforation) or simple septa, never furcate. **Ascospores** *3.8–8 × 3–4.6 µm, non-septate, smooth, ellipsoid to subglobose; **SBs** apically attached to spore wall, 1.5–2 × 0.9–1.8 µm, strongly refractive, (sub)globose (to broadly tear-shaped), apically ± abruptly narrowed to a short, ± thick filum 0.2–0.8 × (0.1–)0.15–0.25 µm. **Paraphyses** apically uninflated or sometimes slightly clavate, straight or slightly to strongly curved, *2.5–7 µm wide, ± equidistantly septate but terminal cells sometimes 2–5 × longer than lower cells, never branched at upper septum. **Medullary excipulum** of dense textura angularis with indistinct orientation, without intermingled hyphae, very indistinctly delimited. **Ectal excipulum** of indistinctly horizontally oriented t. (prismatica-)angularis(-globulosa), (*) thin- to slightly thick-walled (common walls 0.3–0.8 µm thick), cells near base *(8–)10–20(–35) × (7–)9–18(–28) µm, at mid flanks and margin of horizontally oriented t. prismatica-angularis, marginal cortical cells *7–10 µm wide, wall †0.3–3 µm thick, refractive, **glassy processes** and **hairs** absent. **Anchoring hyphae** restricted to base, *(5–)6–13(–17) µm wide, densely septate, often ± constricted at septa, wall *0.2–0.3 µm thick, smooth. **SCBs** refractive, hyaline, cubical to almost globose, 0.4–2 µm diam., present in most vegetative cells, usually in centre of cell, rarely near the septa, accompanied by a few to many minute hyaline **LBs** (carotenoids absent); **WBs** close to septal pores minute (~0.1–0.3 µm diam), globose, rarely seen. **Exudate** absent, **gel** only present as a thin layer on the cell walls, staining distinctly lilac in CRB (but almost negative for ascus wall), paraphyses and asci easily separable. — **ANAMORPH**: **Mycelial hyphae** *(4–)6–9(–11) µm wide, hyaline. **Colonies** slow-growing, greyish to brownish, with aerial mycelium; *L. navicularis* (see also below). **Conidiophores** */†(11–)15–30(–45) × (3.5–)5–7 or 7–14 µm, unicellular, unbranched, cylindrical to slightly capitate above, also clavate or dumbbell-shaped, conidiogenous loci inconspicuous, not protruding, 1–30 conidia synchronously formed at apex in a fascicle. **Conidia** */†28–228 × 6–15(–18) µm, slightly falcate to canoe-shaped, 3–11-septate. **Trapping organs for rotifers and tardigrades**: cylindrical to lageniform adhesive pegs, often with a small, slightly enlarged globose head, unicellular, */†10–24 × 3.5–12 µm, covered by a very thin adhesive gel, entire peg surface staining lilac in CRB; **for nematodes**: sessile globose adhesive knobs. Small refractive cubical **SCBs** occurring in all cells of anamorph. **Chlamydospores** observed in *L. vermicola*.

Habitat: teleomorph on xeric, ± decayed bark and wood of living or dead branches and trunks of angiosperm trees and shrubs, also on gymnosperms in association with resinous wounds; anamorph growing aquatic, in lakes or water-filled treeholes, hygric in soil, manure and moss, or on xeric bark and wood. **Desiccation tolerance**: mature asci survive for a few weeks or over 3 months, mycelial hyphae at least 4 months, conidia at least 2 weeks. **Distribution**: rare, though probably worldwide, in humid to semihumid, hemiboreal to submediterranean areas.

Recognized species: *L. ellipsoideus*, *L. longisporus**, *L. muscicola**, *L. navicularis**, *L. pini*, *L. subglobosus*, *L. vermicola** (* = without known teleomorph).

Taxonomy of teleomorph. The genus *Lecophagus* is characterized by tiny, white, subsessile apothecia, 8-spored asci with short and thick, non-furcate stalks arising either from a simple septum or a crozier, ellipsoid to subglobose spores with a single (sub)globose spore body at one end being attached to the spore wall by a short, rod-like connecting part (filum), and by angular excipular cells and a similarly constructed, hardly delimited medullary excipulum. The genus differs from others of the class in asci with hemispherical to submammiform apices and lens-shaped apical thickenings (dead state, the shape of apex does not depend on the viewing direction), extraordinarily wide anchoring hyphae, characteristic cubical SCBs in anchoring hyphae, ectal and medullary excipulum, and paraphyses, and the capability to capture rotifers and tardigrades, or nematodes.

The cubical SCBs are a characteristic trait of the living vegetative cells of *Lecophagus*. They also occur in the anamorph (see Fig. 89a–e), and have so far not been observed by us in any other genus of the *Orbiliomycetes*, nor in any other class of *Ascomycota*. We classify these cytoplasmic inclusions in the category SCBs because they disappear in KOH and are not stained in CRB. Judging from their crystalloid shape and small size, they might derive from Woronin bodies.

Delimitation from other genera. The ascospores and SBs of *Lecophagus* strongly resemble those of *Orbilia* section *Ovoideae*, but all the other features mentioned above suggest that *Lecophagus* is not closely related to this group, which is confirmed by molecular data. The genus *Hyalorbilia* might be related to *Lecophagus* owing to its hemispherical ascus apices, presence of croziers, and often comparatively wide anchoring hyphae. Species of *Lecophagus* resemble particularly *H. erythrostigma* and similar taxa with broadly ellipsoid but smaller spores. Even a possible connection to a rotifer was observed in a single species of *Hyalorbilia* (see below). However, *Hyalorbilia* differs from *Lecophagus* in the presence of VBs in the living paraphyses, and in the hymenial elements being conglutinated in gel and covered by a thin exudate, also in the absence of cubical SCBs in the anchoring hyphae. Very similar but more or less globose SCBs occur in the living conidia of *Hyalorbilia* and sometimes also in the excipular cells (see, e.g., Pl. 92: 1d, 2e, 3g), and might be homologous to the cubical SCBs in *Lecophagus* (see p. 94–95).

Anamorph (see p. 237–239). Four of the seven accepted *Lecophagus* spp. are only known from their anamorph and two only from the teleomorph. Only for *L. ellipsoideus* both morphs have been observed so far, and only on the natural substrate by emerging from common hyphae.

In *L. navicularis* slow-growing greyish to brownish colonies on PDA were reported by Tzean & Barron (1983), whereas in *L. vermicola* cultivation was unsuccessful (Magyar et al. 2016). Strains of *L. longisporus* (type strain, CBS) and *L. muscicola* (ATCC) exist in culture collections (CBS and ATCC), but no information on colony characteristics was available to us.

The genus *Lecophagus* is named after the capability to prey on rotifers, although tardigrades are likewise captured, whereas a recently described species (*L. vermicola*) traps nematodes. The five known species with anamorph are very similar in their short conidiophores that form large curved phragmoconidia, while they differ in their adhesive pegs (see Fig. 105, Pl. 16). The broad mycelial hyphae resemble the anchoring hyphae of the known teleomorphs not only in their extraordinary width, but also in containing the same cubical SCBs, as can be seen on light micrographs of Tzean & Barron (1983, figs 1–2), Barron et al. (1990, figs 13, 18), Morikawa et al. (1993, fig. 11), and in populations of the anamorphs studied by us (Pl. 47: 2c–h; Pl. 51: 1g, k–m, o; Pl. 52: 1–6). They are also seen in the genus *Haptocara* (Pl. 53: 1–2).

Contrary to the above-mentioned LM observations, TEM micrographs do not always clearly show cubical SCBs. Morikawa et al. (l.c.: figs 2, 7–8) stressed the abundant occurrence of electron-dense vesicles mainly in the upper part of adhesive pegs, but also in the cytoplasm of the hyphae. Groups of small refractive granules are visible under the LM in the apices of living adhesive pegs (Pls 51: 1g,), but it seems that only some of the many electron-dense vesicles seen with the TEM correspond to these refractive granules. Also in *Zoophagus insidians* (*Zoopagales*) Morikawa et al. (1993) reported electron-dense, ± globose vesicles. Yet, crystalloid electron-dense 'vacuoles' reported in *L. muscicola* (erroneously as *Zoophagus insidians*) by Powell et al. (1990, figs 16, 21; see Fig. 89e) appear to represent cubical SCBs.

Based upon the mentioned morphological similarities and the adaptation to rotifers and nematodes, together with molecular results about the relationship of *Lecophagus* with the *Orbiliaceae* (Tanabe et al. 1999, see also p. 239), we conclude that anamorph-typified species recognized in *Lecophagus* and the here reported teleomorphs belong to one genus. The observation by D. Magyar (pers. comm.) and G. Marson of adhesive pegs on broad mycelial hyphae emerging from apothecia of *L. ellipsoideus* (Pl. 46: 2) supported this hypothesis. The occurrence of apothecia and adhesive pegs of *L. ellipsoideus* on xeric bark corresponds to the desiccation tolerance observed by us in *L. muscicola* collected on *Elodea* in an ephemeral pond.

A sequence taken from apothecia of *L. ellipsoideus* confirmed a close relationship to sequenced anamorphs of *Lecophagus*. Therefore, we here adopt the name *Lecophagus* for the holomorph of these fungi. However, a clear connection of a teleomorph-typified species to one of the known anamorph-typified species could not be established so far, particularly because the ascospores did not germinate on agar. Therefore, and because our sequence of *L. ellipsoideus* shows a high distance to *L. muscicola* and *L. longisporus*, we here erect new names for the three recognized teleomorph-typified species.

The genus *Haptocara* Drechsler (see below) is believed here to be closely related to *Lecophagus*, based on its broad hyphae, similar conidiophores and conidia, presence of cubical bodies, and the capability to trap invertebrates, but molecular data were not available. *Haptocara latirostrum* and a similar undescribed species of that genus resemble *L. vermicola* in having sessile adhesive knobs which are formed directly on the conidia (Pl. 53), but differ in a hyphal appendage at the terminal conidial cell. Like *L. vermicola*, *H. latirostrum* is known to trap nematodes instead of rotifers.

Adaptation to rotifers. In several collections of the teleomorph of *Lecophagus*, dead rotifer bodies being completely colonized by hyphae were found in very close proximity to apothecia (*L. ellipsoideus*, Pl. 45: 1d, 2e, IVV: collection on *Betula*, 27.IX.1999). The similarity between hyphae emerging from rotifers and anchoring hyphae emerging from apothecia leave no doubt that these mycelia represent a single fungus: the hyphae correspond not only in their unusual width, but also in the cubical SCBs in all cells of these hyphae. This clearly indicates that *L. ellipsoideus* is able to grow endoparasitically in rotifers, although in some other records of this species as well as in *L. pini* and *L. subglobosus* no trace of a rotifer could be discovered. The adaptation to rotifers seems quite unique within the *Orbiliomycetes*. Only in one collection of a *Hyalorbilia*, apothecia occurred in close association with an infected dead rotifer body (Pl. 145: 2). This rotifer contained distinctly narrower hyphae than known in *Lecophagus*, therefore, these hyphae appeared to be part of the closely associated apothecium, for which reason this species was named *H. rotifera*. Only a few further reports of exceptional rotifer capture other than by *Lecophagus* came to our notice (*Drechslerella bembicodes*, *Gamsylella gephyropaga*), and one case in which eggs of rotifers are infected (*Dwayaangam heterospora*) (see p. 214 ff.). In any case, the parasitic lifestyle of *Lecophagus* is not surprising within the *Orbiliomycetes*, and indicates that trapping capabilities are not restricted to species of *Orbilia* section *Arthrobotrys*.

In *L. ellipsoideus* we observed anchoring hyphae of one apothecium emerging from a single dead rotifer body. A direct connection from an infected rotifer to an apothecium could almost completely be traced in CRB by the selective lilac stain of the hyphal wall. The anchoring hyphae form a loose network within the algal layer and emerge from the rotifer body, which is more or less buried within this biofilm. The rotifer jaws (trophi) inside the pharynx are still clearly visible within the cadaver (Pl. 45: 1j–k, Pl. 46: 2c). The cuticle is either intact, though mostly somewhat crumpled or disintegrated. The cadaver is completely colonized by branched assimilative hyphae of the fungus.

The distance between apothecia and rotifers was 0–0.2 mm, and it seemed that each apothecium is formed by the digestion of a single rotifer body. This is suggested by a similar size of apothecia and dead rotifers, the latter measuring about 0.13–0.2 × 0.12–0.15 mm. Although the apothecia are seated on an algal mat over rotten parts of wood or bark, they appear to be formed predominantly by the consumption of the rotifer: the wide anchoring hyhae are few in number and, due to their width, they do not seem to be adapted to enter cells of woody substrate.

Trapping organs were rarely observed in collections from xeric substrate studied by us. Infection could instead have taken place by ingestion of ascospores, or the trapping organs and their supporting hyphae have disappeared during digestion of the rotifer body. The trapping of rotifers by adhesive pegs could be studied by us in the specimen of *L. muscicola* from a pond (Pl. 51). The wall surface of hyphae and adhesive pegs was here found to be covered by a thin gel layer that stains light lilac in CRB. This gel layer is not thicker at the peg apex. When a rotifer was captured, a hypha grows out from the apex of the adhesive peg, and the peg apex may get more distinctly capitate by increasing up to *6.8–7.3 µm in width. Several branches of assimilative hyphae finally colonize the rotifer body.

Phylogeny. Sequences from five strains of *Lecophagus* were available, three of which comprising SSU and five ITS and LSU. *L. ellipsoideus* and *L. vermicola* were sequenced by G. Marson from apothecia or conidia, respectively. The S1506 intron was consistently absent in all five strains. Some environmental samples from GenBank clustered in the genus and comprise mainly SSU or ITS+LSU (Phyl. 3, L1–L5).

Our molecular analyses confirm the results of Tanabe et al. (1999) who found *Lecophagus* to form a clade with orbiliaceous taxa here recognized in *Orbilia* section *Arthrobotrys*. However, a high distance in the LSU region is noted between *Lecophagus* and the genera *Hyalorbilia* and *Orbilia*, while a closer relationship to *Amphosoma*, *Retiarius*, *Lilapila*, and *Bryorbilia* can be recognized (Phyls 1–2, see also Magyar et al. 2016).

Based on our data, the genus *Lecophagus* forms a strongly supported clade (Phyls 2–4), which clustered within the *Lecophagus*-*Amphosoma* clade with strong support sister to the clade with *Amphosoma* and *Retiarius* (Phyl. 2), but with a high distance in the LSU (D1–D2) to the other included genera (5.2–7.2% to *Amphosoma*, 6.8–9.3% to *Retiarius*, 8.7–10.5% to *Lilapila*, and 11–12% to *Bryorbilia.* Also between the four sequenced *Lecophagus* species a distance of 2.2–3.1% is observed, in spite of their close morphological similarity.

Specific nucleotide positions. *Lecophagus* is characterized in the SSU V9 at pos. 227 by TGGC**C** vs. TGGC**T** in any other *Orbiliomycetes*. At pos. 258–259 and 266–267 (Tab. 60), a variable region which forms a loop by base pairing, *Lecophagus* and *Amphosoma* have AT+AT, whereas other orbiliaceous taxa mainly have TC+GA (*Lilapila*, *Bryorbilia*, *Orbilia*) or GG+CC (*Hyalorbilia*), rarely TT+GA or TT+AA. Also in stem-loop B8 near the 3'-end of 5.8S occur specific positions: pos. 119–120 is TC in *Lecophagus* instead of CT or CC in all other orbiliaceous taxa tested, and pos. 135–136 is GA instead of GG or AG, except for *D. haptotyla* which has also TC and GA but differs at 4–5 positions between 120 and 135 (see also Tab. 18). In the LSU D1–D2 three *Lecophagus*-specific motifs were found: pos. 168–170 GG**TTC**GGAC vs. **TTT**, **TTG**, **CAC** and other combinations, 242–243 TCTC**GT** vs. **TT**, **CT**, **CG**, **GA** and other combinations, and pos. 308 AAAT**G**TC vs. **T** (Tab. 58). A further nucleotide (pos. 396) is diagnostic for *Lecophagus*, *Hyalorbilia*, and *Microdochiella* (AAA**A**AGT), whereas the rest of *Orbiliomycetes* have mostly AAA**C**AGT or sometimes AAA**T**AGT (but never **A**).

In the region of the three '*Orbiliales*-specific' primers (Smith & Jaffee 2009), *Lecophagus* concurs with different other genera of *Orbiliomycetes* (Tabs 18–19). For primer Orb5.8s1F and Orb28s2R this is mainly *Amphosoma*, *Lilapila*, and *Retiarius*, for the former also *Bryorbilia* and the *Vermispora* clade of *Hyalorbilia*. In the primer region of Orb5.8s3F *Lecophagus vermicola* deviates from other *Lecophagus* spp.

Table 58. Specific nucleotides and motifs of *Lecophagus* in the 5.8S (stem-loop B8, see Tab. 18), ITS2, and LSU D1 of rDNA, in comparison with other basal genera and remaining *Orbiliomycetes* (*Hyalorbilia*, *Orbilia*). Position numbers starting with AAAACTTT (5.8S), after GAGCGTC (ITS2), and with TGACCT (LSU, here by omitting predominant gaps in alignment of all groups of *Orbiliomycetes*). Y = C or T, K = G or T, R = A or G. Numbers in brackets give number of species (* = *A. resinicola*, '*A. persooniae*', *A.* aff. *resinicola* G.M. 2015-09-15.2).

Taxa (n)	5.8S pos. 114–120	5.8S pos. 135–140	ITS2 pos. 1–11	LSU pos. 166–174	LSU pos. 238–246	LSU pos. 304–312
Lecophagus (4)	TGCGCTC	GAGCAT	AGTACACACCC	GGTTCGGAC	TCTCGTYCC	AAATGTCAT
Mycoceros (1)	TGCGCCT	AGGCAT	AGAACACATCT	GGTTTGGAC	TCTCTTTCC	AAATTTCAT
*Bryorbilia (*1)	TGCGCCT	AGGCAT	ATATCAC-TCT	GGTTGGGAT	TCTCCGGCT	AAATTTCAT
Lilapila (3)	TGCGCCT	AGGCAT	ATTACAAACCC	GGTTTGGAC	TCTCYTTCC	AAATTTCTT
Retiarius bovicornutus	TGCGCCT	GGGCAT	AGTACACACCT	GGCAGCGAC	TCTGCTGTC	AAATTTCAT
R. revayae	TGCGCCT	GGGCAT	AGTACACACCT	CGCACGGAC	TCTCGAGTC	AAATTTCAT
R. superficiaris	TGCGCCT	GGGCAT	AGTACACACCT	GGCACCGGC	CCTGGAGCT	AAATTTCAT
Amphosoma (3*)	TGCGCCT	GGGCAT	AGTACCCACTC	GGTTTGGAC	TCTCTTTCC	AAATTTCAT
A. atroolivaceum	TGCGCCT	GGGCAT	AGTACCAACTC	GGTTGGGAC	TCTCCTTCC	AAATTTCAT
remaining *Orbiliomycetes*	TGCGCCY	RGGCAY	diverse	diverse	diverse	AKATTYCAT

Ecology. Apothecia of *Lecophagus* have so far only been found on hanging, periodically dry woody substrates, and mostly in small quantities. They completely tolerate desiccation for over 3 months, and the mycelium for at least 4 months. Bdelloid rotifers on which *L. ellipsoideus* preys likewise live on these xeric substrates and similarly overcome drought in a cryptobiotic state of complete water loss. A few dormant, uninfected rotifers were observed on the branches in two of the collections. These individuals rapidly revived and started creeping after spraying with water (Pl. 45: 1l). They possess the very same trophi as those dead infected individuals, and appear to represent the same species.

Mycelia and conidia of *L. ellipsoideus* were observed on xeric substrate at several occasions, e.g., on still-attached bark of *Fagus* and *Platanus* (Pl. 47). Likewise, the so far purely anamorphic *L. vermicola* forms conidia on xeric substrate. This species was found to prey on nematodes which, like bdelloid rotifers, may live on xeric bark and survive drying (Magyar et al. 2016, see under *L. vermicola*, p. 299).

The remaining three accepted species of *Lecophagus* without a known teleomorph were isolated from environments that are continuously moist or wet for a much longer period of time (see p. 237–239). The here studied *L. muscicola* (Pl. 51) formed its adhesive pegs and conidia submerged under water in a pond where it captured a very different type of loricate planktonic rotifer of the ploimoid genus *Lecane*, but exceptionally also a bdelloid rotifer, possibly of the family *Philodinidae*. Mycelium and adhesive pegs in this collection were found to tolerate desiccation on the dry slide for at least 2 weeks, similar as in *L. ellipsoideus* and *L. vermicola*, although the rotifers, protozoans and algae in this aqueous sample did not survive for a single day in the dry state. This result could be explained in a way that the life cycle of *Lecophagus* encompasses an aquatic anamorphic and a terrestrial teleomorphic phase. However, in the here reported samples of teleomorphs of *Lecophagus*, no stagnant or running water was seen in the near surroundings, even after intense rainfalls. It appears, therefore, that only *L. muscicola*, *L. longisporus*, and *L. navicularis* are adapted to a semiaquatic habitat. Whether they are able to form apothecia is unknown.

Key to species of *Lecophagus* based on the teleomorph

1. Spores subglobose, *3.8–4.5(–5) × 3–3.7(–4) µm; paraphyses apically often uncinate; asci *29–39 µm long, arising from croziers, pars sporifera *15–18 µm long; bark of *Ulmus*, mesosubmediterranean (semi)humid, atlantic Europe .... ***L. subglobosus***, p. 296
1. Spores ellipsoid-ovoid, predominantly > 4.5 µm long; paraphyses straight or only sometimes curved at apex; asci *30–68 µm long, pars sporifera *20–40 µm long.. 2

2. SBs with a 0.3–0.8 µm long filum which is ~2–3× longer than wide; spores *(4–)4.5–6.5(–7.3) × (3–)3.3–4(–4.3) µm, ± biseriate within the living asci; asci arising from simple septa or croziers, *(30–)35–45(–55) µm long, pars sporifera *20–36 µm long; marginal cortical cells with †0.3–0.5 µm thick walls; paraphyses apically straight to curved, *3.3–4.5(–5) µm wide; bark & wood of angiosperms, temperate to orotemperate humid Europe .... ***L. ellipsoideus***, p. 291
2. SBs with a 0.2–0.4 µm long filum which is ~1.2–1.5× longer than wide; spores *5–6.3 × 4–4.6 µm, ± uniseriate within the living asci; asci arising from croziers, *45–68 µm long, pars sporifera *37–40 µm long; marginal cortical cells with †1–3 µm thick walls; paraphyses apically straight, *(3.5–)5–6(–7) µm wide; resinous bark of *Pinus*, orosub- to suprasubmediterranean (semi)humid Europe .... ***L. pini***, p. 295

Key to species of *Lecophagus* and *Haptocara* based on the anamorph

(adhesive peg width measured at their base, conidial length straight distance from end to end)

1. Trapping organs elongate cylindrical to conico-lageniform adhesive pegs, apex not or slightly inflated; conidiophores with 1–30 conidia; capturing rotifers and tardigrades in the mouth region..2
1. Trapping organs sessile (sub)globose adhesive knobs; conidiophores with 1–3 conidia; capturing nematodes by adhesion to the cuticle...5

2. Conidia *28–34 × 6–9 µm, (2–)3-septate, canoe-shaped, about 10–30 on each conidiophore; adhesive pegs ± conical, without inflated apex, formed on mycelium; from old manure in a cattle farm, temperate North America (Pl. 16: d) ....***L. navicularis***, p. 299
2. Conidia *73–228 µm long, 5–11-septate, ± falcate 3

3. Conidia *93–133 × 10.5–15.7 µm, 5–8-septate, ± strongly curved; adhesive pegs *20–30 × 7.5–11 µm, apically distinctly inflated; xeric bark & wood of angiosperms, temperate Europe (Pls 45–47)..***L. ellipsoideus***, p. 291
3. Conidia *73–228 × 6–11 µm, 7–11-septate, ± slightly curved; adhesive pegs *10–23 × 5.5–7.5 µm..4

4. Adhesive pegs *17–21 × 3.5–6.5 µm, apically distinctly inflated; conidia slightly curved at the ends, 73–200 × 6–12.5 µm (Pl. 16: a); from moss, soil, or aquatic plants, worldwide, temperate ....***L. muscicola***, p. 297
4. Adhesive pegs *(9–)11–16(–23.5) × (5–)5.5–6(–7.5) µm, apically not inflated; conidia medium curved at the apical end, slightly at the basal end, 125–228 × 8.5–10 µm (Pl. 16: b); from mossy soil or aquatic cyanobacteria, worldwide, arctic to subtropical............ ....***L. longisporus***, p. 299

5. Conidia 5–8-septate, *56–78 × 13–15 µm, distinctly curved (canoe-shaped), without hyphal appendage; often 2–3 adhesive knobs on each conidium (usually at their dorsal side); xeric bark of angio- (and gymno-)sperms, temperate to mediterranean Europe (Pl. 52) ....***L. vermicola***, p. 299
5. Conidia (2–)3(–4)-septate, slightly curved, with a long, narrow, subapically inserted hyphal appendage; one terminal adhesive knob on each conidium..6

6. Conidia slightly obclavate (narrowed towards apex), *24–38 × 9–11 µm, hyphal appendage mainly pointing downwards; from decaying plant material along a roadside, temperate North America (Pl. 53: 3) ....***Haptocara latirostrum***, p. 301
6. Conidia slightly clavate (narrowed towards base), *40–59 × 15–21.5 µm, hyphal appendage pointing laterally; xeric bark of angiosperms, temperate to mediterranean Europe (Pl. 53: 1–2) ....***H.* aff. *latirostrum***, p. 301

However, further evidence for the occurrence of *Lecophagus* in xeric habitats is provided by Hofstetter et al. (2007: 415, 421) who found by molecular methods that *L. muscicola* is present in association with thalli of various lichen genera. Desiccation-tolerant rotifers are known to live on thalli and to feed on the lichen's ascospores (Pyatt 1968), therefore, it can be assumed that *L. muscicola* preys on rotifers in these habitats, either by adhesive pegs or possibly by ingestion of ascospores which may have a similar size and shape as ascospores of many lichens.

The known distribution of the genus *Lecophagus* includes cold-temperate to subtropical, humid regions of Europe, eastern Asia, Australasia, and North America, also tundra vegetation in the Antarctic.

Unrelated genera that resemble anamorphs of *Lecophagus*. Some other genera that prey on rotifers may be confused with *Lecophagus*. The genus *Zoophagus* (*Zoopagales*) was earlier misapplied to species of *Lecophagus* (see p. 238–239) because of similar adhesive pegs and conidia. It differs in having non-septate mycelial hyphae without anastomoses, and another type of conidiophore (see Dick 1990, Morikawa et al. 1993 who observed anastomoses in *L. muscicola* and *L. longisporus*).

Members of two genera of the order *Hypocreales*, *Haptospora* Barron (Barron & Szijarto 1982, Barron 1991b) and *Rotiferophthora* Barron (Barron 1991a), grow endoparasitically in rotifers. In both genera conidiogenesis is phialidic. Their assimilative hyphae inside the dead rotifer body are ± strongly constricted at the septa, with the individual cells often broader at one end, which permits distinction from those of *Lecophagus* which are more rectangular and less constricted.

Lecophagus ellipsoideus Baral & G. Marson, **sp. nov.**, MB 813450 — Pls 45–47, Map 4

Etymology: named according to the ellipsoid ascospores.

Typification: Germany, Baden-Württemberg, Stuttgart, branch of *Lonicera ?tatarica*, 14.V.1994, H.O. Baral (ex H.B. 5078a, M-0276427, holotype).

Latin diagnosis: *Apothecia in statu rehydratato 0.08–0.35 mm diam., sessilia vel breviter stipitata. Asci *24–55 × 6.3–9.3 µm, apice rotundati, in basi non uncinati vel interdum uncinati. Ascosporae *4–7.3 × 3–4.3 µm, ellipsoideae vel ovoideae. Paraphyses sparsae, ad apicem rectae vel leniter curvatae, non vel leniter inflatae ad *3.3–4.5(–5) µm. Excipulum ectale cellulis ad basim *(9–)11–20(–28) µm latis. Hyphae basales *(7.5–)8.5–14(–17) µm latae. Habitat ad lignum vel corticem siccum angiospermarum, in rotiferas parasitans, in zona temperata ad orotemperata humida Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.08–)0.1–0.25(–0.35) mm diam., 0.08–0.18 mm high, white, round, soft, very scattered to subgregarious, rarely gregarious in small groups; disc flat, margin even or very slightly crenulate by the large cortical cells; subsessile on an obconical base or with a ± distinct stipe 15–70(–80) × 40–80(–120) µm, superficial; dry hardly visible, colour unchanged. **Asci** *(24–)29–42(–55) × (6.3–)7–8.5(–9.3)((–11.5)) µm {6}, fully turgescent *7.5–9.5 µm wide, †(23–)27–40(–48) × (5.8–)6–7(–8) µm {4}, 8-spored, spores (*) biseriate to subbiseriate, in lower part also uniseriate, (1–)3–5 upper spores inversely oriented {5} (often ± mixed, often obliquely or laterally oriented), pars sporifera *20–36 → 15–17 µm long (†23–25 µm); **apex** (†) ± hemispherical, slightly mammiform, dome immature or mature *0.8(–1.1) µm thick, mature with refractive inner delimitation, †0.8–1.3 µm thick, endotunica of low refractivity; **base** with ± short and thick stalk, arising from simple septa {6}, but also in some asci from croziers {4}. **Ascospores** *(4–)4.5–6.5(–7.3)((–8)) × (3–)3.3–4(–4.3) µm {6}, ellipsoid, rarely ovoid or slightly clavate, ends rounded, straight, rarely very slightly curved; **SBs** (1.5–)1.6–2(–2.2) × (0.9–)1–1.3(–1.4) ((–1.8)) µm {4}, (sub)globose to broadly tear-shaped, with a short and rather thick or rarely thin, cylindrical or tapering filum, (0.3–)0.4–0.7(–0.8) × (0.1–)0.15–0.25 µm. **Paraphyses** ± sparse, apically uninflated or slightly clavate, straight or sometimes slightly curved or flexuous, terminal cells *10–29 {3} or 30–36 {1} × (3.3–)4–4.5(–5) µm {3}, †2.8–4 µm wide {3}, lower cells *(8–)11–18(–27) × (2–)3–4.5(–5.5) µm {3}, very rarely branched at apex (antler-like), never branched in middle part. **Medullary excipulum** very indistinctly delimited, of dense textura angularis of indistinct orientation, cells guttulate as the ectal excipular cells, without hyphoid elements. **Ectal excipulum** near base of (*) comparatively thin-walled, indistinctly oriented t. angularis(-globulosa), cells *(9–)15–28(–35) × (9–)11–20(–28) µm {3}, at mid flanks and margin of t. prismatica-angularis oriented at a 0–10° angle to the surface, cells *9–18 × 8–12.3 µm {2}, 25–30 µm thick at margin, marginal cortical cells *10–25(–29) × 7–10(–13) µm {4}, wall †0.3–0.4(–0.5) µm thick, refractive. **Anchoring hyphae** sparse, restricted to base, individual cells *(14–)18–30(–35) {4} × (7.5–)8.5–14(–17) µm {5}, †8–12 µm wide, smooth or with an indistinct, very irregular incrustation, wall *0.2–0.3 µm thick {2}, cylindrical to ± moniliform, constricted at septa; individual cells of assimilative hyphae inside the rotifer *10–30(–60) × 5–10(–15) µm {2}. **SCBs** cubical or nearly globose {5}, in paraphyses 1–2 per cell, 0.4–1.2 µm diam., in ectal excipulum and anchoring hyphae ~2–4 per cell, (0.5–)1–1.7(–2) µm diam., in assimilative hyphae 0.5–1 µm diam. **LBs** present in all vegetative cells: small LBs abundant in basal ectal excipulum, sparse towards margin, also in medullary excipulum and paraphyses; sparse to abundant in anchoring and assimilative hyphae (in the latter also large LBs present). — **ANAMORPH**: lecophagus-like (affirmed from natural substrate {2}). **Conidiophores** not seen. **Conidia** strongly curved by ~150–180°, *133 × 15.7 µm {1, *Fagus*}, †90–98 × 10–11 µm {1, *Platanus*}, 5–8-septate. **Adhesive pegs** *(20–)22–28(–29.5) × 9.3–10.8 µm {2, *Clematis*}, †22–26 × 7–8.5 µm {1, *Platanus*}, apex *7.5–9.2 µm wide {2}, lageniform, slightly constricted in upper part, here abruptly thin-walled.

Habitat: collected 0.5–3.5 m above the ground on still-attached, corticated to ± decorticated, dead or sometimes still-living, undecayed, 10–40 mm thick branches but also thick trunks, of *Betula ?pendula* {1}, *Clematis vitalba* {2}, *Cornus sanguinea* {1}, *Fagus sylvatica* {1}, *Lonicera ?tatarica* {1}, *Platanus* × *acerifolia* {3}, *Salix* sp. {1}, *S. cinerea* {1}, on medium to strongly decayed, slightly to strongly eroded bark (bast) {9} and wood {2}, especially on the algae-covered side, often in fissures or old beetle galleries, along the edge between bast and wood, or hidden on inner surface of bark, sometimes on thick algal layer or on excrements of invertebrates, ± strongly greyed, often very close to dead, infected bdelloid rotifer bodies {5}. **Associated**: *Durella connivens* {1}, *Hyalorbilia erythrostigma* {1}, *H. latispora* {2}, *H. subfusispora* {2}, *Karstenia rhopaloides* {2}, *Orbilia clavuliformis* {1}, *O. eucalypti* {1}, *O. filiformis* {1}, *O. obtusispora* {1}, *O. pleioeuonymi* {1}, *O. ungulata* {1}, *O. vinosa* {1}, *O. vitalbae* {1}. **Desiccation tolerance**: fully tolerant for at least 2 weeks, mycelial hyphae for at least 4 months. **Altitude**: 115–1310 m a.s.l. **Geology**: Cambrian pelite, Upper Buntsandstein, Muschelkalk, Middle Keuper (gypsum), Lower Jurassic sandstone & shale, Pleistocene loess; gneiss, marble & amphibolite. **Phenology**: III, V–VII, IX, XI.

Taxonomic remarks. *Lecophagus ellipsoideus* is characterized by ellipsoid ascospores, the upper spores showing a distinct tendency to being inversely oriented within the asci, and by the predominant absence of croziers. However, croziers were present in some asci of four of the six collections with a teleomorph (from Luxembourg and Pyrenees), though only in a few of the tested apothecia. In one of the *Salix* collections (H.B. 6990d) only mycelium was found, and in that on *Fagus* only an infected rotifer and a detached conidium were seen (see below). The mesosubmediterranean *L. subglobosus* differs in subglobose ascospores with narrower SBs, asci consistently arising from croziers, and paraphyses with mostly strongly curved apex. For the more orosubmediterranean *L. pini* see below.

Variation. Ascus length varied among collections between *(24–)29–42 and *35–55 µm, and spore length between *4–

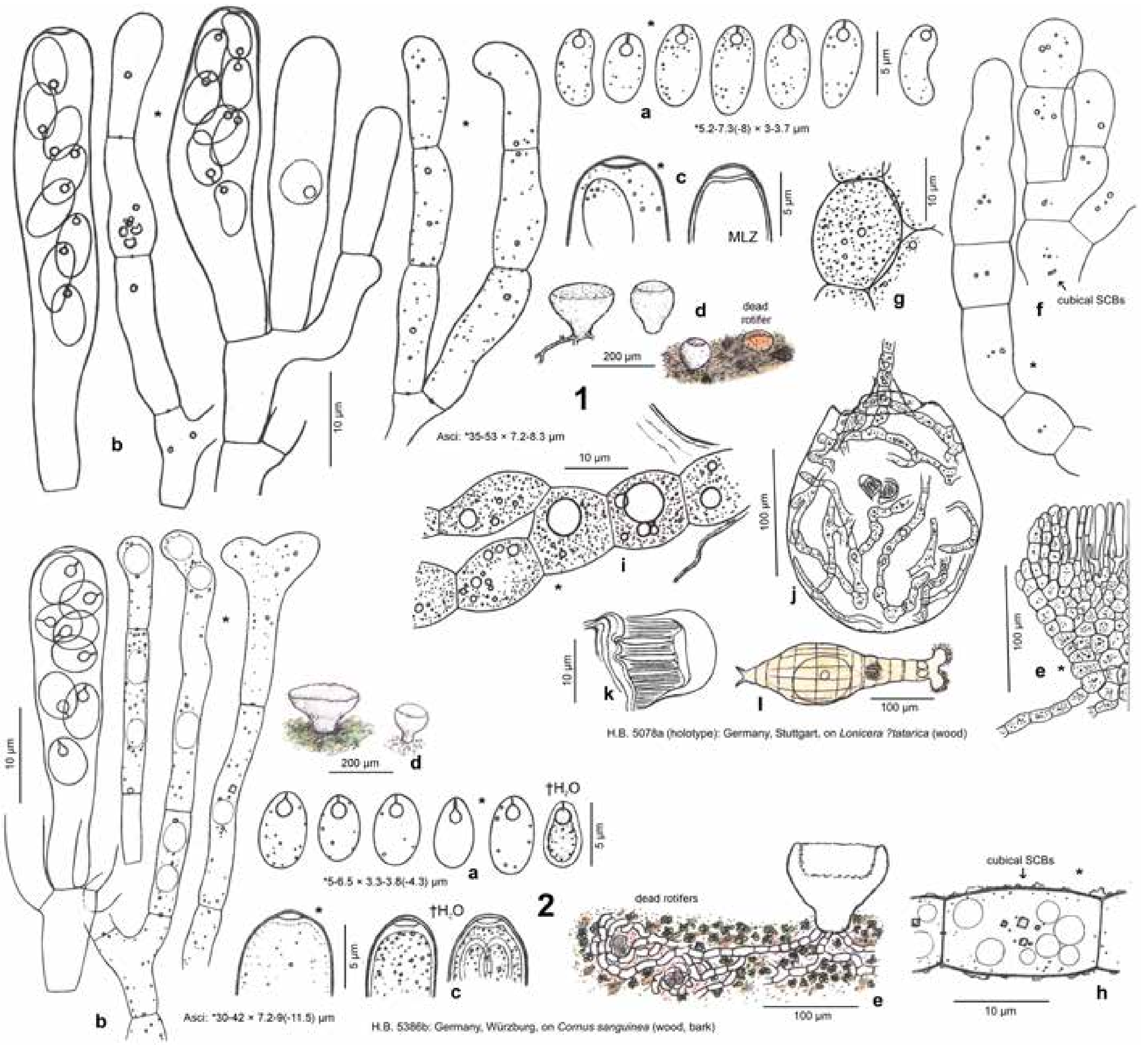


Plate 45. **1–2**: *Lecophagus ellipsoideus*. – **a**. ascospores; **b**. asci and paraphyses (**1b** young ascus with fusion nucleus); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., marginal ectal excipulum; **g**. ectal excipular cell at flanks; **h**. anchoring hypha; **i**. assimilative hypha within rotifer; **j**. dead rotifer with assimilative hyphae inside; **k**. trophi of infected dead rotifer; **l**. living rotifer found on same branch.

5.5 and 5.2–7.3(–8) µm, but some variation occurred also within a population. The most remarkable variation concerns the partial presence of croziers in some of the studied apothecia, but no basal protuberances were observed. The only montane collection (on bark of *Betula*, IVV: 28.IX.1999) comes close to *L. pini* with its large asci (*42–55 × 7.5–8.5 µm) and rather broad spores (*4.2–6 × 3.5–4.3 µm); in the anchoring hyphae the cubical SCBs attained here a maximum size of 2 µm, while the paraphyses and marginal cortical cells were not studied.

Anamorph. A purely anamorphic record with rather large conidia might represent *L. ellipsoideus*, judging from the occurrence on xeric substrate in temperate Europe: a single infected rotifer was found on the inner surface of bark of a standing trunk of *Fagus* 1 m above the ground (Pl. 47: 2). The assimilative hyphae contained cubical SCBs, and a single conidium was detected in vicinity of the cadaver (*133 × 15.7 µm, 8-septate), but no trapping organs, conidiophores, or apothecia. The large size of the conidium appears to exclude any of the described anamorph-typified species of *Lecophagus*.

A record from Hungary (on bark of a standing trunk of *Platanus*, D.M. 102/2) showed adhesive pegs and a few conidia (Pl. 47: 1). When studied by D. Magyar (pers. comm.) in the dead state, these were strongly curved (by ~150–180°) similar to that on *Fagus* but distinctly smaller (†90–98 × 10–11 µm, 5–7-septate). Again no conidiophores were seen. Another Hungarian sample on *Platanus* showed the same adhesive pegs on mycelium, but here connected to minute apothecia (IVV: D.M. 81/5). A detailed microscopic analysis of their asci and spores was not made, but their identity with *L. ellipsoideus* is assumed here. Also in the two apothecial samples from Luxembourg on xeric bark of *Clematis* (Pl. 46: 2–3) the anchoring hyphae carried adhesive pegs, either on the natural substrate or after some weeks of incubation at the lid of a Petri dish. The large size of the adhesive pegs excludes identity with *L. muscicola* or *L. longisporus* (see key p. 290). Ascospores shot on agar from the

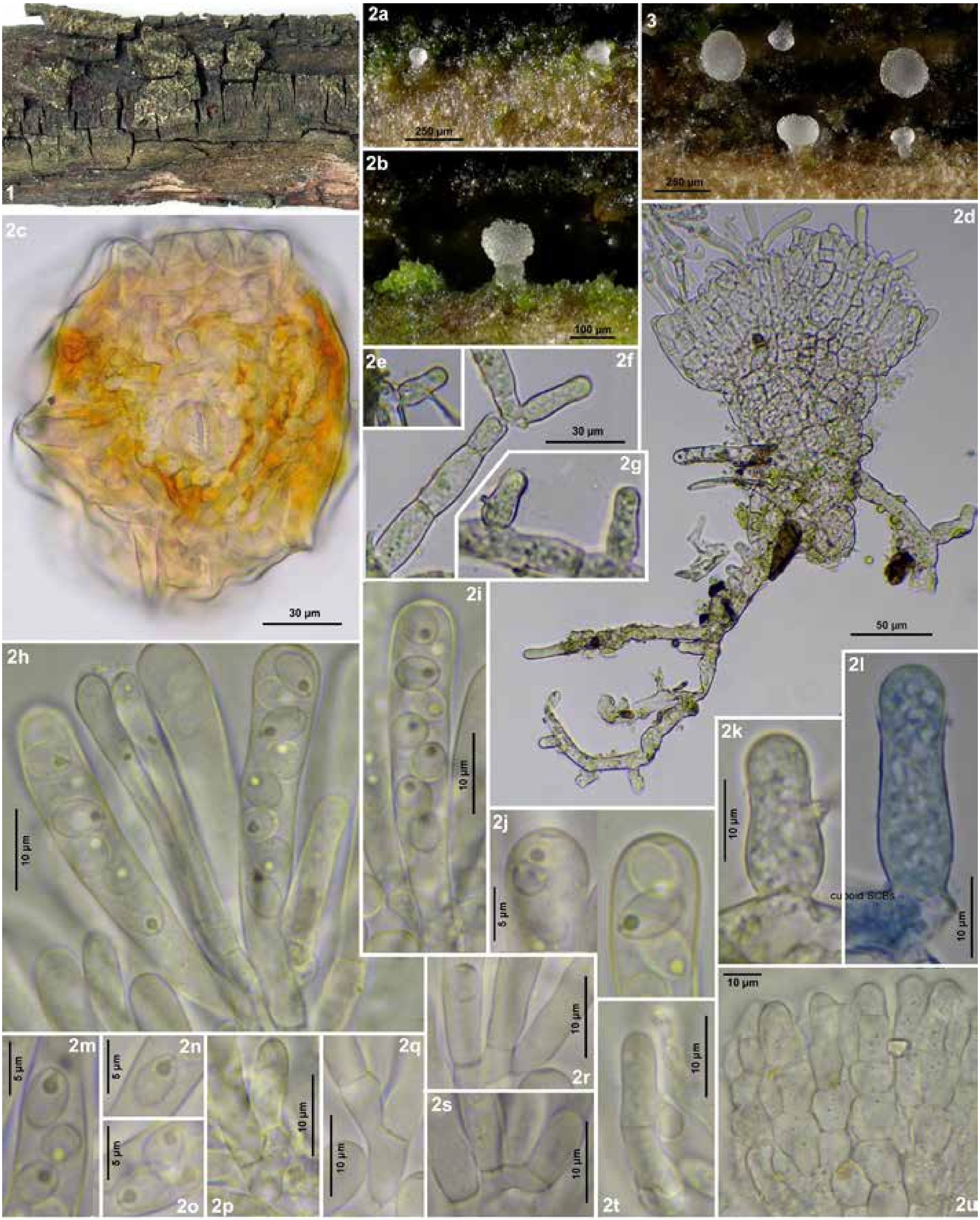


Plate 46. **1–3**: *Lecophagus ellipsoideus*. – **1**. decorticated xeric algae-covered branch of *Cornus sanguinea*; **2a–b**, **3**. rehydrated apothecia; **2h–i**. asci and paraphyses; **2j**. apices of asci, with mature ascospores; **2p–t**. ascus bases (**r–s** simple septate, **p** & **t** with croziers); **2m–o**. ascospores inside asci; **2u**. marginal ectal excipulum (external view); **2d**. apothecium with hyphae and adhesive pegs; **2e–g**, **k–l**. adhesive pegs; **2c**. dead rotifer containing assimilative hypha. – Living state. — **1**. H.B. 5386b: Germany, Würzburg, on *Cornus*; **2a–u**. 16.XI.2013: Luxembourg, Bettembourg, on *Clematis*; **3**. H.B. 9902a: ibid.

two *Clematis* samples failed to germinate. Regrettably, conidia were so far never seen in association with any of the apothecial records of *Lecophagus* reported here.

Phylogeny. A sequence was gained from apothecia of one of the samples on *Clematis* (H.B. 9902a), comprising SSU V1–V9, ITS, and LSU D1–D5 & D9–D12. *L. ellipsoideus* clustered with

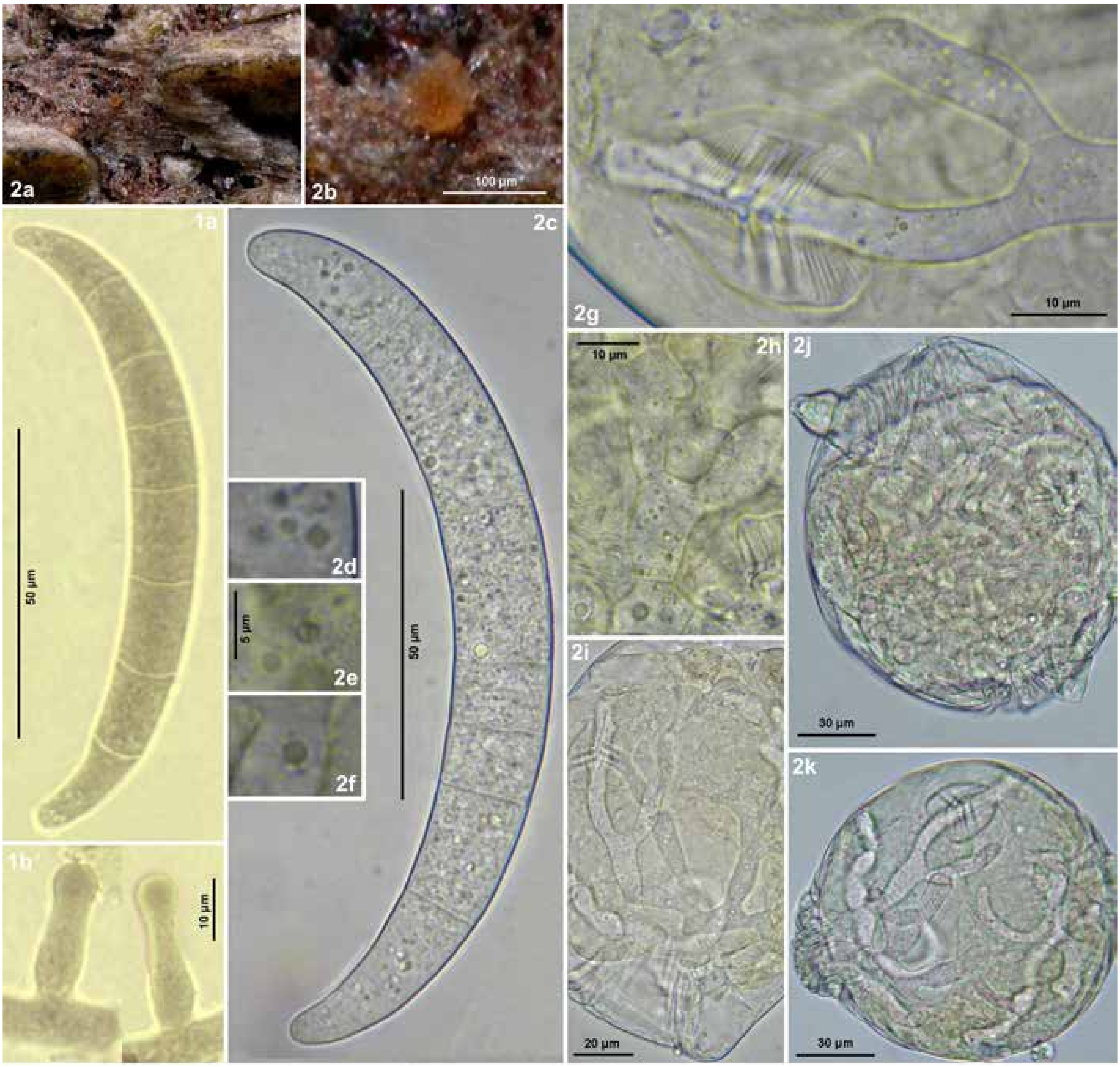


Plate 47. **1–2**: *Lecophagus ellipsoideus*. – **1a**, **2c**. conidia from natural substrate; **1b**. adhesive pegs; **2a–b**. infected rotifer; **2i–k**. rotifer with internal assimilative hyphae; **2d–f**. cubical SCBs in conidium (**2d**) and assimilative hyphae (**2e–f**); **2h**. assimilative hyphae with cubical SCBs; **2g**. assimilative hyphae growing through trophi of rotifer. – Living state, except for **1a–b**. — **1a–b**. D.M. 81/5: Hungary, on *Platanus* (phot. D. Magyar); **2a–k**. 3.I.2010: Luxembourg, on *Fagus*.

high bootstrap support in a clade with *L. muscicola*, *L. longisporus*, and *L. vermicola* (Phyls 2–4). In the ITS region the distance of *L. ellipsoideus* to *L. muscicola* and *L. longisporus* is about 16–17% (15% between the two latter), and 21–23% to *L. vermicola*. Due to their strong distance, the four sequences are difficult to align. *L. ellipsoideus* and *L. vermicola* show 1 larger and 2 smaller inserts in the ITS1. In the LSU the distance of *L. ellipsoideus* to *L. longisporus* is 2.7%, to *L. muscicola* 2.9%, and to *L. vermicola* 3.2% (D1–D2, 633 nucleotides), while the distance between *L. muscicola* and *L. longisporus* is also 2.9%. When including 918 nt (D1–D3), *L. ellipsoideus*, *L. vermicola* and *L. muscicola* show a similar distance among each other (2.2–2.3%, D3 data for *L. longisporus* are lacking), because in the D3 domain *L. ellipsoideus* and *L. vermicola* deviate by only 1 nt (and 4 ambiguities), while *L. muscicola* deviates here by 3 nt from both.

An environmental sequence from Antarctica (MK537054, ITS1) fully matches *L. ellipsoideus*, but was published too late in order to be properly included in this study. Another from a freshwater lake (Lake Biwa) in Shiga, Japan (Bi-F-370) comprises mainly ITS2 and clusters strongly supported with *L. ellipsoideus* (Phyl. 3, L5), though with a distance of 7.5% (15 nt + 5 gaps).

Ecology. *Lecophagus ellipsoideus* was detected on ± decayed bark and wood of xeric branches or on bark of standing living trunks of different angiosperm trees and shrubs or climbers. The known collection sites include cold-temperate (often thermophilous) but also orotemperate areas in subcontinental humid central and southern Europe. A connection to infected cadavers of bdelloid rotifers in close proximity to the tiny apothecia is assumed to be obligatory, although not always easy to observe.

Specimens included. **GERMANY**: **Baden-Württemberg**, 6 km NW of Stuttgart, Weilimdorf, Raiffeisenstraße, 325 m, branch of *Lonicera ?tatarica*, on wood, with infected rotifers, 14.V.1994, H.O. Baral (ex H.B. 5078a, M-0276427, **holotype**). – **Bayern**, **Unterfranken**, 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz,

Map 4. Known distribution of *Lecophagus ellipsoideus* in Europe.

260 m, branch of *Cornus sanguinea*, on bark & wood, 11.XI.1995, H.O. Baral & L.G. Krieglsteiner (H.B. 5386b, Krieglsteiner 1999: 272, as 10.XI., *Orbiliaceae* sp.). — **LUXEMBOURG**: **L'Oesling**, 10 km W of Ettelbruck, 1.5 km NW of Grosbous, near Bruch (an der Wark), 400 m, branch of *Salix cinerea*, on bark, 26.III.2001, G. Marson (H.B. 6990d, myc. only). – **Gutland**, 3.5 km ESE of Ettelbruck, 1.7 km SE of Ingeldorf, Jongeboesch, Béibert, 353 m, branch of *Salix*, on bark (on invertebrate excrements), 17.VI.2001, G. Marson (ø). – 4.2 km S of Bettembourg, 1.7 km E of Dudelange, 2.7 km NW of Zoufftgen, along railway, 290 m, branches of *Clematis vitalba*, on bark, with infected rotifer, 16.XI.2013, G. Marson (ø). – ibid., 25.VII.2014 (G.M. 2014-07-25.2, H.B. 9902a; sq.: KT222385). – 7 km NE of Luxembourg, Waldhaff, 417 m, trunk of *Fagus sylvatica*, on bark, 3.I.2010, G. Marson (only conidium and infected rotifer). — **SPAIN**: **Cataluña**, **Girona**, eastern Pyrenees, 26 km NE of Ripoll, 2.3 km NE of Molló, 2.6 km WSW of Col d'Ares, 1310 m, branch of *Betula ?pendula*, on bark, with infected rotifers, 28.IX.1999, G. Marson (ø). — **HUNGARY**: **Pest**, 4 km E of Budapest, NIEH park, Albert Florian ut, 113 m, trunk of *Platanus* × *acerifolia*, on bark, 7. & 14.V.2010, D. Magyar (D.M. 102/2, pegs and conidia, anam. substr., doc. vid.). – 4.3 km ENE of Budapest, Thököly ut, 113 m, trunk of *P.* × *acerifolia*, on bark, predatory on rotifers, 1.VI.2010, D. Magyar (D.M. 81/5, pegs and apothecia, doc. vid.). – 6 km ENE of Budapest, Róna ut, 117 m, trunk of *P.* × *acerifolia*, on bark, 1.VI.2010, D. Magyar (ø, non vid.).

Lecophagus pini Baral, **sp. nov.**, MB 813451 — Pl. 48

Etymology: named after the host tree, *Pinus sylvestris*.

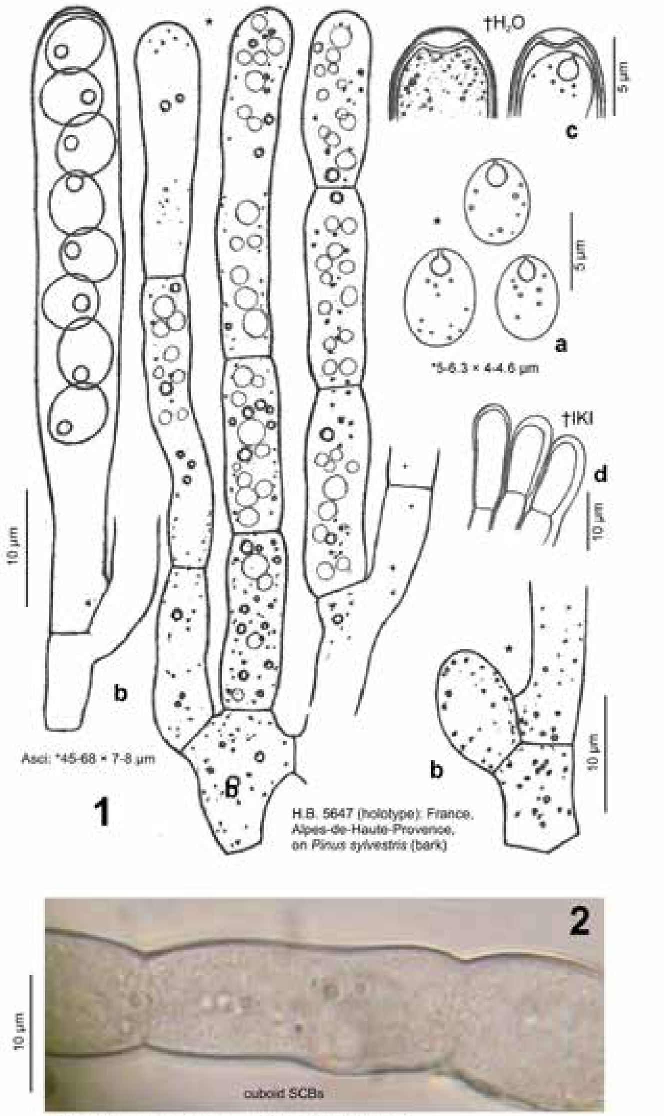
Typification: France, Alpes-de-Haute-Provence, Seyne-les-Alpes, branch of *Pinus sylvestris*, 24.VIII.1996, G. Marson (ex H.B. 5647, M-0276428, holotype).

Latin diagnosis: Lecophago ellipsoideo *similis, sed asci longiores*, *in basi uncinati, ascosporae uniseriatae, leniter latiores*, *paraphyses ad apicem rectae, *(3.5–)5–6(–7) µm latae, excipulum marginale cellulis crassitunicatis. Habitat ad corticem siccum* Pini *in zona orosubmediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.12–0.15 mm diam., ~0.13 mm high (receptacle ~0.1 mm), white, round, scattered; disc flat, margin thin, not protruding, smooth; with a small stipe ~0.03 × 0.05 mm, superficial. **Asci** *45–68 × 7–8 µm {1}, 8-spored, spores (*) ± uniseriate, orientation irregular, pars sporifera *37–40 µm long; **apex** (†) hemispherical to slightly conical, dome †1.3–1.4 → 1–1.2 µm thick {1}; **base** with short to long, thick stalk, arising from croziers {1}. **Ascospores** *5–6.3 × 4–4.6 µm {1}, broadly ellipsoid(-ovoid), ends rounded (to obtuse); **SBs** *1.5–1.8 × 1.3–1.5 µm, globose to ovoid, with a very short and thick connecting part, 0.2–0.4 × 0.15–0.3 µm. **Paraphyses** apically uninflated, straight, terminal cells *(11.5–)14.5–34 × (3.5–)5–6(–7) µm {1}, lower cells *12–25 × 4–6 µm {1}; unbranched at upper septum. **Medullary excipulum** not examined. **Ectal excipulum** of (*) slightly gelatinized t. angularis-prismatica, cells *15–25 × 10–14 µm {1}, common walls *0.5–0.8 µm thick; marginal cortical cells †11.5–17 × 6–7 µm {1}, with up to 1–3 µm thick glassy wall. **Anchoring hyphae** individual cells *15–26 × 10–12.5 µm {1}. **SCBs** in paraphyses roundish to slightly angular, 0.7–1 µm diam., intermingled with non-refractive vacuoles. **Exudate** absent. **— ANAMORPH**: unknown.

Habitat: collected ~3 m above the ground, corticated, 40 mm thick branch of *Pinus sylvestris* {2}, on rather undecayed bark (periderm) {1}, very close to blackened resinous wound {1}, medium greyed, with many green algae. **Associated**: *Amphosoma atroolivaceum* {2}, *Bulbillomyces* sp. {1}, *Resinomyces kirschsteinianus* {2}, *Lilapila oculisporella* {1}, *Orbilia sphaerospora* {1}, *Propolis betulae* {1}, *Sarea difformis* {1}, *S. resinae* {1}. **Desiccation tolerance**: fully tolerant for more than 3 months. **Altitude**: 870–1350 m a.s.l. **Geology**: Cretaceous limestone. **Phenology**: VIII.

Taxonomic remarks. *Lecophagus pini* differs from *L. ellipsoideus* in slightly wider ascospores which are almost uniseriately oriented within the living asci, their SB-containing apex pointing rather irregularly in all directions. Besides, the SBs have a shorter filum, the asci and their pars sporifera are longer, the paraphyses wider and apically always straight, the marginal excipular cells more thick-walled. Finally, *L. pini* differs in the coniferous host and (oro)submediterranean region. Some of these features are only gradual. The ascus base (simple septate vs. croziers) appears to be variable in *L. ellipsoideus*, or perhaps indicative of the existence of further taxa. Because of the paucity of material, the mentioned characteristics of *L. pini* may actually show a higher variation than here reported.



H.B. 9143c; France, Vaucluse, on *Pinus sylvestris* (resin)

Plate 48. **1–2**: *Lecophagus pini*. – **a**. ascospores; **b**. ascus and paraphyses, ascus base; **c**. ascus apices; **d**. marginal cortical cells in median section; **2**. hypha containing cubical SCBs (living state).

Further observations on new records are necessary to clarify the taxonomic value and ecological amplitude of *Lecophagus* species.

A second record on *Pinus sylvestris* (Pl. 48: 2) consisted only of one anchoring hypha that undoubtedly represented a species of *Lecophagus*, probably *L. pini* because of the coniferous substrate. Here *Amphosoma atroolivaceum* grew in very close association.

Ecology. The holotype of *Lecophagus pini*, which consisted of only two apothecia, was found on rather undecayed bark of a xeric branch of *Pinus sylvestris*, on the border of an old resinous wound, at an eastnortheast-exposed steep slope 100 m above a mountain brook in an altimontane, orosubmediterranean humid mixed pine forest in the calcarean Southern French Alps. The mycelial record from Mont Ventoux was also in a resinous wound but at lower altitude in a suprasubmediterranean more semihumid pine forest.

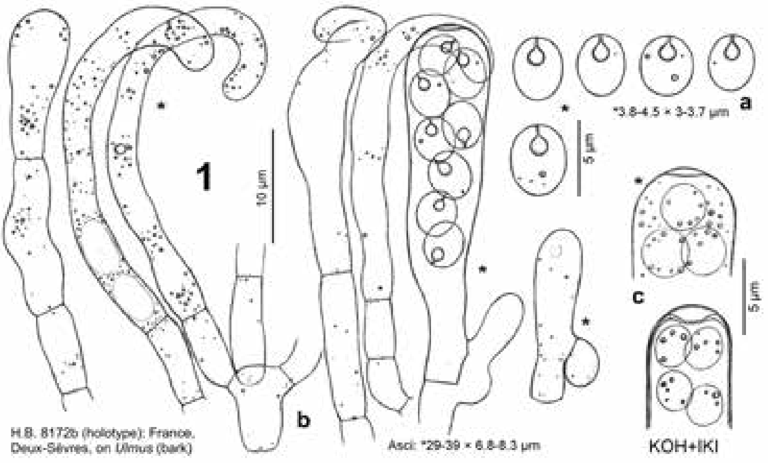


Plate 49. **1**: *Lecophagus subglobosus*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices.

Specimens included. **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, Mercantour, 13.5 km SE of Seyne-les-Alpes, 5.5 km SW of Tête de l'Estrop, SE of Vière, 1350 m, branch of *Pinus sylvestris*, on bark near resin, 24.VIII.1996, G. Marson (ex H.B. 5647, M-0276428, **holotype**). – **Vaucluse**, 10.5 km SE of Mont Ventoux, 3.5 km NW of Sault, 870 m, branch of *P. sylvestris*, on resin, 14.VIII.2009, H.O. Baral & G. Marson (H.B. 9143c ø, myc. only).

Lecophagus subglobosus Baral, B. Coué & M. Hairaud, **sp. nov.**, MB 813452 — Pls 49–50

Etymology: named according to the subglobose ascospores.

Typification: France, Deux-Sèvres, Clussais-la-Pommeraie, trunk of *Ulmus* sp., 6.V.2006, B. Coué (ex H.B. 8172b, M-0276429, holotype).

Latin diagnosis: *Differt ab* Lecophago ellipsoideo *ascis in basi uncinatis, ascosporis subglobosis, *3.8–4.5(–5) × 3–3.7(–4) µm, paraphysibus ad apicem plerumque valde uncinatis, cellulis excipuli minoribus, ad basim *7–12 µm latis, hyphis basalibus *5–9.5 µm latis. Habitat in cortice* Ulmi *in zona submediterranea Europae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.2(–0.25) mm diam., 0.07–0.08 mm high, white, round, very scattered; disc flat, margin even or very slightly crenulate, not protruding, exterior glabrous; subsessile on an obconical base or with a short, ± sharply differentiated stipe 0.03–0.04 × 0.03–0.04 mm, superficial; dry hardly visible, colour unchanged. **Asci** *29–39 × 6.5–8.3 µm {2}, †26–35 × 5.5–6.2 µm {1}, 8-spored, spores (*) biseriate to subbiseriate, in lower part also uniseriate, a few lower spores inversely oriented {1} (often ± mixed, also some spores irregularly oriented), pars sporifera *15–18 µm long; **apex** (†) hemispherical, very slightly mammiform, dome immature or mature *0.4–0.7 µm thick, †0.9–1.1 µm; **base** with ± short and rather thick stalk, arising from croziers {1}. **Ascospores** *3.8–4.5(–5) × 3–3.7(–4) µm {1}, subglobose; **SBs** 1.5–2 × 1–1.2 µm {1}, globose to subglobose, with a short and thick connecting part, 0.5–0.7 × 0.15–0.2 µm. **Paraphyses** apically uninflated, rarely medium clavate, medium to very strongly curved (uncinate) {2}, rarely straight, terminal cells *(13–)25–40 × 2.5–5 µm {1}, lower cells *5–14 × 2.5–3.3 µm {1}, rarely branched at upper septum. **Medullary excipulum** not examined. **Ectal excipulum** near base of comparatively thin-walled textura angularis(-prismatica), cells *8–14(–20) × 7–12(–18) µm {1}, at flanks and margin of horizontally oriented t. prismatica-angularis,

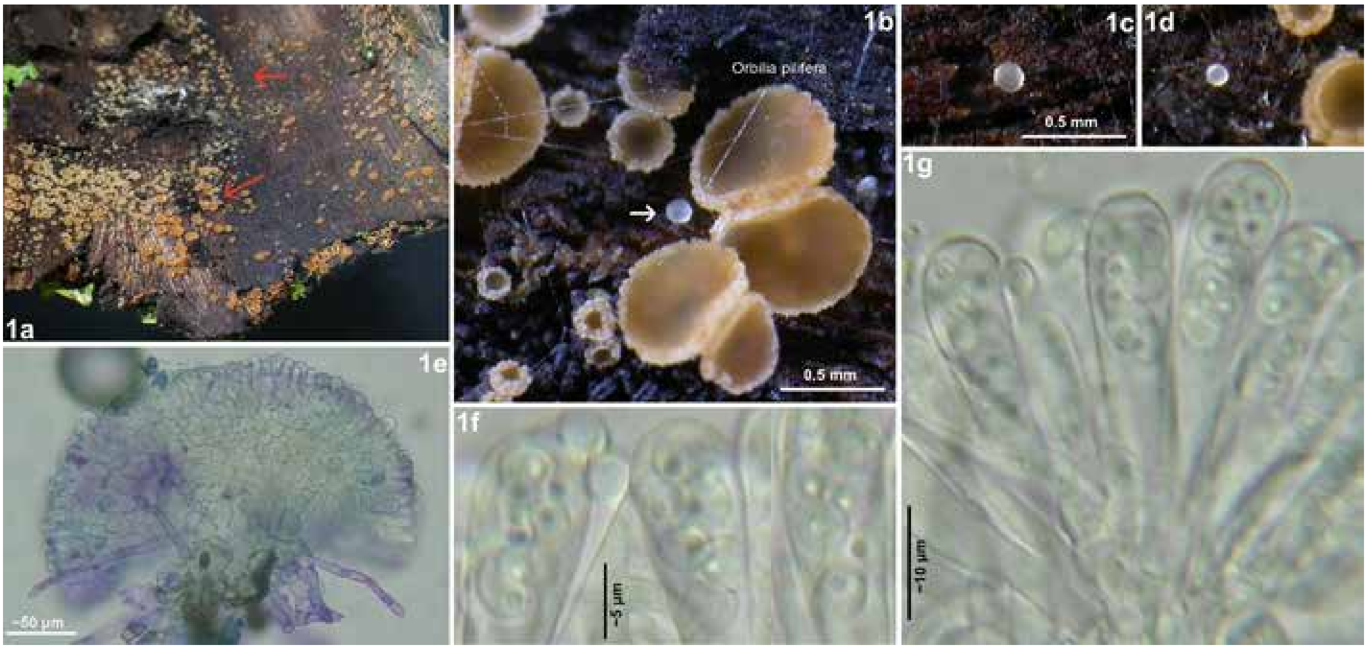


Plate 50. **1**: *Lecophagus subglobosus*. – **1a**. inner surface of xeric *Ulmus* bark, with abundant *Orbilia pilifera*; **1b–d**. rehydrated apothecia (between *O. pilifera*); **1e**. apothecium from below (in CRB); **1f–g**. asci with ascospores, paraphyses. – Living state. – **1e–g**: phot. B. Coué. — **1a–g**. H.B. 8172 (holotype): France, Deux-Sèvres, on *Ulmus*.

marginal cortical cells conglutinated by some gel, †10–12 × 6–11 µm {1}, wall †0.3–0.5 µm thick, refractive. **Anchoring hyphae** sparse, restricted to base, *(5–)6–8(–9) µm wide {1}. **SCBs** in paraphyses not observed, in centre of some excipular cells with globose-cubical SCB 0.5–1 µm diam.; **LBs** in paraphyses and excipular cells scattered, small. — **ANAMORPH**: unknown.

Habitat: on probably recently fallen bark detached from ~5–10 cm thick trunks of dead trees of *Ulmus* sp. {1}, *U.* (?)*minor* {1}, on medium decayed inner surface of bark {2}, ungreyed, without algae, no rotifers observed, outer surface with abundant foliose lichens. **Associated**: *Orbilia pilifera* {2}, *Physcia* sp. {1}, *Xanthoria parietina* {1}. **Desiccation tolerance**: fully tolerant for at least 1–2 weeks. **Altitude**: 130–158 m a.s.l. **Geology**: Tertiary clay over Jurassic and Tertiary limestone. **Phenology**: V, X.

Taxonomic remarks. *Lecophagus subglobosus* is similar to *L. ellipsoideus* and *L. pini*, from which it differs in shorter, subglobose ascospores and mostly strongly curved paraphyses, from the former also in the consistent presence of croziers.

Ecology. *L. subglobosus* was found on medium rotten xeric bark detached from branches of *Ulmus* in ± marshy areas in atlantic, mesosubmediterranean (semi-)humid western Europe. No rotifers or other invertebrates could be found in association with the apothecia.

Specimens included. **FRANCE**: **Poitou-Charentes**, **Deux-Sèvres**, 16 km ESE of Melle, 2 km ENE of Clussais-la-Pommeraie, E of Clussais, 130 m, trunk of *Ulmus*, on bark, 6.V.2006, B. Coué (ex H.B. 8172b, M-0276429, **holotype**). – 13 km ESE of Melle, Coudré, inside of village, 158 m, trunk of *Ulmus* (?)*minor*, on bark, 25.X.2006, B. Coué (ø, non vid.).

Lecophagus muscicola (G.L. Barron et al.) Tanabe, Nagah., Saikawa & Sugiy., Mycologia 91: 835 (1999) — Pl. 51

≡ *Cephaliophora muscicola* G.L. Barron, C. Morik. & Saikawa, Can. J. Bot. 68: 686 (1990)
= *Lecophagus fasciculatus* M.W. Dick, Mycol. Res. 94: 351 (1990)
?= *Lecophagus antarcticus* McInnes (as *L. antarctica*), Polar Biol. 26(2): 79 (2003), nom. inval., Arts 39.1, 40.1 ICN

Etymology: *muscicola*: isolated from mossy soil, *fasciculatus*: from the fasciculate clusters of conidia, *antarcticus*: isolated from Antarctic lakes.

Typification: New Zealand, North Island, from muddy soil in a ditch, 18.XII.1988, G. Barron (OAC 10848, holotype of ***Cephaliophora muscicola***). — USA, Washington, Woodinville, in a small pond, undated, collector unknown (IMI 335522, holotype of ***Lecophagus fasciculatus***, ex-type culture APCC 9000).

Description: — **TELEOMORPH**: unknown. — **ANAMORPH** (collection from Oberlausitz): **Mycelial hyphae** *6–8(–10) µm wide, hyaline. **Conidiophores** *17–17.5 × 6–7 µm, unicellular, unbranched, conidia formed in apical clusters of ~4–10 from broad inconspicuous loci, conidiogenesis synchronous. **Conidia** *83–145 × (9–)9.5–10.5(–12.5) µm, (6–)7–10-septate, fusoid, slightly to medium curved under a wide arch, cells of a conidium of quite different length, terminal cells often longest. **SCBs** in centre of living cells but also near septa, refractive, cubical, 1–1.3 µm diam., present in mycelial hyphae, conidiophores, and conidia. **Trapping organs**: adhesive pegs unicellular, *17–21 × 5.5–6.5 µm, apex *4.2–4.7 µm wide, forming a distinct globose head, sometimes moniliform.

Habitat: isolated from moss and organic debris in wet soil, also from aquatic plants (*Elodea*) in ephemeral ponds, capturing planktonic rotifers of the genera *Adineta* (*Bdelloidea*) or *Lecane* (*Ploima*), also tardigrades. **Desiccation tolerance**: conidia survive for at least 2 weeks. **Altitude**: ~10–300 m a.s.l.

Taxonomic remarks. The synonymy of *L. fasciculatus* with the one month earlier published *L. muscicola* was demonstrated by Morikawa et al. (1993) based on morphological criteria (see p. 238–239). *L. muscicola* and *L. longisporus* were both described in the genus *Cephaliophora* by Barron et al. (1990) and are morphologically as well as ecologically very similar. They are said to differ only in a few details: the adhesive pegs are in *L. muscicola* ± cylindrical, i.e., hardly inflated at the 3.5–5.5 µm wide base, and slightly constricted below the globose apex, whereas in *L. longisporus* they are more conico-lageniform, i.e., inflated to 5.5–7.5 µm at the base but not at the apex (see Pl. 16). The conidia are similar in size and number of septa, but in *L. longisporus* they tend to be more bent near the apex.

We have identified the here illustrated specimen as *L. muscicola* based on the shape of the distinctly subapically constricted adhesive pegs, although their width at the base would better fit *L. longisporus* (it is not quite clear if the measurements in the literature are from living or dead material). Moreover, in our specimen the conidia are never distinctly bent at the apex as is described for *L. longisporus*.

Magyar (2006: fig. 1) identified a fungus as *Cephaliophora muscicola*, sampled in Hungary in a water-filled treehole 1.5 m above the ground. The conidia measured *112–135 × 7.5–8.7 µm and the adhesive pegs *14–15.8 × 4.5–5.5 µm. There is, however, a slight error in these data: the conidia illustrated there and on additional photos kindly sent by D. Magyar (pers. comm.) measure 128–143 × 9–10.5 µm according to the scale, whereas the adhesive pegs on the undulating mycelium are reproduced about 8 % too small on the plate.

Not included collection: *L. antarcticus* was described as predacious on tardigrades (*Acutuncus antarcticus*) and bdelloid rotifers (*Philodina* and others) by McInnes (2003). The author distinguished the species from *L. muscicola* and *L. longisporus* by much broader vegetative hyphae (9 vs. 4–7.5 µm) and larger adhesive pegs (30–40 × 9 vs. 10.5–23.5 × 3.5–7.5 µm), also the conidia are given much wider (170–180 × 13.7–15.5 vs. 125–228 × 6.2–10 µm). However, the indicated dimensions are questionable because there are some striking discrepancies to the dimensions evaluated from the scale: the vegetative hyphae measure 8–9.5 µm from figs 2b and 3a–b and 10–12 µm from fig. 2c, but only ~6–8 µm from fig. 2e; the adhesive pegs measure 33–45 × 7–9 µm from figs 2b–c, but only 13–17 × 6–8 µm from figs 2e, 3a, and 3c; the conidia measure 168–200 × 10–11 µm when evaluated from figs 2e, 2f, and 3c.

Undoubtedly, some of the scales and measurements must be wrong. The illustrated morphology of *L. antarcticus* resembles that of *L. longisporus* and *L. muscicola*, and it is well possible that *L. antarcticus* is conspecific with one of them, when neglecting the very different climatic region from which it derives. In any case, the name *L. antarcticus* is invalid because it lacks a Latin diagnosis and statement where the type was deposited (which was sent to CABI, UK, S. McInnes pers. comm.). No molecular data of *L. antarcticus* was available.

Phylogeny. Sequences from three strains of the *L. muscicola*/*L. longisporus* complex were available in GenBank, comprising SSU (V1–V9), in two of them also ITS and LSU. In the 1769 overlapping nucleotides of SSU, *L. longisporus* (CBS 845.91, New Zealand, holotype) differs from *L. muscicola* (IAM 14638, Japan) by 5 nt, which is a 0.3 % distance in this gene region, whereas the third strain (*Lecophagus* sp., ATCC 56071, ?USA) differs from Japanese *L. muscicola* by only 1 nt and from *L. longisporus* by 4 nt. This appears to indicate that the two strains with a 1 nt distance represent the same species, *L. muscicola*.

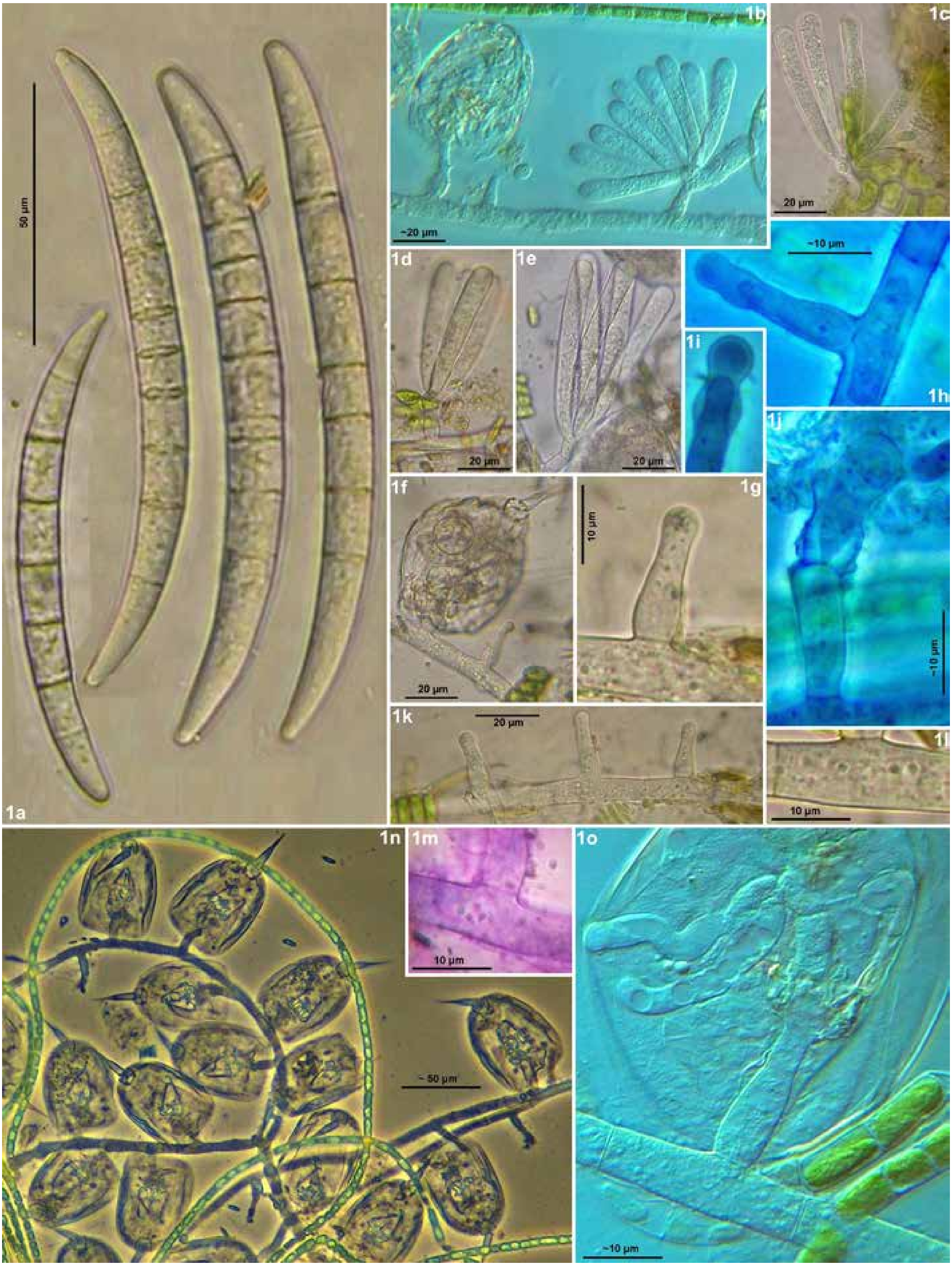


Plate 51. **1**: *Lecophagus muscicola*. – **1a**. mature conidia; **1b–e**. conidiophores with young conidia; **1b**, **f–k**, **n–o**. adhesive pegs (**1b**, **f**, **j**, **n–o** with captured ploimoid rotifers of the genus *Lecane* and assimilative hyphae within rotifer); **1l–m**. cubical SCBs in hyphae. – Living state in water (**1m** in CRB) except for **1h–j** (in CB_L), **n**. – **1b**, **h–j**, **n–o**: phot. P. Bergmann (**b**, **n–o**: DIC). — **1a–o**. Germany, Sachsen, Oberlausitz, Löbau, on *Elodea* (H.B. 7771)

In the LSU (overlapping 563 nt), the difference between *L. muscicola* (ATCC 56071) and the type of *L. longisporus* is 13 nt (2.3 %), and in the 5.8S rDNA it is 2 nt, whereas in the ITS1 and less so in the ITS2 the divergence is so high that an alignment is almost impossible (no data on ITS and LSU are available for the Japanese strain). The high distance of ~15 % in the ITS region confirms separation between *L. muscicola* and the morphologically similar *L. longisporus* at the species level. For the distances to *L. ellipsoideus* see p. 294.

Ecology. The population illustrated here was collected by Peter Bergmann (pers. comm.) in a garden pond in the region of Oberlausitz at the easternmost edge of Germany. The fungus occurred here in close association with trichomous algae attached to decaying shoots of *Elodea*. Barron et al. (1990, as *C. muscicola*) isolated the fungus from muddy soil in a ditch in Egmont Park on North Island (New Zealand), from muddy soil in a rainforest at Milford Sound, and from moss beside a woodland path at Geraldine (both on South Island), also from leaf mould in a subtropical lowland riverside bank of Agano river (Saitama, Japan). The type of *L. fasciculatus* was from a small pond at Woodinville at the cool-maritime westcoast of North America. *L. muscicola* was also recorded from a water-filled treehole on a standing trunk of *Acer platanoides* in Hungary (Magyar 2006, as *Cephaliophora muscicola*). For more details see also under Ecology of the genus *Lecophagus*, p. 290. All these records concern lowland areas with a more or less temperate, humid climate.

The not included *L. antarcticus* was isolated from benthic cyanobacterial mats and sediments in maritime Antarctic lakes in the tundra vegetation of Signy Island, a part of the South Orkney Islands in the Antarctic Ocean about 600 km NE of the tip of the Antarctic Peninsula (McInnes 2003).

Specimens included. **GERMANY**: **Sachsen**, Oberlausitz, 10 km SE of Löbau, Berthelsdorf, S of Zinzendorf Castle, 300 m, on *Elodea canadensis*, parasitic on *Lecane*, III.2005, P. Bergmann (H.B. 7771 ø). — **NEW ZEALAND**: **North Island**, Mt. Egmont Park, muddy soil in ditch, parasitic on *Adineta* and *Tardigrada*, 18.XII.1988, G. Barron no. 169 (**holotype** of *L. muscicola*, OAC 10848, doc. vid.). — **USA**: **Washington**, small pond near Woodinville, on twigs and leaves, parasitic on *Lecane*, date and collector not stated (**holotype** of *L. fasciculatus*, IMI 335522, ex-type culture APCC 9000). – ?**USA**: unlocalized, James et al. 2006 (AFTOL-ID 183, ATCC 56071, as *Lecophagus* sp.; sq.: AY635836, AY997058, DQ273799). — **JAPAN**: **Honshu**, **Tokyo**, Saitama, Agano, river side, leaf mold, M. Saikawa (IAM 14638, isolated by Morikawa et al. 1993, as *C. muscicola*; sq.: AB001108).

Not included. **ANTARCTICA**: **South Orkney Islands**, Signy Island, 0 m, parasitic on *Acutuncus antarcticus* and *Philodina* sp., undated, S.J. McInnes (CABI, **type** of *L. antarcticus*, doc. vid.).

Lecophagus longisporus (G.L. Barron, C. Morik. & Saikawa) Tanabe, Nagah., Saikawa & Sugiy. [as '*longispora*'], Mycologia 91: 835 (1999) — Pl. 16: b

≡ *Cephaliophora longispora* G.L. Barron, C. Morik. & Saikawa, Can. J. Bot. 68: 688 (1990)

Taxonomic remarks. *Lecophagus longisporus* differs from *L. muscicola* mainly in the shape and size of the adhesive pegs (see under *L. muscicola*, p. 297). However, the morphological distinction between the two species is not very clear.

Phylogeny. Sequence data exist in GenBank for the holotype of *L. longisporus* (CBS 845.91, New Zealand), showing to the Japanese strain of *L. muscicola* a distance of 0.3 % in the SSU, ~15 % in the ITS, and 2.3 % in the LSU D1–D2 (see p. 297).

Ecology. *Lecophagus longisporus* was isolated by G.L. Barron from mossy soil in a subtropical humid kauri wood at Birkenhead (Auckland, New Zealand, 25.XII.1988, CBS 845.91, holotype), also from moss on a rock in a cold-temperate humid region at Eramosa River bank near Guelph (Ontario, Canada), using tardigrades and rotifers of the genus *Adineta* as prey. Cultures earlier misidentified as *Zoophagus insidians* are APCC 9000 (H.C. Whisler), and ATCC 48646 (S. Warner no. 65-6) (Dick 1990, Morikawa et al. 1993), but their geographical origin is not indicated.

Lecophagus navicularis (Tzean & G.L. Barron) M.W. Dick, Mycol. Res. 94: 352 (1990) — Pl. 16: d

≡ *Cephaliophora navicularis* Tzean & G.L. Barron, Can. J. Bot. 61: 1345 (1983)

For a description see Tzean & Barron (1983).

Taxonomic remarks. The canoe-shaped conidia of *Lecophagus navicularis* resemble those of *L. vermicola* but are smaller and with only 3 septa. *L. navicularis* forms conical adhesive pegs in contrast to the globose ones of *L. vermicola*. No molecular data of *L. navicularis* was available.

Ecology. *L. navicularis* was reported as predacious on bdelloid rotifers of the genus *Adineta*, being isolated from old manure in a beef (cattle) farm near Toronto, Ontario, in cold-temperate (hemiboreal) humid North America.

Lecophagus vermicola D. Magyar, G. Marson, Z. Merényi & Baral, in Magyar et al., Mycol. Progr. 15: 1139 (2016) — Pl. 52

Etymology: named after the ability to prey on nematodes.

Typification: Hungary, Budapest, infected nematodes on trunk of *Platanus* × *acerifolia*, 24.VII.2011, D. Magyar (BP 107927, holotype).

Description: — **TELEOMORPH**: unknown. — **ANAMORPH**: **Assimilative hyphae** septate †(3–)5–7(–11) µm wide, completely colonizing the nematode's body, arranged longitudinally as 1 or 2 parallel, anastomosing threads. **Conidiophores** micronematous, mononematous, †11–13 × 8–9 µm {Hungary}, conical to clavate, 0–1-septate, with 2 conidiogenous scars. **Conidia** *56–86 × (11.5–)13–17 µm {12}, †(44.5–)50–55(–61.5) × (8–)10.5–11.5(–12.5) µm {Hungary} or †58–63 × 12–15 µm {Canada} (in situ, actual length *~65–90, †~55–75 µm), (3–)7(–8)-septate, fusoid to fusiform, canoe-shaped, slightly tapered at the slightly to medium curved base, sometimes forming a pedicellate 'foot-cell', straight in middle part, strongly tapered and curved (sometimes hooked) at the apex. **SCBs**: living cells containing small, globose to rectangular (cubical to hexagonal), refractive bodies 0.7–1.5 µm, rarely 2–3 µm diam. **Trapping organs**: capturing nematodes by globose sessile adhesive knobs formed on conidia or hyphae erupting from the host's body, 1–5 knobs at dorsal side of conidia, also on apical cell, sessile, globose, *7.5–9 µm diam. (†7–7.5 µm {Hungary}); adhesive knobs on assimilative hyphae breaking through the cuticle of the nematode, globose to elliptic, †8–12 × 6–8 µm, sometimes short-stalked with a broad basal cell. **Chlamydospores** globose, 16.5–36.5 µm diam. {Hungary}.

Habitat: ~1–2 m above the ground, on standing living trunks or dead, corticated, rarely decorticated, ~2–30 cm thick xeric twigs and branches of *Cercis siliquastrum* {2}, *Cornus* sp. {2}, *Elaeagnus angustifolia* {3}, *Fagus sylvatica* {1}, *Gymnocladus dioicus* {1}, *Platanus* × *acerifolia* {3}, *Populus ?balsamifera* {1}, *Salix* sp. {1/1}, *Sorbus aucuparia* {1}, *Taxus baccata* {1}, *Thuja plicata* {1}, on bark {10} or wood {1}, rarly boring dust {1}, mycelium repeatedly observed to emerge from infected nematodes. **Associated**: *Claussenomyces* sp. {1}, *Hyalorbilia helicospora* {1}, *Hysterobrevium mori* {1}, *Nitschkia broomeana* {1}, *Orbilia arachnovinosa* {1}, *O. cejpii* {1}, *O. cercidicola* {1}, *O. flagellispora* {1}, *O. gambelii* {1}, *O. myriolentiformis*

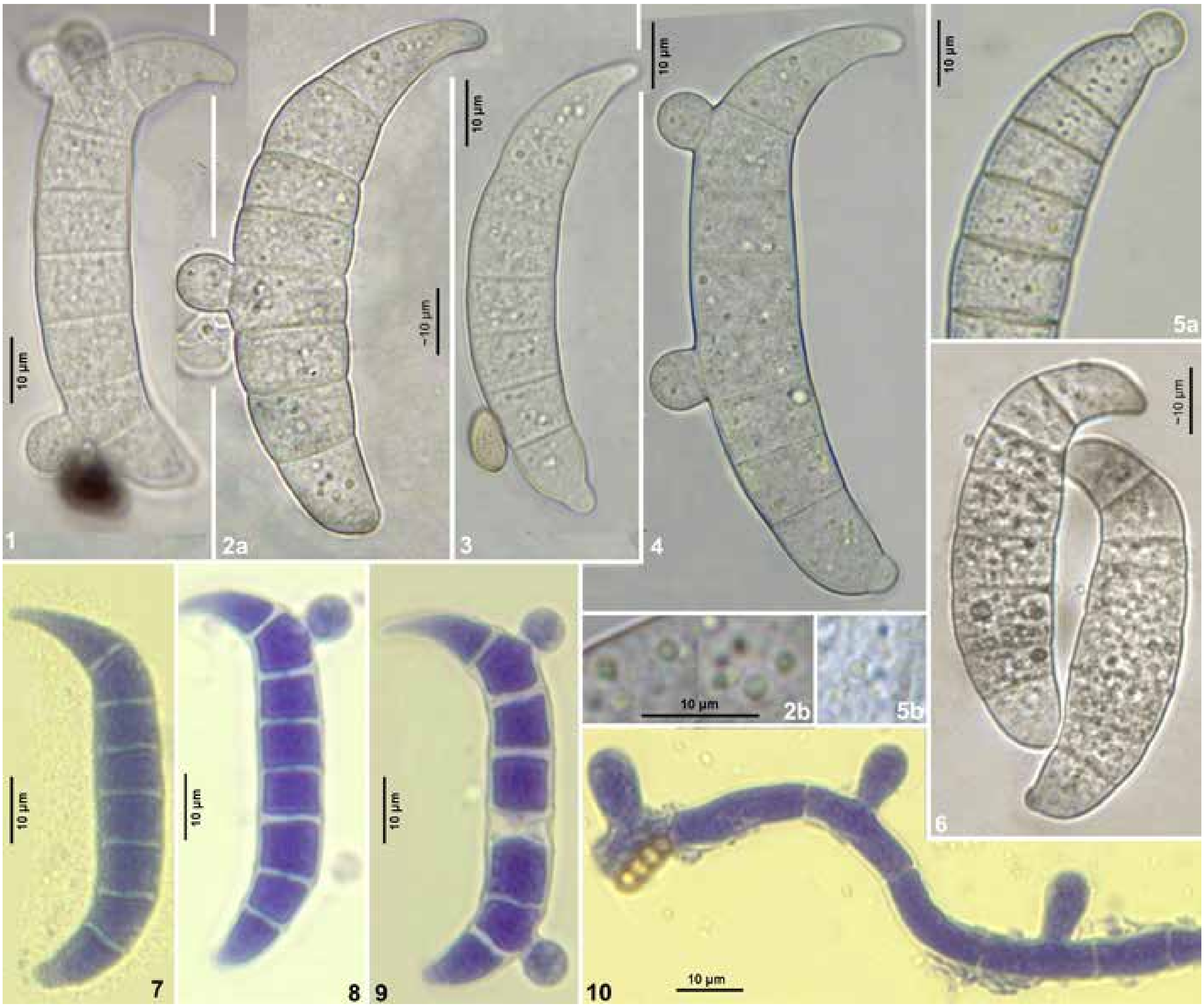


Plate 52. **1–10**: *Lecophagus vermicola*. – **1–9**. conidia with sessile adhesive knobs; **10**. hypha with adhesive knobs; **2b**, **5b**. cubical SCBs in conidial cells. – Living (**1–6**) and dead state (**7–10**, in methylene blue). — **1**. VIII.2005: Luxembourg, unlocalized, substrate unknown; **2a–b**. 9.X.2002: France, Venasque, on *Cornus*; **3**. 27.VII.2005: Luxembourg, Alzingen, on *Fagus*; **4**. H.B. 9151k: France, Nyons, on *Cercis*; **5a–b**. 19.III.2005: Luxembourg, Berchem, on *Thuja*; **6**. undated, unlocalized; **7–10**. BP 107927, Hungary, Budapest, on *Platanus* (holotype).

{1}, *O. myriosphaera* {1}, *O. ocellata* {1}, *O. subaristata* {1}, *O. subclavuliformis* {1}, *O. trapeziformis* {1}, *O. vinosa* {1}. **Drought tolerance**: conidia survive in the dry state for probably several months. **Altitude**: 114–485 m a.s.l. (Europe), 30 m (North America). **Geology**: Canada: Permian sedimentary rock; Europe: Keuper & Lower Jurassic sandstone & Minette, Cretaceous limestone, Miocene sandstone; granitoid granulite & gneiss. **Phenology**: I, III, V, VII–XI (throughout the year).

Taxonomic remarks. *Lecophagus vermicola* forms very large conidia which produce laterally or apically 1–5 sessile, globose adhesive knobs, apparently without presence of nematodes. Uninfected nematodes added to conidia on the natural substrate, which was rehydrated with distilled water, were trapped by the adhesive and got invaded by the fungus, while germination of conidia without presence of nematodes was not observed.

Conidia of *L. vermicola* resemble those of *Lecophagus navicularis* but are distinctly larger and have 5–8 septa instead of (2–)3, also they are formed in much smaller number on the conidiophores. Cubical bodies are regularly present in the living cells (Pl. 52: 2b, 5b). In the samples from Luxembourg and France only conidia were observed, which were detected by one of us (G.M.) on bark of xeric branches of various angio- but also gymnosperms (Pl. 52: 1–6). D. Magyar demonstrated that the fungus captures nematodes on xeric bark (Magyar et al. 2016). Apothecia of a presumed teleomorph could never be observed in association.

Haptocara latirostrum s.l. (see below) has similar conidia which deviate in having a single sessile adhesive knob at the apex when still on the conidiophore, and by forming a lateral hyphal appendage at their apical cell already before the knob appears.

Variation. The rather strong size difference between Hungarian and Luxembourg samples is in part due to the shrinking effect. The extent of shrinkage was so far only tested for conidia from Canada (A. Carter pers. comm.), measuring *~57–68 × 15–17(–19?) µm vs. †58–63 × 12.5–15 µm which is a ~3% shrinkage in length and 12–18% in width.

Phylogeny. A sequence of *L. vermicola* from Hungary comprising ITS and LSU falls in the *Lecophagus-Amphosoma* clade, showing in the ITS region a distance of 17–23 % to the so far sequenced typical species of *Lecophagus*, which is not higher than the distance between them (~15–17 %). In the LSU (D1–D2) the distance is 2.2–3.2 % to typical *Lecophagus* species (to other genera, e. g. to *Amphosoma*, the minimum LSU distance is 7 %).

Ecology. Conidia of *Lecophagus vermicola* were harvested on bark of xeric branches and trunks of different angio-, rarely gymnosperms in subcontinental, cold- to orotemperate humid and mesosubmediterranean semihumid Europe, and in cold-temperate humid eastern Canada.

Specimens included. **LUXEMBOURG**: **Gutland**, **Esch-sur-Alzette**, 8 km S of Luxembourg, 1 km NW of Berchem, Angelsbierg, 295 m, trunk of *Thuja plicata*, on bark, 19.III.2005, G. Marson (ø). – 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, on *Cornus*, 17.VII.2001, G. Marson (ø). – **Luxembourg**, 6.5 km SE of Luxembourg, 2.5 km ESE of Alzingen, Kircheboesch, 316 m, trunk (or branches?) of *Fagus sylvatica*, on bark, 27.VII.2005, G. Marson (ø). – 11 km ESE of Luxembourg, 2 km E of Oetrange, Draf, 268 m, branch of *Salix*, 8.IX.1998, G. Marson (ø). – 3 km NE of Luxembourg, 1 km NE of Kirchberg, Kirchbierg, 350 m, branch of ?*Salix*, 25.VIII.1998, G. Marson (ø). – 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, host not noted, on bark, 19.XI.2000, G. Marson (ø). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, Col du Pontias, 460 m, branch of *Cercis siliquastrum*, on boring dust, 13.VIII.2009, G. Marson, H.O. Baral, B. Liu (H.B. 9151k, ø). – **Loire**, 1.9 km NNE of Le Bessat, 1145 m, branch of *Sorbus aucuparia*, 13.IX.2018, G. Marson (G.M. 2018-09-13.3). – **Provence-Alpes-Côte d'Azur**, **Vaucluse**, 14 km SE of Carpentras, 4 km SE of Venasque, Aire de Pic-Nique de Venasque, 485 m, branch of *Cornus*, 9.X.2002, G. Marson (ø). — **HUNGARY**: **Pest**, unlocalized, trunk of *Gymnocladus dioicus*, on bark, 28.VI.2009, D. Magyar (ø). – 4.5 km SE of Budapest, 114 m, trunk of *Platanus × acerifolia*, on bark on infected nematodes, 24.VII.2011, D. Magyar (BP 107927, **holotype**). – ibid., 21.VII.2011, D. Magyar (K07/15). – ibid., 16.V.2013, D. Magyar (K07/36; sq.: KU955283 [MD12], KU955284 [MD19]). – ibid., trunk of *Cercis siliquastrum*, on bark, 25.VII.2008, D. Magyar (ø). – ibid., trunk of *Taxus baccata*, on bark, 5.V.2012, D. Magyar (ø). – 5 km NE of Budapest, 113 m, trunk of *Elaeagnus angustifolia*, on bark, 20.VII.2008, 20.III.2009, 20.IX.2009, D. Magyar (ø). — **CANADA**: **Prince Edward Island**, 7.7 km SSW of Charlottetown, Cumberland, 30 m, branch of *Populus* ?*balsamifera*, on wood, 5.I.2019, A. Carter (doc. vid.).

Haptocara Drechsler, Am. J. Bot., Suppl. 62: 1073 (1975)

Type species: *H. latirostrum* Drechsler

Etymology: *Haptocara*: from the capture of nematodes by means of an adhesive bulb at the conidial apex; *latirostrum*: referring to the broad adhesive bulb ('wide beak').

Description (according to Drechsler 1975, modified): — **TELEOMORPH**: unknown. — **ANAMORPH**: **Mycelial hyphae** *4–13 µm wide, septate, hyaline, scanty. **Colonies** slow-growing (maize-meal agar). **Conidiophores** *40–80 × 6.5–9 µm, apically not narrowed, septate only at base, unbranched, conidia formed in apical parallel clusters of ~3 from broad inconspicuous loci, conidiogenesis synchronous. **Conidia** phragmosporous, *(24–)30–38 × 9–10(–11) µm (excluding knob), with 2 septa near the middle, inequilateral to slightly curved, subapically forming 1 lateral, filiform, nonseptate **hyphal appendage** *24–34 × 1.7–2 µm directed ± downwards, apically later developing a broadly ellipsoid to subglobose **adhesive knob** of *8–9.5 × 6–7 µm, eventually (2–)3(–4)-septate. **Trapping organs**: capturing nematodes by small globose adhesive knobs on short lateral branches of the mycelium, or, more often, by the larger subglobose adhesive knobs on the conidia; extending an infection tube to the animal, producing only one endozoic hypha 4–13 µm wide.

Habitat: isolated from plant remains from a ruderal roadside, capturing nematodes. **Desiccation tolerance**: unknown. **Altitude**: 40 m a.s.l.

Recognized species: 1, plus 1 unnamed species.

Taxonomic remarks. The above description is based on the type species, *H. latirostrum* (Pl. 53: 3). A short generic characterization is given on p. 235. *Haptocara* is probably very closely related to *Lecophagus*, if not conspecific, but molecular data were not available. It is mainly the conidial hyphal appendage and the less curved conidia that distinguish *H. latirostrum* from *L. vermicola*, to which it is otherwise very similar.

Cubical bodies in the conidial cells are not or only indistinctly seen in Drechsler's (1975: fig. 12c) drawing which was undoubtedly made on living cells. In any case, they are clearly visible in another, apparently undescribed species of *Haptocara*, here referred to as *H.* aff. *latirostrum*, which has very similar

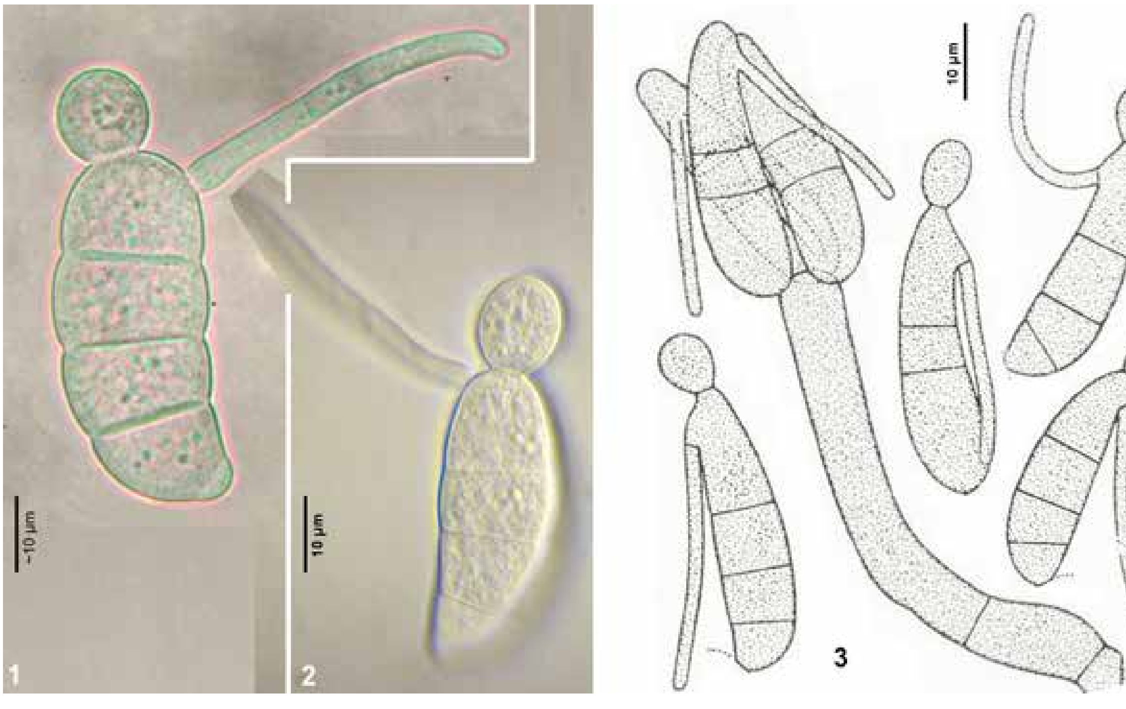


Plate 53. **1–2**: *Haptocara* aff. *latirostrum*; **3**: *H. latirostrum*. – Conidiophore and conidia with sessile adhesive knobs (**1–3**) and hyphal appendages (**1–3**; all in living state). — **1**. 3.II.2007: Luxembourg, Beaufort, on *Fagus*; **2**. 20.III.2003: France, Nyons, on *Cercis*; **3**. from Drechsler (1975), holotype.

conidia, differing in much larger (*~38–47 × 15–20 µm), consistently 3-septate conidia of a somewhat different shape, the hyphal appendage projecting more upwards and the knob of more (sub)globose shape (Pl. 53: 1–2).

Conidia of *H.* aff. *latirostrum* were found at least two times on xeric branches and trunks of angiosperms in cold-temperate humid and mesosubmediterranean semihumid Europe. Although conidiophores have not been seen, the conidia were undoubtedly formed on the xeric substrate and found to be viable when later examined, suggesting considerable drought tolerance of this species.

Haptocara latirostrum: **USA**: **Maryland**, 16 km NE of Washington DC, Beltsville, 0.5 km S of National Agricultural Library, roadside, 40 m, obtained from indet. plant material on agar, 28.V.1969, C. Drechsler (**holotype**, doc. vid.).

Haptocara* aff. *latirostrum: **LUXEMBOURG**: **Gutland**, **Echternach**, 10 km WNW of Echternach, 1.2 km SW of Beaufort, Längt, 340 m, trunk of *Fagus sylvatica*, on bark, 3.II.2007, G. Marson (ø). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, le Devés, 460 m, branch of *Cercis siliquastrum*, ~20. III.2003, G. Marson (ø).

Bryorbilia Baral & E. Rubio, **gen. nov.**, MB 825640

Type species: *B. arenicola*

Etymology: referring to the associated growth with a moss and the relationship to the genus *Orbilia*.

Latin diagnosis: *Apothecia in statu vivo 0.4–0.5 mm diam., orbicularia, sessilia, tota alba, hymenio plano, margine subglabro. Asci fusoideo-clavati, apice conico-truncati, in statu emortuo maturitatem tenuitunicati sed immaturitatem ad latera crassetunicati, non amyloidei (IKI), octospori, stipitati, bifurcati. Ascosporae distichae in asco viventi, ellipsoideae, clavatae, vel ovoideae, aseptatae, hyalinae, in statu vivo plures corpuscula refringentia, globosa continentes. Paraphyses ad apicem plus minusve clavatae, flexuosae, plerumque rostratae, ramosae, corpusculum refringentem unum globosum continentes, exsudato hyalino tectae, non cohaerentes. Excipulum ectale e textura globulosa-prismatica tenuitunicata. Habitat ad solum argillaceum inter muscum* Ceratodonis purpurei *Europae occidentalis*.

Recognized species: *B. arenicola*.

Bryorbilia arenicola E. Rubio & Baral, **sp. nov.**, MB 825641 — Pls 54–55

Etymology: referring to the sandy soil on which it grows.

Typification: Spain, Asturias, Carcedo de Lomes, on sandy soil among *Ceratodon purpureus*, 11.III.2017, E. Rubio (ex E.R.D. 6987 & ex H.B. 10121, AH 52844, holotype, sq.: MK514443, MK514443).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.4–0.5 mm diam., 0.21 mm high, white, slightly translucent, subturbinate, round, non-gelatinous, scattered; disc flat, margin distinct, thin, finely rough; broadly sessile to substipitate. **Asci** *82–99 × 9.5–11 µm, †(60–)70–80(–93) × 6–7(–8) µm, 8-spored, fusoid-clavate, spores obliquely biseriate, lower spores not inverted, pars sporifera *~50 µm long, †27–35 µm; **apex** (†) conico-truncate irrespective of the viewing direction, thin-walled (in KOH 0.3 µm), entire lateral wall thick-walled when mounted in KOH (0.4–0.5 → 0.6–1 µm), immature with a ring-like plasmatic structure; **base** with (*) short and thick, (†) short to long and thin, often flexuous stalk, bifurcate (h- to H-shaped), arising from simple septa. **Ascospores** *9–13(–14) × (4–)4.5–5.2(–5.5) µm, †8.5–12 × 3.5–4.5(–5) µm, non-septate, smooth, narrowly ellipsoid to clavate-ovoid, both ends rounded to obtuse, straight; **SBs** numerous (~20–30), 0.5–1 µm diam., globose, attached to wall all over the spore, together with 1 **LB** 1–2.7 µm in each half; overmature *10–10.5 × 5.5–7 µm, †9.5–12.5 × 4.3–5.5 µm, during germination 0–1-septate, germ tubes moniliform and irregularly bent. **Paraphyses** apically uninflated or usually slightly to medium clavate to spathulate, often beaked, sometimes 2–3-lobed, always ± flexuous, terminal cells *17–27 × 2.5–4 µm, lower cells *(7–)10–14 × 1.7–2.5 µm; sometimes branched at upper septum, not immersed in gel. **Medullary excipulum** 80–110 µm thick, of dense, small-celled non-gelatinized textura angularis-intricata, medium sharply delimited from ectal excipulum by a thin t. prismatica. **Ectal excipulum** at base and lower flanks of (*) thin-walled t. globulosa-prismatica, 35–40 µm thick, oriented at a (10–)30–50(–80)° angle to the surface, cells *7–14 × 4.5–9.5 µm, 20 µm at mid flanks and margin, of t. prismatica oriented at 10–50°, cells *10–24 × 7–12 µm, marginal cortical cells *9–15 × 3–5 µm, †9–13 × 2.5–4.3 µm, *thin-walled, in KOH slightly gelatinized; **glassy processes** and **hairs** absent. **Anchoring hyphae** medium abundant at base, hyaline, †1.5–2.5 µm wide, walls 0.2 µm thick, smooth. **VBs** absent. **SCBs** globose, 2–2.8 µm diam., subapically and singly in each paraphysis. **Exudate** over paraphyses and marginal excipulum 0.7–1.5 µm thick, cloddy, loosely attached, hyaline. **— ANAMORPH**: unknown.

Habitat: on burnt, sandy soil under *Ceratodon purpureus*, green algae abundant below apothecia. **Associated**: *Octospora rustica*. **Desiccation tolerance**: probably desiccation-intolerant, dead in all parts after 3 months in dry state. **Altitude**: 692 m a.s.l. **Phenology**: III. **Geology**: Neoproterozoic sandstone, slate & greywacke.

Taxonomic remarks. *Bryorbilia arenicola* resembles members of *Helotiales* in shape of ascospores and upper part of asci, but it discloses its genuine relationship in having a bifurcate, h- to H-shaped ascus base (Pl. 55: 1i), apically inflated and flexuous paraphyses with globose SCBs (Pl. 55: 1j–l) reminiscent of, e. g., *Orbilia* section *Ovoideae*, and KOH-soluble guttules (SBs) in the spores (Pl. 55: 1m). The large spore drops sometimes seem to be situated in the middle of each spore half, but in such cases they are actually out of focus while under another viewing direction they appear closely associated with the lateral spore wall. On the other hand, in a later reexamination two large drops remained visible in KOH (Pl. 55: 1p), suggesting that they were LBs, whereas other spores appeared in H_2O or IKI like vacuolated (Pl. 55: 1n–o). No tests with KOH or CRB were undertaken when studied in the fresh state (E. Rubio pers. comm.). In order to better understand the nature of the small and large drops in the spores, future collections should be studied in different reagents.

The inamyloid ring-like structure at the ascus apex (Pl. 55: 1e) was only seen in a few immature asci. Because of its obviously cytoplasmic nature it cannot be homologous with amyloid or congophilous apical rings which always represent a component of the ascus wall.

Phylogeny. A BLAST search for ITS or LSU yields only *Orbiliomycetes* as closest hits, although in the ITS region solely the 5.8S did align. When analysing SSU+ITS+LSU, *B. arenicola* clustered with *Amphosoma, Retiarius*, *Lecophagus*, and *Lilapila* in a weakly supported clade (Phyl. 2), whereas in separate analyses of ITS and LSU it stands unresolved (Phyls 3–4). In our analysis of LSU, seven uncultured fungus clones from Papua New Guinea, Madagascar, Panama, Puerto Rico, and Chile, submitted by Tedersoo et al. (2017) to GenBank, comprising LSU, ITS and mostly SSU, and one by Mueller et al. (2014) from North Carolina (only LSU), belong to at least four unknown species and cluster in the strongly supported *Bryorbilia* clade (Phyl. 4, B2–B5), though with a distance in the D1–D2 domain of 7–18% to each other (called GS33 clade by Tedersoo et al.). Also when analysing the ITS region, they cluster together but with only low support (Phyl. 3).

Various further uncultured fungus clones from America and one from Australasia, from the studies by Hartmann et al. (2009, 'LTSP_EUKA'), Jumpponen et al. (2010, 'OTU'), Mueller et al. (2014, 'NCD_LSU_otu'), Tedersoo et al. (2017, 'GL'), and Urbina et al. (2010, 'OTULB'), comprise ITS2 and/or LSU

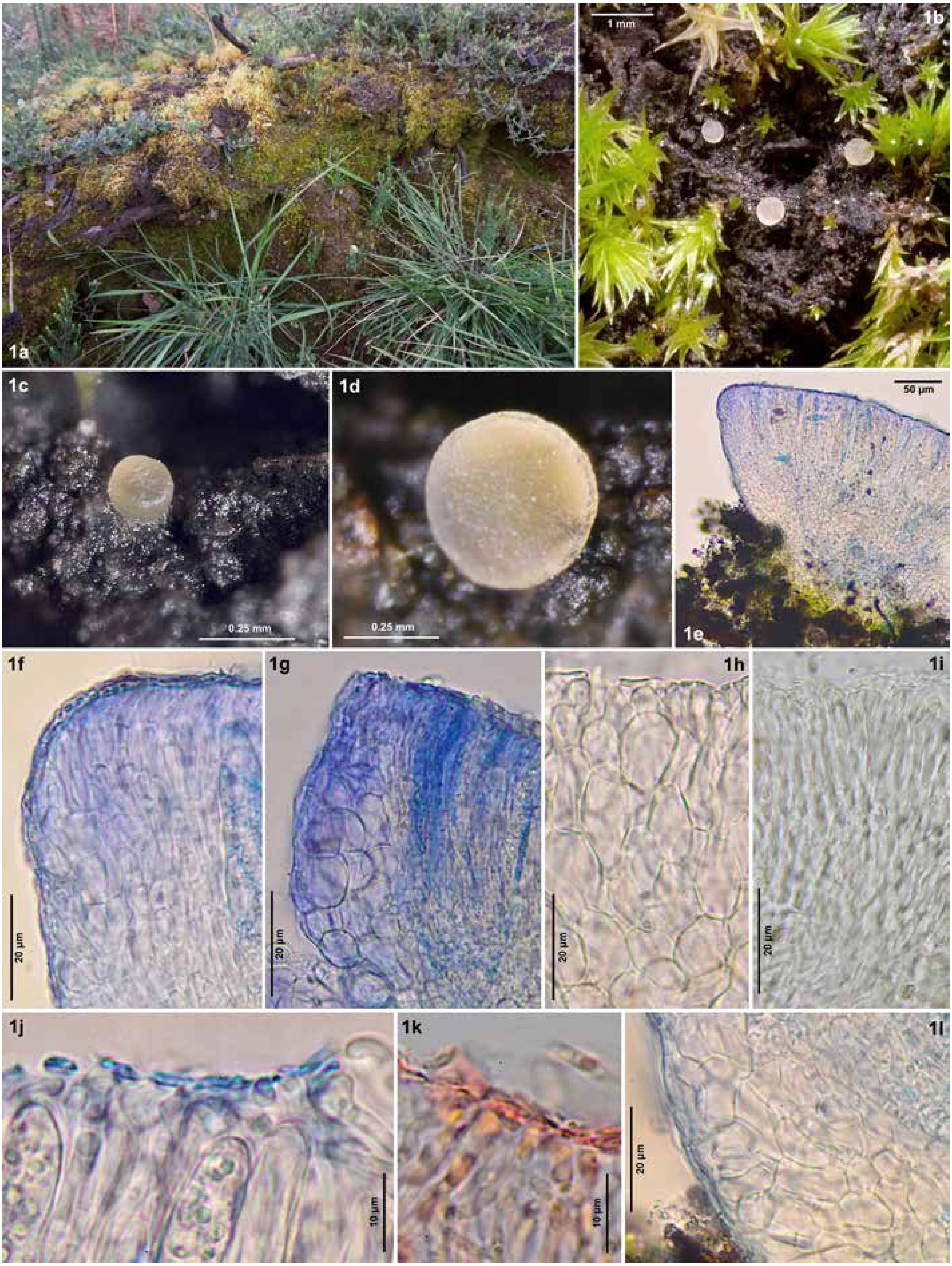


Plate 54. **1**: *Bryorbilia arenicola* (holotype). – **1a**. Burnt down *Quercus robur-Betula celtiberica* forest with *Ulex europaeus*, poor sandy soil covered by *Ceratodon purpureus*, *Funaria hygrometrica* etc.; **1b**. fresh apothecia on burnt soil between *C. purpureus*; **1c–d**. fresh apothecia; **1e**. apothecium in median section; **1f–g**. id., marginal ectal excipulum; **1l**. do, at flanks; **1h–i**; marginal ectal excipulum in external view; **1j–k**. upper part of hymenium with exudate (stained). – Living state (**1e–g**, **j**, **l** in CRB), except for **1i** (in KOH), **1k** (in CR). – **1a–h**, **j–l**: phot. E. Rubio. — **1a–l**. E.R.D. 6987: Spain, Asturias, on soil.

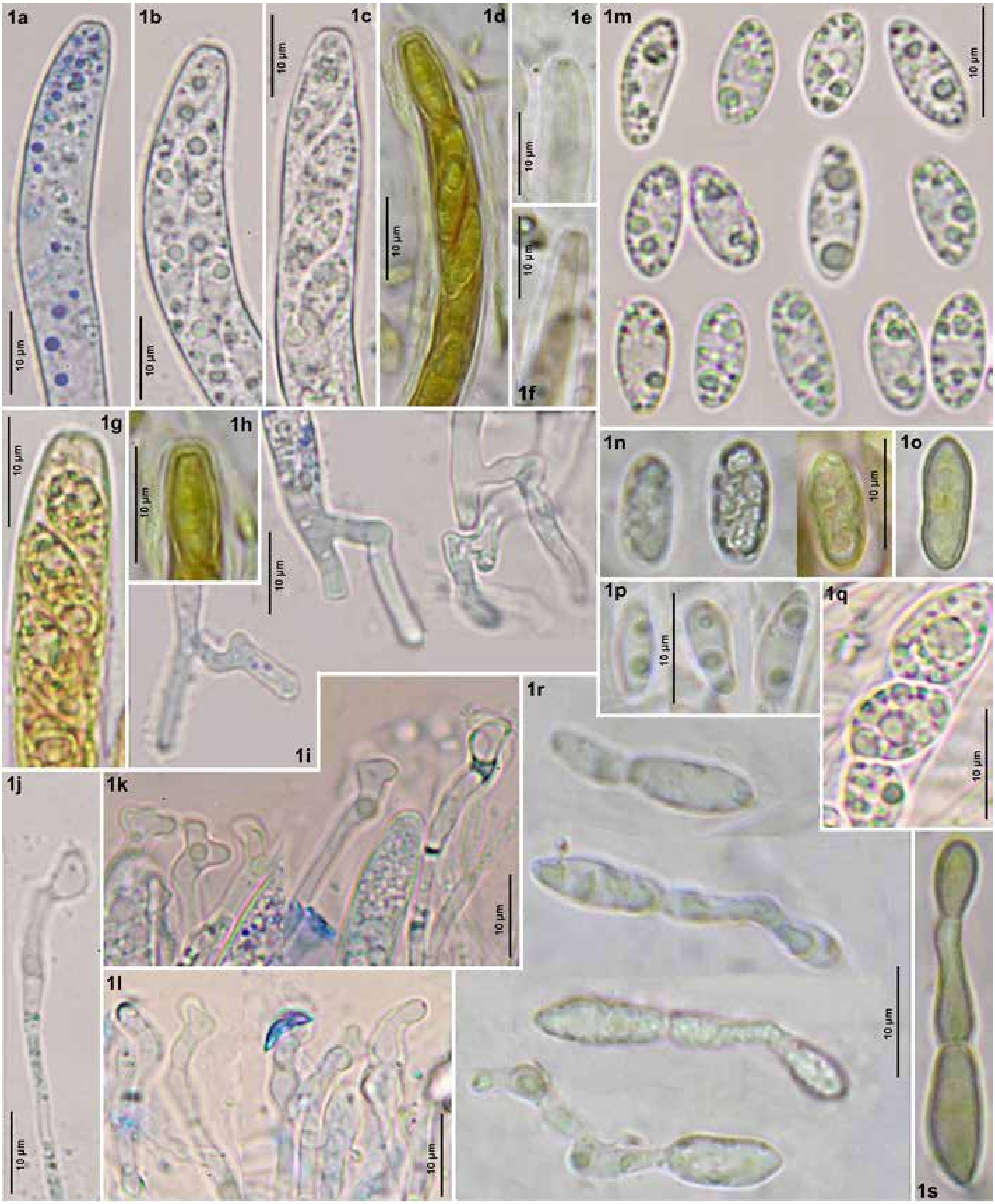


Plate 55. **1**: *Bryorbilia arenicola* (holotype). – **1a**, **e–f**. upper part of young asci; **1b–d**. upper part of mature asci; **1g–h**. ascus apices; **1i**. ascus bases; **1j–l**. paraphyses; **1m–p**. mature ascospores; **1q**. swollen, overmature ascospores within ascus; **1r–s**. germinating ascospores. – Living state (**1a**, **i**, **k**, **l** in CRB), except for **1d**, **h**, **o**, **s**, spores in **1g** (in IKI), **1n**, ascus in **1q** (in H_2O), **1p**, **r** (in KOH), **1e–f** (in KOH+CR). – **1a–c**, **g**, **i–m**, **q**: phot. E. Rubio. — **1a–s**. E.R.D. 6987: Spain, Asturias, on soil.

and clustered unresolved and distant from the *Bryorbilia* clade (U1–U4, U7). That they belong to *Orbiliomycetes* is supported by their motifs in the *Orbilia*-specific primer regions (Tabs 18–19) and by BLAST searches for each gene region. In our phylogenetic analyses a strongly supported clade is obtained (Phyls 3–4, U1 clade) which Tedersoo et al. named GS32 clade, but some other strains clustered separate hereof.

Specific nucleotide positions. In the Orb5.8s1F primer region, *B. arenicola* concurs with members of *Amphosoma*, *Lecophagus*, *Lilapila*, *Retiarius*, and the *Vermispora* clade of

Hyalorbilia, whereas in the other two *Orbilia*-specific primers and in stem-loop B8 of 5.8S it differs from all other taxa of *Orbiliomycetes* in at least 1 nucleotide position, and in and around the LR4 primer even in 5 positions (Tab. 21).

Five of Tedersoo's seven uncultured clones match *B. arenicola* in the Orb5.8s1F primer, while two (KY687745, KY687746, [B2]) differ at 1 position (Tab. 18). In the Orb28s2R region most of them concur with *Hyalorbilia erythrostigma* and a majority of *Orbilia*, and also in Orb5.8s3F they deviate by 1–3 nt from *B. arenicola* (Tabs 18–19). Very remarkable is that all those four clones which cover the D3 domain, including the L4 primer region, fully match *B. arenicola* in all 5 aberrant nucleotides around this primer, two of them being part of the primer region (Tab. 21). Only a few members of *Dothideomycetes*, *Lecanoromycetes*, *Leotiomycetes*, and *Xylonomycetes* were found to concur with *Bryorbilia* at the 2 aberrant positions within the LR4 primer. The paired change of nucleotides in this primer region, which is also observed in *Orbilia septispora*, though at adjacent positions, is due to base pairing between reverse-complementary motifs in a stem-loop, here the stem-loop H700 of LSU (see Gillespie et al. 2005).

Other motifs specific to the *Bryorbilia* clade are difficult to find. Predominant motifs in the LSU are CT**T**GGATGCT or CT**C**GGATGCT in the D2 (pos. 605) and **GA**CTGTTGGGA in the D3 (pos. 784–785) vs. mostly CT**A**GGATGCT (D2) and **AG**CTGTTGGGA or sometimes **GG**CTGTTGGGA (D3) in other *Orbiliomycetes*.

Ecology. *Bryorbilia arenicola* grew on poor acidic sandy soil among the moss *Ceratodon purpureus*, together with apothecia of *Octospora rustica*. The soil was burned 2 years ago and is now colonized by *C. purpureus*, *Funaria hygrometrica*, and other pioneer mosses. Before the fire, the place was covered with *Quercus robur* and *Betula celtiberica*, now young *Ulex europaeus* is growing. Whether a connection between *Bryorbilia* and *Ceratodon* exists was not investigated. The holotype now contains only a single apothecium without the moss, but it seemed clear in the field that the fungus has close relations to it. The location lies in the suprasubmediterranean slightly semihumid atlantic Cantabrian Mountains of Asturias (southwestern Europe).

Specimens included. **SPAIN**: **Asturias**, Allande, 3.5 km NNW of Cangas del Narcea, 1.2 km WSW of Carcedo de Lomes, 692 m, on burnt, sandy soil among *Ceratodon purpureus*, 11.III.2017, E. Rubio (ex E.R.D. 6987, ex H.B. 10121, AH 52844, **holotype**, sq.: MK514443, MK514443).

Pseudorbilia Ying Zhang, Z.F. Yu, Baral & K.Q. Zhang, Fungal Diversity 26: 306 (2007)

Type species: *Pseudorbilia bipolaris* Ying Zhang et al.

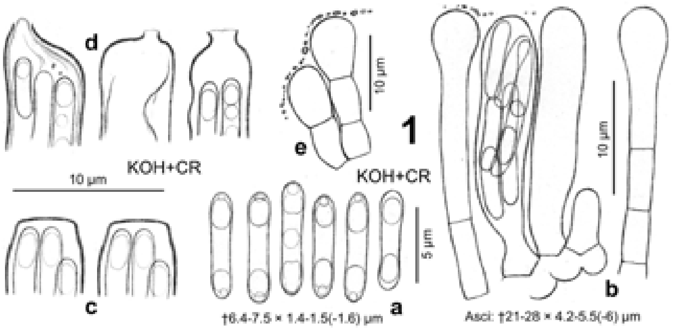
Etymology: named after its similarity to the genus *Orbilia*.

Recognized species: *P. bipolaris*.

Pseudorbilia bipolaris Ying Zhang, Z.F. Yu, Baral & K.Q. Zhang, Fungal Diversity 26: 307 (2007) — Pls 56–57

Etymology: referring to the bipolar arrangement of the spore bodies within the ascospores.

Typification: China, Yunnan, Yi Liang, wood of gymnosperm, IX.2005, Y. Zhang (ex H.B. 8310, M-0140896, holotype).



H.B. 8310 (holotype): China, Yunnan, on indet. coniferous tree (wood)

Plate 56. **1**: *Pseudorbilia bipolaris*. – **1a**. ascospores; **1b**. asci and paraphyses; **1c–d**. ascus apices (**d** apically opened); **1e**. marginal ectal excipulum (median section). All elements in dead state.

Description: — **TELEOMORPH**: **Apothecia** 0.09–0.2(–0.35) mm diam., ~0.07–0.1 mm thick (receptacle 0.055–0.07), whitish to pale cream-yellowish, medium translucent, gregarious to fasciculate in small groups; disc flat to slightly convex, margin thin, smooth to very finely rough; superficial or with ± immersed, obconical, stipe-like base, dry light ochraceous. **Asci** *23.5–34 × 5.5–6.8 µm {2} or *31–41 × 7.5–8.5 µm {1}, †20–28 × 4.2–5.5(–6) µm {2}, 8-spored, spores (*) 2–4-seriate, pars sporifera *(9–)13–17(–19) {2} or *19.5–21 {1} µm; **apex** (†) medium to strongly truncate, but hemispherical to slightly or strongly conical in profile view, without apical thickening, rupturing by a central or eccentric pore; **base** with short, thick stipe, arising from croziers (without perforation) {2}. **Ascospores** *6.8–8.5 × 1.5–1.8 {T} or *(4.5–)5–6(–7) × 1.3–1.8(–2) {France} µm or *6.5–7.8 × 1.6–2.1 µm {Norway}, †6.4–7.5 × 1.4–1.5(–1.6) {T} or †5–6 × 1.3–1.5 {France} µm, cylindric-bacilliform to very slightly dumbbell-shaped, rounded at both ends, straight or sometimes very slightly curved; containing 2 ± lens-shaped refractive **SBs** broadly attached to the terminal spore wall, one at each end, *0.6–1 × 1.3–1.8 µm {2}, *0.4–0.5 × 0.9–1.1 µm {1}, inner surface of SBs ± flattened; containing also 2 subterminal, large, ellipsoid, non-refractive **vacuoles**, one in each half, selectively staining violet in CRB (Pl. 15 Fig. 1g), vacuoles in dead spores still visible when mounted in KOH+IKI (light yellowish-brown, refractive) or KOH+CR (light purplish-red, Fig. 1f, h). **Paraphyses** not embedded in gel, apically (*) uninflated or slightly capitate-clavate (†slightly to medium so), terminal cells *12–19 × 3.8–4.5 µm {1}, †11–19 × 3–5 µm {2}, lower cells †(2–)4–7(–10) {2} × 2–2.2(–3) {T} or 2.5–3(–4.5) {1} µm. **Medullary excipulum** hyaline, ~10–15 µm thick, of dense, not or ?slightly gelatinized t. intricata. **Ectal excipulum** pale yellowish-ochraceous near base (very pale so at flanks), of (†) ± thin-walled, indistinctly (?vertically) oriented t. globosa-angularis from base to mid flanks, ~10–30 µm thick, cells †6–18 × 5–11 µm {2} (in surface view partially tangentially elongated), at margin 6–8 µm thick, of t. prismatica-angularis oriented at a ~10–30° angle to the surface, marginal cortical cells †5–9 × 4–6 {T} or †11–15 × 5–7 {1} µm, thin-walled, **glassy processes** and **hairs** absent. **Anchoring hyphae** sparse, †1.2–2.5 µm wide, wall 0.1–0.2 µm thick {2}, sparsely septate. **VBs** in terminal cells of paraphyses large, very elongate, hyaline, refractive. **Exudate** over paraphyses and margin absent or scattered, granular, 0.2–0.5 µm thick, hyaline, at lower flanks continuous, 0.2–0.3 µm thick, pale yellowish-ochraceous. **— ANAMORPH**: unknown.

Habitat: lying on the moist ground, decorticated, thick branch of unidentified conifer {T}, on deeply very decayed wood (ungreyed, no algae) {1}; on necrobiotic leaves of ?*Hypnum cupressiforme* {1}, on 1 cm thick branch of *Ulex* sp. {1}, droppings of *Capreolus capreolus* {1}. **Associated**: *Orbilia rubrovacuolata* {1}. **Desiccation tolerance**: no elements viable after 3 weeks in the dry state. **Altitude**: 24–285 m a.s.l. (Europe), 1843 m (China). **Geology**: China: Paleozoic sedimentary rock; France: Ordivician sand- & siltstone; Norway: granite & quartzite. **Phenology**: III, IX–X.

Taxonomic remarks. *Pseudorbilia bipolaris* is easily recognized in the living state by its cylindrical ascospores containing two lens-shaped spore bodies, one at each end. The species includes characters typical of *Orbilia* (ectal excipulum of globose

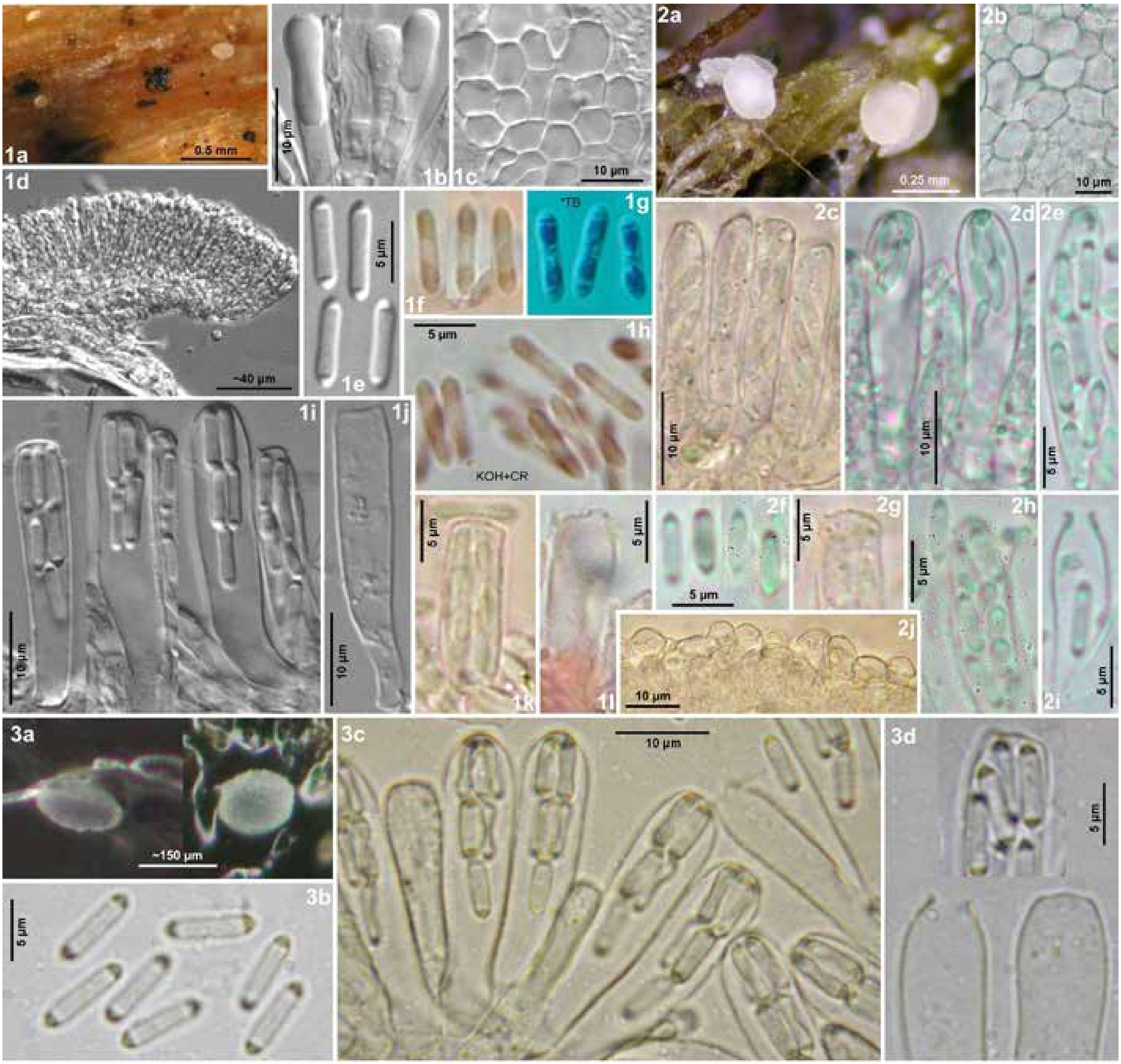


Plate 57. **1–3**: *Pseudorbilia bipolaris*. – **1a**, **2a**, **3a**. fresh apothecia; **1d**. apothecium in median section; **1c**, **2b**. ectal excipulum in external view; **2j**. margin in top view; **1b**. paraphyses; **1i**, **2c–d**, **3c**. mature asci; **1j**. young ascus; **1k–l**, **2g**, **i**, **3d**. ascus apices; (**1l**, **2i**, **3d**, below, emptied); **1e–h**, **2e–f**, **h–i**, **3b**. ascospores. – Living state, except for **1d**, **j**, **2j**, **3d** (asci) (in H_2O); **1k**, **2c**, **g** (in KOH); **1f**, **h**, **l** (in KOH+CR), right ascus in **1i**, asci in **2e**, **2h–i**. – **1a–e**, **g**, **i–j**: phot. Y. Zhang (DIC, p.p. in Zhang et al. 2007); **2a–b**, **d–f**, **h–i**: phot. J.P. Priou; **3a–d**: phot. M. Depont. — **1a–l**. H.B. 8310 (holotype): China, Yunnan, on indet. gymnosperm; **2a–h**. H.B. 8794: France, Bretagne, on ?*Hypnum*; **3a–d**. 3.X.2014: Norway, Arendal, on *Capreolus* dropping.

to angular cells, asci with a truncate, shouldered apex, hymenial elements not embedded in gel), but also characters typical of *Hyalorbilia* (asci arising from croziers, paraphyses containing large refractive vacuoles, spores with bipolar SBs). The genus *Amphosoma* resembles *P. bipolaris* in the bipolar arrangement of the lens-shaped SBs, but differs in rounded, mostly thick-walled ascus apices, the predominant absence of croziers, ellipsoid spores, and multiguttulate VBs in the paraphyses. Therefore, *P. bipolaris* is recognized in a separate genus.

Pseudorbilia bipolaris may easily be mistaken for a member of the *Helotiales*. The whitish translucent apothecia resemble genera of *Hyaloscyphaceae* such as *Calycellina*. The truncate, biradial-symmetrical ascus apex and the characteristic SBs in the living ascospores are the reason for including this species in the *Orbiliomycetes*.

Variation. The spores in the holotype vary between cylindrical and dumbbell-shaped with a very slight median constriction. The European collections fit quite well the holotype, particularly that from Norway, which differs in longer asci with a longer pars sporifera, although the spore characters are quite similar, and the apothecia only slightly smaller (90–150 µm diam. vs. 150–200 µm). The collection from France on bryophyte differs in shorter, not dumbbell-shaped spores with smaller SBs, longer marginal cortical cells, and the bryophilous habitat; also the apothecia tend to be larger (~150–350 µm). It might well represent a different species, but this cannot be decided at present based on the three sparse collections.

A correction is necessary for fig. 2 in the protologue (Zhang et al. 2007): the bar is not 10 µm as stated in the legend but 15 µm. Hardly any apothecia remain in the holotype, whereas the entire specimen from France was lost during examination, and that from Norway got destroyed in the mails.

Ecology. *Pseudorbilia bipolaris* is only known from three very sparse collections. The holotype was detected on a decorticated, very decayed hygric branch of a coniferous tree in a shady subtropical humid (winter-dry) forest in southeastern Asia. The two European collections were from a living moss on a hygric branch of an *Ulex* shrub in mesotemperate humid, atlantic western Europe and from excrements of *Capreolus* in hemiboreal northern Europe, both on acidic soil.

Specimens included. **CHINA**: **Yunnan**, **Kunming**, 37 km ESE of Kunming, 8.5 km WNW of Yiliang, Xiaobailong Forest Park, 1843 m, on wood of indet. gymnosperm, IX.2005, Y. Zhang (ex H.B. 8310, M-0140896, **holotype**). — **FRANCE**: **Bretagne**, **Morbihan**, 4.5 km SE of La Gacilly, 2.6 km E of Cournon, Pinguily, 24 m, branch of *Ulex europaeus*, on ?*Hypnum cupressiforme*, 19.III.2008, J.P. Priou (J.P.P. 28039 ø, H.B. 8794 ø). — **NORWAY**: **Aust-Agder**, 29 km NW of Arendal, NW of Ytre Lauvrak, 285 m, on droppings of *Capreolus capreolus*, 3.X.2014, J. Fournier, vid. M. Delpont (ø, doc. vid.).

Hyalorbilia Baral & G. Marson, Micologia 2000: 44 (2001)

Type species: *H. berberidis* (Velen.) Baral

= *Orbilia* subgroup *Spirospora* Velen. (part 'a', with unstalked asci), Monogr. Discomyc. Bohem.: 99 (1934, unranked) – Type: not designated

?= ***Vermispora*** Deighton & Piroz., Mycol. Pap. 128: 87 (1972) – Type species: *Vermispora grandispora* Deighton & Piroz.

= ***Dwayaangam*** Subram., Kavaka 5: 96 (1978) – Type species: *D. quadridens* (Drechsler) Subram. (≡ *Hyalorbilia quadridens*)

?= ***Curucispora*** Matsush., Matsush. Mycol. Mem. 2: 4 (1981) – Type species: *C. ponapensis* Matsush.

≡ *Cruciconidiifera* Matsush., Matsush. Mycol. Mem. 2: 145 (2005), replacement name for the intended spelling *Crucispora*, non *Crucispora* Horak (*Agaricales*)

= ***Brachyphoris*** Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu, Fungal Diversity 26: 128 (2007). – Type species: *B. oviparasitica* (G.R. Stirling & Mankau) Juan Chen, L.L. Xu, Bin Liu & Xing Z.Liu (≡ *Hyalorbilia oviparasitica*)

= ***Microdochiella*** M. Hern.-Restr. & Crous, Persoonia 36: 62 (2015) [2016] – Type species: *M. fusarioides* (D.C. Harris) M. Hern.-Restr. & Crous (Pl. 17)

Etymology: *Brachyphoris*: after the short conidiophores; *Curucispora*: referring to the cross-shaped conidia; *Dwayaangam*: named after the conidia with normally 4 arms formed by repeated dichotomous branching (from Sanskrit: 'dwaya' = 2, 'angam' = branch); *Hyalorbilia*: referring to the pale-coloured, ± translucent apothecia and the relationship to *Orbilia*; *Microdochiella*: after the morphological similarity with *Microdochium*; *Spirospora*: with curled ascospores (but Velenovský referred here taxa with falcate spores); *Vermispora*: after the worm-shaped conidia.

Description: — **TELEOMORPH**: **Apothecia** fresh (0.05–)0.1–2(–5) mm diam., (0.03–)0.05–0.25(–0.4) mm thick [receptacle (0.03–)0.05–0.13(–0.2) mm], whitish to often pale cream-chlorinaceous (chlorinaceous-yellow under LED), also light (to bright) yellowish- or orange-ochraceous, often ± translucent, not or very slightly to rather strongly gelatinous, sessile on a broad or narrow base but often substipitate on an obconical base, or with a distinct cylindrical stalk (0.01–)0.02–0.2(–0.5) × 0.04–0.4(–0.7) mm, disc cup- to saucer-shaped, or flat, finally sometimes convex, margin usually ± even, in large apothecia often undulating or notched, rarely crenulate or denticulate, exterior glabrous but sometimes hairy due to anchoring hyphae which are often seen (mainly in dry state) as a whitish subiculum, especially near the base, superficial, dry hardly to strongly contracted with incurved margin, more intensely ochraceous or yellow, sometimes red-brown. **Asci** *(13.5–)16–40(–50) × (3–)3.5–7(–8) µm, †(9–)12–40(–53) × (2.6–)3–6(–7) µm, 8-, rarely 16-spored, inverse spore orientation only rarely observed (if spores with 1 eccentric SB, or heteropolar in shape); **apex** of dead asci hemispherical or slightly (rarely medium) truncate or often subconical to submammiform, apical wall thin- to firm-walled (†0.2–0.4 µm); **base** with or without short, thick, not or only slightly flexuous stipe, consistently arising from croziers (some with a round to slit-like, rarely large, medaillon-shaped perforation). **Ascospores** *(2–)3–14(–17.5) × 0.7–2.8(–3.8) µm, non-septate, smooth, of various shape (cylindrical, fusoid to fusiform, fusoid-clavate, ellipsoid, subglobose to ovoid), never consistently heteropolar in shape, straight or slightly to strongly curved (falcate to helicoid); living spores with 1–4(–5) low- to high-refractive, globose (rarely subglobose, tear-, or lens-shaped) **SBs** in each half, especially near the ends, 0.2–1.2(–1.5) × 0.2–1(–1.5) µm, sometimes without SBs or only 1 eccentric SB present, attachment by a filum only exceptionally seen, if hemispherical then broadly attached to wall; usually a few minute **LBs** present; **glycogen** not observed; spores in senescent apothecia never seen to germinate or to form a septum. **Paraphyses** apically uninflated or slightly to medium, rarely strongly clavate(-capitate), terminal cells (1–)1.5–4(–5.5)× as long as lower cells, unbranched or often dichotomously branched (usually only in their lower part), anastomoses rarely seen near the base. **Subhymenium** not differentiated. **Medullary excipulum** hyaline, (5–)10–50(–110) µm thick, of non- or slightly to strongly gelatinized textura angularis-prismatica of small to medium-sized cells of usually indistinct orientation, partially also mixed with hyphae or purely t. intricata, indistinctly to very sharply delimited. **Ectal excipulum** hyaline, near base (10–)20–150(–250) µm thick, of ± vertically oriented t. angularis or t. prismatica, from lower flanks up to margin of horizontally oriented t. prismatica-porrecta, sometimes t. prismatica-angularis, exceptionally t. angularis (mainly in *H. subfusispora*, *H. resinae*, *H. rotifera*); texture in external view with a distinct radial orientation, individual cells never tangentially elongated (never wider than long); cells at flanks *(4–)8–45(–80) × (3–)6–25(–40) µm, walls (†) non- or slightly to strongly gelatinized (common walls †0.3–3 µm thick); 10–40(–80) µm thick at flanks, (5–)10–20(–30) µm thick at margin, marginal cortical cells narrowly cylindrical (t. porrecta) or often clavate to obovoid (vesiculous), exceptionally globose and thick-walled by forming denticulate protrusions; **glassy processes** absent, exceptionally with glassy caps (*H. nodulosa*); **septate hairs** absent. **Anchoring hyphae** sparse to often abundant at base, sometimes also at lower flanks, usually long and straight, radiating ± vertically from excipular surface, (1.3–)2–5(–10) µm wide, sparsely to rather densely septate, partially branching, sometimes anastomosing, walls smooth, 0.2–1(–2) µm thick. **Globose SCBs** usually absent (but refractive SCBs inconsistently observed in the excipulum in a few species, partially ring- or irregularly shaped); **crystalloid SCBs** rarely present in excipulum and anchoring hyphae (*H. ulicicola*); **VBs** usually abundant in paraphyses and marginal cortical cells, globose, medium-sized, slightly to medium refractive, hyaline to often pale chlorinaceous, later fusing to form large, angular or elongate bodies (also from the beginning large and elongate); **carotenoids** in LBs of paraphyses rarely present (*H. erythrostigma*, *H. anonyma*). **Exudate** forming a continuous, refractive, (0.1–)0.2–0.6(–1.2) µm thick layer over hymenium and marginal excipulum, exterior of exudate either ± smooth or usually densely covered by minute, angular, pale chlorinaceous granules or clods; paraphyses and asci usually conglutinated with the paraphyses in a hymenial **gel** (gel invisible, staining faintly to distinctly lilac in CRB), in some species freely separable. — **ANAMORPH**: mainly brachyphoris-like, also trinacrium-, curucispora-, or dwayaangam-like (the latter is presumed). **Mycelial hyphae** *1–5 µm wide, hyaline. **Colonies** ± slow-growing, whitish to yellowish or brownish, with ± aerial mycelium. **Conidiophores** emerging from mycelial hyphae, 1.5–50(–100) µm when unbranched, (1.5–)2–4(–7) µm wide at the base, (1–)1.3–2(–2.5) µm at the tip, up to 95(–200) µm when branched. **Conidiogenous cells** monoblastic or sometimes sympodial with 2–4 lateral nodules or denticles. **Conidia** predominantly unbranched (brachyphoris-like), cylindrical to narrowly-ellipsoid, or often fusoid to fusiform, straight or only slightly curved towards their ends, rarely flexuous to S-shaped, *(12–)20–96(–120) × (2–)3–8(–10) µm, (0–)3–8(–12)-septate; rarely branched: T-, Y- to K-shaped or 4-armed, *(10.5–)15–45 × 10–25 µm (in *H. quadridens* *75–95 × 61–77 µm), branches (1.2–)2–4(–4.5) µm wide, 0–2(–4)-septate, arms ± tapering, straight, also strongly curved (C-shaped); living cells often containing refractive globose **SCBs** 0.4–2 µm diam. aggregated in small groups (so far only seen in unbranched conidia); large **glycogen** regions sometimes present; wall surface either lilac or hardly stained by CRB.

Chlamydospores absent or present. **Trapping organs**: capturing rhizopods with adhesive knobs (so far known only in a few species), also invading nematode eggs and cysts, rotifers, and oospores of *Pythium*.

Habitat: saprobiontic on dead bark and wood, rarely woody fruits or herbaceous stems of mono- and dicots, often on dead or living fungal fruitbodies (perennial polypores, gelatinous basidiomycetes, pyrenomycetes, apothecia of *Orbilia* spp.), exceptionally on dung; substrate usually ± decomposed (optimal to often final stage), when fungicolous then partially parasitic; substrate permanently moist (hygric) or periodically dry (xeric, then sometimes in tight association with green algae and black yeasts); sometimes capturing testaceous rhizopods or parasitic on nematode eggs and oomycete oospores. **Desiccation tolerance**: mature asci intolerant or tolerating 1 week up to 3 months, immature asci rarely up to 11 months, excipular cells, ascospores and conidia a few days up to 1–5 months, rarely 11–17 months. **Distribution**: worldwide, in boreal-montane, temperate, subtropical or tropical, humid to semihumid, rarely semiarid climates, the highest species number observed in temperate to tropical (semi)humid regions, recorded from arctic-alpine areas so far only by DNA isolates.

Recognized species: 44 (7 of them without known teleomorph), plus 7 unnamed species (‘affinis’).

Generic concept. The genus *Hyalorbilia* forms a comparatively small, natural group within the *Orbiliomycetes*, being easily recognizable in almost every case. In the present monograph we accept 44 species, 7 of which being only known from their anamorph and 7 further unnamed taxa mentioned as *affinis* (aff.) under the related species. *Hyalorbilia* is sharply delimited from *Orbilia* based on various characteristics (Tab. 59), some of which occur with high consistency across the genus. The most important are: (1) spore bodies usually near both ends of the ascospores; (2) croziers always present at the ascogenous hyphae, sometimes perforated; (3) paraphyses and asci usually firmly embedded in gel; (4) numerous minute angular clods of exudate usually covering the gel surface on hymenium and margin; (5) ascus apex in dead state never distinctly truncate or thick-walled; (6) ectal excipulum at flanks of a horizontally oriented textura (angularis-)prismatica.

Morphologically, the anamorphs of *Hyalorbilia* and *Orbilia* are not easily distinguishable. Yet, many species of *Hyalorbilia* possess a rather uniform and quite diagnostic type of fusiform phragmoconidia, which were described under the names *Dactylella passalopaga*, *D. lignatilis*, *Brachyphoris oviparasitica*, and *B. brevistipitata*. In addition to their shape, these conidia often contain refractive, small, globose SCBs which are unknown in *Orbilia*, and which appear to be homologous to the cubical SCBs in *Lecophagus*.

The genera *Pseudorbilia* and *Amphosoma* resemble *Hyalorbilia* in some micromorphological characteristics, e. g., in their bipolar-symmetrical spore bodies (see Tab. 56), but they share also features with *Orbilia* (*Amphosoma*: furcate ascus base, *Pseudorbilia*: truncate ascus apex).

Within *Hyalorbilia*, a division into a small group of species with globose to subglobose ascospores and a large group with elongate ascospores could be made. However, the two groups are not clear-cut (see Pl. 58), and a correlation with features of the anamorph is not recognizable. Since the genus is rather poor in morphological characteristics, correlations of features are difficult to detect, and further subdivisions can hardly be made based on morphology alone.

With some experience the genus *Hyalorbilia* can be recognized in the field by the usually pale yellowish-chlorinaceous-brownish, often translucent, substipitate apothecia with a thin margin. By external appearance alone, however, *Orbilia* species with hyaline apothecia, such as *O. leucostigma*, can easily be confounded with members of *Hyalorbilia*. At the time the

Table 59. Comparison of characters of the teleomorph between *Hyalorbilia* and *Orbilia*.

		Hyalorbilia	*Orbilia*
1a	Asci	*(13.5–)16–40(–55) × (3–)3.5–7(–8) µm, 8(–16)-spored	*(24–)30–100(–140) × (2.8–)4–11(–15.3) µm, 8–128-spored
1b	Ascus base	unstalked or with short and thick stalks, arising from croziers	with short to very long, often thin and flexuous, usually furcate stalks arising from simple septa
1c	Apex of dead asci	hemispherical to slightly (rarely medium) truncate or conical, shape scarcely depending on the viewing direction, never with distinct internal wall thickenings	either hemispherical and ± thick-walled (often with an apical chamber), or ± saddle-shaped (truncate but hemispherical in profile view) and then usually thin-walled
2a	Ascospores	shape never predominantly heteropolar, never with a tail	shape homo- to strongly heteropolar, with or without a tail
2b	Spore bodies (SBs)	spore guttulation bipolar-symmetrical (one or more SBs near each spore end), rarely one eccentric SB per spore but then spores subglobose or ovoid, no clear inverse spore orientation	spore guttulation unipolar-asymmetrical (1 SB per spore), SBs inserted in spore apex, rarely laterally, inverse spore orientation frequent
3	Paraphyses	uninflated to slightly, rarely strongly capitate, not distinctly protruding beyond hymenial surface, terminal cells usually longer than lower cells, rarely of ± equal length	uninflated to strongly capitate, sometimes spathulate-lanceolate and then often distinctly protruding beyond hymenial surface (sometimes only the cap-like exudate), terminal cells longer than lower cells or ± equal with them
4a	Ectal excipulum	at flanks of horizontally oriented textura prismatica, rarely t. globulosa-angularis (cells isodiametric)	at flanks of vertically oriented t. angularis(-prismatica), very rarely of horizontally oriented t. prismatica
4b	Medullary excipulum	composed of isodiametric to prismatic cells, partly intermingled with hyphoid elements, sometimes purely of interwoven hyphoid elements	composed of interwoven hyphae, usually intermingled with inflated cells that form chains, sometimes purely of isodiametric cells
4c	Anchoring hyphae	usually ± straight, rarely forming strands, (1.3–)2–5(–10) µm wide	usually irregularly oriented, ± undulating, often forming a thick loose or dense layer or strands, (1.5–)2–3.5(–6) µm wide
5	Intercellular gel	hymenial elements often embedded in abundant gel, mostly very difficult to separate, medullary and ectal excipulum gelatinized or not	hymenial elements with a thin gel layer on the wall surface, therefore usually easy to separate, medullary and ectal excipulum rarely gelatinized
6	Exudate on exterior of apothecium	mostly present, hyaline to often pale yellowish-chlorinaceous, forming minute, ± angular granules or clods on a firm continuous layer, ~0.2–1 µm thick	present or absent, hyaline or pale to light yellow, rarely dark olive, continuous to granular or often cloddy, also forming individual caps, (0.2–)1–3(–5) µm thick
7	SCBs	rarely present, crystalloid or globose (in anchoring hyphae and excipular cells)	globose and/or crystalloid SCBs frequently present in the living paraphyses and excipular cells
8	VBs	regularly present in paraphyses and marginal cortical cells, rarely absent	irregularly present in desiccation-sensitive taxa, absent in desiccation-tolerant taxa

concept of the genus was established, exclusively European material was available for study. Later examined collections from other continents and even from tropical regions fully supported this concept.

Ad (1a). *Hyalorbilia* has shorter asci on average compared to *Orbilia*, due to the lack of a distinct ascus stalk and because polyspory occurs only exceptionally (asci 16-spored in *H. pleioerythrostigma*). The shortest asci were noted in *H.* cf. *japonica* (†9–17 µm, H.B. 7994a), *H. ulmi* (†12–17 µm), and *H. inflatula* (*13–21 µm, H.B. 8221), the longest in *H. anonyma* (†40–53 µm) and *H. fusispora* (*30–50 µm).

Ad (1b). Though not very easily visible, the consistent presence of croziers in *Hyalorbilia* provides a valuable feature which none of the many examined species of *Orbilia* have. Nevertheless, some variation must be mentioned. On the one hand, the occurrence of perforated, medaillon-shaped croziers in some species of *Hyalorbilia* may simulate a bifurcate ascus base, especially if the perforation is large (e.g., in some collections of *H. fusispora*, Pl. 114: 5b). On the other hand, in a few species of *Amphosoma* and *Orbilia* the two legs of the bifurcate ascus base of a few asci may be connected to form a medaillon-shaped crozier (e.g., in *A. resinicola*, Pl. 34: 1b).

Ad (1c). The apex of dead asci is typically rounded, but often it tends to be somewhat conical or truncate. Its shape apparently does not or only slightly depend on the direction of view. Sometimes the ascus wall is distinctly more thick-walled at the apex compared to the lateral wall, but a low-refractive endotunica was never observed in dead asci.

Ad (2a). Ascospore shape diversity in *Hyalorbilia* is confined to a few types, ranging between globose, ellipsoid, cylindrical, and fusiform, with only a slight tendency towards heteropolar (Pl. 58). Depending on the species, the spores vary between straight and strongly curved. In contrast to this, spore shape in *Orbilia* is much more diverse, comprising also strongly heteropolar, clavate to tailed, or highly asymmetrical spores.

Ad (2b). The general bipolar-symmetrical arrangement of SBs in living ascospores (2 or more SBs per spore) provides a valuable characteristic to recognize the genus *Hyalorbilia*. Only in three species with subglobose spores (*H. erythrostigma*, *H. anonyma*, *H. ulmi*) there is only a single eccentric SB in each spore. The generally small, globose SBs in *Hyalorbilia* (in *H. subfusispora* sometimes tear-shaped, in *H. multiguttulata* hemispherical and broadly attached) are difficult to distinguish from the often only slightly smaller LBs (a similar situation is noted in the group around *Orbilia eucalypti*). In *Hyalorbilia*, both SBs and LBs are medium to strongly refractive and grouped near each spore end, but they are sometimes also scattered over both spore halves. 1, 2, or up to 5 SBs occur in each spore half. In a few species (*H. pleioerythrostigma*, *H. oreadum*, *H. rotifera*, *H. texensis*) SBs are often or perhaps consistently absent. In a few collections of *H. subfusispora* and *H. erythrostigma* a very fine filum that connects the SBs to the terminal spore end could be observed. It is assumed that the SBs in *Hyalorbilia* are always connected by delicate fila to the apical or lateral spore wall, including species with more than two SBs per spore. Evidence for this is difficult to obtain with the TEM as filaments are easily missed in sections. Staining the SBs with CRB proved difficult because the stain penetrated the spore wall often very slowly, even after adding low-concentrated KOH. Distinction between SBs and LBs is rather easy based on the stability of the latter in KOH.

Ad (3). The paraphyses of *Hyalorbilia* are quite uniform in shape. They are never apically spathulate, lageniform or lanceolate, and they never protrude distinctly beyond the hymenial surface, i.e., the exudate always forms a rather even layer over them. Only in a few species are the apices strongly inflated (capitate-clavate). Usually the terminal cells are much longer (2–4×) than the lower cells, but in some small-spored taxa, such as *H. brevistipitata*, *H. erythrostigma*, *H. herbicola*, *H. pleioerythrostigma*, *H. rotifera*, or *H. resinae*, the cells tend to be of rather equal length, with the terminal cell up to twice as long as a maximum. The paraphyses emerge from partially inflated cells of the medullary excipulum. Dichotomous branches generally occur only in their lower part, but in species with short terminal cells branches may also occur in the upper part. Anastomoses were only occasionally seen in some species, either between the lower cells or especially between inflated cells from which the paraphyses emerge.

Ad (4a). With its characteristic prismatic cells at the flanks being oriented at a very low angle to the surface, the ectal excipulum of *Hyalorbilia* provides one of the most striking differences against the genus *Orbilia*. Nevertheless, this feature was only rarely reported in the literature, e.g., by Spooner (1987: 177, fig. 23 D) and Romero (1994, fig. 15 B) for *H. inflatula*. Particularly in those species with rather large apothecia, in which the excipular cells are usually strongly elongated at the flanks, this character can easily be observed, either in a median section (e.g., Pl. 126: 1g; Pl. 114: 1e; Pl. 106: 3f; Pl. 77: 1d, 10f) or in surface view in a squash mount (Pl. 116: 1g). Especially in minute but sometimes also in large apothecia the cells may be more isodiametric and then the parallel orientation to the surface is only indistinctly seen (see, e.g., Pl. 67: 2d, 11b, 13c). Rarely, a t. globulosa-angularis without a clear orientation is observed (e.g., Pl. 117: 3f, Pl. 67: 4c, Pl. 92: 1c, 2b). Near the base of the apothecium, however, the texture is often composed of indistinctly or more vertically oriented isodiametric to prismatic cells.

Ad (4b). In the medullary excipulum of *Orbilia* there are often ± horizontally oriented chains of distinctly inflated roundish cells among the narrow hyphae, while in *Hyalorbilia* such cell dimorphism was only indistinctly noted, e.g., in *H. erythrostigma*. In *Hyalorbilia* the two excipular layers are often difficult to distinguish, except that the medullary excipulum was gelatinized, or the cells of the ectal excipulum were comparatively large.

Ad (4c). The anchoring hyphae of *Hyalorbilia* are often long and ± straight by radiating more or less perpendicular to the excipular surface, comparatively wide and somewhat thick-walled. They strongly differ herein from the mostly narrow, more inconspicuous, undulating hyphae in *Orbilia*. Yet, some of those *Hyalorbilia* species with rather small apothecia possess narrow undulating hyphae very similar to *Orbilia*.

Ad (5). The gel between asci and paraphyses in *Hyalorbilia* is not easily seen, even when stained by various dyes. It becomes manifest when trying to separate the hymenial elements. Separation of living asci from the hymenium was usually impossible, with a few exceptions (e.g., Pl. 80: 9a). In KOH-mounts, separation was sometimes successful to a certain degree. Separation of the hymenial elements in *Orbilia* is generally easier, but it may similarly be hampered by an overlying continuous exudate attached to the paraphyses by some gel, and separation also often becomes more difficult with apothecial senescence. The intercellular space of medullary and ectal excipulum in

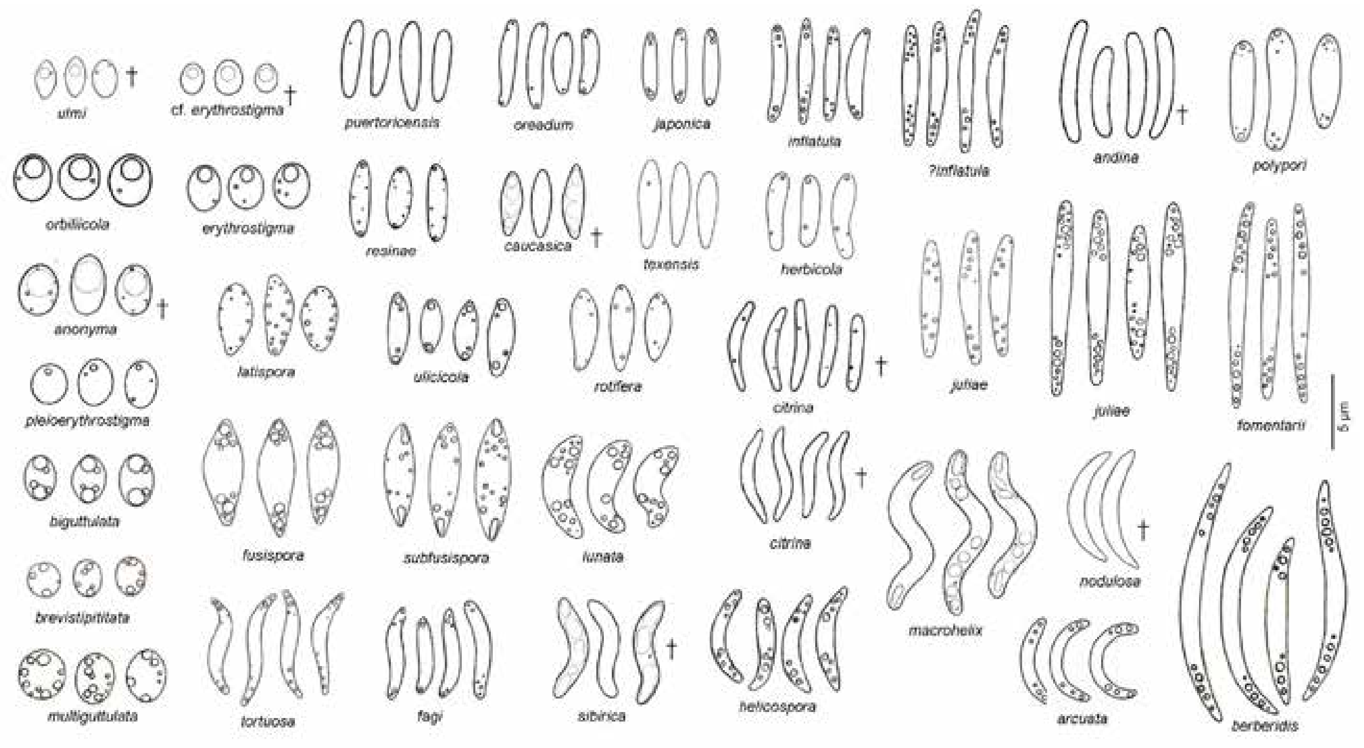


Plate 58. Ascospore diversity within the genus *Hyalorbilia*.

Hyalorbilia may be strongly gelatinized or nearly without gel, but in the former the gel is not always refractive and then not easy to see. In *Orbilia* such gelatinization is rarely seen.

Ad (6). The exudate in *Hyalorbilia* forms a coherent, inelastic layer which may sometimes get folded in squash mounts (Fig. 95: a–d) and probably also in the dry state. The cloddy warts obviously do not join when the apothecia shrink during drying, whereas in desiccation-tolerant species of *Orbilia* the large isolated clods of exudate get closer packed in the dry state to form a compact covering layer. The cloddy warts in *Hyalorbilia* might develop by splitting of an inelastic outer layer during growth of the very young apothecia.

Ad (7). Although quite frequently occurring in *Orbilia*, especially in desiccation-tolerant species, SCBs in *Hyalorbilia* were only occasionally seen. Crystalloid SCBs occur in *H. ulicicola*, and here usually in the basal excipular cells and in the anchoring hyphae, but never in the paraphyses, whereas in *Orbilia* they were never encountered in the anchoring hyphae. Globose SCBs commonly occur in *Orbilia* in the paraphyses and marginal ectal excipulum, but were never seen in the paraphyses of *Hyalorbilia*, and only very incosistently in the excipular cells of a few species (*H. erythrostigma*, *H. fagi*, *H. juliae*). Contrary to *Orbilia*, they tend in *Hyalorbilia* to be quite refractive and partially ring-shaped (Pl. 92: 1d). Rather small, ± globose, strongly refractive SCBs were rather frequently found in the cells of living conidia of *Hyalorbilia* (see below under Anamorph). Similar bodies occur in the genus *Lecophagus*, whereas conidia of *Orbilia* are generally without them.

Ad (8). Slightly to strongly refractive VBs are present in the living paraphyses and marginal cortical cells of almost every species of *Hyalorbilia*, irrespective of being desiccation-tolerant or not. In *Orbilia* VBs occur only in more or less desiccation-sensitive taxa, though only in some of these species.

Species delimitation, diversity of teleomorph. In contrast to the genus *Orbilia*, the morphological diversity of the teleomorph of *Hyalorbilia* is comparatively low. Species delimitation within *Hyalorbilia* is very complicated, because the morphological differences between closely related taxa are often only slight, and a more or less pronounced variation among the collections was noted in almost every species. Intermediate collections have actually been encountered between most of the here recognized taxa. This complex situation cannot be improved by applying a wider species concept, because species limits would thereby remain unsharp. We were also unable to recognize infrageneric groups within *Hyalorbilia* based on a combination of morphological traits of both teleomorph and anamorph.

The most reliable characteristics at the species level were found in the ascospores (size, shape, curvature), in combination with the number of SBs which they contain. Some species differ merely in spore curvature, others in spore length or width, and others only in spore guttulation (number and size of SBs). A severe complication with herbarium material is that SBs are invisible or only very faintly seen (Fig. 3). The strength of spore curvature in *Hyalorbilia* does not as markedly decrease in the dead state as observed in *Orbilia* section *Arthrobotrys* (see Pl. 104: 2a, 4a; Pl. 89: 1a; Pl. 100: 1a, 2a).

A majority of elements of the teleomorph are morphologically rather concordant within *Hyalorbilia* and, therefore, usually of little value for species delimitation (a similar conformity is noted in the anamorph, see below). This more or less concerns: ascus apex (shape and wall thickness), croziers, spore number, paraphysis characters (cell length, apical inflation, contents), exudate, excipular texture, anchoring hyphae, colour of apothecia. Also the presence of gel in the hymenium was found to be a rather constant feature across the genus. The gelatinization of the medullary and ectal excipulum, however, strongly varied among the species but often also within a species, being abundant preferably in the more tropical collections. A crenulate to denticulate margin made up of thick-walled cells is typical of *H. citrina*, but populations with smooth margins also appear to represent this species. Size and colour of apothecia as well as features of the margin provide hints to a species at best, and most of the species are impossible to identify by macroscopy alone. Strong difference in width of the marginal cortical cells was found to support separation of some closely related species, for instance, *H. fusispora* vs. *H. subfusispora*, *H. anonyma* vs. *H. erythrostigma*, or *H. ulicicola* vs. *H. caucasica*. In other taxa (e. g., *H. inflatula*, *H. fagi*) the marginal cells seem to be very variable, with frequent intergradations, and cell width was usually not correlated with other features. Preliminary results using molecular data, however, suggest that marginal cell width might permit distinction of at least two taxa within *H. inflatula* (Phyl. 5).

Characteristics of the living cytoplasm in *Hyalorbilia* have a similar importance as in *Orbilia.* Number and size of SBs in the spores serve as a valuable tool, e. g., in separating *H. multiguttulata* from *H. biguttulata* and *H. erythrostigma*. In contrast to *Orbilia*, SB shape is uniformly globose, rarely flattened where they are attached to the wall (*H. multiguttulata*), or ellipsoid to tear-shaped as in *H. subfusispora* in comparison with the similar *H. fusispora*. VBs in the paraphyses are present in almost every species of *Hyalorbilia*, and are, therefore, taxonomically unimportant at the species level.

Some of these spore features are coupled with ecological differences such as desiccation tolerance, or with those of the marginal excipulum, or with a different anamorph. However, spore and also ascus size may vary considerably. Likewise, the width of the marginal excipular cells may do so in some of the species. Hence, delimitation among closely related taxa based upon metric data is often problematic. For example, within *H. juliae* spore length varies from 7–9 up to 11–15 µm; yet, collections with an intermediate spore length were frequently seen, therefore, separation into two taxa was abandoned for the moment.

Nomenclature of teleomorph. A number of generic names, being today applied to non-orbiliaceous, mainly helotialean fungi, were used in the past for species here assigned to *Hyalorbilia*. The genus *Calloria* (*Calloriaceae*), was in use for, e. g., *Hyalorbilia ?fagi* by Saccardo (1882a, as *C. chrysocoma* var. *microspora*), for *H. inflatula* by Phillips (1887), and for *H. citrina* by Smith (1901). *Pithyella* (= *Helotiopsis*, *?Helotiaceae*), a genus comprising bryophilous taxa with globose, warted ascospores, was applied to *Hyalorbilia erythrostigma* and *H. anonyma* by Korf & Zhuang (1987), to the former species also by Boudier (1907), to the latter by Höhnel (1910: 623, 1926a: 68, as *Helotiopsis*, see also under *Calloria* (p. 205) and *Pithyella* (p. 209)). Species of *Hyalorbilia* were placed in further helotialean genera such as *Mollisiella*, *Pezizella* etc.

Among the orbiliaceous genera, the name *Hyalinia* was applied to *Hyalorbilia inflatula* and *H. ?fagi* by Boudier (1907, as *Hyalinia inflatula*), Rehm (in Straßer 1910, as *H. inflata* var. *lonicerae*), Kanouse (1939, as *H. breviasca*), and Grelet (1948b, as *H. rectispora* var. *majuscula*). A majority of the hitherto known species of *Hyalorbilia* have been considered as representing typical members of *Orbilia*, even by modern authors, although they lack the furcate ascus base, the truncate ascus apex, and the capitate paraphyses, previously estimated as key characteristics of *Orbilia*. In the absence of authentic material of the common ly known *H. inflatula*, the little-known but well typified *H. berberidis* was chosen in Baral & Marson (2001) as type species of the newly erected genus *Hyalorbilia.*

Anamorph. In six species a connection to an anamorph could be established in pure culture or when formed at the lid of the Petri dish (*H. brevistipitata*, *H. fagi*, *H. inflatula*, *H. latispora*, *H. polypori*, *H. tortuosa*), and in one by DNA extract from conidia (*H. orbiliicola*). In further 12 species conidia and sometimes also conidiophores were only observed on the natural substrate near apothecia (see Appendix 4). As in many sections of *Orbilia*, we use the current generic names of anamorphs in the sense of form genera when describing different conidial types within *Hyalorbilia*: unbranched conidia are referred to as brachyphoris- (straight) or vermispora-like (± curved), and branched conidia as trinacrium-like, curucispora-like, or dwayaangam-like, depending on the number of branches.

Unbranched septate conidia (phragmoconidia) were observed in most *Hyalorbilia* species with a known anamorph. Conidia of this type have earlier been accomodated in *Dactylella*. The term 'dactylella-like' is used here in a restricted sense, particularly for anamorphs of series *Neodactylella* (section *Arthrobotrys*) and *Hyalinia* (section *Aurantiorubrae*) with usually long, unbranched conidiophores. Similar anamorphs are found in *Orbilia* series *Orbilia* which, however, deviate from typical dactylella-like anamorphs in shorter conidiophores.

A morphologically different type of stauroconidia (T- to Y-shaped, trinacrium-like) characterizes two *Hyalorbilia* species with subglobose ascospores, *H. erythrostigma* and *H. orbiliicola*. Their anamorph strongly resembles those observed in various sections of *Orbilia*, but also in *Amphosoma*. Another type of stauroconidia (curucispora flabelliformis-like) occurs so far solely in *H. latispora*, whereas two other subglobose-spored species, *H. brevistipitata* and *H. multiguttulata*, form unbranched conidia. K-shaped, curucispora ponapensis-like conidia were several times seen on the natural substrate in association with apothecia of *H. subfusispora*. Dwayaangam-like conidia are typical for *H. quadridens*.

The anamorph-typified genera *Brachyphoris* and *Vermispora* or *Microdochiella* can only be recognized with certainty by molecular or cultural methods as belonging to *Hyalorbilia* s.l. As already mentioned above, several observations on living conidia of *Hyalorbilia* s.str. indicate that an organelle in the cytoplasm might serve as a characteristic of the genus: in the phragmoconidia of *H. citrina*, *H. fagi*, *H. inflatula*, *H. polypori,* and *H. tortuosa* (perhaps also in *H. arcuata*) we observed medium-sized, strongly refractive drops which resemble LBs but which irreversibly disappear in KOH or in dead material (Pl. 59: a, see also Fig. 89: f–g). With CRB they cannot be stained, even in a slightly alkalinized medium, hence they should be classified as SCBs (or WBs). These bodies also occur in the K-shaped conidia found associated with *H. subfusispora* (Pl. 118) and probably in the dwayaangam-like conidia of *H. quadridens*.

In the remaining groups of *Hyalorbilia* s.l. these bodies have so far not been seen: neither in the branched conidia of *H. orbiliicola* and *H. latispora*, nor in the unbranched conidia of the *Vermispora* clade. They have also never been seen in any of the many anamorphs of *Orbilia*, with rare exceptions (*O.* cf. *bembicodes* Pl. 1000). The bodies resemble those more or less cubical SCBs that occur in mycelial and excipular cells and conidia of *Lecophagus*, but whether they are homologous to them is uncertain. As in *Lecophagus*, these bodies have also been observed in the excipular cells of *Hyalorbilia*, though only exceptionally (see Pl. 92: 1d).

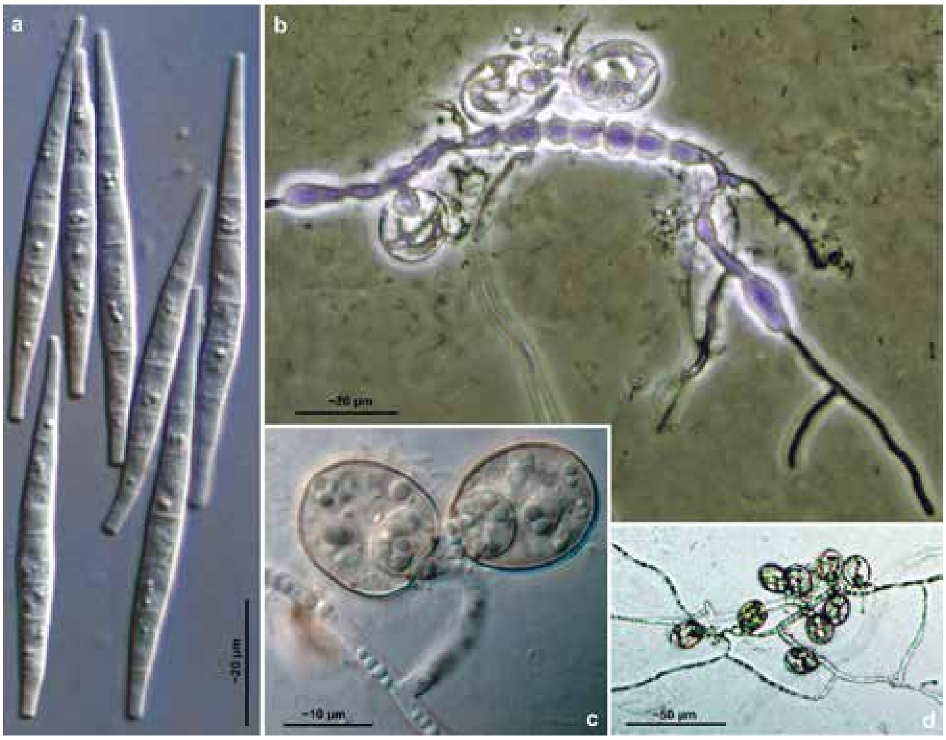


Plate 59. '*Dactylella*' *passalopaga* (anamorph of *H.* ?*inflatula*). – a. conidia containing globose SCBs; b, d. germinated conidium with captured testaceous rhizopods; c. two captured rhizopods. – phot. G. Barron (DIC), http://www.uoguelph.ca/~gbarron/2008/passalop.htm.

Despite these remarkable conidial characters, anamorphs of many *Hyalorbilia* spp. exhibit a rather poor morphological diversity, to the present knowledge. In fact, various closely or distantly related species possess very similar, often indistinguishable, elongate fusoid to fusiform, ± straight to slightly curved, multiseptate conidia. Taxa with this conidial type represent about a third of the genus and include (1) the anamorph-based taxa *H. lignatilis*, *H. oviparasitica*, '*D.*' *passalopaga*, and *H. tenuifusaria* in *Hyalorbilia* s.str., and *H. fusarina*, *H. fusarioides*, *H. leguminacea*, and *H. spermatophaga* in the *Vermispora* clade (see Pls 3 & 59) and (2) the teleomorph-based taxa *H. brevistipitata*, *H. caucasica*, *H. citrina*, *H. fagi*, *H. helicospora*, *H. inflatula*, *H. japonica*, *H. lunata*, *H. oreadum*, *H. resinae*, *H. rotifera*, and *H. ulicicola*. Whether differences in size, curvature or septation of the conidia, or in branching of the conidiophores exist, is unclear due to the low number of observed conidia and unknown conidiophores in some taxa and the few obtained cultures.

Predatory capabilities. Four species are known to prey on invertebrates but are only known from their anamorph (*H. oviparasitica* and *H. fusarina* invading nematode eggs, *H. tenuifusaria* and '*D.*' *passalopaga* capturing rhizopods). DNA sequences were available for the former three taxa, which fall into *Brachyphoris* and *Vermispora*, according to Chen et al. (2007a), but do not fit sequences of a teleomorph. For '*D.*' *passalopaga* a connection to a teleomorph (*H. inflatula*) is presumed here, based on very similar conidia (Pls 59, 77, 82).

In a few species with similar teleomorphs, differences in conidial shape support their delimitation. For instance, *H. erythrostigma* differs in Y-shaped conidia from *H. brevistipitata* and probably *H. multiguttulata* with unbranched phragmoconidia. *H. polypori* and *H. tortuosa* differ in cylindric-ellipsoid phragmoconidia from *H. fagi* and *H. inflatula* and probably *H. helicospora* with fusoid to fusiform phragmoconidia. *H. tortuosa* appears to be phylogenetically related to *H. berberidis* (see below), but anamorphs are unknown in *H. berberidis* as well as in the similar *H. fomentarii*, *H. juliae*, and *H. fusispora*. In several samples of *H. herbicola*, *H. rotifera*, *H. fusispora*, *H. juliae*, and *H. subfusispora*, narrow, filiform to fusoid phragmoconidia were encountered on the natural substrate (*28–77 × 1.5–3 µm, 3–6-septate). This conidial type was so far not obtained in pure culture, but it possibly corresponds to that in *H. fusarioides* (20–60 × 2–3 µm, 1–5-septate). We are somewhat doubtful about its connection to teleomorphs of *Hyalorbilia*, nevertheless we have figured them on the plates. In a few species conidia with more than two arms (curucispora- or dwayaangam-like) were observed, but their connection to the genus *Hyalorbilia* was so far demonstrated only for *H. latispora* (in pure culture and by molecular methods).

Nomenclature of anamorph. Because of the often very short conidiophores observed in *Hyalorbilia* (often shorter than the conidia) and particularly because of molecular results, Chen et al. (2007a, c) proposed the new genus *Brachyphoris* to accomodate the anamorphs of *Hyalorbilia* (see p. 217–219). Conidiophore length is not a very reliable characteristic of this group, however, because several *Hyalorbilia* species produce rather long though often strongly branched conidiophores with short to medium long side branches (*H. fagi*, *H. lignatilis*, *H. polypori*, *H. tortuosa*). On the other hand, the authors were unaware that in different sections of *Orbilia*, e.g., *Aurantiorubrae* and *Helicoon*, short conidiophores occur which produce unbranched conidia. Due to their strong morphological similarity these phragmoconidia are termed 'vermispora-like' here when more or less curved (C-shaped), or 'anguillospora-like' when very long and narrow. The limits to brachyphoris- and dactylella-like anamorphs with straight conidia is unsharp, however. One species assigned by Chen et al. to *Brachyphoris* without molecular data (*B. stenomeces*) resembles anguillospora-like anamorphs and might rather belong to *Orbilia* (perhaps in section *Helicoon*).

With the new nomenclatural rules (ICN Art. F.8.1), the later established phragmoconidial genera *Brachyphoris* and *Microdochiella* fall in synonymy with *Hyalorbilia*. Also the earlier established genera *Vermispora* with phragmosporous conidia and *Dwayaangam* and *Curucispora* with stauroconidia, though having priority, do not automatically displace *Hyalorbilia*. In order to avoid a large number of recombinations, Baral et al. (2017b) proposed to protect *Hyalorbilia* over all these names. However, synonymy with *Hyalorbilia* is only affirmed for *Brachyphoris* and *Microdochiella*, because molecular data of the type species of the other three genera were unavailable.

In fact there is a high probability that some of these genera are heterogeneous. For instance, Chen et al. (2007c) accepted five species in *Vermispora* by excluding *V. obclavata* by faintly pigmented conidiophores and firm-walled conidia. Synonymy with *Hyalorbilia* is affirmed here only for three species which we therefore combine as *H. fusarina*, *H. leguminacea*, and *H. spermatophaga*, whereas *V. grandispora* (type species), *V. obclavata*, and *V. cauveriana* are without molecular data. In our opinion, *V. cauveriana* could instead belong to *Orbilia* section *Arthrobotrys* because of very large conidia producing microconidia. Hernández-Restrepo et al. (2015) proposed the new genus *Microdochiella* for *M. fusarioides* which clustered sister to the three *Vermispora* species. However, scarcely any striking morphological and ecological differences to *Vermispora* exist, the only worth mentioning being narrower conidia with a drop of moisture at their mid-point, and presence of chlamydospores. Therefore, we here combine this species as *H. fusarioides*. For a more detailed historical review of *Curucispora* (p. 219), *Dwayaangam* (p. 232–234), *Microdochiella* (p. 239), and *Vermispora* (p. 246–247) see there.

Phylogeny. Molecular data from 21 validly described and accepted species of *Hyalorbilia* with a known teleomorph were available, and six further species with sequence data are without a known teleomorph (*H. fusarina*, *H. fusarioides* *H. leguminacea*, *H. oviparasitica*, *H. spermatophaga*, *H. tenuifusaria*). Many environmental strains belong to various unidentified species (in Phyl. 5, S6 H1–H33, V1–V16). The genus shows an extraordinarily high diversity in the ITS rDNA region. Nevertheless, it formed in previous phylogenetic analyses of ITS or LSU a more or less well-supported monophyletic group within the *Orbiliomycetes* (Liu et al. 2006a, Chen et al. 2007a, Smith & Jaffee 2009, Yang et al. 2012b). Smith & Jaffee named it '*Brachyphoris* clade' after its anamorph, and Yang et al. 'DO clade' after *Dactylella oviparasitica*, the object of their population dynamics study. Also in our combined analysis (Phyl. 2) it formed a weakly supported group.

The genus includes four supported clades with unresolved position: the 'core clade of *Hyalorbilia*' (= *Hyalorbilia* s.str., i. e., the majority of *Hyalorbilia* species), the *erythrostigma-orbiliicola* clade, *H. latispora*, and the *Vermispora* clade. Each of these clades received strong support even in single analyses of most regions (Phyls 5, 6, S5). The phylogenetic analyses by M. Weiß (in Baral et al. 2017b) and Magyar et al. (2017b) yielded a bootstrap value of 99–100 for *Hyalorbilia* s.l. *Hyalorbilia* s.str. and the *Vermispora* clade appear to be sharply separated by their molecular data, but also the *erythrostigma-orbiliicola* clade and *H. latispora* as well as some environmental taxa show a high distance to them and cannot be assigned to either clade: *H. latispora* is found in the *Vermispora* branch in M. Weiß' analysis and in Phyls 6 and S05 (ITS+LSU, LSU), but in the *Hyalorbilia* branch in Phyl. 5 (ITS), and likewise *H. erythrostigma* and *H. orbiliicola* clustered unresolved between the two groups (Phyls 5–6). One species with the typical teleomorph characteristics of *Hyalorbilia*, *H. rotifera*, clustered strongly supported in the *Vermispora* clade (Phyl. 6), and some species without molecular data might also belong there (*H. herbicola*, *H. resinae*). This placement prompted us to combine *Microdochiella fusarioides* and the three species of *Vermispora*, for which DNA data were available, with *Hyalorbilia*. Sequence data were not available for *Pseudorbilia* which appears to belong to the closest relatives of *Hyalorbilia*.

In Chen et al.'s (2007a) ITS analysis the three former *Vermispora* species formed a strongly supported but distant clade with *Orbilia* series *Neodactylella* (as *Dactylella*), whereas *Hyalorbilia* (as *Brachyphoris*) formed a basal sister clade. Further groups of *Orbiliomycetes* were not included in this analysis. Our studies confirm the high distance to the large genus *Orbilia*: analyses of either 5.8S, ITS, LSU, or SSU+ITS+LSU placed *Vermispora* always outside *Orbilia*, and in most analyses to *Hyalorbilia* in a strongly (Baral et al. 2017b) or weakly supported relationship (Phyls 1–2).

The phylogenetic position among the three large groups of *Orbiliomycetes* (*Hyalorbilia*, *Lecophagus-Amphosoma* clade, *Orbilia*) remained unresolved in maximum likelihood analyses. In those of SSU+ITS+LSU in Baral et al. (2017b, erroneously as 'SSU+5.8S+LSU') and ITS+LSU in Magyar et al. (2017b), *Hyalorbilia* formed a sister clade to *Orbilia*, and the *Lecophagus-Amphosoma* clade clustered sister to them. A different result was obtained in the present analyses of 5.8S+LSU D1–D6 or SSU+ITS+LSU (Phyls 1–2), in which *Orbilia* clustered sister to the *Lecophagus-Amphosoma* clade and *Mycoceros*, and *Hyalorbilia* sister to those. The support at the main branches was always low or absent under ML. Also Magyar et al.'s Bayesian/ML analysis yielded no or weak bootstrap support at these branches: 0.96/– at the first branch and 0.99/60 at the clade containing *Hyalorbilia* and *Orbilia*. The rather isolated position of *Hyalorbilia* is even obvious when analysing only 5.8S (not shown). Also within the genus, our NJ analysis of this region (Phyl. S3) shows the core clade of *Hyalorbilia* to differ sharply from the remaining groups which also are also separated into the *Vermispora* clade, *H. latispora*, the *erythrostigma-orbiliicola* clade, and H30–H31.

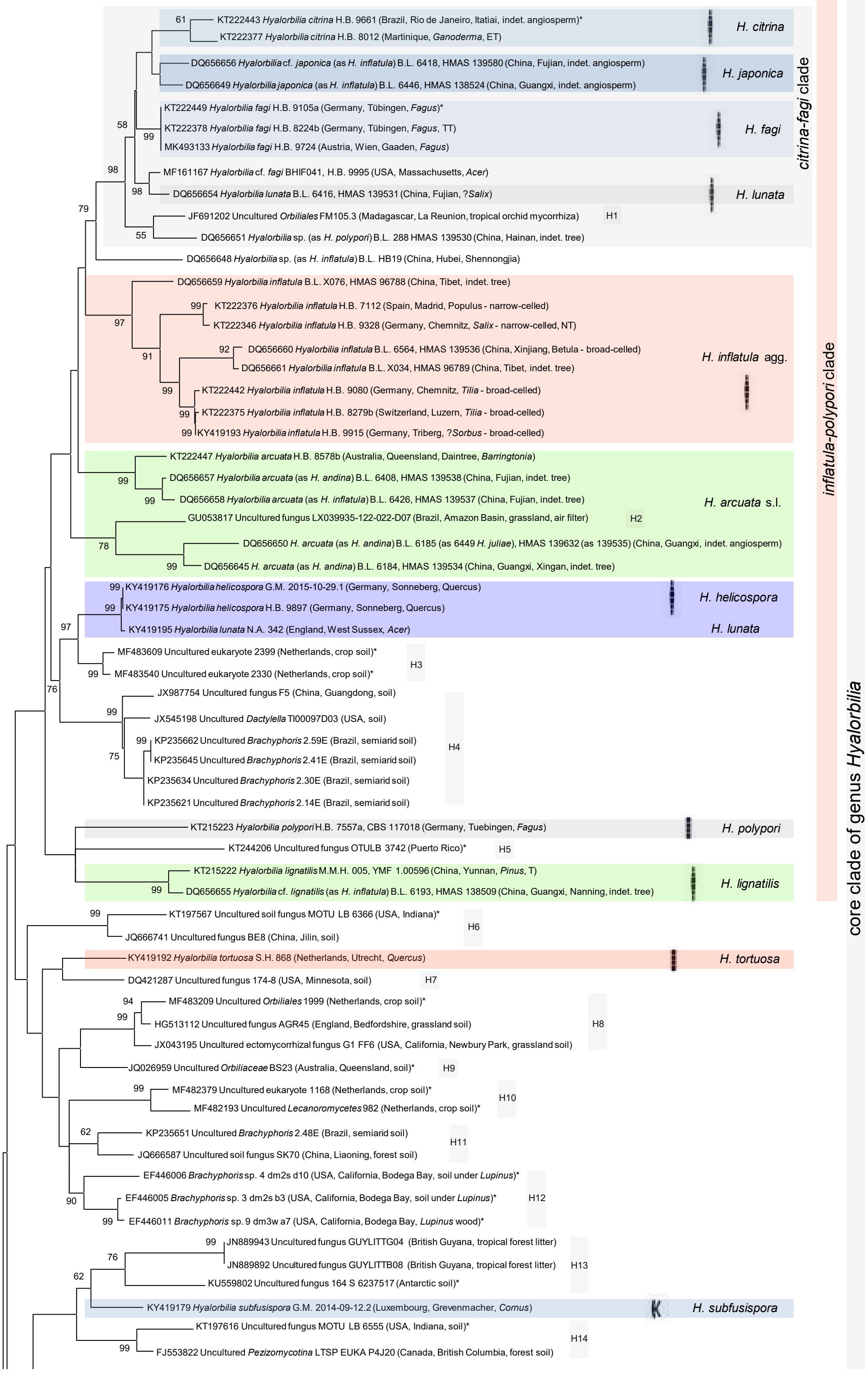
H. brevistipitata and *H. multiguttulata* clustered together with the anamorph-typified *H. oviparasitica* in the core clade of *Hyalorbilia* by forming a very distinct subclade which received strong support in analyses of ITS, ITS+LSU or LSU. *H. oviparasitica* and the undescribed *H.* aff. *multiguttulata*, which is only known from non-sporulating mycelium and DNA (including DoUCR50, in GenBank as *Dactylella oviparasitica*), infect nematode eggs and females. This group, here called *oviparasitica-multiguttulata* clade, differs from *H. erythrostigma* and *H. latispora* in fusoid phragmoconidia very similar to those of most remaining clades of *Hyalorbilia*.

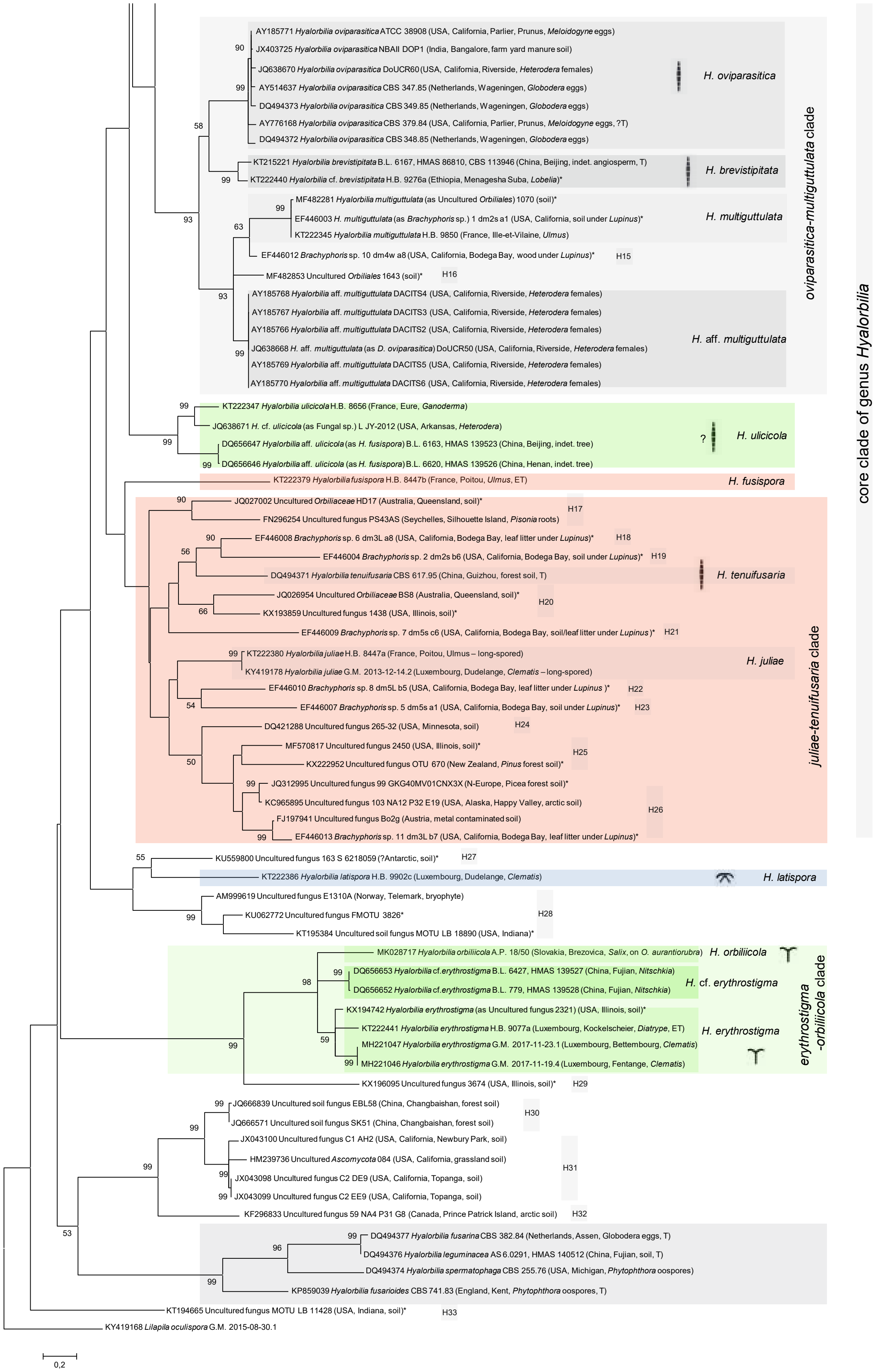
A large group of the *Hyalorbilia* core clade, characterized by elongate, mostly subcylindrical ascospores, is called *inflatula-polypori* clade here and includes *H. arcuata*, *H. citrina*, *H. fagi*, *H. helicospora*, *H. inflatula*, *H. japonica*, *H. lunata*, and *H. polypori*. The clade received rather strong support when analysing ITS+LSU and especially LSU (Phyls 6, S5), but no support when analysing ITS (Phyl. 5). These fungi have in common more or less large and predominantly desiccation-sensitive apothecia. Fusoid phragmoconidia are known in several of them, except for *H. polypori* which has cylindric-ellipsoid conidia. With the presumption that '*D.*' *passalopaga* is the anamorph of *H. inflatula* agg., the ability to capture rhizopods occurs in this clade.

H. subfusispora formed a clade with some environmental strains (Phyls 5, S5, H13–14, H36) and clustered with strong support sister to the *oviparasitica-multiguttulata* clade (Phyl. 6). *H. ulicicola* s.l. with short fusoid ascospores formed a strongly supported clade which clustered either with medium support sister to the *inflatula-polypori* clade (LSU, Phyl. S5), or unresolved (Phyl. 5, ITS) or weakly supported (Phyl. 6, ITS+LSU) with the *oviparasitica-multiguttulata* clade and *H. subfusispora*. An environmental isolate from Arkansas (USA), which like *H. oviparasitica* infects nematode eggs, belongs to *H. ulicicola* s.l. Narrowly fusoid conidia which represent the predominant conidial type in *Hyalorbilia* were repeatedly observed in association with *H. ulicicola*.

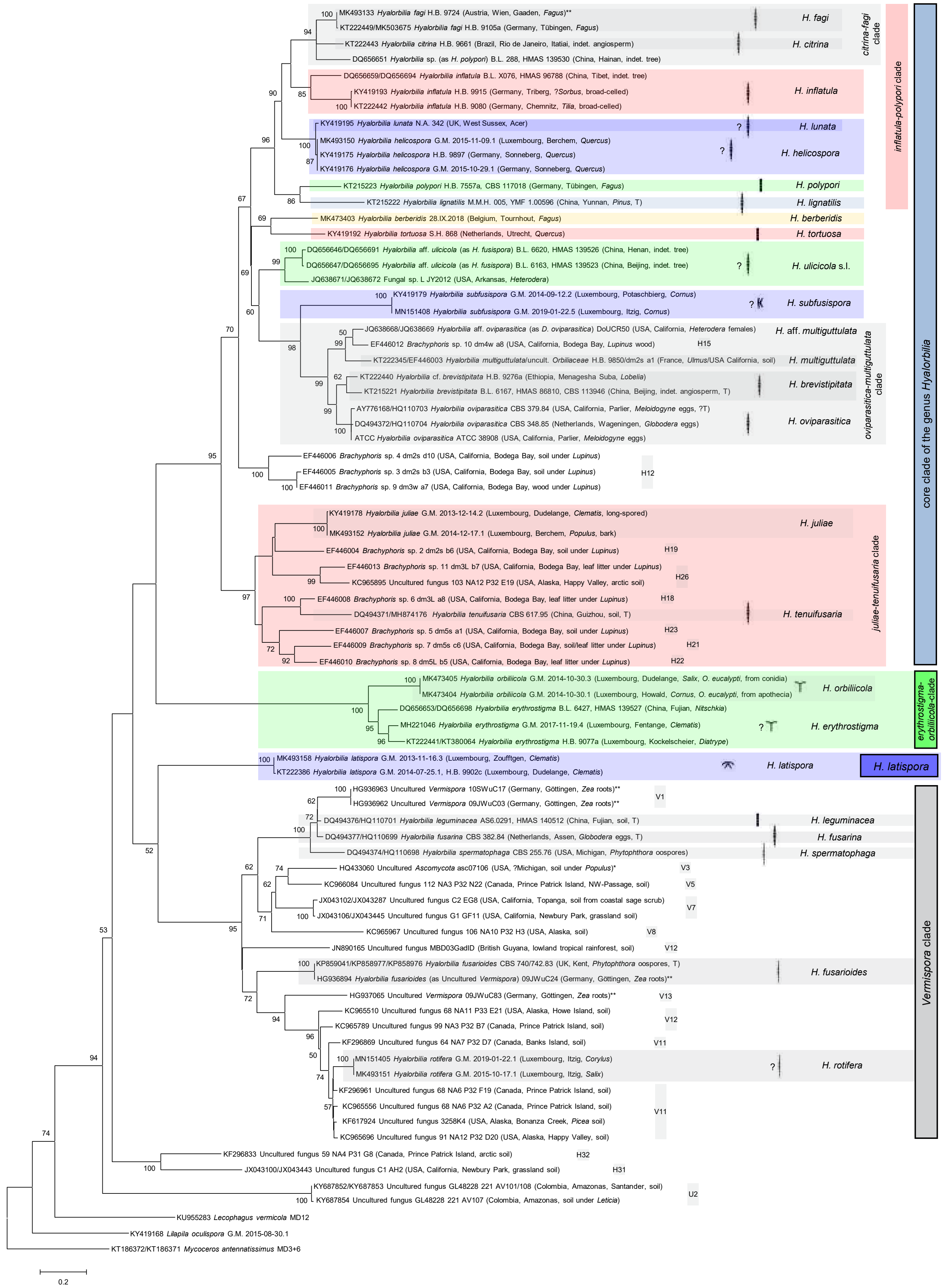
Some other species with elongate, fusoid to subcylindrical ascospores (*H. fusispora*, *H. juliae*, *H. berberidis*, *H. tortuosa*) clustered in different, mostly unsupported clades. In our combined analysis (Phyl. 6), only *H. juliae* formed with the anamorphic *H. tenuifusaria* a strongly supported clade (here called *juliae-tenuifusaria* clade), to which also some environmental isolates from soil and litter are associated (see also Phyl. 5, H18–H26). A soil isolate from Minnesota (H7) clustered unsupported with *H. tortuosa* (Phyl. 5). However, the recent sequence of *H. berberidis*, the type species of *Hyalorbilia*, formed with *H. tortuosa* a weakly supported clade in the combined analysis (Phyl. 6), although the support was strong in an earlier analysis, and in this clade falls also the soil isolate which lacks LSU.

Several species without molecular data are expected to fall in some of these clades, based on their similar morphology. For instance, *H. fomentarii* is probably closely related to *H. juliae*. *H. resinae* and *H. herbicola* might belong in relationship of *H. rotifera* in the *Vermispora* clade.





Phylogenetic analysis 5. Phylogram of genus *Hyalorbilia* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (133 sequences, 991 positions, aligned with MUSCLE) using the GTR+G+I model in MEGA6 (100 replicates). Various environmental strains from GenBank are included, most of which representing unidentified species of *Hyalorbilia* (as H1–H32). The tree is rooted with *Lilapila oculispora*. For a more detailed *Vermispora* clade see S6. T = type, ET = epitype, TT = topotype; * = without ITS1 and often also partial 5.8S.



Phylogenetic analysis 6. Phylogram of genus *Hyalorbilia* inferred from combined ML analysis of ITS1-5.8S-ITS2+LSU (D1–D2) rDNA dataset (79 sequences, 1694 positions, aligned with MAFFT) using the GTR+G+I model in MEGA6 (500 replicates). The included sequence of *H. multiguttulata* is a chimere of KT222345 (H.B. 9850) and EF446003 (uncultured *Orbiliaceae* dm2s_a1). Various environmental strains from GenBank are included, most of which representing unidentified species of *Hyalorbilia* (as H15, H18–H19, H21–H23, H26, H32, V1, V3, V5, V7–8, V11–12). The tree is rooted with *Lilapila oculispora.* T = type, ET = epitype, * = without ITS1, ** = without LSU (D2).

Environmental sequences. Various more or less supported clades in our phylogenetic analyses include mainly environmental DNA isolates of unknown morphology retrieved from GenBank (clones H1–37, V1–V16), and in most cases no name could be attached to them. Sequences of our teleomorph-typified species clustered only sometimes with them, and only rarely they could be considered as conspecific.

Eleven uncultured DNA-isolates (H12, H15, H18–19, H21–23, H26) gained by Smith & Jaffee (2009, 'dm') from wood, litter, and soil in California (as 'uncultured *Orbiliaceae* clone') clustered in their '*Brachyphoris* clade', and only one isolate showed a high similarity to one of our new species: dm2s_a1 clustered with *H. multiguttulata* and an unlocalized strain (Phyl. 5) with a 0.3% distance in the 5.8S+ITS2. Another isolate (dm4w-a8) clustered in the same clade but with a 9% distance. Also for *H. berberidis* conspecific clones exist in GenBank. Among the isolates which clustered in the supported *Vermispora* clade (V1–V16), only one teleomorph (*H. rotifera*) clustered with them (V12), though with a 9.5–10.5% ITS distance.

Specific nucleotide positions. Various specific nucleotides of the rDNA characterize the genus *Hyalorbilia* or some subgroups of it (see Tabs 60–61). Their partial interlacing with other orbiliaceous genera suggests possible evolutionary pathways within the *Orbiliomycetes*.

In the SSU V8–V9 region about 12 nucleotides were found to be more or less diagnostic of the genus *Hyalorbilia*, based on available data from 15 species, including the two environmental taxa H14 and H37 (Tab. 60). A correlation with members of section *Arthrobotrys* forming adhesive traps is noted at 2 positions in an otherwise conservative region downstream of V8 (pos. 109 and 126: ATAG**G**GCATTGCAATTATTGC**C**CTT). Besides these groups, only two further taxa of *Orbiliomycetes* show this motif (U2, U3, Tab. 60). *H. latispora* is the only representative of the *Vermispora* clade for which SSU was available, and it concurs at these 2 positions with *Orbilia* p.p.maj. and the remaining orbiliaceous genera.

In the 5.8S region (Tab. 61 left part) 1 nucleotide (pos. 30) characterizes *Hyalorbilia* s.str. and the *erythrostigma-orbiliicola* clade by showing the motif GGTTC**C**CGCAT, compared to the current motif GGTTC**T**CGCAT in *H. latispora* and the *Vermispora* clade and many other *Orbiliomycetes*. However, this deviation (**C**) also occurs in a few subgroups within *Orbilia*, particularly section *Ovoideae* (see p. 1241) and all predacious members of section *Arthrobotrys* (see Tab. 76), whereas **T** also occurs in other classes of *Ascomycota*. At another nucleotide (pos. 11) the *Vermispora* clade (including clones V1–V13) and a few *Bryorbilia* spp. (clones B1, B2 p.p.) have G but almost any other *Orbiliomycetes* A (Tab. 61).

In Smith & Jaffee's (2009) Orb5.8s1F primer region (pos. 47–64, Tab. 18), *Hyalorbilia* s.str. concurs with *Orbilia*, but the *erythrostigma-orbiliicola* clade, *H. latispora*, and the *Vermispora* clade matches other orbiliaceous genera (*Amphosoma*, *Bryorbilia*, *Lecophagus*, *Lilapila*, and *Retiarius*). Primer Orb5.8s3F (pos. 137–157, Tab. 18) varies within *Hyalorbilia* with one frequent and several more rare variants. Most of these variants are unique, with a few exceptions: *H. tortuosa* concurs with *Orbilia* p.p.min., *H. fusarioides* with *Retiarius* and *Amphosoma* p.p., and species of the *Vermispora* clade (*Hyalorbilia*) with *Saccharomycetales* and *Boletales*. Also in stem-loop B8 of 5.8S (pos. 117–138, Tab. S4) *Hyalorbilia* is diverse and partially unique, some members concurring with *Mycoceros* and *Lilapila*, the *oviparasitica-multiguttulata* clade with some *Orbilia* spp., *H. latispora* with the *Vermispora* clade, and *H. rotifera* with some environmental clones of that clade (V7, V11–V12).

In the LSU (Tab. 61 right part) 5 nucleotides characterize the genus *Hyalorbilia* in the present sense (including *Vermispora* clade): pos. 112, 152/155, 266, and 311 are CA**G**AT, **C**TG**G**A or **C**TG**C**A (rarely **C**TG**A**A), A**C**GA, and T**C**C, whereas all other orbiliaceous genera consistently have CA**A**AT, **T**TG**A**A (rarely **T**TG**T**A), A**A**GA, and T**T**C, except for some sequences of series *Dactylellina* with A**C**GA at pos. 266. Pos. 123 is very diagnostic for the core clade of *Hyalorbilia* which has AATC**C** (including *H. latispora* and V3–V16) or sometimes AATC**G** (*erythrostigma-orbiliicola* clade) or AATC**A** (H21–23, H31–32), whereas the remaining *Vermispora* clade and other orbiliaceous genera consistently have AATC**T**. Similarly, pos. 534 is AA**A**GT or AA**C**GT in *Hyalorbilia* p.p.maj., but AA**T**GT in the *Vermispora* clade and most other orbiliaceous taxa.

Pos. 219 is **C**CCCG in *Hyalorbilia* p.p.maj. (including species previously assigned to *Vermispora* and *Microdochiella*), but **T**CCCG in the *erythrostigma-orbiliicola* clade, *H. latispora*, and most environmental clones of the *Vermispora* clade (including *H. rotifera*). At 2 positions (328 and 608) the *Vermispora* clade has **T**GC and **G**TG unlike all other *Orbiliomycetes* and most other ascomycetes which have **G**GC and **A**TG, respectively. At pos. 332 variant CG**G** characterizes *Hyalorbilia* s.str. and the *erythrostigma-orbiliicola* clade but also predacious members of *Orbilia* section *Arthrobotrys* (Tab. 76), *Mycoceros*, and some *Orbilia* spp. (series *Abutilones*, section *Ovoideae*, *O. dryadum*), whereas remaining orbiliaceous taxa have CG**A**

In Smith & Jaffee's (2009) Orb28s2R primer region (pos. 606–626, Tabs 19 & 61), *Hyalorbilia* s.str. is unique, while *H. erythrostigma* and *H. orbiliicola* concur with *Orbilia* p.p.maj., and *H. latispora* with the *Vermispora* clade. The latter group is unique because of a rare deviation at pos. 608 (G vs. A), but varies at pos. 616 (C vs. T). At pos. 616 the character C was otherwise only found in *Hyalorbilia* p.p.maj.

In the available LSU D3 domain, species previously assigned to *Vermispora*/*Microdochiella* share with the environmental clone V14 a unique motif (GTG**A**GAGCCCGCAAG) which deviates in *H. rotifera* and clones V11 and V15 by 3 gaps (GTG**A**GAGCCGC--AA-) and in *Amphosoma* and *Retiarius revayae* at the fourth position (pos. 722, GTG**G**GAGCCCGCAAG). Among other *Orbiliomycetes* pos. 722 is A only in *Hyalorbilia latispora* (GTG**A**GAT), *H. subfusispora* (GTG**A**GAG), *H. brevistipitata* and *H. oviparasitica* (GCG**A**GAG).

Ecology. Species of *Hyalorbilia* usually form their ascomata on decayed bark and wood, some also on herbaceous stems. Many of them exhibit a more or less pronounced tendency to grow on or close to other fungi, like resupinate basidiomycetes and pyrenomycetes, also apothecia of *Orbilia*, or gelatinous basidiomata. Usually the hosts are rather senescent and the *Hyalorbilia* appears to grow as a saprobiont on them. Yet, *H. erythrostigma* and particularly *H. orbiliicola* grow parasitic on fungi: they form apothecia and conidia on living fruitbodies, the latter exclusively on apothecia of *Orbilia* spp.

Trapping of rotifers was only once observed (*H. rotifera*) and firm evidence for this is lacking. *H. oviparasitica*, *H. tenuifusaria*, and *H. fusarina* are known to prey on nematode eggs and cysts, and arguments are presented above that also

Table 60. Informative nucleotides in the SSU (V8–V9) rDNA, about 12 of which being more or less specific for *Hyalorbilia* in comparison with other genera of *Orbiliomycetes*, based on available sequences of 11 species (*H. brevistipitata*, *H. citrina*, *H. erythrostigma*, *H. fagi*, *H. inflatula*, *H. lignatilis*, *H. lunata*, *H. orbiliicola*, *H. polypori*, *H. rotifera*, *H. tortuosa*) and two environmental taxa of the genus (clades H37–38). Note concordance between *Hyalorbilia* and five species of section *Orbilia* (*T. subuliphora*, *O. xanthostigma*, *O. leucostigma*, *O. liliputiana*, *O. eucalypti* clade D) at pos. 40 & 90, between *Hyalorbilia* and members of section *Arthrobotrys* with adhesive traps at pos. 109 & 126, and between *Hyalorbilia* p.p.maj. and the *Lecophagus-Amphosoma* clade at pos 141–142. Numbers of species are given in brackets (incomplete sequences after slash). Position numbers start with CCTTAGAT downstream of primer NS7. In *Amphosoma* (A6) only SSU pos. 190–362 was available and in *H. orbiliicola* only pos. 218–362.

Taxa (n)	36–42	55–58	88–94	107–111	124–128	139–144	258–261	264–267	279–284
Lilapila (3)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATTCCT	TCGG	ACGA	CGGAAA
Amphosoma (1/3)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATTCCT	ATGG	ACAT	CGGAAA
Amphosoma (A6)	?	?	?	?	?	?	ATGG	ACAT	CGGAGA
Lecophagus (2)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATTCCT	ATGG	ACAT	CGGAAA
Bryorbilia (4)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATTCCT	TCGG	ACGA	CGGAAA
Bryorbilia (2)	ACAGAGC	TCCT	ACTCTGT	AGAGC	GCTCT	ATTCCT	TCGG	ACGA	CGGAAA
Uncultured Colombia (U2)	ACAGGGC	TCCT	ACCCTGT	AGGGC	GCCCT	ATTCCT	TCGG	ACGA	CGGGAA
Uncultured Italy (U3)	ACGGGGC	TTCC	ACCCCGT	AGGGC	GCCCT	ATTCCT	TTGG	ACGA	CGGAAA
Hyalorbilia (9 + H14, H37)	ACGGGGC	TCCT	ACCCCGT	AGGGC	GCCCT	ATTCCT	GGGG	ACCC	CGAGAA
H. fagi, H. citrina	ACGGGGC	TCCT	ACCCCGT	AGGGC	GCCCT	ATACCT	GGGG	ACCC	CGAGNA
H. erythrostigma	ACAGAGC	TCCT	ACTCTGT	AGGGC	GCCCT	ATACCT	TTGG	ACGA	CGAGAA
H. orbiliicola	?	?	?	?	?	?	TTGG	ACGA	CGAGAA
H. rotifera	ACAGAGC	TCCT	ACTCTGT	AGAGC	GCTCT	ATTCCT	GGGG	ACTC	CGAGAA
Orbilia (~85–95)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATATCT	TCGG	ACGA	CGGAAA
Orbilia (2–10)	ACAGAGC	(CCCT) (TCCT)	ACTCTGT	AGAGC	GCTCT	ATATCT	TTGG (GCGG)	ACAA (ACGT)	CGAAAA (CGGGAA)
section *Orbilia* p.p. (5)	ACAGGGC	ACCT	ACCCTGT	AGAGC	GCTCT	ATATCT	TCGG	ACGA	CGGAAA
O. guyanensis	ACGGAGC	CCCT	ACTCTGT	AGAGC	GCTCT	ATATCT	CGGG	ACTG	CGGGAA
O. pleistoeuonymi	ACAGTCC	--CT	AGACTGT	AGAGC	GCTCT	ATATCT	TCGG	ACGA	CGGAAA
series *Neodactylella* (8) series *Neodactylella* (3)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATATCT	TCGG TTGG	ACGA	CGGAAA
series *Drechslerella* (4)	ACAGAGC	ACCT	ACTCTGT	AGAGC	GCTCT	ATATCT	TCGG	ACGA	CGGAAA
Arthrobotrys adhesive (~28–32)	ACAGAGC	ACCT	ACTCTGT	AGGGC	GCCCT	ATATCT	TCGG	ACGA	CGGAAA
Arthrobotrys adhesive (1–4)	ACAGAGC	CCCT	ACTCTGT	AGGGC	GCCCT	ATATCT	(TTGG)	ACGT (ACAA)	(CGGGAA) (CGAGAA)

H. ulicicola has such capabilities. ‘*Dactylella*’ *passalopaga* captures rhizopods (Pl. 59), and we strongly presume that a species of the *inflatula-polypori* clade is the teleomorph of this species. Two further species assigned to *Brachyphoris*, *B. helminthodes* and *B. stenomeces*, and *H. fusarioides* and *H. spermatophaga*, previously assigned to *Vermispora*, infect oospores, *B. helminthodes* also zygospores (see Tab. 43), but molecular data were not available to confirm their connection to the genus *Hyalorbilia*.

Members of *Hyalorbilia* were recorded from boreal to tropical, humid to subhumid, more rarely semihumid and exceptionally semiarid regions. Similar as in *Orbilia*, desiccation tolerance strongly differs between the taxa, with the tolerant species showing a tendency to produce smaller apothecia. However, the power of tolerance is less pronounced in *Hyalorbilia*, therefore, species diversity in semiarid regions is very low. The tolerance of mature asci usually did not exceed 1–4 weeks in our tests. Some species appear to be desiccation-sensitive, e. g., the asci of

Table 61. Specific nucleotides in the 5.8S rDNA (155 nt) and LSU D1–D2 (635 nt) of the *Hyalorbilia* clade or its subgroups, in comparison with other taxa of *Orbiliomycetes* (position numbers for 5.8S: 1 = **A**AAACTTT, 155 = GAGCGT**C**, for LSU starting with TGACCT by omitting predominant gaps in alignment of all groups of *Orbiliomycetes*. Pos. 138–141 and 152–155 are part of Orb5.8s3F primer (see Tab. 18). * = *V. spermatophaga*/*V. fusarina*/*V. leguminacea*. Rare or exceptional motifs are given in small font. Note more or less unique nucleotides of (1) the *Vermispora* clade (green) at pos. 11 and 85 of 5.8S and at pos. 328 and 608 of LSU, (2) *Hyalorbilia* p.p.maj. (orange) at pos. 140 of 5.8S, and (3) the e*rythrostigma-orbiliicola* clade (yellow) at pos. 83–84 (but concurring with H30–H32) and 155 (but concurring with H29) of 5.8S. Note also coincidence between *Hyalorbilia* p.p.maj. and *Orbilia* at pos. 64 and 98 of 5.8S.

Taxa	9–13	28–32	62–66	81–86	96–100	138–141	152–55	1–6	110–114	119–123	150–154	219–223	263–266	308–312	328–332	529–533	608–616
Hyalorbilia core clade (incl. H4–32)	CAACA cagca	TCCCG tctcg taccg	AGTTA aatta aggta	ATTCAG atctag atccag	GAGTC gaatc gagtt	CACG catg	CGTC	TGACCT	CAGAT	AATCC AATCA	CTGGA ctgca ctgaa	CCCCG tcccg	ACGA	TCCAT tccgt	GGCGG ggcga	AAAGT- AACGT aatgt	ATGCTGGCC atgctagcc
H. erythrost./orbiliic.	CAACA	TCCCG	AGGTA	ATCTAG	GAATC	CATG	CGTG	TCACCT	CAGAT	AATC–	CTGCA	TCCCG	ACGA	TCCAT	GGCGG	AACGT	ATGCTGGCT
H. latispora	CAACA	TCTCG	AGGTA	ATTCAG	GAATC	CACG	CGTC	TGACCT	CAGAT	AATCC	CTGGA	TCCCG	ACGA	TCCAT	GGCGA	AACGT	GTGCTGGCT
Vermispora clade*	CAGCA	TCTCG	AGGTA	ATTCCG	GAATC	CATG	CGTC	TGACCT	CAGAT	AATCT	CTGCA	CCCCG	ACGA	TCCAT	TGCGA	AATGT	GTGCTGGCT
Vermispora clade (V1–V16)	CAGCA	TCTCG tcccg	AGGTA	ATTCCG attcag	GAATC	CATG cata	CGTC	TGACCT	CAGAT	AATCC aatct	CTGCA CTGGA ctgta	TCCCG ccccg	ACGA gcga	TCCAT cccat	TGCGA	AATGT	GTGCTGGCC GTGCTGGCT gtactgact
H. fusarioides	CAGCA	TCTCG	AGGTA	ATTCCG	GAATC	CATG	CGTC	TGACCT	CAGAT	AATCT	CTGGA	CCCCG	ACGA	TCCAT	TGCGA	AATGT	GTGCTGGCC
Lilapila	CAACA	TCTCG	AGGTA	ATTCAG	GAATC	CATG	CGTC	TGACCT	CAAAT	AATCT	TTGAA	TCCCG	AAGA	TTCTT	GGCGA	AATGT	ATGCTGGCG
Lecophagus	CAACA	TCTCG	AGGTA	ATTCAG ATTCCG	GAATC	CATG	CGTC	TGACCT	CAAAT	AATCT	TTGAA	TCCCG	AAGA	GTCAT	GGCGA	AATGT	ATGCTGGCG
Amphosoma/*Reti-arius*/*Bryorbilia*	CAACA cagca	TCTCG	AGGTA	ATTCAG	GAATC	CATG	CGTC agtg	TGACCT	CAAAT	AATCT	TTGAA	TCCCG	AAGA	TTCAT	GGCGA	AATGT	ATGCTGGCG
Mycoceros	CAACA	TCCCG	AAGTA	ATTCAG	GAATC	CATG	CGTC	TGACCT	CAAAT	AATCT	TTGAA			TTCAT	GGCGG	AATGT	ATGCTGGCG
Orbilia	CAACA	TCTCG TCCCG tcccc	AGTTA agcta	ATTCAG atttag	GAGTC gaatc gagta	CATG CACG tatg	CGTC	TGACCT	CAAAT	AATCT	TTGAA ttgta	TCCCG ccccg	AAGA acga	TTCAT ttctt	GGCGA ggcgg ggtgg ggggg	AATGT aacgt	ATGCTGGCT atgctggcg atgctggca acgctggct

Key to species of *Hyalorbilia* based mainly on teleomorph

1. Spores ovoid to subglobose or globose, *(1.8–)2.2–5(–5.7) × 1.3–3.7 µm, length/width ratio 1–1.5(–2); asci 8(–16)-spored; apothecia 0.05–0.9 mm diam. 2
1. Spores cylindrical to ellipsoid or fusiform, *(3.2–)3.5–17.5 × 0.6–2.8 µm, length/width ratio (1.5–)1.8–10(–15); asci 8-spored; apothecia 0.1–4 mm diam. 10

2. Asci 16-spored; spores subglobose, *2.6–3.8 × 2–2.8 µm, SBs apparently lacking; xeric bark of *Melaleuca*, subtropical semiarid western Australia .... ***H. pleioerythrostigma***, p. 430
2. Asci 8-spored 3

3. Living spores with 2 or more bipolar symmetrically arranged SBs; apothecia mainly on hygric substrate 4
3. Living spores with a single eccentric SB; apothecia mainly on xeric substrate 6
If without distinct SBs compare *Hyalorbilia hergiswiliana* (lead 22)

4. Spores broadly ellipsoid, *(3.3–)3.6–5(–5.7) × (2.2–)2.4–2.9 µm; 1(–2) SBs of 0.8–1.5 µm diam. near each spore end; angiosperm wood, subtropical humid eastern Asia .... ***H. biguttulata***, p. 412
4. Spores globose to broadly ellipsoid, *2–4.2 × 1.8–3.8 µm; 3–6 SBs of 0.3–0.8(–1.5) µm diam. peripherally dispersed in each spore half (multiguttulate) 5

5. Spores *(2.5–)3–3.8(–4.2) × 2.2–3.8 µm; asci †18.5–30 × 4–5.6 µm; bark & wood of angiosperms (including *Rubus*), temperate humid Europe, subtropical eastern Asia and western North America .... ***H. multiguttulata***, p. 414
5. Spores *2–2.8 × 1.7–2.5 µm; asci †15.5–25 × 3–4.5 µm; bark & wood of angiosperms, stems of bamboo, temperate to subtropical humid eastern Asia & Macaronesia .... ***H. brevistipitata***, p. 408

6. Asci †12–17 × 3–4 µm; spores ellipsoid-ovoid, *2.4–3.2 × 1.4–1.8 µm, SBs 0.6–0.8 µm diam.; apothecia 0.07–0.16 mm diam.; anamorph unknown; bark of *Ulmus* (on pyrenomycete), temperate humid atlantic northwestern Europe .... ***H. ulmi***, p. 436
Collections from Australia and Ethiopia with larger apothecia (0.15–0.65 mm), partly longer asci (†13–24.5 µm) but shorter spores (†1.7–2.4 µm) resemble *H. brevistipitata* but appear to contain one eccentric SB (p. 409–410)
6. Asci min. †18–21 µm long; spores *1.7–3.5 µm wide, SBs 0.8–1.5 µm diam.; apothecia 0.06–0.4 mm diam.; conidia Y-shaped, arms ± curved downwards 7

7. Conidia with 0–1-septate stipe and ± asymmetrical, non-septate arms; spores ± globose, *3–3.5 µm diam.; asci †29–35 µm long; parasitic on apothecia of *Orbilia* spp. (mostly only conidia present), subtropical subhumid to arid Australia .... ***H.* aff. *erythrostigma***, p. 419
7. Conidia with 1–4-septate stipe and ± symmetrical, 0–2-septate arms (unknown in *H. anonyma*); spores globose to broadly ellipsoid, *(1.7–)1.9–2.7(–3) µm wide 8

8. Asci †40–53 × 3.8–4.8 µm; spores †3–4 × 2.4–2.8 µm; paraphyses apically uninflated, terminal cells 13–28 × 1.2–2.3 µm; marginal cortical cells †1.5–3 µm wide; anamorph unknown; branch of *Melastoma* (on stromata of *Valsaria*), tropical humid South America .... ***H. anonyma***, p. 429
8. Asci †(18–)21–33(–38) × (3.2–)3.5–5(–6) µm; spores †(2–)2.2–2.8(–3.3) × (1.4–)1.7–2.4 µm; paraphyses apically often ± inflated, terminal cells 8.5–20 × 2–5.5 µm; marginal cortical cells †(2–)2.5–6(–7) µm wide; temperate to mesomediterranean humid to semihumid Europe, South America, Macaronesia, Asia, Australia 9

9. VBs ± globose, in paraphyses and marginal cortical cells 1.5–5 µm long; trinacrium-like conidia often present; parasitic on apothecia of *Orbilia* spp. .... ***H. orbiliicola***, p. 424
9. VBs ± elongated, in paraphyses and marginal cortical cells (2–)3–10(–13) µm long; trinacrium-like conidia rarely observed; ± parasitic on pyrenomycetes and gelatinous basidiomycetes, saprobic on bark & wood of angiosperms .... ***H. erythrostigma***, p. 417

10. Spores *9.5–17.5 µm long, with 3–5 or more SBs and some minute LBs near each end; apothecia hydrated 0.1–0.5(–0.9) mm diam. 11
10. Spores *3.5–10 µm long, with 1–2 or 3–5 SBs and some minute LBs near each end; apothecia hydrated 0.1–5 mm diam. 14

11. Spores slightly to strongly curved, rarely a few straight 12
11. Spores straight or only exceptionally slightly curved 13

12. Spores strongly helicoid, *9.5–12(–13) × 1.4–1.7 µm, intertwined within asci, ends only slightly tapered, SBs 0.7–1.1 µm diam.; hygric angiosperm wood, subtropical humid southeastern Asia .... ***H. macrohelicospora***, p. 376
12. Spores slightly to medium falcate, *(10–)11–14(–17.5) × (1.1–)1.2–1.6(–1.8) µm, not intertwined, ends distinctly tapered, SBs 0.3–0.8 µm diam.; hygric to mesic old polypores or angiosperm wood & bark, boreal to subtropical humid Europe, Macaronesia, eastern Asia .... ***H. berberidis***, p. 393

13. Spores *10–13(–15) × (1.1–)1.2–1.6(–1.9) µm (†1–1.5 µm wide); xeric bark & wood of angiosperms, also polypores, boreal to subtropical humid to semihumid Europe, Asia, Australia .... ***H. juliae***, p. 384
13. Spores *(11–)12–14.5(–15.5) × 1.1–1.2(–1.3) µm (†0.8–1.2 µm wide); hygric *Fomes fomentarius*, orotemperate humid Europe .... ***H. fomentarii***, p. 392

14. Spores *(1.2–)1.4–2.5(–3) µm wide 15
14. Spores *0.7–1.3(–1.5) µm wide 28

15. Spores slightly or strongly curved (falcate or helicoid), *(4.5–)5–7 × (1.5–)1.6–1.8(–2) µm, SBs 0.5–1(–1.3) µm diam.; apothecia 0.25–3 mm diam.; hygric bark & wood of angiosperms, temperate to subtropical humid to subhumid atlantic Europe, Macaronesia, eastern Asia .... ***H. lunata***, p. 381
15. Spores straight or only some spores slightly curved, rarely most spores slightly curved (then on xeric substrate) 16

16. Spores *(4.5–)5.5–8.5(–10) µm long 17
16. Spores *(3.5–)4.5–6.5 µm long 19

17. Spores cylindric-ellipsoid to subfusoid, *(1.3–)1.5–1.9(–2.3) µm wide, with 1(–2) globose SBs 0.2–0.5 µm diam. at each end; spores inside living asci usually in two superimposed bundles; apothecia 0.3–2 mm diam.; hygric gymno- & angiosperm wood, polypores, pyrenomycetes, boreal to temperate humid Europe . ... ***H. polypori***, p. 328
If spores somewhat narrower and more fusoid, with several SBs in each half, apothecia on xeric substrate: see *H. juliae* (p. 384).
17. Spores ellipsoid-fusoid to fusiform, *(1.7–)2–2.5(–3) µm wide, with 1–5 SBs 0.3–0.8(–1) µm diam. in each half; xeric bark & wood, atlantic to subcontinental, temperate to submediterranean humid to semihumid Europe 18

18. Apothecia 0.2–2 mm diam., yellowish-cream to ochraceous-orange; marginal cortical cells 3–5(–6) µm wide in surface view; terminal cells of paraphyses 18–33 µm long; all SBs globose; angiosperm bark (rarely wood)........ ***H. fusispora***, p. 397
18. Apothecia 0.08–0.5 mm diam., whitish to pale chlorinaceous; marginal cortical cells (5–)6–10 µm wide in surface view; terminal cells of paraphyses (10–)13–19(–25) µm long; SBs globose but polar ones often subglobose to tear-shaped; gymno- & angiosperm bark & wood, hemiboreal to mesosubmediterranean (semi- or sub)humid Europe, eastern & western North America.....***H. subfusispora***, p. 401

19. Marginal cortical cells thick-walled, forming a protruding collar; apothecia 0.7–2.8 mm diam.; spores †4–6.3 × 1.2–1.4 µm; hygric wood of angiosperms, tropical humid Middle America .... ***H. puertoricensis***, p. 334
19. Marginal cortical cells always ± thin-walled........ 20

20. Apothecia 0.2–2 mm diam., usually cream-chlorinaceous 21
20. Apothecia 0.08–0.2(–0.3) mm diam., usually whitish-greyish; always on xeric substrate........ 24

21. Apothecia mainly 0.2–0.6 mm diam.; spores without SBs, with or without a few minute LBs; on xeric substrate........ 22
21. Apothecia mainly 0.5–2 mm diam.; spores with 1–2 or more SBs and a few minute LBs near each end; on hygric substrate........ 23

22. Spores *5.2–6.5 × 1.3–1.5 µm, fusoid; ectal excipulum at lower flanks of horizontal t. prismatica, marginal cortical cells †4–5 µm wide; wood & bark of *Campsis*, subtropical humid North America .... ***H. texensis*** p. 333
22. Spores *3.2–4.4 × 1.6–2.1 µm, broadly ellipsoid-fusoid to subclavate; ectal excipulum at lower flanks of roundish, indistinctly vertically oriented cells, marginal cortical cells †2–3.5 µm wide; angiosperm wood, oro- to mesotemperate humid central Europe........ ***H. hergiswiliana***, p. 433

23. Marginal excipular cells in median section 6–13 µm wide; spores †4.2–5 × 1.3–1.5 µm; wood of *Platanus*, subtropical (semi)humid southeastern Europe .... ***H. caucasica***, p. 327
23. Marginal excipular cells in median section 3–6(–7) µm wide; spores mainly *4–6 × 1.4–1.7 µm; gymno- & angiosperm bark (& wood), polypores, warm-temperate to mediterranean (semi)humid atlantic Europe, eastern Asia, Australasia .... ***H. ulicicola***, p. 322

24. Spores *3.5–4.3 × 1.8–2 µm, broadly ellipsoid to subclavate .... see under 22 (*H. hergiswiliana*)
24. Spores *(3–)4–5.5(–6) µm long, cylindrical, ellipsoid, or fusoid........ 25

25. Paraphyses apically partly slightly to sometimes strongly inflated (up to *3–5 µm); spores mainly *4–5.3 × 1.3–1.6 µm, mostly straight and homopolar, narrowly ellipsoid, without or with one minute SB at each end; xeric to hygric bark or blackened resin of conifers, temperate humid Europe ....***H. resinae***, p. 437
25. Paraphyses apically usually not inflated (*2–3 µm); on angiosperms 26

26. Spores *1.3–1.5 µm wide; montane northeastern Africa .... see under 31 (*H.* aff. *herbicola*)
26. Spores mainly over *1.5 µm wide; (oro)temperate humid Europe........ 27

27. Spores *4–6 × (1.4–)1.6–1.8(–2) µm, homo- or sometimes heteropolar (subclavate), often without SBs; marginal cortical cells (3–)4–8(–9) µm wide; bark (rarely wood) of angiosperms .... ***H. rotifera***, p. 440
27. Spores *3–6 × (1.8–)2–2.3(–2.5) µm, ± homopolar, with ~3–5 SBs in each half; marginal cortical cells 3–6.5 µm wide; stems of *Senecio* & *Rubus*, bark & wood of *Clematis*, cupules of *Fagus* ....***H. latispora***, p. 431

28. Spores *(3–)4–5.5(–6.5) µm long (in situ, if curved then actual length partly exceeding 6 µm)........ 29
28. Spores predominantly over *5.5 µm long (in situ)........ 32

29. Spores †(4–)4.5–5.5(–6.3) × 1.2–1.4 µm, straight; marginal cortical cells thick-walled, forming a protruding collar; apothecia 0.7–2.8 mm diam. .... see under 19 (*H. puertoricensis*)
29. Spores predominantly < *1.2 µm wide (if > *1.2 µm then apothecia < 0.3 mm diam.), straight or slightly curved; margin usually not forming a protruding collar 30

30. Spores *(3.5–)4.5–6(–6.5) × 0.8–1.1(–1.2) µm; medullary excipulum often gelatinized; marginal cells thin- or thick-walled; apothecia 0.25–2.5 mm diam.; hygric angiosperm bark & wood, temperate to tropical humid eastern Asia, South Africa, Middle America (not sharply delimited from *H. citrina* and *H. oreadum*) .... ***H. japonica***, p. 354
A sample from central Europe on *Populus* wood deviates by partly helicoid spores (p. 367).
30. Spores *3.5–5.7 µm long; medullary excipulum non-gelatinized; marginal cells thin-walled........ 31

31. Spores *(3.5–)4–5.7 × (0.9–)1–1.1(–1.4) µm; apothecia 0.15–0.3 or 0.2–1(–2) mm diam.; excipular cells at lower flanks min. 9–25 × 5–15 µm; terminal cells of paraphyses 9–18.5 µm long, 2–4× longer than lower cells; spores *4-seriate in two superimposed bundles; xeric coniferous and angiosperm wood, temperate to montane humid Europe, ?Asia........ ***H. oreadum***, p. 335
Collections from the Antilles (H.B. 8036) and Azerbaijan (TAAM 68123, p. 355) mentioned under *H. japonica* are somewhat intermediate in having thick-walled excipular cells and slightly curved spores (†4.8–5.5 × 1–1.1 µm and †5.3–5.7 × 0.9 µm, respectively). Both have rather large apothecia.
31. Spores mainly *3.5–5 × 1.2–1.3 µm; apothecia 0.1–0.16 mm diam.; excipular cells at lower flanks 5–8 × 5–6 µm; terminal cells of paraphyses (4–)7–9(–10) µm long, 1.5–2× longer than lower cells; spores *2–4-seriate; hygric herbaceous stems (*Reynoutria*, *Phleum*), temperate humid Europe........ ***H. herbicola***, p. 438
A specimen from Ethiopia on angiosperm bark differs in slightly wider spores (*1.3–1.5 µm, p. 439).

32. Spores straight to partly slightly curved (sickle-shaped, never helicoid) 33
32. Spores consistently slightly to strongly curved (sickle-shaped to helicoid) 35

33. Spores with 1–2 minute SBs close to each end, mainly *5–7.5 × 0.9–1.2 µm, in living asci mostly in two superimposed bundles; apothecia mainly 0.4–2 mm diam., often cupulate to saucer-shaped, also flat from the beginning; conidia fusoid, (3–)4–8(–12)-septate; ± hygric (gymno- &) angiosperm wood & bark, also pyrenomycetes & polypores, boreal to subtropical (semi)humid, worldwide .... ***H. inflatula***, p. 339
33. Spores with usually 3–4(–6) SBs in each half, mainly *7.5–9.5 µm long, in living asci rarely in two superimposed bundles; xeric bark & wood, rarely hygric culms of *Poaceae* 34

34. Spores *6.5–9.7 × 0.9–1.1 µm; apothecia (0.4–)0.7–1.3 mm diam., saucer-shaped; wood of *Quercus*, temperate humid Europe (Luxembourg) .... ***H.* cf. *inflatula*** (H.B. 6819), p. 349
34. Spores *8–10 × 1.1–1.5 µm; apothecia 0.15–0.7(–0.9) mm diam., flat or only slightly concave; bark & wood of angio-, rarely gymnosperms, boreal to subtropical (semi)humid Europe .... ***H. juliae***, p. 384
A collection on hygric culms of *Phleum* from Poland (H.B. 9138b) is hardly different (apothecia 0.12–0.2 mm diam., p. 388).

35. Ectal excipulum at flanks often strongly gelatinized, margin 10–90 µm protruding, composed of globose thick-walled cells forming distinct lobes or teeth or a crenulate collar; spores *4.5–7 × 0.8–0.9 µm, distinctly helicoid (somewhat stair-like); apothecia (0.3–)0.6–3(–4.5) mm diam.; hygric angiosperm bark & wood, petioles, fruits, also polypores & pyrenomycetes, tropical to temperate humid Middle & South America, southern Africa, Asia, Australia (not sharply delimited from *H. japonica*) .... ***H. citrina***, p. 359
35. Excipular cells ± thin-walled (though cortical cells rarely with small glassy caps), never forming marginal teeth 36

36. Spores slightly to strongly sickle-shaped, only exceptionally slightly helicoid, */†5–8 × 0.9–1.3 µm; subtropical South America, Asia & Australasia 37
36. Spores partly or predominantly helicoid, temperate (to subtropical) 39

37. Spores slightly curved; asci †26–30 µm long; apothecia 1–5 mm diam., concave, margin curved upwards; stem of bamboo, angiosperm branches, subtropical humid South America & eastern Asia .... ***H. andina***, p. 337
The Asian collections differ in smaller (0.3–1 mm), flatter apothecia and shorter asci (†17–22.5 µm).
37. Spores medium to strongly curved; asci †18–26(–29) µm long; apothecia 0.14–1.8 mm diam., flat or only slightly concave; (sub)tropical humid eastern Asia, Australia 38

38. Marginal cortical cells without glassy caps; paraphysis apices uninflated, †2–2.5 µm wide; apothecia 0.4–1.8 mm diam.; gymno- & angiosperm bark & wood .... ***H. arcuata***, p. 377
38. Marginal cortical cells with small, knob-like glassy caps; paraphysis apices clavate, †2.5–4.2 µm wide; apothecia 0.14–0.24 mm diam.; angiosperm wood .... ***H. nodulosa***, p. 380

39. Spores †5.5–7.7 × 1.1–1.4 µm, rather strongly helicoid; asci †24–30 × 4–4.7 µm; apothecia 0.4–1 mm diam.; xeric wood of *Larix*, cold-continental humid central Asia .... ***H. sibirica***, p. 375
39. Spores max. †1–1.2 µm wide; asci †(13–)15–23(–26) × (3–)3.3–4.3(–4.7) µm 40

40. Apothecia 0.12–0.8(–1.4) mm diam.; spores *(5.5–)5–7.5(–8) × 1–1.3(–1.4) µm, with 2–4 SBs in each half; xeric angiosperm wood & bark, temperate humid Europe .... ***H. helicospora***, p. 372
40. Apothecia 0.2–0.4 up to 1–2.5(–4) mm diam.; spores with 1–2(–4) SBs in each half; hygric wood & bark 41

41. Spores *(4.3–)4.7–6.5(–7) × (0.9–)1–1.2 µm, slightly to medium helicoid, 1(–2) SBs at each end; conidia fusoid to fusiform, 3–5-septate; (gymno- &) angiosperm wood & bark, also polypores, pyrenomycetes, temperate humid Europe, eastern North America, eastern Asia .... ***H. fagi***, p. 368
41. Spores *(5–)6–7.5(–8) × (0.7–)0.8–1(–1.2) µm, medium to rather strongly helicoid, 1–2(–4) SBs at each end; conidia cylindric-ellipsoid with obtuse ends, 1–3(–4)-septate; angiosperm wood, bamboo, polypores, temperate to subtropical (sub)humid Europe, eastern North America, eastern Asia .... ***H. tortuosa***, p. 364

Key to species of *Hyalorbilia* based on anamorph

1. Conidia branched (staurosporous, trinacrium- to dwayaangam-like or K-shaped) 2
1. Conidia unbranched (phragmosporous, brachyphoris-like) 6

2. Conidia 2-armed (trinacrium-like), *20–35 × 15–24.5 µm, arms ± curved downwards 3
2. Conidia 3–4-armed 4

3. Conidia formed on pyrenomycetes, basidiomycetes, bark and wood, worldwide .... ***H. erythrostigma* s.l.**, p. 417
3. Conidia formed on apothecia of *Orbilia* spp., Europe, North America, Australia .... ***H. orbiliicola* s.l.**, p. 424

4. Conidia 4-armed (dwayaangam-like), *75–95 × 61–77 µm, arms diverging; parasitic on rhizopods, North America .... ***H. quadridens***, p. 407
If only *35 × 20 µm and arms more parallel see under *H. fusispora*.
4. Conidia 3-armed (K-shaped) 5

5. Conidia *27–45 × 11–22 µm, with straight arms; bark & wood, Europe & North America .... ***H. subfusispora***, p. 401
5. Conidia *11–13.7 × 9.5–12 µm long, with strongly curved arms; woody & herbaceous substrates, Europe .... ***H. latispora***, p. 431

6. Conidia filiform to fusoid, *2–3 µm wide 7
6. Conidia fusoid to fusiform, min. *(2.5–)3–4 µm wide 8

7. Conidia 30–60 × 2–3 µm, slightly falcate, 3-septate; parasitic on oospores, Europe .... ***H. fusarioides***, p. 443

7. Conidia *44–77 × 2.1–2.4 µm, slightly flexuous (S-shaped), 3–6-septate; bark, Europe .... ***H. rotifera***, p. 440
Similar type of conidia observed in *H. texensis* and *H. multiguttulata* (46–51 × 2.7–3 µm, 5–6-septate).

8. Conidia 160–180 × 10–22 µm, 6–9-septate; leaves of *Ficus*, India .... ‘***Vermispora’ cauveriana*** (see p. 247)
Possibly belonging to *Orbilia* section *Arthrobotrys* because the conidia produce microconidia.

8. Conidia < 100 × 6 µm 9

9. Conidia cylindric-ellipsoid, (1–)3(–6)-septate 10

9. Conidia fusoid to fusiform, 3–4 up to 5–8-septate 11

10. Conidia *26–45 × 8–10 µm; wood & polypores, Europe .... ***H. polypori***, p. 328

10. Conidia *15.5–35 × 4–7.3 µm; wood & polypores, Europe, eastern North America, eastern Asia .... ***H. tortuosa***, p. 364

11. Conidiophores 1.5–10(–28) µm long, non-septate, unbranched, unilocular or with nodulous scars when multilocular 12

11. Conidiophores (7–)15–50(–100) long, partly septate, branched or not, branches unilocular 13

12. Conidiophores unilocular or sometimes with one additional scar; conidia *31–65 × 3–5 µm, (4–)6–7(–9)-septate; parasitic on nematode cysts & eggs, western North America, Europe, southern Asia .... ***H. oviparasitica***, p. 247, 410

12. Conidiophores partly multilocular; conidia †23–52 × 3–4 µm, 3–5-septate; bark & wood, eastern Asia, Macaronesia .... ***H. brevistipitata***, p. 408

13. Conidia 73–120 µm long 14

13. Conidia 20–70(–83) µm long 15

14. Conidia 88–120 × 4–6 µm, 9–14-septate, apical end tail-like; parasitic on rhizopods, eastern Asia .... ***H. tenuifusaria***, p. 408

14. Conidia 73–96 × 4.5–5 µm, 5–8-septate, apical end not tail-like; hyperparasite of *Meliolaceae*, western Africa .... ***Vermispora grandispora*** (see p. 247)

15. Conidia ± straight, *(25–)40–70(–83) × (3–)4–8(–9) µm, (1–)3–8(–12)-septate; hygric bark & wood, parasitic on rhizopods .... ***Hyalorbilia* spp**.

15. Conidia slightly curved near the ends 16

16. Conidia 20–34 × 4–5 µm, cylindric-fusoid, 1–5-septate; parasitic on nematode eggs, eastern Asia .... ***H. leguminacea***, p. 442

16. Conidia 30–65 × 3.5–5 µm, fusoid-fusiform, (1–)3(–5)-septate 17

17. Conidia 30–50(–55) µm long, partly slightly widened at basal hilum; parasitic on nematode eggs, Europe .... ***H. fusarina***, p. 442

17. Conidia 35–65 µm long, not widened at basal hilum; parasitic on oospores, eastern North America .... ***H. spermatophaga***, p. 443
Compare also *H. lunata* (H.B. 7906a) with conidia *36–45 × 3.5–4 µm, ~4–5-septate (p. 382), and *H. brevistipitata* with conidia †23–52 × 3–4 µm, 3–5-septate (p. 410).

H. berberidis, *H. fomentarii*, *H. inflatula*, *H. lunata*, *H. polypori*, and *H. tortuosa* did not survive for a longer period than ½–2 days. Only in a few cases were mature asci still alive after 3 months (*H. subfusispora*), and immature asci after 11 months (*H. arcuata*). Excipular cells, ascospores, and conidia usually survived for a maximum of 1–5 months, in *H. arcuata*, *H. juliae* even 11–13 and in *H. pleioerythrostigma* 17 months. Because of a comparatively low tolerance, populations of *Hyalorbilia* species on xeric substrate often contain only dead asci when collected after a longer period of drought. The so far single population of a *Hyalorbilia* collected in a semiarid subtropical area, the Australian *H. pleioerythrostigma*, is extraordinary in several respects: it represents the only known species of the genus with 16-spored asci, its apothecia are at the lowermost range (0.15–0.25 mm diam.), and its excipular cells and ascospores showed the highest tolerance observed during storage in the herbarium, while this population has certainly been under dry condition in the field for an unknown period of time.

Hyalorbilia ulicicola Baral & Priou, **sp**. **nov**., MB 813466 — Pls 60–62, Map 5

Etymology: named after the predominant host plant, *Ulex europaeus*.

Typification: France, Morbihan, Île de Creïzic, on *Chaetosphaerella phaeostroma*, also on bark of *Ulex europaeus*, 11.III.2000, J.P. Priou, (ex H.B. 6612, M-0276421, holotype).

Misapplied names: Korf (1992: 508), as *O. inflatula*; Liu (2006: 33, 2007b), as *H. fusispora* (?= *H. ulicicola*); Guo et al. (2014b), as *H. fusispora* (?= *H. texensis* or *H. ulicicola*).

Latin diagnosis: Hyalorbiliae inflatulae similis sed ascosporae multo breviores et latiores, plerumque fusoideae.

Description: — **TELEOMORPH**: **Apothecia** fresh (0.3–)0.4–1.5 or 1.5–2.5(–3) mm diam., 0.14–0.2(–0.3) mm high (receptacle 0.08–0.13(–0.2) → 0.06–0.07 µm), pale or light chlorinaceous to cream-ochraceous, round, when large slightly to very strongly undulating or lobate, hardly to distinctly gelatinous, ± gregarious in small groups; disc ± concave, also flat to finally medium convex, margin thin, smooth, slightly raised; stipe ill-defined or obconical, 0.06–0.1 × 0.16–0.3 mm, superficial; turning light reddish-brown (to amber-orange) with age, dry concave, olivaceous-yellow to orange-brown, often with distinct white subiculum. **Asci** *(20–)25–36(–39) × 4.3–5.2(–5.5) µm {9}, †20–33 × 3.5–4.2 µm {3}, 8-spored, spores 2–3-seriate, pars sporifera *10.5–20 µm long (†16–21 µm); **apex** (†) hemispherical to slightly truncate; **base** with or without medium long, thick, ± flexuous stalk, arising from croziers {9} without perforation. **Ascospores** *(3–)4–5.5(–6) × (1.2–)1.4–1.7(–2) µm {22}, †3.8–4.8 × 1.3–1.6 µm {2}, ellipsoid to mostly fusoid or fusiform, sometimes slightly to distinctly heteropolar (fusoid- or fusiform-clavate), ends obtuse to subacute, straight, sometimes slightly inequilateral; exceptionally medium curved, 1–2 globose **SBs** (0.3–)0.4–0.5(–0.6) µm diam. {4} and 1–2 minute LBs at each end. **Paraphyses** apically uninflated or slightly (rarely medium) clavate-capitate, terminal cells *(14–)17–30(–37) × (2.5–)3–4.3(–4.8) µm {6}, †13.5–18.3 × 3–3.3 µm {1}, lower cells *5–8(–12) × 2–3.5 µm {5}, †5–9.5 × 2.5–3 µm {1}. **Medullary excipulum** 15–50 µm thick, of non- or slightly gelatinized textura globulosa-prismatica mixed with t. porrecta-intricata, cells up to *6–10 µm wide, medium to sharply delimited. **Ectal excipulum** non- or slightly gelatinized, at base of t. angularis 80–170 µm thick, from lower to mid flanks of horizontal t. prismatica 35–50 → 15–20

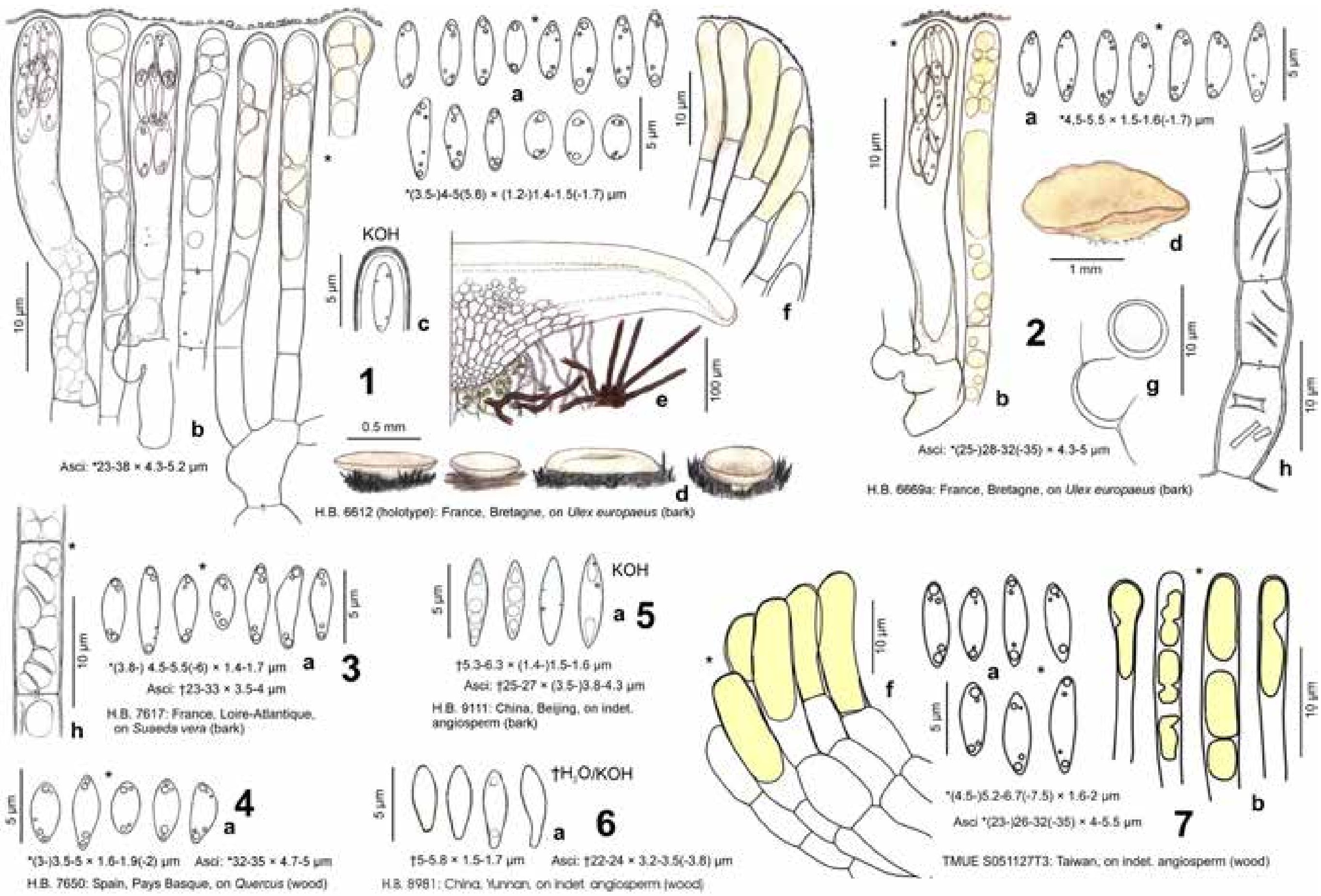


Plate 60. **1–4**: *Hyalorbilia ulicicola*; **5–7**: *H.* cf. *ulicicola*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. ascus apex; **d**. apothecia (fresh); **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. crystalloid SCBs in ectal excipulum; **h**. anchoring hyphae containing SCBs. – **7**: del. Y.C. Su.

µm thick, cells *(10–)20–40(–53) × (6–)10–17(–26) µm {5}, common walls *0.3–0.5 µm thick; cells towards margin in surface view *10–17 × 5–8 µm {1}; margin not or distinctly gelatinized, cortical cells cylindrical to slightly clavate, */†(7–)9–18(–24) × (2.5–)3–5(–7) µm {8}. **Anchoring hyphae** abundant, loose, long, radiating, *(3–)4–6(–8) µm wide, walls *(0.2–)0.3–1(–1.3) µm thick {9}, †(2–)3–5.5 µm, walls 0.2–0.6 µm thick {1}, individual cells *(6–)14–23 µm long. **SCBs** crystalloid, in basal cells of ectal excipulum and also in anchoring hyphae often present, low- to medium refractive, needle-, rod-, ring-, C-, S- or spool-shaped {11}, less often absent {3}. **VBs** in terminal cells of paraphyses very pale to light yellowish-chlorinaceous, very low to usually medium refractive, globose to elongate-angular; excipular cortical cells at mid flanks and margin sometimes filled with medium to large, globose, chlorinaceous, low- to medium refractive VBs; cells of medullary excipulum sometimes with 1 globose **LB** 1–3 µm diam. {1}, or with 1–6 medium refractive globose bodies (?VBs) moving inside vacuoles {1}. **Exudate** over paraphyses 0.3–0.6 µm thick, continuous, mostly strongly warted by small clod-shaped granules; over margin and flanks thin, minutely granular. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate {4}). **Conidiophores** not observed. **Conidia** unbranched, ± straight, narrowly fusoid, †29–37 × 2.3–4.3 µm, 4–7-septate {3}, or *75 × 4.5 µm, ~9–10-septate {1}.

Habitat: lying on ground, covered by moss, grass, or dead *Pteridium*, also 0.1–0.6 or rarely 2–3 m above the ground, ± corticated to decorticated, 6–80 mm thick branches, also thick logs, of *Alnus glutinosa* {1}, *Ceratonia siliqua* {1}, *Clematis vitalba* {1}, *Cytisus scoparius* {2}, *Eucalyptus camaldulensis* {2}, *Fagus sylvatica* {1}, *Fraxinus excelsior* {1}, *Malus domestica* {3}, *Pinus* sp. {1}, *Populus nigra* '*italica*' {1}, *Quercus* sp. {1}, *Robinia pseudoacacia* {2}, *Sambucus nigra* {2}, *Suaeda vera* {2}, *Tamarix africana* {2}, *T. anglica* {1}, *Ulex europaeus* {21}, medium to strongly decayed bark {23} (periderm, also bast), more rarely wood {14}; on pores (also upper side of pileus) of sometimes very old *Fuscoporia ferrea* {1}, *Phylloporia ribis* {1}, *Ganoderma applanatum* {1}, *G. australe* {1/2}, *Inonotus* sp. {1}, gills of *Cellulariella warnieri* {1}; on setae and old perithecia of *Chaetosphaerella phaeostroma* {2}, stromata of ?*Hypoxylon* {1}, green algae very abundant or sparse to absent. **Associated**: *Ascocorticium anomalum* {2}, *Athelia* ?*arachnoidea* {1}, *Calycina* sp. (?heterosporous) {1}, *Cosmospora episphaeria* {1}, ?*Diplodia* sp. {1}, *Duportella halimi* {1}, *Frullania dilatata* {1}, *Hyalorbilia erythrostigma* {1}, *H. fusispora* {1}, *H. juliae* {1}, *Karstenia rhopaloides* {1}, *Lasiosphaeria ovina* {1}, *Lophiostoma angustilabrum* {1}, *Mollisia* sp. {1}, *Neodasyscypha cerina* {1}, *Orbilia eucalypti* {1}, *O.* ?*xantho-*/*leucostigma* {1}, *Phaeangella* ?*ulicis* {1}, *Pyrenopeziza dextrinospora* {1}, *Ramicola obscura* {1}, *Tubeufia cerea* {1}. **Desiccation tolerance**: excipular cells survive for max. 1–2 days, some asci 1 week. **Altitude**: 1–475 m a.s.l. **Geology**: Cambrian siltstone & quartzitic wacke, Ordivician sandstone, Jurassic dolomite, Cretaceous sand-, marl- & limestone, Pleistocene sand; granite, migmatite, porphyry, gneiss, mica schist, ophite etc. **Phenology**: throughout the year (long-lived), collected especially in winter.

Phenology of *H. ulicicola*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
3	10	3	4	1	2	4	2	4	4	10	4

Taxonomic remarks. *Hyalorbilia ulicicola* is characterized by comparatively small, ellipsoid to fusoid or fusiform ascospores, and rather large, ± desiccation-sensitive apothecia. *H. caucasica* is very closely related (see below). *H. fusispora* and *H. subfusispora* differ in longer and wider spores, and in desiccation-tolerant apothecia, the latter also in usually

Plate 61. **1–10**: *Hyalorbilia ulicicola*. – **1a**. *Ulex* shrubland, **9a**. *Eucalyptus* log in an open *Pinus halepensis* forest; **2a–b**, **3a–b**, **4a**, **5**, **6a–b**, **8b**. fresh apothecia; **6d**, **7b**. apothecia in median section; **4d**, **7a**. id., marginal region; **1b**. id., near base; **1c**. id., region of lower flanks; **1d–e**, **4b**. ectal excipular cells near base, with SCBs; **4e**. exudate on hymenium; **6c**. anchoring hyphae; **2c**. paraphyses with VBs; **9b**. mature asci; **2d**, **4c**, **6e**, **8a**. ascospores; **10**. conidia from substrate. – Living state. – **1a**, **2a–b**, **5**: phot. J.P. Priou; **9**: phot. R. Tena. — **1a–e**. H.B. 8048: France, La Gacilly, on *Ulex*; **2a–d**. H.B. 8656: France, Rouen, on *Ganoderma*; **3a–b**. H.B. 8808: France, Île de Ré, on *Cellulariella*; **4a–e**. H.B. 7617: France, Mesquer, on *Suaeda*; **5**. J.P.P. 28032: ibid., on *Ulex*; **6a–e**. H.B. 8357: France, Île-de-France, on *Fagus*; **7a–b**. H.B. 7650: Spain, Gipuzkoa, on *Quercus*; **8a–b**. H.B. 9427: France, Deux-Sèvres, on *Ganoderma*; **9a–b**. 25.IX.2010: Spain, Valencia, on *Eucalyptus*; **10**. H.B. 6864: France, Muzillac, on *Ulex*.

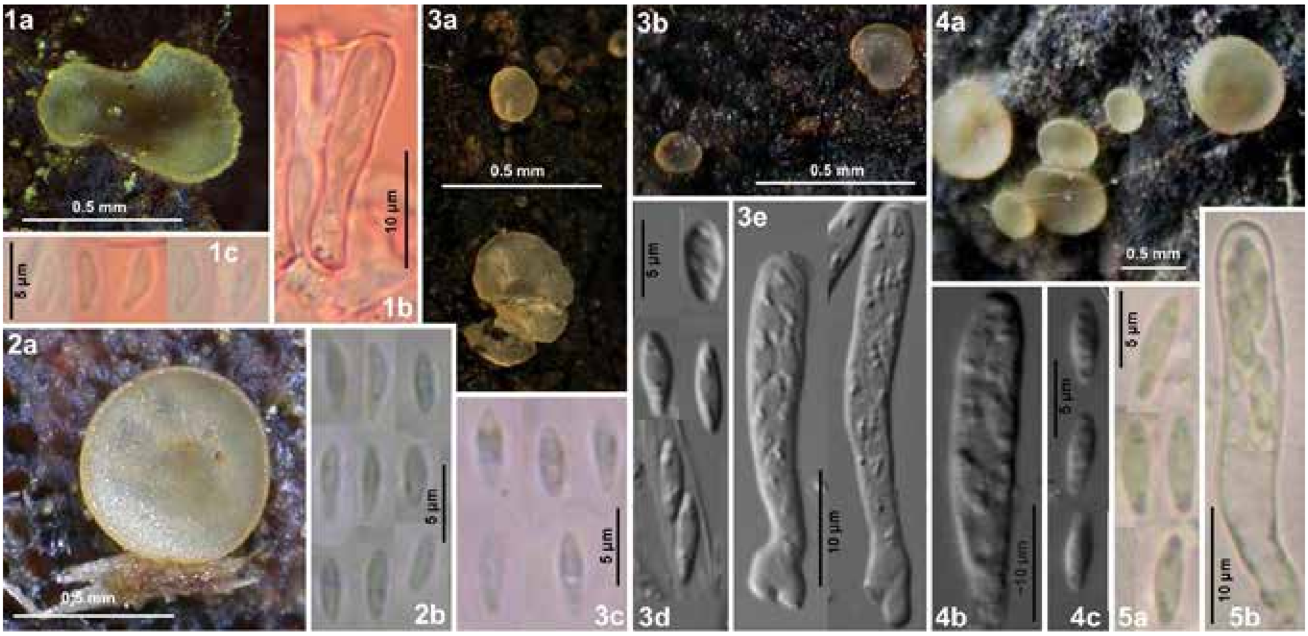


Plate 62. **1–5**: *Hyalorbilia* cf. *ulicicola*. – **4a**. ?fresh apothecia; **1a**, **2a**, **3a–b**, **4a**. apothecia rehydrated from herbarium; **1b**, **3e**, **4b**, **5b**. asci; **1c**, **2b**, **3c–d**, **4c**, **5a**. ascospores. – Dead state (**1b–c** in KOH+CR), except for spores in **3d–e**, **4b–c**. – **1**: from Quijada et al. (2014a); **3a**, **d–e**: phot. H.Y. Su (**d–e**: DIC); **4**: from Liu et al. (2007b), **5**: phot. Y.C. Su. **— 1a–c**. CUP-MM 2487: Azores, São Miguel, on ?*Erica*; **2a–b**. PDD 60056: New Zealand, Auckland, on polypore; **3a–e**. H.B. 8981: China, Yunnan, Jizushan, on indet angiosperm; **4a–c**. HMAS 139546: Henan, Jigongshan, on indet. angiosperm; **5a–b**. TMUE S051127T3: Taiwan, Kaohsiung, on indet. angiosperm.

much smaller apothecia and wider marginal cortical cells. *H. puertoricensis* differs in subcylindrical spores and thick-walled excipular cells, *H. inflatula* in distinctly longer and narrower spores, and *H. texensis* in somewhat longer and narrower spores which apparently do not contain SBs, and in desiccation-tolerant apothecia.

Variation. The spores vary between 3 and 6 µm in length, but this variation can be observed within a single apothecium. The width of the marginal cortical cells varies among the collections between usually 2.5–4 to 3–6 or rarely (on *Populus*) 5–7 µm. The observation of crystalloid SCBs in the anchoring hyphae and excipular cells is so far unique within the genus *Hyalorbilia*, but these cell inclusions were absent or often only very faintly visible in some of the collections. The apothecia vary in size, often attaining 1–2.5 mm but sometimes only 0.4–1 mm.

Not included collections. Under the name *H. fusispora*, Liu (2006: 33, fig. 6; 2007b) reported 13 collections from various provinces of China (Beijing, Henan, Hubei, Jiangsu, Jiangxi, Liaoning, Xinjiang, altitude 400–1000 m), and Guo et al. (2014b) eight collections (from Anhui, Jiangsu, Jiangxi, Zhejiang, Yunnan), but the small size of the spores given there (4.2–6.5 × 1.3–2 µm) clearly excludes *H. fusispora*. The fusoid spore shape and polar SBs resemble instead *H. ulicicola*. One of Liu's collections was reexamined (Beijing, Pl. 60: 5): the spores are slightly longer than in European *H. ulicicola*, and the apothecia measured rehydrated only 0.25–0.35 mm diam. To a different collection (from Henan) belongs his photo plate (Pl. 62: 4), with spores †5–5.2 × 1.5–1.7 µm (*~5.5 × 1.7 µm) and apothecia of 0.35–0.8 mm diam., according to scale. Slightly longer spores occurred also in a specimen from Taiwan studied by Y.C. Su and M.L. Wu (pers. comm., Pls 60: 7; 62: 5), with apothecia 0.4–0.7 mm diam. Another examined Chinese collection (H.Y. Su, pers. comm., Yunnan, Pls 60: 6; 62: 3) has partially heteropolar spores, rather narrow asci, and small apothecia (rehydrated 0.13–0.33 mm diam.). Apothecia reported by Guo et al. (2014b) measured 0.3–1.5 mm, and the similarity in spore shape prompted us to place his samples closer to *H. texensis* (see Pl. 69: 2).

As in European *H. ulicicola*, the living spores in these Asian collections contained 1–2 globose SBs 0.4–0.6 µm diam. at each end. The comparatively narrow marginal cortical cells (3–7 µm wide) seem to exclude *H. caucasica*. The apparently desiccation-sensitive apothecia grew on bark and wood of twigs and branches of angiosperms. Because of available molecular data (see below) we refrain from including these Asian specimens in the description of *H. ulicicola*.

A sample from New Zealand is shown in Pl. 62: 2. In its spore size of †(3.3–)3.5–4.8 × (1–)1.2–1.4 µm it falls in the scope of European *H. ulicicola*, though the spores and also the asci [†(15–)19–25 × 3–3.3 µm] are slightly too narrow. The apothecia measure rehydrated 0.4–1.3 mm, and the marginal cortical cells are 3–5(–6) µm wide and gelatinized. It grew as a mixture with the macroscopically hardly distinguishable *Orbilia cunninghamii*.

Two specimens from Azores identified by Korf (1992) as *Orbilia inflatula* were reexamined by L. Quijada (Quijada et al. 2014a) and resemble the preceding one. That from São Miguel (CUP-MM 2487, Pl. 62: 1) has rather small asci (†19.5–25 × 3.7–4.3 µm) and spores (†3.7–4.3 × 1–1.2 µm). Although its spores are distinctly fusoid, they are too narrow to be included in *H. ulicicola*, besides the apothecia have a distinctly crenulate margin. For the specimen from Flores (CUP-MM 2126) see under *H. texensis* (p. 334).

Anamorph. Conidia were detected near apothecia in four collections of *H. ulicicola*, though only a single conidium in each of them. Those found in three collections from Bretagne (Pl. 61: 10) resemble in shape and size species having smaller conidia, such as *H. brevistipitata*, *H. lignatilis*, or *H. oviparasitica*. In a collection from Valencia (IVV: 25.IX.2010) a much larger conidium was found that resembles those seen in *H. caucasica*.

Phylogeny. An ITS sequence was obtained from apothecia of a French collection of *H. ulicicola* (on *Ganoderma*, H.B. 8656), while two ITS and four LSU sequences were gained by B. Liu from apothecia of four Chinese specimens of *H.* aff. *ulicicola* (as *H. fusispora*). In the ITS region the European sample deviates from the two Chinese ones by 12 %, which suggests that different species are involved, although in the 5.8S region they are identical. A sequence of an unidentified fungus (strain L or ARF-L) comprising ITS and LSU, isolated from eggs of the nematode *Heterodera glycines* in soybean fields in Arkansas (USA) by Yang et al. (2012b), shows a 9 % ITS distance to H.B. 8656 and 12 % to *H.* aff. *ulicicola*. In Liu et al.'s (2006a) and our analyses of ITS, LSU, or ITS+LSU (Phyls 5–6, S5) all these samples form a strongly supported monophyletic clade.

In the LSU (D1–D2), the four Chinese samples show a distance of 0.6–1.5 % to each other. Between HMAS 139526 from Henan and HMAS 139523 from Beijing the distance is 1.5 %, although in the ITS region it is only 0.8 % (5 nt and 2 gaps). However, the two Chinese LSU sequences differ almost only near the 3'-end of D2. Also here the clade of *H. ulicicola* s.l. contains the sample from Arkansas, which shows a distance of 1.5–2.5 % to the Chinese samples.

H. ulicicola s.l. clustered in our combined analysis with weak support sister to *H. subfusispora* and the *oviparasitica-multiguttulata* clade (Phyl. 6)). In our analysis of LSU, however, it formed with moderate support a sister clade to the *inflatula-polypori* clade (Phyl. S5) and in that of ITS it clustered unresolved (Phyl. 5). To European *H. subfusispora* the three ITS sequences of *H. ulicicola* s.l. show a very high distance of ~20 %, while in the 5.8S region they deviate by only 2 nt in the Orb5.8s3F primer region.

Ecology. *Hyalorbilia ulicicola* was found on rotten bark (rarely wood) of hygric branches of angio-, rarely gymnosperm shrubs and trees, predominantly of *Ulex*, also on polypores or pyrenomycetes. It shows a striking restriction to the (south)atlantic area of western and southwestern Europe with a supra- to thermotemperate or mesosubmediterranean humid climate at planar to colline altitude. The vegetation includes *Ulex* shrubs, sometimes with *Rubus*, salt marshes, and forests of *Pinus maritima* or *Quercus*/*Castanea* with tall *Ulex*. In two coastal collections from southern Europe, the climate is mesosubmediterranean semihumid (Montenegro) or thermomediterranean semihumid (almost semiarid, Valencia), and in the not included collection from Azores it is thermotemperate semihumid oceanic (almost humid).

The not included collections from China were from temperate to tropical, humid, monsoon-influenced (winter-dry), sometimes montane forests, and that from New Zealand from a subtropical humid, oceanic climate with damp winters. Based on the genetic similarity with an isolate from northwestern Arkansas, *H. ulicicola* s.l. also occurs in warm temperate humid south of Northern America. The Arkansas fungus was found to infect eggs of the nematode genera *Cactodera*, *Heterodera* and *Meloidogyne* but not *Globodera* (Kim & Riggs 1991). We may assume that also European and Asian *H. ulicicola* s.l. is able to infect nematode eggs.

Map 5: Known distribution of *H. ulicicola* in Europe.

Specimens included. **FRANCE**: **Haute-Normandie**, **Eure**, 16 km SSW of Rouen, 1 km NW of Martot, Forêt de Martot, on *Ganoderma australe*, 6 m, 10.XI.2007, A. Delannoy, vid. J.P. Priou (*Ganoderma* collected X.2006, apothecia developed in garden at Rouen and La Gacilly a year later, J.P.P. 27120, 27130, H.B. 8656, sq.: KT222347). – **Île-de-France**, **Seine-St.-Denis**, 16 km NE of Paris, 2 km NE of Aulnay-sous-Bois, Parc de Sausset, 60 m, branch of *Fagus sylvatica*, on bark, 25.X.2006, G. Eyssartier (H.B. 8357). – **Bretagne**, **Finistère**, 1.7 km NNW of Crozon, SW of Landaoudec, 25 m, branch of *Ulex europaeus*, on wood, 16.II.2002, J.P. Priou (J.P.P. 22025, doc. vid.). – **Morbihan**, 1.7 km NNE of La Gacilly, NE of Les Villes Geffs, Pont des Boussards, rivulet of Rahun, 11 m, branch of *Fraxinus excelsior*, on wood, 16.IX.2011, J.P. Priou (J.P.P. 11091, doc. vid.). – 6.5 km NNW of La Gacilly, 2.5 km W of Carentoir, Tréhandin, 37 m, branch of *Malus domestica*, on bark, 29.XII.2011, J.P. Priou (J.P.P. 11269, doc. vid.). – 12.5 km NNW of La Gacilly, N of La Grée Basse, Le Pouilo, 115 m, branch of *Cytisus scoparius*, on wood, 19.II.2009, J.P. Priou (J.P.P. 29025, doc. vid.). – 3.8 km WNW of La Gacilly, N of St.-Jugon, 80 m, branch of *U. europaeus*, on bark, 19.I.2006, J.P. Priou (J.P.P. 26014, H.B. 8048). – 7.5 km NW of La Gacilly, 4 km W of Carentoir, St.-Adrien, 50 m, branch of *Ulex europaeus*, on bark, 22.II.2001, J.P. Priou (J.P.P. 21034 ø, H.B. 6866a). – 1.4 km WNW of La Gacilly, SW of Talhuart, Buhan, 50 m, of *U. europaeus*, on bark, 11.XI.2001, J.P. Priou (J.P.P. 21111, doc. vid.). – 9.5 km N of La Gacilly, 4 km NNE of Carentoir, Le Marchix, 64 m, branch of *Cytisus scoparius*, on bark, 2.II.2005, J.P. Priou (J.P.P. 25024, doc. vid.). – 2.5 km SSE of La Gacilly, 2 km NNE of Glénac, Pré Naval, 8 m, branch of *Ulex europaeus*, on wood, 21.XI.2001, J.P. Priou (J.P.P. 21123, non vid.). – 6 km W of La Gacilly, 3 km N of Les Fougerêts, Couesme, 80 m, branch of *U. europaeus*, 14.XI.2003, J.P. Priou (J.P.P. 23101, non vid.). – 9 km SE of Malestroit, 3 km NW of St.-Gravé, NE of La Secouette, 80 m, branch of *U. europaeus*, 28.XII.2003, A. Delannoy, vid. J.P. Priou (J.P.P. 23159, non vid.). – 5.5 km SE of Vannes, 1.5 km E of Séné, Falguérec, 2 m, on branch of *U. europaeus*, on bark, 31.I.2014, J.P. Priou (J.P.P. 14028, doc. vid.). – 10 km SSE of Vannes, WSW of St.-Armel, N of Lasné, 1 m, branch of *Suaeda vera*, on bark, 25.XI.2004, J.P. Priou (J.P.P. 24257, H.B. 7651c ø, non vid.). – 8.5 km SSE of Vannes, 2.3 km NW of St.-Armel, Île de Tascon, 9 m, branch of *U. europaeus*, on bark, 25.III.2000, J.P. Priou (J.P.P. 20092, non vid.). – ibid., on *Chaetosphaerella phaeostroma* on *U. europaeus*, 18.X.2001, J.P. Priou (J.P.P. 21093, doc. vid.). – Île de Groix, 15 km SW of Lorient, NW of Kervédan, 38 m, branch of *U. europaeus*, on bark, 22.III.2012, B. Duhem, vid. J.P. Priou (J.P.P. 12070, non vid.). – 15 km SE of Quiberon, Île d'Houat, SW of Houat, above l'Eclosarium, 25 m, branch of *U. europaeus*, on bark, 19.V.2000, J.P. Priou (J.P.P. 20154 ø, H.B. 6669a). – 24 km SE of Quiberon, Île de Hoedic, SW of Hoedic, 7 m, *U. europaeus*, on bark, 25.XI.2009, J.P. Priou (J.P.P. 29231, non vid.). – 12 km S of Auray, 1.5 km SW of Locmariaquer, SE of St.-Pierre Lopérec, Breneguy, 2 m, branch of *Tamarix anglica*, 29.XII.2003, J.P. Priou & A. Delannoy (J.P.P. 23151, non vid.). – 12 km SW of Vannes, 2.5 km SE of Larmor Baden, Île de Creïzic, 14 m, on *Chaetosphaerella phaeostroma* and bark of *Ulex europaeus*, 11.III.2000, J.P. Priou (J.P.P. 20090 **isotype**, doc. vid.; ex H.B. 6612, M-0276421, **holotype**, anam. substr.). – ibid., on *Phylloporia ribis* on stump of *U. europaeus*, 19.II.2000, J. Guillet (J.P.P. 20083b, H.B. 6619). – ibid., on *Fuscoporia ferrea* on *U. europaeus*, 3.XII.2000, J.P. Priou (J.P.P. 20200, non vid.). – 9.5 km SE of Muzillac, 1.9 km NE of Camoël, Barrage d'Arzal, 10 m, branch of *U. europaeus*, on bark, 23.II.2001, J.P. Priou (J.P.P. 21038 ø, H.B. 6864, anam. substr.). – 14.5 km WNW of Herbignac, 2 km NW of Pénestin, Pointe du Halguen, 6 m, branch of *U. europaeus*, on bark, 5.II.2005, B. Fréchet, vid. J.P. Priou (J.P.P. 25028, doc. vid.). – **Ille-et-Vilaine**, 11.5 km WSW of Bruz, 3.3 km ESE of Baulon, Landes blanches, 64 m, branch of *U. europaeus*, on bark, 22.II.2008, J.P. Priou (J.P.P. 28032, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 2.3 km NE of Mesquer, l'Île de Rostu, 2 m, branch of *Suaeda vera*, on bark, 10.XI.2004, J.P. Priou (J.P.P. 24228, H.B. 7617). – 3 km ESE of Piriac-sur-Mer, E of St.-Sébastien, 20 m, branch of *U. europaeus*, 12.XI.2004, J.P. Priou & B. Duhem (J.P.P. 24221, non vid.). – 2.4 km NE of Piriac-sur-Mer, SW of Kerdrien, Pors er Ster, 12 m, branch of *U. europaeus*, on bark, 11.XI.2006, J.P. Priou (J.P.P. 26181, doc. vid.). – **Poitou-Charentes**, **Deux-Sèvres**, 12.5 km WSW of Niort, 1 km ENE of Le Vanneau-Irleau, Marais Poitevin, 4 m, stump of *Populus nigra* '*italica*', on wood, 28.VII.2007, B. Coué (H.B. 8592, anam. substr.). – 14.5 km WSW of Niort, 1.5 km NNW of Amuré, Marais Poitevin, Port Goron, 5 m, on *Ganoderma applanatum*, 26.IV.2011, E. Weber (H.B. 9499 ø). – 9 km N of Aulnay, 2 km SW of Chizé, near river La Boutonne, 40 m, on *Ganoderma* (?)*australe* on *Populus* log, 28.VIII.2010, M. Hairaud (H.B. 9427 ø). – **Charente-Maritime**, Ile de Ré, 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, on *Cellulariella warnieri*, 16.IV.2008, A. Gardiennet (H.B. 8808). – ibid., branch of *Pinus*, on bark, 16.IV.2008, collector unknown (H.B. 8811). – ibid., branch of *Tamarix africana*, on bark, 16.IV.2008, N. Van Vooren (H.B. 8807). – 13.5 km ENE of Saintes, 2.5 km E of St.-Bris-de-Bois, 65 m, pores of *Ganoderma ?australe*, 23.VII.2018, P. Tanchaud (doc. vid.). – **Midi-Pyrénées**, **Ariège**, 12 km ENE of St.-Girons, 2 km NNE of Rimont, Las Muros, 475 m, on pyrenomycete on branch of *Robinia pseudoacacia*, on wood, 27.X.2011, J.P. Priou (J.P.P. 11150, doc. vid.). – 16.5 km ENE of St.-Girons, 0.7 km NE of Castelnau-Durban, les Mouns, 450 m, branch of *R. pseudoacacia*, on wood, 26.X.2011, J.P. Priou (J.P.P. 11170b, doc. vid.). — **SPAIN**: **Asturias**, 2.6 km NNW of Unquera, 1.4 km NE of Pimiango, near Cueva del Pindal, 35 m, branch of *Ulex europaeus*, on bark, 26.XI.2016, E. Rubio (E.R.D. 6895, doc. vid.). – **País Vasco**, **Gipuzkoa**, 30 km SSW of San Sebastián, 0.5 km W of Altzaga, 235 m, branch of *Quercus*, on wood, 2.I.2005, J.P. Priou (J.P.P. 25006, H.B. 7650 ø). – 26 km S of San Sebastián, 3 km SE of Lizartza, Basabe river, 255 m, branch of *Sambucus nigra*, on wood, 19.VII.2015, J. Martin (ARAN-F 01564, doc. vid.). – 6 km SSW of Zarautz, 4.5 km ESE of Zestoa, NW of Altzola, 111 m, branch of *Clematis vitalba*, on wood, 25.VII.2015, J. Martin (ARAN-F 01566, doc. vid.). – **Navarra**, 31 km N of Pamplona, 1 km E of Almándoz, Regata de Marin, 350 m, log of *Alnus glutinosa*, on old pyrenomycete, 5.IX.2014, J. Balda (F.J.B. 50914, doc. vid.). – ibid., 345 m, branch of *Sambucus nigra*, on wood, 29.VIII.2017, F.J. Balda (F.J.B., doc. vid.). – **Com. Valenciana**, **Valencia**, 16 km SSE of Valencia, 2.4 km SSE of Les Gavines, Casal d'Esplai, 2 m, stump of *Eucalyptus camaldulensis*, on wood, 5.II.2010, J. Ormad (J.O. 20100205.03, non vid.). – 14 km SSE of Valencia, El Saler, Gola de Pujol, 4 m, of *Ceratonia siliqua*, on wood, 12.II.2011, J. Ormad (doc. vid.). – 11.5 km SSE of Valencia, 1 km SE of El Saler, Tallafoc de la Rambla, 3 m, log of *Eucalyptus camaldulensis*, on wood, 25./26.IX.2010, R. Tena & J. Ormad (R.T.L. 10092601, anam. substr., doc. vid.). – ibid., branch of *Malus domestica*, on bark, 11.VI.2011, R. Tena (R.T.L. 11061102, doc. vid.). — ibid., branch of *M. domestica*, on bark, 24.IX.2011, R. Tena (R.T.L. 11092401, doc. vid.). — **MONTENEGRO**: 1.5 km NW of Herceg Novi, SW of Trebesinj, 185 m, on *Inonotus*, 22.VI.2019, D. Savić (FG-1095, doc. vid.).

Not included. **MACARONESIA**: **Azores**, **São Miguel**, 5 km NE of Ponta Delgada, ~10 km SW of Ribeira Grande, ~150 m, stump of ?*Erica*, on wood, 27.IV.1978, R.P. Korf, L.M. Kohn & N. Korf, vid. L. Quijada (CUP-MM 2487, as *O. inflatula*, doc. vid.). — **CHINA**: **Beijing**, **Mentougou**, 23 km WNW of Beijing, Xiangshan, 450 m, branch of indet. angiosperm, on bark, 24.VI.2002, B. Liu (B.L. 6165, HMAS 139524 as *H. fusispora*, H.B. 9111; sq.: DQ656692). – ibid., on indet. wood, 24.VI.2002 (B.L. 6163, HMAS 139523; sq.: DQ656647, DQ656695). – ibid., on indet. wood (B.L. 6169, HMAS 139542 [?= 139543 in Liu 2006]; sq.: DQ656696). – **Henan**, **Xinyang**, 35 km S of Xinyang, Jigongshan, 750 m, on indet. wood, 16.XI.2003, B. Liu & W.Y. Zhuang (B.L. 6620, HMAS 139526, as *H. fusispora*, non vid.; sq.: DQ656646, DQ656691). – ibid., on indet. bark (HMAS 139546, doc. vid.). – **Yunnan**, **Dali**, 42 km NNE of Dali, Binchuan, Jizushan Nature Reserve, 2700 m, branch of indet. angiosperm, on wood, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (H.Y.S. jz-4, CBCD, H.B. 8981). – **Taiwan**, **Kaohsiung**, 54 km NE of Kaohsiung, 4.5 km SE of Liouguei, Shanping Natural Education Center, 520 m, branch of indet. angiosperm, 27.XI.2005, Y.C. Su (TMUE S051127T3, TNM, doc. vid.). — **NEW ZEALAND**: **North Island**, Auckland, 21 km SW of Auckland, 2.5 km N of Cornwallis, Waitakere Ranges, Mill Bay, 47 m, on pores of ?*Phellinus*, 17.III.1992, P.R. Johnston (P.R.J. D795, PDD 60056; H.B. 9885a ø). — **USA**: **Arkansas**, soybean field, *Heterodera glycines* eggs (L JY-2012, ARF-L, JQ638671, JQ638672).

Hyalorbilia caucasica Baral & E. Weber, **sp. nov.**, MB 813467 — Pls 63–64

Etymology: named according to the geographical origin, the Kolkheti National Park in th wider Caucasus region (towards Pontic Mts.).

Typification: Georgia, Poti, Kolkheti National Park, branch of *Platanus orientalis*, 7.VIII.1977, V. Puusepp (TAAM 109530, holotype).

Latin diagnosis: Hyalorbiliae ulicicolae *valde similis sed cellulae excipuli marginalis latiores*, *conidia multo longiora et latiora.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.5–1.5(–2) mm diam., 0.16–0.22 mm high (receptacle 0.09–0.1 → 0.05–0.06 mm), pale chlorinaceous-ochraceous, slightly translucent, round, gregarious; disc (slightly concave to) flat, margin not raised, smooth; broadly sessile, superficial; dry light dirty ochre(-brown), ± cupulate. **Asci** †(20–)22–27(–30) × 3.8–4.2 µm, 8-spored, spores ± biseriate; **apex** (†) hemispherical to slightly subconical; **base** unstalked, with croziers. **Ascospores** †4.2–5 × 1.3–1.4(–1.5) µm, fusoid (to fusiform), homopolar, both ends obtuse to subacute, straight to very slightly inequilateral; **SBs** unknown († always with 4 large vacuole-like non-refractive structures). **Paraphyses** apically slightly capitate, terminal cells †(18–)22–25 × 2.7–3.5 µm, lower cells †4–7 × 1.8–2 µm. **Medullary excipulum** 10–20 µm thick, small-celled, slightly gelatinized, medium sharply delimited. **Ectal excipulum** of slightly gelatinized (common walls 0.5–1 µm thick), horizontally oriented textura prismatica at flanks, 70–100 µm thick near base, cells †21–40 × 10–20(–30) µm; 15 µm thick near margin, marginal cortical cells †8–19 × 6–13 µm, thin-walled (0.2 µm). **Anchoring hyphae** abundant near base, very long, straight, radiating, †3.3–5.5(–6.3) µm wide, walls 0.2–0.5(–0.8) µm thick. **Exudate** over paraphyses and margin 0.1–0.2 µm thick, with scattered to dense warts. **— ANAMORPH**: brachyphoris-like (presumed, from natural substrate). **Conidiophores** not observed. **Conidia** unbranched, fusiform, straight, †63–67 × 4–4.8 µm, 7–8-septate.

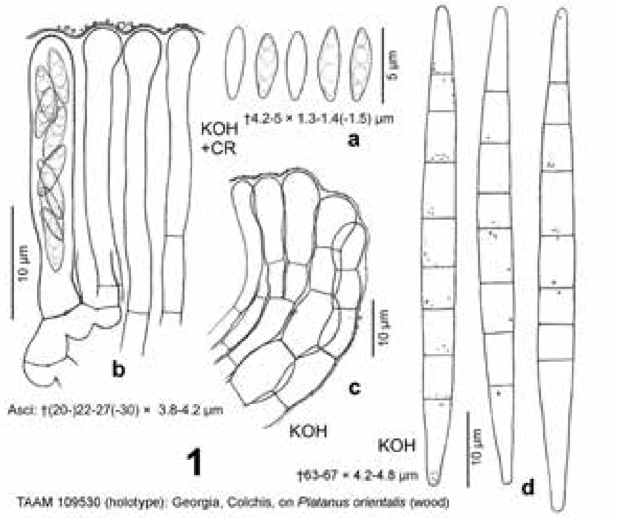


Plate 63. **1**: *Hyalorbilia caucasica*. – **a**. ascospores; **b**. ascus (with croziers) and paraphyses; **c**. marginal ectal excipulum (median section); **d**. conidia from substrate.

Habitat: on fallen, decorticated, 30 mm thick branch of *Platanus orientalis*, on 0.1 mm deep medium decayed wood, ± blackened, no algae, sometimes on old *Lasiosphaeria*. **Associated**: *Chaetosphaeria myriocarpa*, *Lasiosphaeria hirsuta*. **Desiccation tolerance**: unknown (probably intolerant). **Altitude**: ~5 m a.s.l. **Geology**: Cretaceous and Eocene sediment. **Phenology**: VIII.

Taxonomic remarks. *Hyalorbilia caucasica* strongly resembles the ozeanic *H. ulicicola* in size and shape of the ascospores. The single collection is tentatively separated here at the species level by its rather strongly inflated marginal cortical cells and the presumed anamorph having distinctly larger conidia with more septa (however, a single conidium detected in a collection from Valencia closely resembles those of *H. caucasica*). *H. rotifera* differs from *H. caucasica* in wider ascospores and much smaller apothecia.

Ecology. *Hyalorbilia caucasica* was found on medium rotten wood of a hygric branch of *Platanus orientalis* in the warm-temperate humid (somewhat summer-dry) Kolkheti riparian forest, a marshy delta of the Rioni river east of the Black Sea at the Eurasian, Turco-Caucasian border between Caucasus and Pontic Mts.

Specimens included. **GEORGIA**: **Samegrelo-Zemo Svaneti**, Kolkheti (as Colchis), ?15 km E of Poti, 5 m, branch of *Platanus orientalis*, on wood, 7.VIII.1977, V. Puusepp (TAAM 109530, **holotype**; H.B. 7966 ø, anam. substr.).

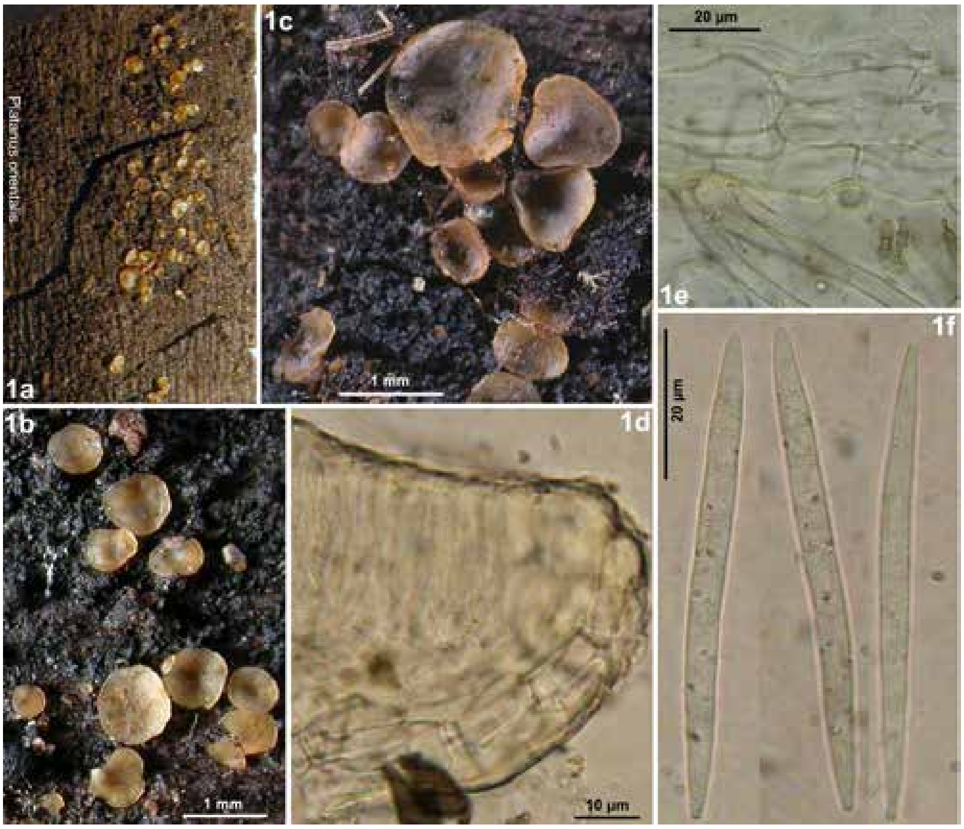


Plate 64. **1**: *Hyalorbilia caucasica*. – **1a**. decorticated wood; **1a–c**. rehydrated apothecia; **1d**. median section of marginal region; **1e**. id., ectal excipulum at lower flanks with anchoring hyphae; **1f**. conidia from substrate. – Dead state (in KOH). — **1a–f**. TAAM 109530 (holotype): Georgia, on *Platanus*.

Hyalorbilia polypori (Velen.) Baral & E. Weber, in Quijada et al., Nova Hedwigia 100: 10 (2014) — Pls 65–67, Map 6

≡ *Orbilia polypori* Velen., Monogr. Discom. Bohem.: 99, pl. 11 fig. 41 (1934)
= *Orbilia cryptocarpa* Svrček, Česká Mykol. 40: 215, pl. 4 fig. 3 (1986)
?= *Orbilia abietina* Velen., Opera Bot. Čech. 4: 103 (1947)

Etymology: *polypori*, *abietina*: named after the substrate (*Ganoderma*, *Abies*); *cryptocarpa*: growing hidden on inner surface of bark.

Typification: Czechia, Central Bohemia, Jevany, *Ganoderma lucidum*, 15.IX.1924, J. Velenovský (PRM 149743, holotype of ***Orbilia polypori***). — Czechia, Dobřichovice, log of *Quercus*, 4.VII.1985, M. Svrček (PRM 842957, holotype of ***O. cryptocarpa***). — Czechia, Mnichovice, log of *Abies alba*, 20.VIII.1941, J. Velenovský (PRM 152436, holotype of ***O. abietina***).

Misinterpretation: Liu (2006, B.L. 288, HMAS 139530), = *Hyalorbilia* sp. (*H.* aff. *citrina*).

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated (0.2–)0.3–1.2(–2) mm diam., (0.08–)0.11–0.25(–0.27) mm high (receptacle 0.06–0.14 → 0.04–0.07 mm), pale yellowish-chlorinaceous-cream, rarely light yellow, slightly to medium translucent, round, margin only very slightly undulating when large, very slightly to sometimes rather strongly gelatinous, scattered to subgregarious, also gregarious in small groups; disc slightly (to medium) concave or often flat, sometimes umbilicate, margin thin, not or only very slightly protruding, smooth or slightly rough; sessile on an obconical base or with a distinct stipe 0.08–0.12 × 0.12–0.4 mm, superficial; dry pale to light yellow-ochraceous. **Asci** *(25–)27–38(–43) × ((4.5–))(5–)5.3–6.3(–6.8) µm {9}, †(20–)22–34(–39) × ((3.5–))(4–)4.5–5.5(–6) µm {11} [Macaronesia: *(23–)25–33(–39) × (4–)4.5–5.5(–6.2) µm {3+}, †(18–)22.5–26.5(–29) × (3.2–)3.5–4 µm {2+}], 8-spored, spores *4-seriate, always or mostly in two superimposed bundles, also ± 3-seriate, rarely some heteropolar spores clearly inversely oriented, pars sporifera *(11–)12–15.5(–17) µm long; **apex** (†) hemispherical (to slightly truncate); **base** only slightly narrowed, arising from croziers {11}, sometimes with small perforation. **Ascospores** *(5–)5.5–8.5(–10)((–11)) × (1.3–)1.5–1.9(–2.3) µm {14}, †(4.5–)5–7.7(–8.5) × ((1.1–))(1.2–)1.3–1.8(–2.2) µm {10} [Macaronesia: *(5–)6–6.5(–7.5) × (1.3–)1.4–1.7(–2.1) µm {4+}, †4.9–6.7 × 0.9–1.4 µm {2+}], (sub)cylindric to slightly fusoid or sometimes fusoid-clavate, exceptionally ellipsoid to fusiform, both ends rounded to obtuse, straight or only slightly curved or inequilateral; **SBs** *0.2–0.5 µm diam. {5}, globose, 1–2 at each end; with a few minute LBs. **Paraphyses** apically uninflated to slightly (rarely medium to strongly) clavate-capitate, terminal cells *(15–)19–28(–30) × (2.5–)3–4(–5) µm {3}, †15–22(–26) × (2–)2.5–3.5(–4.8) µm wide {3}, lower cells *(3–)4–9(–10) × 2–3(–3.7) µm {4}, †3–9(–10) × 1.8–2.7(–3.5) µm {4}. **Medullary excipulum** 10–40 µm thick, of small-celled, medium dense textura globulosa-angularis with hyphoid elements, medium sharply delimited, very slightly to strongly gelatinized. **Ectal excipulum** at base of t. prismatica-globulosa-angularis, (†) slightly to medium gelatinized (common walls 0.3–1 µm thick, at edges up to 2–3 µm), (25–)70–170(–200) µm thick near base, vertically or obliquely oriented, cells */†18–40(–70) × (12–)17–30(–37) µm {8}; 40–60 → 20–25 µm thick at flanks, of horizontal t. globulosa-angularis to short-celled t. prismatica, cells */†(8–)10–25(–30) × (5–)8–15(–20) µm {6}, 10–20 µm thick near margin, marginal cortical cells */†(6–)10–21(–26) × (3–)5–12(–15)((–20)) µm {9}. **Anchoring hyphae** ± abundant at base, */†(2–)2.5–4.5(–7) µm wide, walls 0.2–0.4(–0.7) µm thick {8}, vertically radiating. **VBs** in living terminal cells of paraphyses low to medium refractive, (very) pale chlorinaceous, at a length of 10–23 µm from tip. **Exudate** over paraphyses and ectal excipulum smooth or usually finely to roughly granular, 0.2–0.4 µm thick. **— ANAMORPH**: brachyphoris-like (from ascospore isolate {1} and natural substrate {4}). **Conidiophores** mostly branched (often several side branches in opposite arrangement), hyaline, up to 95(–200) µm long, side branches *40–100 × 3–3.5(–4.5) µm, not or scarcely attenuated above, conidiogenous cells monoblastic. **Conidia** cylindrical to narrowly ellipsoidal, the upper end rounded or obtuse, the lower end with abrupt basal protrusion, *26–45 × 8–10 µm {4}, (0–)3(–6)-septate, †26–34 × 7.8–9 µm {1}, cells containing strongly refractive, globose **SCBs** (0.5–)1–2 µm diam. {1}, often aggregated in groups, instantly disappearing in KOH, not stained in CRB+KOH, and small peripheral LBs (KOH-resistant); large glycogen regions visible in IKI. **Trapping organs** were not formed when nematodes (*Acrobeloides maximus*) were added.

Habitat: decorticated, 22–200 mm thick branches and logs (also stumps and roots), lying on moist ground, of *Abies nordmanniana* {1}, *Acer pseudoplatanus* {1}, *Alnus alnobetula* {1}, *A. incana* {1}, *Betula pubescens* {1}, ?*Corylus avellana* {1}, *Erica arborea* {1}, *Fagus orientalis* {1}, *F. sylvatica* {5/1}, *Laurus novocanariensis* {2}, *Myrica faya* {1}, *Ocotea foetens* {2}, *Picconia excelsa* {1}, *Picea abies* {2}, *Pinus sylvestris* {1}, *Populus* sp. {1}, *Prunus lusitanica* subsp. *hixa* {2}, *Pseudotsuga menziesii* {1}, *Quercus* sp. {1}, *Salix* sp. {1}, indet. gymnosperm {2}, usually on underside, on 0.3 mm deep up to very deeply medium to strongly decayed wood {27}, rarely bark {1}, often blackened; sometimes on senescent stromata of *Eutypa maura* {1}, also on pores of old *Fomes fomentarius* {1}, *Ganoderma lucidum* {1}, *Ischnoderma benzoinum* {1}, *Phellinus* sp. {1}, no or only a few green algae seen. **Associated**: *Ascocoryne inflata* {1}, *Botryobasidium aureum* {1}, *Brachysporium obovatum* {1}, *Calycina citrina* {1}, *Chaetosphaeria* sp. {1}, *C. myriocarpa* {1}, *Diatrype flavovirens* {1}, *Eutypa maura* {1}, *Hyalorbilia berberidis* {1}, *H. inflatula* {1},

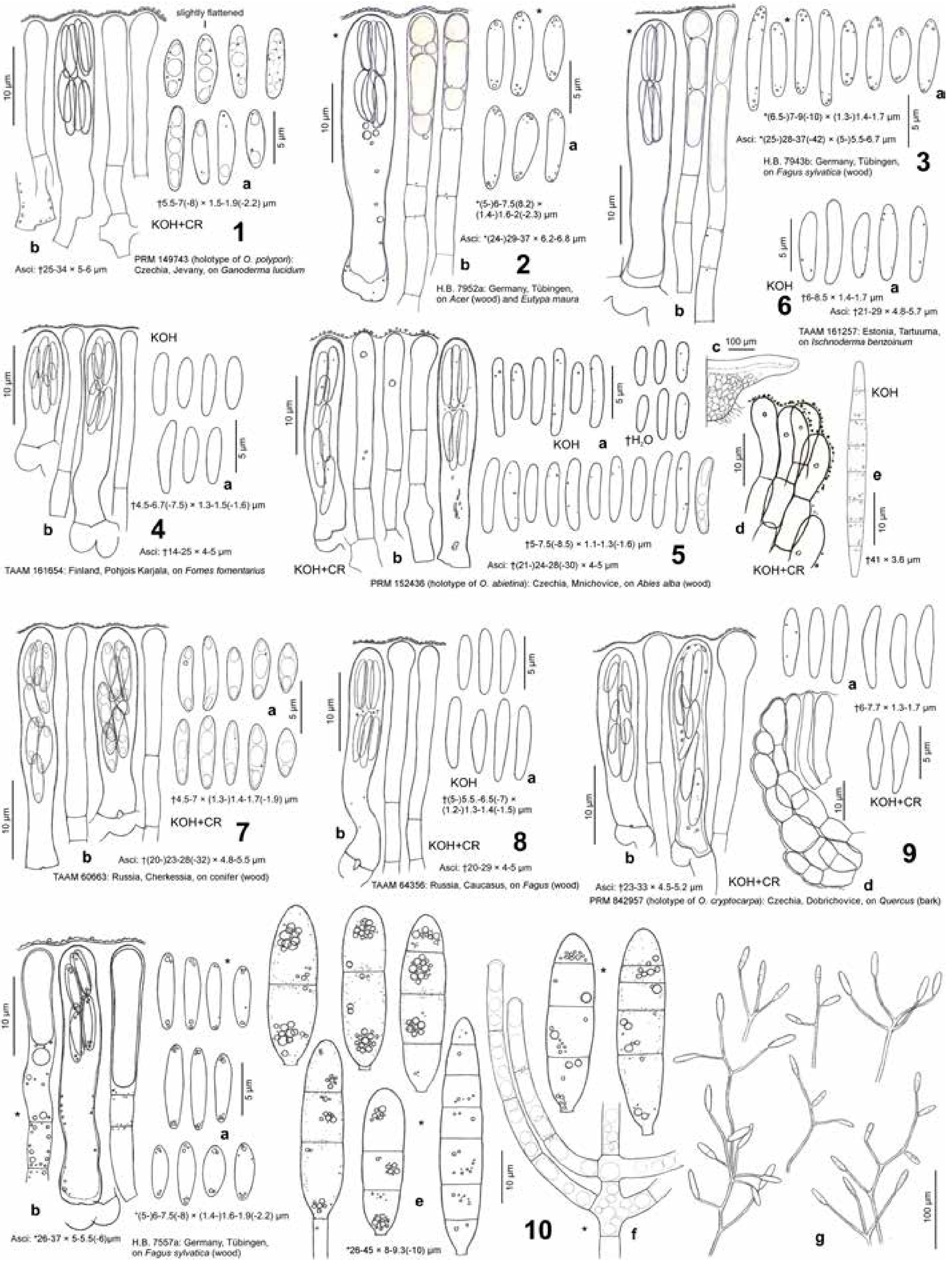


Plate 65. **1–4**, **6–10**: *Hyalorbilia polypori*; **5**. *H.* cf. *polypori*. – **a**. ascospores; **b**. asci (croziers) and paraphyses; **c**. apothecium in median section; **d**. marginal ectal excipulum (median section); **e**. conidia; **f–g**. conidiophores (from culture).

Hyaloscypha leucostigma {1}, *Jackrogersella multiformis* {1}, *Mollisia ?oblonga* {1}, *Natantiella ligneola* {1}, *Orbilia dryadum* {2}, *O. flavovacuolata* {1}, *O. leucostigma* {2}, *O. ?xantho-/leucostigma* {1}, *Psilocistella quercina* {2}, *Scutellinia* sp. {1}, *Trichia decipiens* {1}, *Trichosphaeriaceae* {1}. **Desiccation tolerance**: only ascospores survived for 15 h in the dry state. **Altitude**: 67–715 m a.s.l. (Scandinavia & Baltic), 300–1620 m (central Europe), 775–1700 m (southern Europe & Caucasus), 665–1136 m (Macaronesia). **Geology**: Cambrian and Devonian sedimentary rock, Ordovician shale, silt- & sandstone, Keuper (Stubensandstein, Knollenmergel), Upper Jurassic limestone, Cretaceous mudstone, Tertiary molasse, peat; granite, granodiorite, quartz diorite, amphibolite, tephritic and phonolitic mafic or basaltic flows, phyllosilicate & gneiss, mica schist. **Phenology**: (II–)VI–X(–XI).

Phenology of *H. polypori*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
0	2	0	2	0	2	5	10	6	6	2	0

Taxonomic remarks. *Hyalorbilia polypori* differs from *H. inflatula* in much wider ascospores, also in a tendency to wider and somewhat longer asci. Usually, the two species are sharply delimited, but in the holotype collection of *O. abietina* spore width was found to be intermediate. The ectal excipulum of *H. polypori* is at the flanks mostly composed of rather short and wide, almost isodiametric cells, whereas in *H. inflatula* they are more elongate and prismatic. Only in a few specimens of *H. polypori* (H.B. 7965, 8245) the excipular cells tended to be more elongated in some apothecia. Macroscopically *H. polypori* differs from *H. inflatula* in apothecia being never distinctly cupulate, but *H. inflatula* also occurs in a form with flat apothecia. *H. andina* appears to be closely related to *H. polypori*, but differs in narrower, more curved spores, larger apothecia with inrolled margins (rehydrated) and an ectal excipulum of more elongated prismatic cells (similar as in *H. inflatula*). For the differences to *H. juliae* see p. 386.

Variation in *H. polypori* was mainly observed concerning spore size, though often within a collection or apothecium. Considerably long and narrow spores occurred in the sample from Huesca [*(7–)8–9(–11) × 1.2–1.5 µm]. Collections from Macaronesia studied by L. Quijada (Quijada et al. 2014a) and in the present study (Pl. 67: 6) differ in somewhat shorter spores (mainly *6–6.5 µm) and narrower asci (mainly *4.5–5.5 µm), therefore, their values are given separately in the description. Yet, such short spores occurred also in some European samples. The medullary excipulum was most often found to be not or only slightly gelatinized, though a strong gelatinization was noted in the holotype of *H. polypori*.

Type studies: Already when examined by Velenovský (1934), the holotype of ***O. polypori*** consisted of apparently only one apothecium (1 mm diam. in the protologue, rehydrated 0.8 mm in the present study). Svrček (1954: 19) found the asci (30 × 3–4 µm) and spores (5–7 × 0.8–1 µm) to fit *O. inflatula* and, therefore, placed it in synonymy. Velenovský's description (asci 25 × 5 µm, spores 4–5 µm long, narrowly acicular) also fits quite well Svrček's data, but his drawing on the uncalibrated manuscript sheet shows distinctly wider spores. Together with Svrček's data, a spore size of ~5.5–7 × 1–1.1 µm can be assumed. However, in the present study of the very same apothecium the asci and spores were found to be much wider (Pl. 65: 1). This strong divergence can hardly be explained by different preparation media, or by flattened spores in dead material: a slightly flattened spore showed a width of 2.2 µm, but when seeing it in profile view during floating its width was still 1.8 µm. In Velenovský's manuscript sheet (Pl. 66: a) the spores are also sketchily drawn inside an ascus, and here their width much better corresponds to the present data.

Svrček (1986a) segregated ***O. cryptocarpa*** from *O. inflatula* on the basis of strong differences in spore width [*O. cryptocarpa*: *5–8.5(–9) × 1.3–1.8 µm]. That his description was made from living apothecia can be seen from his drawing which shows a turgescent mature ascus with a compact spore fascicle, and from the regular presence of a small droplet at each spore end (Pl. 66: b), a feature that also Svrček stressed ('always biguttulate'). This drop undoubtedly represents the spore body because in the present reexamination of the holotype no such drop could be seen at the spore ends when mounted in KOH (Pl. 65: 9). The spores slightly deviate from those of typical *H. polypori* in a sometimes more fusoid to fusiform and slightly heteropolar shape, with some spores inversely oriented within the asci, though they look quite homopolar in Svrček's drawing. The paraphyses, which Svrček did not see, are more capitate than in the other collections here assigned to *H. polypori*. Svrček reported the species to grow on the inner surface of bark of a large fallen trunk of *Picea abies*. However, the label on the holotype written by him says '*Quercus*', and the microanatomy of the bark clearly excludes a coniferous substrate. Svrček reported numerous algal cells referred to *Stichococcus bacillaris* as occurring among the excipular cells. Only a few algal cells were seen in the examined type specimen, and the apothecia were found to grow among and sometimes on abundant perithecia of a *Chaetosphaeria*.

A few doubts remain on the correct placement of *O. cryptocarpa* since all the other collections here referred to *H. polypori* were not on bark, and since a number of features of *O. cryptocarpa* somewhat resemble those of the type of *H. juliae* which frequently grows on bark. However, in the present concept of *H. juliae* the living spores usually contain several SBs in each spore half, whereas the SBs in *O. cryptocarpa* as drawn by Svrček match very well those in recent collections of *H. polypori*. The anchoring hyphae are in *O. cryptocarpa* with 3–6(–7) µm rather wide for typical *H. polypori* and even more so for *H. juliae*. The excipular cells at the lower flanks fit with mainly †11–30 × 12–19 µm better typical *H. polypori* (*/†10–25 × 8–15 µm) than the type of *H. juliae* (†10–14 × 6–9

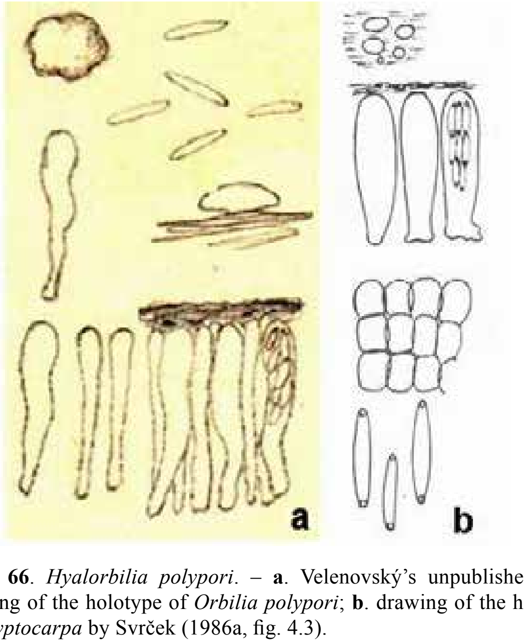


Plate 66. *Hyalorbilia polypori*. – **a**. Velenovský's unpublished original drawing of the holotype of *Orbilia polypori*; **b**. drawing of the holotype of *O. cryptocarpa* by Svrček (1986a, fig. 4.3).

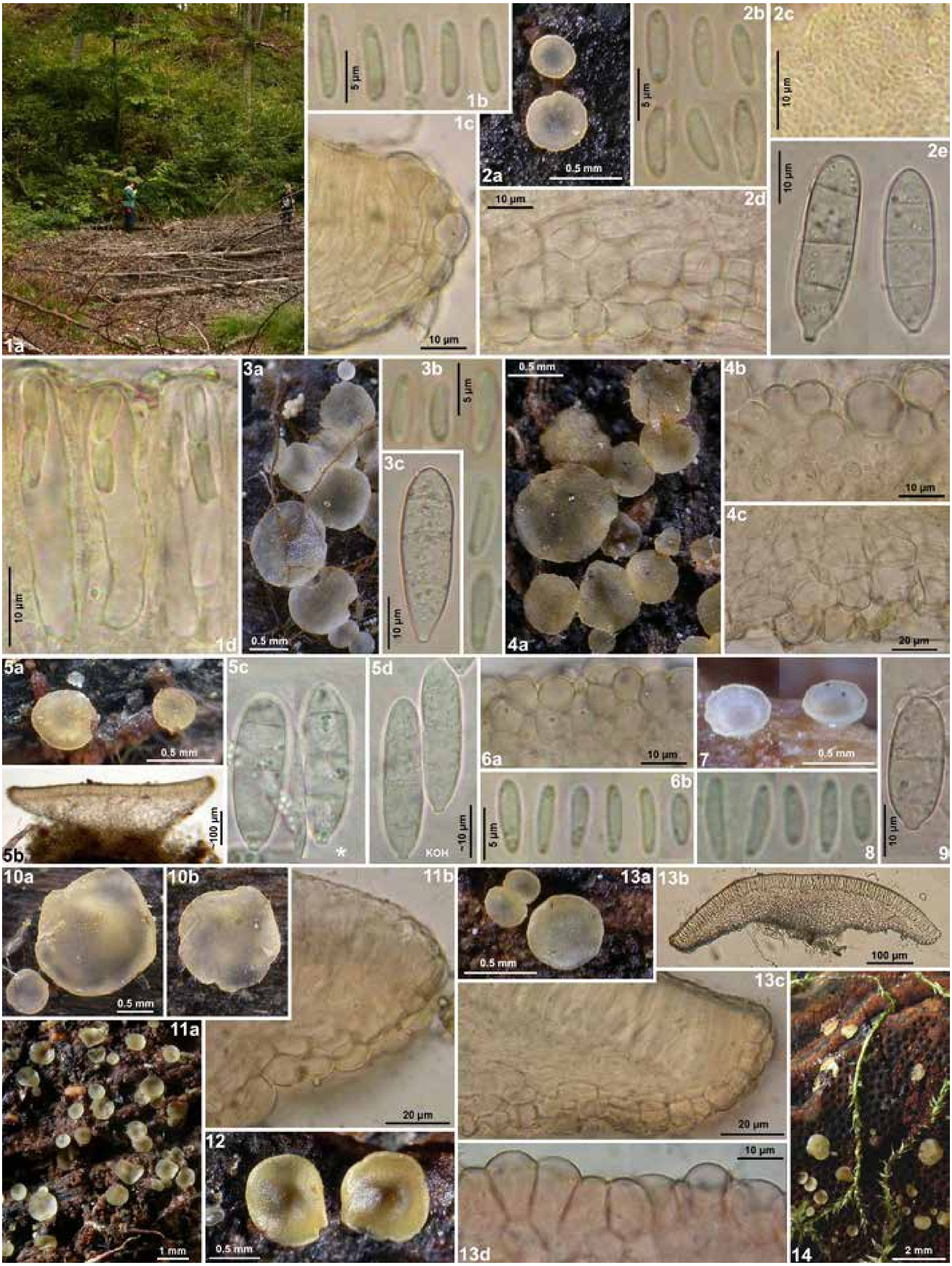


Plate 67. **1–14**: *Hyalorbilia polypori*. – **1a**. usually water-filled pond over Knollenmergel in a ?*Melico-Fagetum*; **2a**, **3a**, **5a**, **7**, **10a–b**. fresh apothecia; **4a**, **11a**, **12**, **13a**, **14**. rehydrated apothecia; **5b**, **13b**. apothecia in median section; **1c**, **11b**, **13c**. id., ectal excipulum at margin and flanks; **2d**, **4c**. id., lower flanks; **4b**, **6a**, **13d**. margin in top view; **2c**. exudate on hymenium; **1d**. mature asci; **1b**, **2b**, **3b**, **6b**, **8**. ascospores; **2e**, **3c**, **5c–d**, **9**. conidia (from substrate, **5** from culture). – Living state, except for **4b–c**, **5d**, **11b**, **13b–c** (in KOH); **13d** (in KOH+CR). – **8**: phot. P. Perz. — **1a–d**. H.B. 7943b: Germany, Tübingen, on *Fagus*; **2a–e**. H.B. 7952a: ibid., on *Eutypa*; **3a–c**. H.B. 8245: Switzerland, Luzern, on indet. gymnosperm; **4a–c**. PRM 842957 (holotype of *H. cryptocarpa*): Czechia, on *Quercus*; **5a–d**. H.B. 7557a: Germany, Tübingen, on *Fagus*; **6a–b**. H.B. 9211: Madeira, on *Ocotea*; **7**. H.B. 9361: Sweden, Saxnäs, on *Betula*; **8**. H.B. 8654a: Poland, on *Acer*; **9**. TAAM 161257: Estonia, on *Ischnoderma*; **10a–b**. H.B. 8243: Switzerland, Luzern, on *Salix*; **11a–b**. TAAM 64356: Russia, Kaukasus, on *Fagus*; **12**. TAAM 64387: ibid., on *Abies*; **13a–d**. TAAM 60663: Russia, Cherkessia, on indet. gymnosperm; **14**. TAAM 161654: Finland, Lieksa, on *Fomes*.

µm). Finally, the size of the rehydrated apothecia (Pl. 67: 4a) fits with (0.25–)0.5–1(–1.3) mm much better *H. polypori*, as does the growth on a fallen trunk. The SBs drawn by Svrček is also reminiscent of *H. subfusispora*, but in that species the spores are wider and, as in *H. juliae*, the distinctly smaller apothecia grow on xeric substrate.

Not included collections. The holotype of ***O. abietina*** (PRM 152436) consists of a piece of rotten decorticated coniferous wood from a thick log, with ~20 well-preserved apothecia. This taxon was likewise placed in synonymy with *O. inflatula* by Svrček (1954: 8) because of narrow spores (6–7 × 1 µm). Actually, the spores were found in the present study to measure only 3.3–5 × 0.9–1.1 µm when mounted in water, but in KOH they swelled to 5–7.5(–8.5) × (1.1–)1.2–1.3(–1.6) µm. Spore width is at the lower limit of *H. polypori*, therefore, this taxon is somewhat intermediate to *H. inflatula*. However, the anchoring hyphae measured only 2–4 µm in width which is a bit too narrow for *H. inflatula*, The excipular cells at the flanks, though prismatic and quite variable (10–50 × 8–20 µm), tend to be rather short and thick, and the spores are a bit too wide. Therefore, we did not include this collection in either description. The apothecia of *O. abietina* were distinctly larger (rehydrated 0.3–0.7 mm) than indicated by Svrček (0.1–0.3 mm, ?dry), but much smaller than stated by Velenovský (1–3 mm). A *Cladonia* grew on the *Abies* log 1–2 cm away from the apothecia on an apparently rather xeric wood area. Probably the area of the *Hyalorbilia* was more protected against drying since Velenovský wrote 'ad lignum humidum'. Velenovský reported dark brown setae (100–150 × 2–3 µm) near the apothecia which were not detected here.

Liu (2006: 45, pl. 10) reported under the invalidly combined name *Hyalorbilia polypori* two Chinese collections, one from temperate Jilin (on wood of *Liquidambar*, IVV: HMAS 96786) and one from tropical Hainan (on unidentified wood, B.L. 288, unillustrated). Spore (†5.2–7 × 1.2–1.5 µm) and ascus size (†21.7–28 × 3.2–4 µm) of the combined diagnosis well correspond to the included Macaronesian samples. Judging from the photo plate of the Jilin sample, spore shape is a bit too fusoid-clavate, and some living spores inside the asci contain one comparatively large SB at each end, which would be untypical for *H. polypori*. The scale bar of the two shown dead spores of HMAS 96786 (fig. E) is erroneous (B. Liu pers. comm.) as it would result in a size of 9.5–10 × 1.9–2.1 µm. The identity of the two records remains uncertain, but a relationship to a specimen from Azores (CUP-MM 2126) mentioned under *H. texensis*, or perhaps to the type of *Orbilia cryptocarpa*, cannot be excluded with certainty. Only the Hainan specimen was sequenced by B. Liu (see below).

Anamorph. The brachyphoris-like anamorph of *H. polypori* resembles *Dactylella tenuis* and *D. coccinella* in conidial shape and to some extent also in size. Yet, these two taxa differ in unbranched conidiophores, *D. coccinella* also in smaller conidia. In *D. zhongdianensis* the conidia are likewise slightly smaller, but the conidiophores are branched similar as in *H. polypori*. However, *D. coccinella* is genetically not a *Brachyphoris* but related to *Orbilia dryadum*, according to Yang & Liu (2005, as *O. alnea*) (see under *O. dryadum*, p. 1390). Also *D. zhongdianensis* clustered in the phylogenetic analysis of Chen et al. (2007a) in *Dactylella* s.str., distant from *Brachyphoris* (see also p. 1472). *H. tortuosa* has a very similar anamorph which differs from that of *H. polypori* in smaller, especially narrower conidia. In the type of *O. abietina* a single conidium (†41 × 3.6 µm, 7-septate) was observed on the substrate, which would fit, e. g., *H. inflatula* but not *H. polypori*.

Phylogeny. A sequence gained from apothecia of *H. polypori* (Germany, H.B. 7557a) comprises SSU (with S1506 intron), ITS, and LSU. When analysing ITS or ITS+LSU, *H. polypori* clustered unsupported or with medium support in a clade with *H. lignatilis*, respectively (Phyls 5–6), as a part of the *inflatula-polypori* clade. When analysing LSU, it clustered with medium support with a strain from Thailand (as *H.* cf. *inflatula*) (Phyl. S5), with a distance of 2.6 % in the D1–D2 domain. However, in previous analyses without the latter strain it clustered in a supported clade with *H. lignatilis*, with a distance of 2.4 % in the D1–D2 (in contrast to ~23 % in the ITS).

A sequence of one of the not included Chinese collections of *H.* '*polypori*' (as *Hyalorbilia* sp., Hainan, B.L. 288, ITS+LSU) clustered strongly supported with *H. citrina* (H.B. 9661) when analysing ITS+LSU, with an LSU distance of 2.5 %, whereas European *H. polypori* deviates from the Hainan collection by 4.5 %. In the ITS region, the Hainan collection showed a distance of 14–15 % to *H. citrina* (H.B. 8012) and *H. japonica* (HMAS 138524), and ~20 % to European *H. polypori*.

Ecology. *Hyalorbilia polypori* was found on rotten wood (very rarely bark) of hygric branches and logs of various gymno- and mainly angiosperm trees and shrubs lying on the moist ground, sometimes on polypores and pyrenomycetes. Similar as *H. inflatula*, *H. polypori* grows predominantly on their underside. *H. polypori* was found in humid, atlantic to continental Europe, at colline to subalpine altitude from hemi- to oroboreal and supra- to orotemperate and orosubmediterranean. Vegetation types include shady deciduous or mixed forests such as *Querco-Fagetea* (*?Stellario holosteae-Fagetum*, *Abieto-Fagetum*), subalpine birch forest, e.g., in ravines close to rivulets. In Macaronesia *H. polypori* was recorded in mesosub- to thermomediterranean (subhumid to) humid laurel forests (*Lauro novocanariensis-Perseetum indicae*) at four sites in the northeast of Tenerife (Anaga) and two in the north of Madeira.

Specimens included. **SWEDEN**: **Västerbotten**, 4.5 km SW of Saxnäs, Satsfjället, Pojken, 715 m, branch of *Betula pubescens*, on wood, 24.VII.2010, T. Læssøe (H.B. 9361). — **FINLAND**: **North Karelia**, 26 km SSW of Lieksa, 1.5 km SE of Koli, ENE of Forest Research Institute, ~180 m, on *Fomes fomentarius* on *Alnus incana*, 11.VIII.1995, K. Põldmaa (TAAM 161654, H.B. 7980). — **RUSSIA (West)**: **Leningrad**, **Vyborg**, Gulf of Finland, 120 km SW of Vyborg, 97 km ESE of Primorsk, Gogland Island, 67 m, on wood of indet. angiosperm, 5.VIII.2007, E.S. Popov (LE 248028, as *H. inflatula*, doc. vid.). — **ESTONIA**: **Tartumaa**, 15.5 km E of Võnnu, 1.4 km NNE of Järvselja, primeval forest, 47 m, on *Ischnoderma benzoinum* on *Picea abies*, 2.IX.1994, K. Põldmaa (TAAM 161257, H.B. 7981 ø, anam. substr..). — **POLAND**: **Lower Silesia**, Kotlina

Map 6: Known distribution of *H. polypori* in Europe and Macaronesia.

Kłodzka, 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 420 m, stump of *Pinus sylvestris*, on wood, 21.XI.2006, P. Perz (P.P. 20070820-3, H.B. 8605b ø). 25km SSE of Kłodzko, 11 km SW of Stronie Slaskie, 1.5 km SE of Miedzygorze, way towards Śnieżnik, 700 m, branch of *Acer pseudoplatanus*, on wood, 31.VII.2007, P. Perz (P.P. 20070731-2, H.B. 8654a). — **GERMANY**: **Baden-Württemberg**, 5 km ENE of Tübingen, 1 km SSE of Pfrondorf, Haldenbach, 330 m, on *Eutypa maura* and wood of *Fagus sylvatica*, 30.X.2005, E. Weber (H.B. 7952a, anam. substr.). – ibid., Bitzle, 350 m, branch of *Fagus sylvatica*, on wood, 25.VII.2004, E. Weber & H.O. Baral (H.B. 7557a, CBS 117018, anam. cult.; sq.: KT215223). – 1 km E of Pfrondorf, Hinterpfand, 410 m, branch of *Fagus sylvatica*, on wood, 22.X.2005, E. Weber (H.B. 7943b, in M-0276481 [H.B. 7943a, *O. flavovacuolata*]). – 4.3 km E of Heidenheim, 2.7 km SW of Nattheim, Wagnersgruben, 608 m, root of *Picea abies*, on wood, 7.VII.2012, G. Schabel (ø, doc. vid.). — **SWITZERLAND**: **Uri**, 9.7 km ESE of Altdorf, 1.7 km SSW of Unterschächen, N of Sittlisalp, 1620 m, branch of *Alnus alnobetula*, on wood, 21.VIII.2006, E. Weber (H.B. 8268 ø). – **Nidwalden**, 8 km SSW of Luzern, 2.5 km WSW of Hergiswil, NW of Renggeli, W of Brunni, Mülibach, 960 m, branch of *Salix*, on wood, 16.VIII.2006, V. Baral (H.B. 8243). – ibid., 2 km WSW of Hergiswil, Renggeli, 840 m, branch of indet. gymnosperm, on wood, 18.VIII.2006, E. Weber (H.B. 8245, anam. substr.). – **Fribourg**, 9 km ESE of Fribourg, 1.3 km ENE of Rechthalten, 860 m, branch of ?*Corylus*, on wood, 21.VI.2012, M. Hairaud (ø, doc. vid.). – **Graubünden**, 4.3 km ENE of Landquart, 2 km WSW of Seewis, NE of Crupspitz, Mannaswald, 1000 m, log of ?*Fagus sylvatica*, on wood, 8.XI.2018, U. Roffler (doc. vid.). — **AUSTRIA**: **Steiermark**, 6 km WNW of Feldbach, ENE of Rohr a. d. Raab, 335 m, log of *Populus*, on wood, 20.VIII.2015, A. Gallé, vid. G. Friebes (ø, doc. vid.). — **CZECHIA**: **Central Bohemia**, 30 km ESE of Praha, around Jevany, ?450 m, on *Ganoderma lucidum*, 15.IX.1924, J. Velenovský (PRM 149743, **holotype** of *O. polypori*, H.B. 6270 ø). – 22 km SSW of Praha, 1 km SW of Dobřichovice, Brdské hřebeny, above ravine Malá rokle (as Buková rokle), ~300 m, log of *Quercus*, on bark, 4.VII.1985, M. Svrček (PRM 842957, **holotype** of *O. cryptocarpa*, H.B. 6939a ø). — **SPAIN**: **Asturias**, 9.5 km SW of Cangas de Onís, 2 km SE of El Pico, NE of Casa de Fontecha, 775 m, log of *Pseudotsuga menziesii*, on bark, 6.IX.2013, E. Rubio (ø, doc. vid.). – **Aragón**, **Huesca**, 9 km NE of Benasque, SW of Hospital de Benasque, Los Llanos, 1700 m, log of *Fagus sylvatica*, on wood, 31.VIII.2015, R. Blasco (R.B. 31-08-15-857-BE, anam. substr., doc. vid.). – ibid., 26.IX.2015 (R.B. 26-09-15-877-BE, non vid.). – 12.5 km NNE of Jaca, 2.7 km E of Villanúa, Fuente el Paco, 1270 m, log of *F. sylvatica*, on wood, 6.IX.2016, R. Blasco (R.B. 06-09-16-978-VI, doc. vid.). — **RUSSIA (West)**: **Krasnodar**, Caucasus Mts., 80 km ENE of Sochi, 3 km NNE of Umpyr, Malaya Laba, 1100 m, branch of *Abies nordmanniana*, on wood, 12.VIII.1976, M. Pallo (TAAM 64387, H.B. 7965b ø). — ibid., on branch of *Fagus orientalis*, on wood, 12.VIII.1976, M. Pallo (TAAM 64356, as '*Abies nordmanniana*', H.B. 7965a ø). – **Karachayevo-Cherkesiya**, 90 km SW of Tscherkessk, 32 km WNW of Teberda, Arkhyz, ~1400 m, log of indet. gymnosperm, on wood, 24.IX.1968, L. Järva, E. Parmasto & A. Raitviir (TAAM 60663, H.B. 7971 ø). — **MACARONESIA**: **Madeira**, 4.7 km SSE of Ribeira da Janela, 3.5 km SW of Seixal, 1136 m, branch of *Ocotea foetens*, on wood, 15.X.2009, J.P. Priou (J.P.P. 29185, H.B. 9211 ø). – 4.5 km W of Seixal, 2.5 km S of Ribeira da Janela, 885 m, on *Phellinus* on *Ocotea foetens*, 15.X.2009, J.P. Priou (J.P.P. 29184, doc. vid.). – **Canary Islands**, **Tenerife**, Tegueste, Anaga, 5 km NNW of San Cristóbal de La Laguna, 1.5 km NE of Tegueste, La Hoya del Palomo, 665 m, branch of *Picconia excelsa*, on wood, 16.VI.2012, L. Quijada & E.V. Rodríguez (TFC Mic. 23540, doc. vid.). – Santa Cruz de Tenerife, 3 km ESE of Taganana, near to El Pijaral, 765 m, branch of *Prunus lusitanica* subsp. *hixa*, on wood, 13.VIII.2013, L. & C. Quijada (TFC Mic. 24282, doc. vid.). – 3.3 km ESE of Taganana, El Pijaral, 775 m, branch of *Laurus novocanariensis*, on wood, 14.II.2012, L. & C. Quijada (TFC Mic. 23365, non vid.). – ibid., branch of *Myrica faya*, on wood, 14.II.2012, L. & C. Quijada (TFC Mic. 23369, doc. vid.). – ibid., branch of *Prunus lusitanica* subsp. *hixa*, on wood, 24.X.2012, L. & C. Quijada (TFC Mic. 23689, doc. vid.). – ibid., branch of *Erica arborea*, on wood, 24.X.2012, L. & C. Quijada (TFC Mic. 23693, doc. vid.). – 4.3 km E of Taganana, 2 km SW of Chamorga, Chinobre, 895 m, branch of *Laurus novocanariensis*, on wood, 7.IV.2013, L. & C. Quijada (TFC Mic. 24027, doc. vid.). — **AUSTRALIA**: **Tasmania**, Tasmanian Northern Slopes, 20 km S of Devonport, 10 km WSW of Sheffield, SW corner of Lake Barrington, Billet Creek Gully, ?200 m, branch of indet. tree, on wood, 13.IV.1996, E. Batten (E.B. 3357A, K(M) 199708, doc. vid.).

Not included. **CZECHIA**: **Central Bohemia**, 3 km SE of Mnichovice, Hrusice, 360 m, log of *Abies alba*, on wood, 20.VIII.1941, J. Velenovský (PRM 152436, **holotype** of *O. abietina*, H.B. 6058a ø). — **CHINA**: **Jilin**, **Yanbian**, Antu, ~400 m, on wood of *Liquidambar formosana*, 19.IX.2004, B. Liu (HMAS 96786, as *H. polypori*, doc. vid.). – **Hainan**, **Wuzhishan**, Suiman, 700 m, on indet. wood, 15.XII.2003, B. Liu, M.H. Sun, X.Z. Liu (B.L. 288, HMAS 139530, as *H. polypori*, non vid.; sq.: DQ656651, DQ656697).

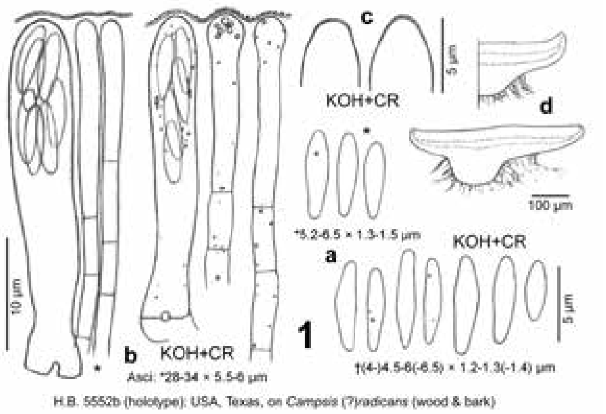


Plate 68. **1**: *Hyalorbilia texensis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section.

Hyalorbilia texensis Baral & G. Marson, **sp**. **nov**., MB 813468 — Pls 68–69

Etymology: From the geographical origin, Texas (USA).
Typification: USA, Texas, Houston, branch of *Campsis* (?)*radicans*, 20.VI.1996, G. Marson (ex H.B. 5552b, M-0276419, holotype).
Misapplied name: Guo et al. (2014b), as *H. fusispora* (?= *H. texensis*).
Latin diagnosis: Hyalorbiliae polypori *similis sed ascosporae minores*. *Habitat ad corticem putridum siccum*, *etiam lignum*, *ramorum fruticis* Campsidis (?) radicantis *in zona subtropica humida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.6(–0.8) mm diam., 0.11–0.14 mm high (receptacle 0.07–0.1 → 0.06 mm), light cream-yellowish to orange-brownish, scarcely translucent, round, medium to strongly gelatinous, very scattered; disc slightly concave to flat with raised smooth margin; with ± distinct stipe 0.05–0.06 × 0.12–0.15 mm, superficial; dry dirty red-brown. **Asci** *28–34 × 5.6–6 µm, †25–30 × 4–4.4 µm, 8-spored, spores *2–3-seriate; **apex** (†) hemispherical to subconico-subtruncate; **base** unstalked, with croziers. **Ascospores** *5.2–6.5 × 1.3–1.5 µm, †(4–)4.5–6(–6.5) × 1.2–1.3(–1.4) µm, fusoid, sometimes fusoid(-clavate), ends rounded to obtuse, rarely one end subacute, straight to very slightly inequilateral; **SBs** (*) apparently absent. **Paraphyses** apically uninflated to slightly capitate(-clavate), terminal cells †13–17 × (2–)2.5–3.3 µm, lower cells †5–7 × 1.8–2.2 µm. **Medullary excipulum** 20–40 µm thick, of dense, non-gelatinized textura prismatica-angularis, indistinctly delimited. **Ectal excipulum** of thin-walled to slightly gelatinized t. angularis(-prismatica), 30–60 µm thick near base, cells †17–23 × 6–10 µm; at flanks of 20 µm thick horizontally oriented t. prismatica, near margin 10 µm thick, marginal cortical cells †9–12 × 4–5 µm. **Anchoring hyphae** abundant, †(2–)2.5–4(–5) µm wide (near insertion 5–6 µm), walls 0.2–0.3(–0.5)((–1)) µm thick, vertically radiating. **Exudate** over paraphyses and excipulum 0.2 µm thick, densely finely granular-warted. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate). **Conidiophores** not observed. A single **conidium** found, †46 × 2.7 µm, narrowly fusoid, slightly curved at apex, ?5-septate.

Habitat: decorticated to partially corticated, attached, 10–20 mm thick stems of *Campsis* (?)*radicans*, on 1 mm deep strongly decayed wood and mainly bark (periderm & bast), slightly greyed, covered by green algae. **Associated**: *Orbilia cejpii*, *O. hesperidea*. **Desiccation tolerance**: fully tolerant for at least 1–2 weeks. **Altitude**: 35 m a.s.l. **Geology**: Pleistocene clay and mud. **Phenology**: VI.

Taxonomic remarks. *Hyalorbilia texensis* is tentatively separated from *H. polypori*, *H. fusispora*, and *H. subfusispora* based on the living spores being smaller and eguttulate, from *H. polypori* also by desiccation-tolerant apothecia. *H. caucasica* differs in wider marginal cortical cells and shorter spores, and *H. ulicicola* in slightly shorter and wider spores with several distinct SBs, and in desiccation-sensitive apothecia. *H. juliae*

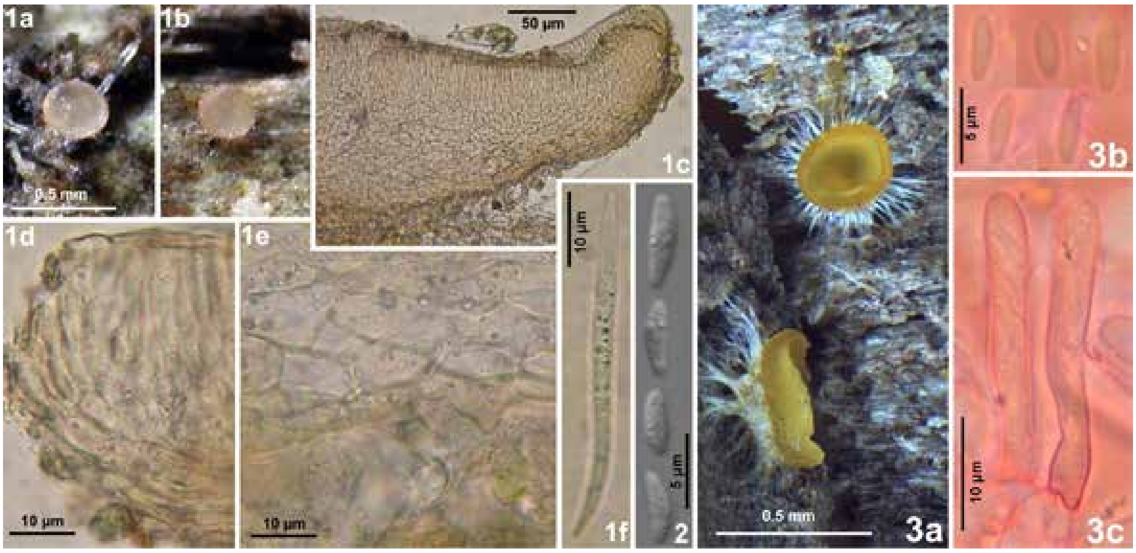


Plate 69. **1**. *Hyalorbilia texensis*; **2–3**. *H.* cf. *texensis*. – **1a–b**, **3a**. rehydrated apothecia; **1c**. apothecium in median section; **1d**. id., marginal ectal excipulum; **1e**. id., ectal excipulum at lower flanks; **3c**. asci; **2**, **3b**. ascospores; **1f**. conidium from substrate. – Dead state: **2** (in H_2O), **1c–f** (in KOH), **3b–c** in KOH+CR. – **2**: from Guo et al. (2014b, DIC), **3a–c**. from Quijada et al. (2014a). — **1a–f**. H.B. 5552b (holotype): USA, Texas, on *Campsis*; **2**. J.W.G. ym-j-179: China, Yunnan, on indet. tree; **3a–c**. CUP-MM 2126: Azores, Flores, on indet angiosperm.

differs in much longer spores. A similar sparse collection from Texas (285 km to the west, altitude 380 m higher) on *Vitis* (IVV: H.B. 5554c) differs in distinctly wider spores (*5–7.5 × 1.8–2 µm) with small to medium-sized drops and is tentatively included in *H. subfusispora*.

Not included collections. Eight Chinese collections reported by Guo et al. (2014b) under the name *H. fusispora* are mainly known in the dead state. Judging from spore size and shape (Pl. 69: 2, †4.2–6.3 × 1.3–1.8 µm) this could well belong to *H. texensis*. However, the asci are given much shorter (16.6–26.2 × 2.8–5.9 µm) and the apothecia which grew on hygric branches of indet. angiosperms or indet. trees attained a much larger size (0.3–1.5 mm). Guo et al. did not indicate which collection is figured on his fig. 3, but when he earlier sent this plate to us he referred it to ym-j-179 (J.W. Guo pers. comm.). Caution is advised with the published plate which is vertically 10 % shorter compared to the original plate. Measurements taken by us from the original plate confirmed those in the description: †4.3–6 × 1.3–1.5 µm, †18.7–20.3 × 3.4–3.7 µm, and 0.7–1.3 mm, respectively. The description includes also living spores containing 2 elongate terminal and several globose peripheral SBs, therefore, it is also mentioned under *H. ulicicola*.

A specimen from Azores (CUP-MM 2126) identified by Korf (1992) as *Orbilia inflatula* was reexamined by L. Quijada (Quijada et al. 2014a; Pl. 69: 3). The size of asci (†23.5–30 × 3.8–4 µm) and spores [†4–5(–5.8) × 1.3–1.6(–1.9) µm] fit quite well the North American *H. texensis*, but the specimen resembles also the smaller-spored collections of *H. polypori* from Tenerife reported by Quijada et al. (l.c.). Korf erroneously believed that the conspicuous subiculum was characteristic solely of *H. inflatula*.

Anamorph. The single fusoid conidium found near the apothecia is slightly narrower (†46 × 2.7 µm) than typical conidia of *Hyalorbilia* spp.

Ecology. *Hyalorbilia texensis* grew on rotten wood and bark of a xeric branch of *Campsis* (?)*radicans* cultivated in the northern suburb of Houston in the subtropical humid south of USA. The not included collections from Azores and China are from evergreen forests with a thermotemperate or subtropical humid climate, respectively.

Specimens included. **USA**: **Texas**, 32 km N of Houston, Motel 6, 35 m, branch of *Campsis* (?)*radicans*, on wood & bark, 20.VI.1996, G. Marson (ex H.B. 5552b M-0276419, **holotype**, anam. substr.).

Not included. **MACARONESIA**: **Azores**, **Flores**, ?SW of Cedros, Ribeira do Cascalho, Alagoa, ?200 m, indet. angiosperm, on wood, 13.IV.1978, R.P. Korf, L.M. Kohn & N. Korf, vid. L. Quijada (CUP-MM 2126, as *O. inflatula*, doc. vid.). — **CHINA**: **Yunnan**, **Yuxi**, Yimen, 54 km NW of Yuxi, 3 km NW of Fangtunxiang, Dalongkou, Longquan, 1750 m, branch of indet. tree, 23.VIII.2006, J.W. Guo (J.W.G. ym-j-179, YMFT, doc. vid.).

Hyalorbilia puertoricensis Baral, **sp. nov.**, MB 813469 — Pls 70–71

Etymology: named after the geographical origin, Puerto Rico (Middle America).
Typification: Puerto Rico, El Yunque, log of indet. angiosperm, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (ex D.H.P. PR 111, FH, holotype).

Latin diagnosis: Hyalorbiliae citrinae *similis sed ascosporae rectae*, *latiores*, *excipulum ectale textura prismatica crassitunicata*, *ad marginem textura angularis*, *valde gelatinosum.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.7–2.8 mm diam., 0.09–0.15 mm high (receptacle 0.08–0.11 → 0.05–0.06 mm), light chlorinaceous-yellow, translucent, round, slightly gelatinous, scattered to gregarious; disc medium concave to flat, margin ± thick, 20–40 µm rising above disc, even or often with fine lobes 5–20 × 40–70 µm; broadly attached to substrate, superficial; dry cupulate to flat with inrolled margin, light cream-yellowish to bright chlorinaceous-yellow. **Asci** †18–26 × 3.3–4.5 µm {2}, 8-spored, spores ~3-seriate; **apex** (†) hemispherical; **base** with very short, thick stalk arising from croziers {2}. **Ascospores** †(4–)4.5–5.5(–6.3) × 1.2–1.4 µm {2}, subcylindric, rarely slightly (fusoid-)clavate, ends rounded to obtuse, straight; **SBs** not seen in dead state; with 1–3 minute LBs. **Paraphyses** apically uninflated, terminal cells †18–25 × 1.4–2 µm {2}, lower cells †4.5–6.5 × 1.5–2.3 µm. **Medullary excipulum** 15–20 µm thick, of slightly to strongly gelatinized, dense textura prismatica-angularis, sharply delimited. **Ectal excipulum** from base to mid flanks of thick-walled, horizontal t. prismatica, 40–110 µm thick near base, cells †15–50 × 10–24 µm {1}, common walls 0.5–2 µm thick, frequently containing large **LBs** 2–10 µm diam.; 20 µm thick at mid flanks and margin, upper 100–140 µm of margin composed of a gelatinized t. globulosa-angularis (common walls 0.4–1.2 µm thick), marginal cortical cells †5–13.5 × 4–6 µm {1}, 5–9 µm wide in surface view, upper margin terminated by a 1–3 µm thick gel layer. **Anchoring hyphae** abundant, †(3–)4–6 µm wide {2} (near insertion 5.5–7.5 µm), walls (0.3–)0.5–1 µm thick {2}. **Exudate**

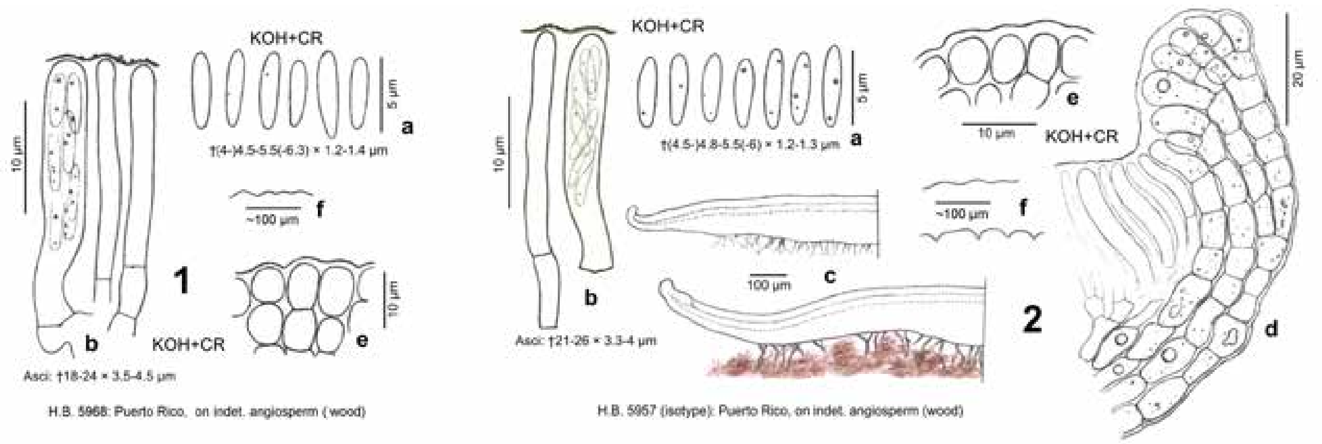


Plate 70. **1–2**: *Hyalorbilia puertoricensis*. – **a**. ascospores; **b**. asci (**1b**: showing crozier) and paraphyses; **c**. apothecia in median section; **d**. id., ectal excipulum at margin and mid flanks; **e**. margin in top view; **f**. id., undulating outline of apothecia.

over paraphyses 0.2 µm thick, continuous, smooth to finely rough; over margin and flanks externally smooth or with very indistinct warts. — **ANAMORPH**: unknown.

Habitat: probably lying on ground, decorticated logs of unidentified angiosperm trees {2}, on entirely or only 1 mm deep medium to strongly decayed wood {2}, on dark detritus or boring dust, no algae. **Associated**: *Orbilia nemaspora* {1}. **Desiccation tolerance**: unknown (probably sensitive). **Altitude**: 20–450 m a.s.l. **Phenology**: I (tropical belt).

Taxonomic remarks. *Hyalorbilia puertoricensis* seems to be closely related to *H. citrina* in having yellowish apothecia and a strongly gelatinized ectal excipulum that forms a projecting, sometimes finely undulating or lobate margin of thick-walled, ± isodiametric cells. The straight, much wider ascospores sharply segregate it from *H. citrina* and *H. japonica*. *H. inflatula*, *H. andina* and *H. oreadum* differ in a less or non-gelatinized ectal excipulum and a tendency to longer and narrower spores.

Variation. The two collections are microscopically very similar. They vary mainly in the excipular margin which is less gelatinized in the paratype (Pl. 70: 1e, 2d–e), the gel layer at upper margin 1–1.5 vs. 2–2.5 µm thick. In some apothecia of the holotype the margin forms distinct incisions while in the remaining apothecia it is only minutely wavy (Pl. 70: 1f, 2f).

Ecology. *Hyalorbilia puertoricensis* was collected on ± rotten wood of unidentified angiosperm trees and is only known from tropical humid rainforests in Puerto Rico (Caribbean belt of Middle America). The ecological data and large apothecia suggest that *H. puertoricensis* is a desiccation-sensitive species comparable to *H. citrina*.

Specimens included. **PUERTO RICO**: Sierra de Luquillo, El Yunque, ?7 km S of Rio Grande, Guzman Obajo Camino Los Tapia, ~450 m, log of indet. angiosperm, on wood, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (D.H.P. PR 111, FH, **holotype**, H.B. 5957 **isotype**). — N of El Yunque, 2.5 km SSW of Luquillo, near Rio Sabana, hill above chicken farm, 20 m, log of indet. angiosperm, on wood, 17.I.1996, D.H. Pfister, F.A. Harrington, D.J. Lodge & S. Hundorf (D.H.P. PR 31, FH, H.B. 5968 ø).

Hyalorbilia oreadum (Velen.) Baral, J.W. Guo & K.Q. Zhang, Mycosystema 33: 749 (2014) — Pls 72–74

≡ *Orbilia oreadum* Velen., Monogr. Discom. Bohem.: 100, pl. 11 fig. 26 (1934)

Etymology: derived from the climatic zone (montane).

Typification: Slovakia, Tatranská Lomnica, branch of *Pinus*, VIII.1926, A. Pilát (PRM 151736, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.27 {T} or (0.2–)0.4–1(–2) mm diam. {1}, 0.1–0.125 mm high (receptacle 0.05–0.09 → 0.03–0.05 mm), whitish to pale yellowish-chlorinaceous, ± translucent, round but ± strongly lobate when large,

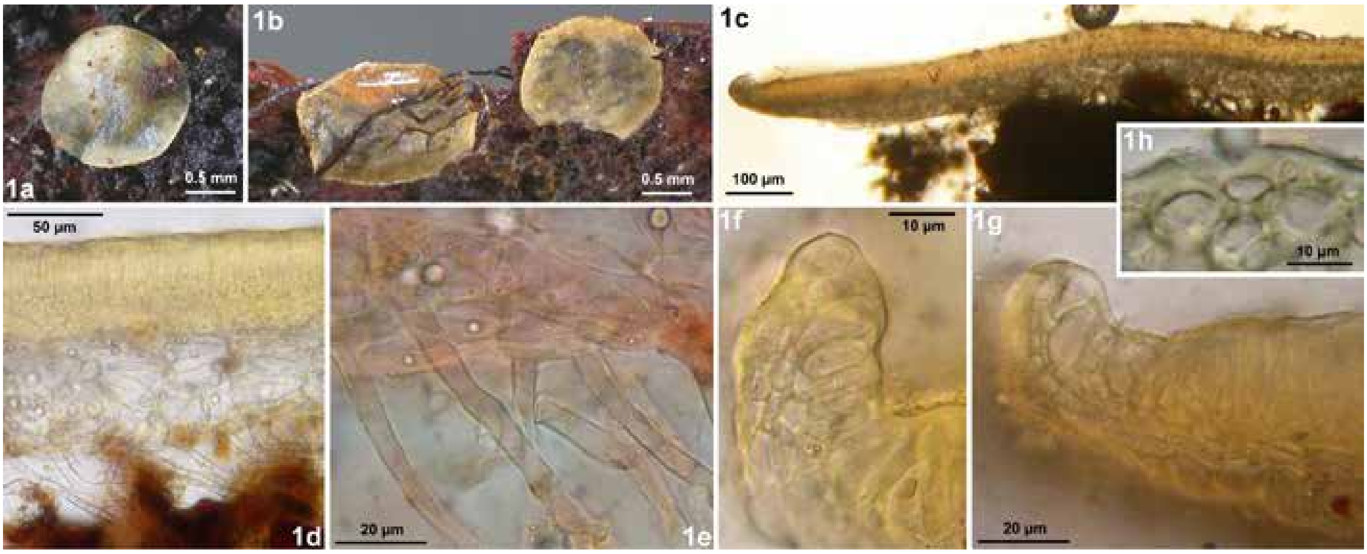


Plate 71. **1**: *Hyalorbilia puertoricensis*. – **1a–b**. rehydrated apothecia; **1c**. apothecium in median section; **1d**. id., central part of apothecium; **1f–g**. id., marginal ectal excipulum; **1h**. top view of marginal cells; **1e**. anchoring hyphae. – Dead state (in KOH, **1e** in KOH+CR). — **1a–h**. H.B. 5957 (isotype): Puerto Rico, on indet. angiosperm.

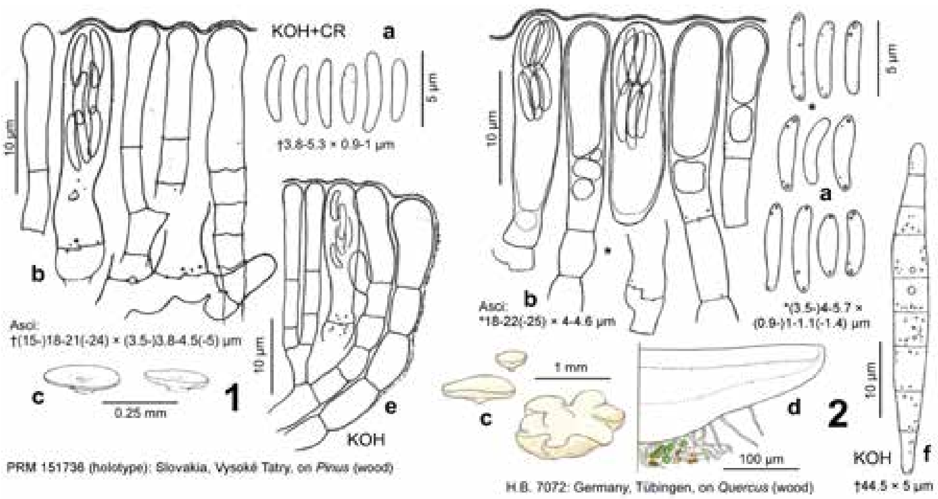


Plate 72. **1–2**: *Hyalorbilia oreadum*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. rehydrated apothecia; **d**. apothecium in median section; **e**. id., ectal excipulum at margin and mid flanks; **f**. conidium from substrate.

slightly gelatinous, ± gregarious over smaller or larger areas; disc (medium concave to) flat (to medium convex), margin thin, smooth; sessile or often with an abrupt stipe 0.02–0.08 × 0.06–0.15 µm, superficial. **Asci** *18–22(–25) × 4–4.6 µm {1}, †15–20 × 3–3.5 {1} or †(15–)18–21(–24) × (3.5–)3.8–4.5(–5) {T} µm, 8-spored, spores *4-seriate (in two superimposed bundles), pars sporifera *9.5–11 µm long; **apex** (†) ± hemispherical; **base** ± unstalked or with short, thick stalk, with croziers {2}, sometimes with small perforation. **Ascospores** *(3.5–)4–5.7 × (0.9–)1–1.1(–1.4) µm {1}, †3.8–5.3 × 0.9–1 µm {T}, subcylindrical or sometimes slightly fusoid or fusoid-clavate, both ends rounded to obtuse, straight to slightly, rarely medium curved; **SBs** *(0.1–)0.2 µm diam. {1}, globose, 1 at each end, sometimes absent. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cells *12–18.5 × 3.5–6 µm {1}, †9–15 × 2–3.3(–4) µm {T}, lower cells *4–7 × 3–3.5 µm {1}, †2.5–6 × 1.8–3 µm {T}, sometimes branched near base. **Medullary excipulum** 10–15 {T} or 40 {1} µm thick, of dense, non-gelatinized textura globulosa-angularis-prismatica, medium sharply delimited. **Ectal excipulum** in stipe of vertically oriented t. globulosa-angularis-prismatica 50–80 µm thick, at flanks 25–30 µm, of horizontal t. prismatica(-angularis), cells thin- to firm-walled (common wall †0.2–0.4 µm thick), *17–25 × 10–16 or up to 30–80 × 14–30 µm {1}, †9–10 × 5–7 or 14–20 × 8–10 µm {T}, 8–10 µm thick at margin, marginal cortical cells †10–12.5 × 3–6 µm {2}, clavate, ± firm-walled, somewhat immersed in gel. **Anchoring hyphae** medium abundant, */†2–4 µm wide, near insertion */†3.8–5.5 µm wide, walls 0.2–0.3(–0.4) µm thick {2}, radiating. **VBs** in paraphyses medium refractive, subhyaline. **Exudate** over paraphyses and marginal excipulum 0.2–0.3 µm thick, continuous, smooth or very finely rough. **— ANAMORPH**: brachyphoris-like (presumed, from natural substrate {1}). **Conidiophores** not observed. A single **conidium** fusiform, straight, †44.5 × 5 µm, 8-septate.

Habitat: collected 4 m above the ground {1}, corticated or decorticated, 25–40 mm thick branches of *Quercus* sp. {1}, *Pinus* sp. {T}, on 0.3–1 mm deep or entirely strongly decayed wood {2}, not or slightly greyed, with or without algae. **Associated**: *Rhizodiscina lignyota* {1}, ?*Lasiosphaeriaceae* {1}. **Desiccation tolerance**: only spores survived for 5 days in the herbarium. **Altitude**: 345–1800 m a.s.l. **Geology**: Slovakia: Pleistocene fluviatile sandy clay; Germany: Keuper (Stubensandstein). **Phenology**: VIII, XI.

Taxonomic remarks. Besides the holotype (on *Pinus*), only one further collection (on *Quercus*) was included in the description of *Hyalorbilia oreadum*. *H. inflatula* closely resembles *H. oreadum*, e.g., in the rather straight, narrowly cylindrical ascospores that are arranged in the living asci in two superimposed bundles, but differs in distinctly longer spores. *H. japonica* has about the same spore length as *H. oreadum* but differs in slightly narrower spores, more thick-walled anchoring hyphae, and a different geographical and climatic distribution. However, some collections appear to be intermediate (see under *H. japonica*, p. 355). *H. puertoricensis* and *H. resinae* both resemble *H. oreadum* in the spores. The former differs in thick-walled marginal excipular cells and wider spores, the latter in apically more inflated paraphyses, wider spores and asci, and very minute apothecia. Since all these taxa have rarely been recorded, their taxonomic limits need to be explored from further collections. *H. herbicola* resembles *H. oreadum* in the spores, but differs in various respects (see p. 438).

Variation. The *Quercus* collection from southern Germany differs from the holotype in larger apothecia, also in somewhat longer and wider terminal cells of paraphyses, and in smaller asci, but this might fall in the scope of variation of the species. Great variation is noted in the size of the ectal excipular cells at the flanks between the two samples, but this variation is also observed within each population in correlation with apothecial size.

Type studies. The holotype of *H. oreadum* contains about a hundred, rehydrated flat to medium convex, fully mature apothecia, which Velenovský (1934) reported as 0.1–0.2 mm, gregarious, pale yellow. The author described and depicted the ascospores as filiform, strongly curved (± semicircular), 3–4 µm long. On his manuscript sheet the spores are drawn distinctly wider than in the published drawing (see Pl. 73). Svrček (1954: 17) revised the holotype and found only slightly curved or sometimes even almost straight spores 3–5.5 × 0.8 µm. Due to the strong discrepancy in spore curvature he doubted that Velenovský's drawing was correct. In the present study 5 apothecia of the holotype were examined, and the spores, though seen only inside the asci, fully concur with Svrček's observation (Pl. 72: 1).

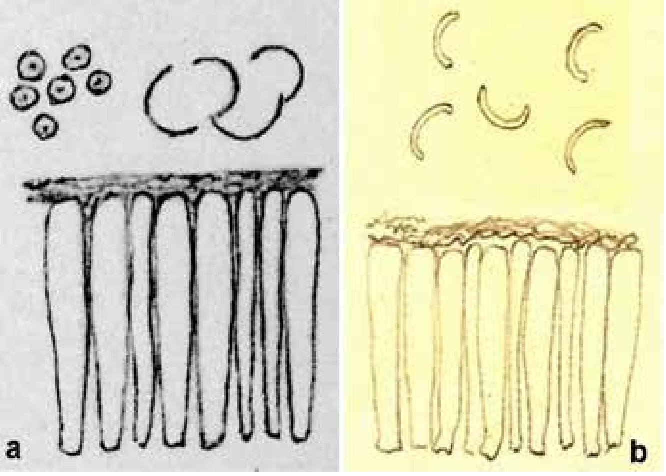


Plate 73. *Hyalorbilia oreadum*. – **a**. from Velenovský's published plate (1934: pl. 11 fig. 26); **b**. from his original drawing.

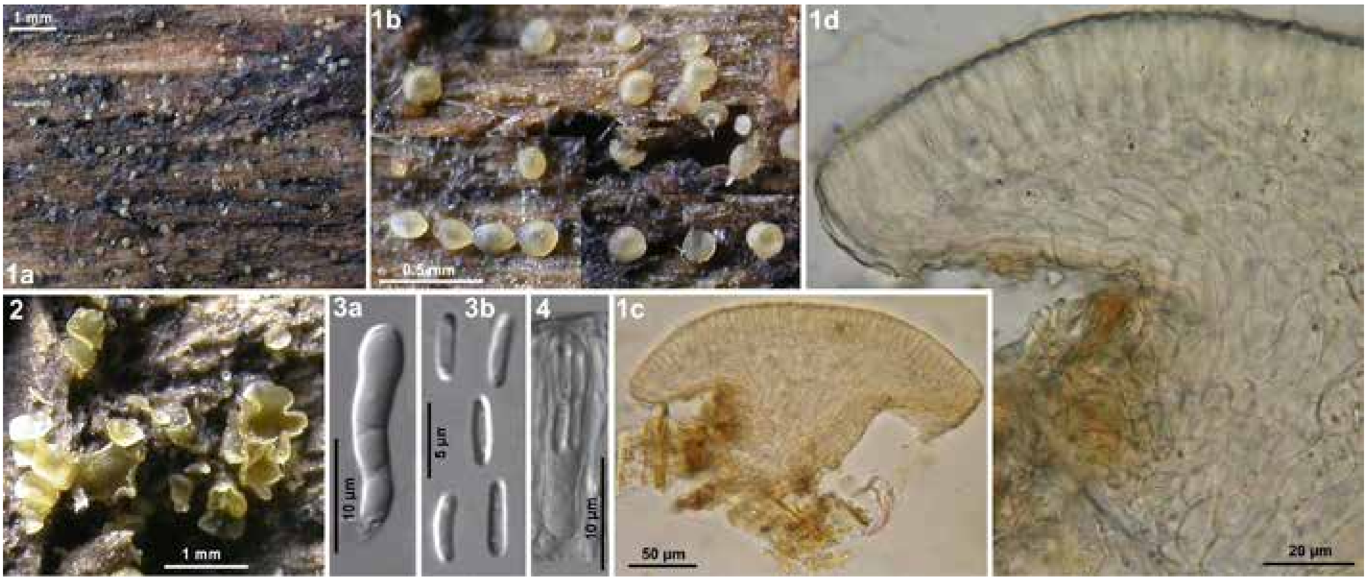


Plate 74. **1–2**: *Hyalorbilia oreadum*; **3–4**: *H.* cf. *oreadum*. – **1a–b**, **2**. rehydrated apothecia (**1**: after 79 years, **2**: after 3 years); **1c–d**. apothecia in median section (in KOH); **3a**. paraphysis; **3b**. ascospores; **4**. mature ascus. – Dead state: **1–2**, living state: **3–4**. – **3–4**: phot. J.W. Guo (DIC; **3**: from Guo at al. 2014a). — **1a–d**. H.B. 6188 (holotype): Slovakia, Vysoké Tatry, on *Pinus*; **2**. H.B. 7072a: Germany, Tübingen, on *Quercus*; **3a–b**. Guo et al. (2014a): China (data not specified), on indet. tree; **4**. J.W.G. zcw-j-2: China, Sichuan, on indet. tree.

Despite the rather homogeneous appearance of the dense population in the holotype, a mixture of two species cannot be excluded with certainty. Considering such a possibility, the name *H. oreadum* is to be considered as tentatively applied here. The more or less semicircular spores seen by Velenovský could belong to the Asian *H. arcuata*, or perhaps to *H. berberidis* in the case that his spore measurements are erroneous. Since Velenovský did not draw the spores within the asci he might also have described stray spores.

Not included collections. Five Chinese collections assigned to *H. oreadum* in Guo et al. (2014a) show apothecia 0.3–1 mm diam., asci †18.5–21.6 × 3.4–4.2 µm, and spores *(4.7–)5.0–6.1 × (0.8–)0.9–1.1(–1.3) µm (a range of 4.2–5 × 1.1–1.2 µm is obtained when evaluated from their scale of fig. 2). The droplets in the spores are very minute so that it is difficult to decide whether the polar ones are SBs or LBs. The ectal excipular cells at the flanks were rather small (†4.2–6.4 × 3.1–5 µm), but they attain 9 µm length on their fig. 2B. Guo et al. (2014a) did not indicate from which collection their data were gained and to which the photo plate refers (another unpublished plate refers to zcw-j-2, see IVV). We refrained from including these samples in the description, although we agree that the available data suggest conspecificity with European *H. oreadum*. However, we see problems in separating *H. oreadum* from *H. japonica*, for instance to their *H. japonica* gz-5 (see p. 354). Also a collection from which the anamorph of *Orbilia xiushanensis* (YMF 1.03033), a member of series *Orbilia*, was erroneously thought to originate (Zhang et al. pers. comm.), could belong here (IVV: 15.VIII.2008, see also p. 1425).

Guo et al.'s (2014a) article was published by four authors, though without involvement of its second author (H.O.B.).

Anamorph. The single conidium found on the natural substrate in our collection of *H. oreadum* (Pl. 72: 2f) matches those observed in *H. inflatula*.

Ecology. *Hyalorbilia oreadum* appears to be a rare species. The two known collections from cold-temperate humid, subcontinental Europe are otherwise ecologically quite different: the type was on rotten wood of a ?hygric branch of *Pinus* in a montane forest of the High Tatras, the other on wood of a xeric branch of *Quercus* in a colline, thermophilous broad-leaved forest with *Robinia*. The *Pinus* branch was possibly collected from the ground, as can be seen from the appearance of the wood. The slightly greyed and algae-covered *Quercus* branch was hanging 4 m above the ground, and the apothecia grew only in the area of a small and deep cavity probably caused by picking of a bird. Despite growing on a dry branch, the large apothecia surprisingly did not survive repeated desiccation. Not included collections from southern China were on hygric branches of unidentified trees, in evergreen broad-leaved or mixed orotemperate to subtropical humid (winter-dry) forests.

Specimens included. **GERMANY**: **Baden-Württemberg**, Schönbuch, 5 km ENE of Tübingen, 1 km SE of Pfrondorf, SE of Rauhalde, 345 m, branch of *Quercus*, on wood, 18.XI.2001, H.O. Baral (H.B. 7072a, anam. substr.). — **SLOVAKIA**: **Prešov**, Vysoké Tatry, above Tatranská Lomnica, 1800 m, branch of *Pinus*, on wood, VIII.1926, A. Pilát (PRM 151736, **holotype**, H.B. 6188 ø).

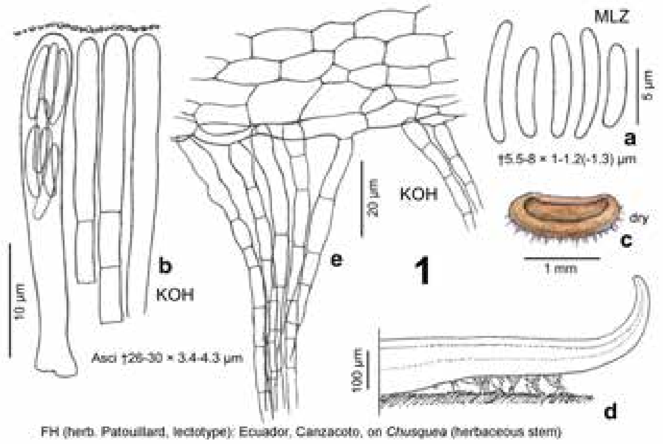
Not included. **CHINA**: **Sichuan**, **Ngawa** (Aba), Jiuzhaigou, 2000–2500 m, branch of indet. tree, 8.X.2006, J.W. Guo (J.W.G. zcw-j-2, YMFT, doc. vid.). – **Yunnan**, **Kunming**, Songming, branch of indet. tree, 6-IX.2006, J.W. Guo (J.W.G. azy-j-1, YMFT). – **Dali**, Yongping, Baotai Shan, branch of indet. tree, 14.VI.2006, J.W. Guo (J.W.G. yp-j-2, YMFT). – **Yuxi**, Yimen, Dalong Shan, branch of indet. tree, 23.VIII.2006, J.W. Guo (J.W.G. ym-j-166, YMFT). – Xinping, ?18 km S of Xinping, Mopanshan, ?1800 m, branch of indet. tree, V.2009, J.W. Guo (J.W.G. mp2-34, YMFT). – Tonghai, 35 km SE of Yuxi, ~2 km S of Tonghai, Xiushan Forest Park, ~1900 m, twigs of indet. angiosperm, 15.VIII.2008, Z.F. Yu & S.F. Li (YMFT 1.03033, but the culture YMF 1.03033 is *Orbilia xiushanensis*). (Guo et al. 2014a did not specify which collection was illustrated in their fig. 2.).

Hyalorbilia andina (Pat.) Baral, J.W. Guo & K.Q. Zhang, in Guo et al., Mycosystema 33: 747 (2014) — Pls 75–76

≡ *Orbilia andina* Pat., in Patouillard & Lagerheim, Bull. Soc. Mycol. Fr. 11: 218 (1895)

Etymology: named after the geographical origin, the Andes (South America).
Typification: Ecuador, San Jorge, stem of *Chusquea*, VII.1892, G. Lagerheim (FH, lectotype, designated here, MBT202370).
Misinterpretation of *H. andina*: Liu (2006: 26), = *H. arcuata*.

Description: — **TELEOMORPH**: **Apothecia** dry 1–3.8 mm diam. (up to 5 mm in protologue), rehydrated 0.15 mm high (receptacle 0.09–0.1 → 0.04 mm), [protologue: amber-coloured, translucent,



FH (herb. Patouillard, lectotype): Ecuador, Canzacoto, on *Chusquea* (herbaceous stem)

Plate 75. **1**: *Hyalorbilia andina*. – **1a**. ascospores; **1b**. asci and paraphyses; **1c**. apothecium (dry); **1d**. apothecium in median section; **1e**. id., ectal excipulum at lower flanks, with anchoring hyphae.

moderately gelatinous], round; disc flat but concave near strongly upwards curved, smooth margin, ± sessile, superficial; dry honey-yellow-ochraceous, margin strongly inrolled, with white subiculum. **Asci** †26–30 × 3.4–4.3 µm, 8-spored, spores 4-seriate; **apex** (†) hemispherical; **base** with or without ± thick stalk, with croziers. **Ascospores** †5.5–8 × 1–1.3 µm, cylindrical, sometimes very slightly narrower towards base, ends rounded, consistently slightly curved; **SBs** not seen in dead state. **Paraphyses** apically uninflated, terminal cells †15–18 × 2–2.5 µm, lower cells ~5–5.5 × 1.6–1.8 µm. **Medullary excipulum** ~50–60 µm thick, not examined. **Ectal excipulum** at base of thin-walled textura angularis 60–70 µm thick, at flanks of horizontal t. prismatica, cells †10–23 × 6–15 µm; at mid flanks and margin of thin-walled t. porrecta ~10 µm thick. **Anchoring hyphae** very abundant, †3.5–5 µm wide, walls 0.3 µm thick, forming long radiating strands. **Exudate** over paraphyses 0.2–0.4 µm thick, granular-cloddy. **— ANAMORPH**: unknown.

Habitat: on dead, medium decayed, 15 mm thick herbaceous stem of *Chusquea* sp. **Associated**: none observed. **Desiccation tolerance**: unknown. **Altitude**: ?1940 m a.s.l. **Phenology**: VII (tropical belt).

Taxonomic remarks. *Hyalorbilia andina* is tentatively accepted as distinct from *H. inflatula* because of its broader ascospores which are consistently slightly curved. With an inrolled margin of hyphoid elements (textura porrecta), *H. andina* resembles those populations of *H. inflatula* with narrow marginal cortical cells. Some collections of *H. inflatula* resemble *O. andina* in their cylindrical instead of narrowly fusoid spores, e. g., the examined syntype of *Orbilia sinuosa*, but these tend to have somewhat shorter and narrower, also less distinctly curved spores. A species mainly known from Europe, *H. polypori*, differs from *H. andina* in smaller apothecia with a hardly raised margin, and in wider, straight spores. The spores in the holotype of *O. abietina*, tentatively referred here to synonymy with *H. polypori*, resemble those of *H. andina*, but the small (0.3–0.7 mm) and flat, stipitate apothecia fit more *H. polypori*.

Type studies. In the protologue Patouillard (1895) assigned at least two collections to *Orbilia andina*, one on *Chusquea* which bears Patouillard's original sketch and on which the present redescription is based, and another on an apparently unidentified host from the same locality which was not received. In the same paper, Patouillard also described *O. andina* var. *lateritia* which is referred to synonymy with *H. citrina* in the present study.

Patouillard's data on the label of the *Chusquea* collection slightly deviate from the protologue: asci 23–30 × 6 µm (23–33 × 6–7 µm in the protologue), excipular cells 20–26 × 13 µm (20–30 × 13–15 µm), anchoring hyphae 6 µm wide (60–150 × 6–8 µm). The sketch on the *Chusquea* label figures acicular, slightly curved spores of rather equal length (no size indicated), whereas the protologue says 'straight or slightly curved, 5–13 × 1 µm'.

When erecting the new genus *Orbiliaster*, Dennis (1954: 294, fig. 6 H) briefly treated *O. andina* and pointed out that the 'hairs' mentioned in the protologue do not emerge from the margin but are, in fact, anchoring hyphae growing out from the lower part of the excipulum. Dennis mentioned several collections (probably all from K) which were referred by Patouillard to *O. andina* (one on a 'log'), and for which different spore measurements were noted by Patouillard (5–7 × 1 and 13 × 1 µm). This high variation and the different substrates suggest that the included specimens were not conspecific. We here designate the *Chusquea* specimen in FH as **lectotype** of *H. andina*.

Dennis (1954) appears to have figured the *Chusquea* collection, for which he found narrow, slightly allantoid spores (no size given, see Fig. 159H). Later, Dennis (1970: 352) referred *O. andina* (the *Chusquea* collection) to synonymy with *Orbilia auricolor* (s.auct., = *H. inflatula*). The data given there for asci (22–23 × 4–5 µm) and spores (5–6 × 0.5 µm) deviate from the here presented values (Pl. 75) especially in a much shorter ascus length and in much too narrow spores.

Misinterpretation. Six Chinese specimens named *H. andina* by Liu (2006) have rather strongly curved spores which fit *H. arcuata* (for more details see p. 377).

Not included collections. Three Chinese collections (Yunnan, hygric branches of unidentified trees) were referred by Guo et al. (2014a) to *H. andina* (Pl. 76). They resemble the type in their slightly allantoid spores *5.7–7.3 × 1–1.2(–1.4) µm, but the asci were said to be much shorter (†17–22.5 × 2.9–4.3 µm) and the translucent white apothecia only 0.3–1 mm diam. when fresh, almost flat, without a raised margin in median section. Together with ecological deviations, conspecificity of these records with the type remains uncertain. The ascospores contained in the living state 1–3 globose SBs of 0.3–0.7 µm diam. near each end. Guo et al. stressed the almost isodiametrical cells of the ectal excipulum in the Chinese specimens, and their similarity to *H. inflatula* and *H. erythrostigma*. These findings are in contrast to the present study which presents prismatic cells for *H. inflatula* as well as the type of *H. andina*.

It must be mentioned that Guo et al.'s article was written and published without involvement of its second author (H.O.B.). Because of this, the article does not mention and discuss the here presented reexamination of the type of *H. andina*.

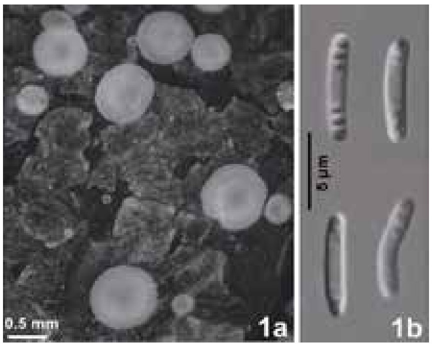


Plate 76. **1**: *Hyalorbilia* cf. *andina*. – **1a**. fresh apothecia; **1b**. ascospores (3 in living state). **— 1a–b**: China, on indet. tree (phot. Guo et al. 2014a).

Ecology. The lectotype of *Hyalorbilia andina* grew on herbaceous stems of *Chusquea* (*Bambusoideae*) under a subtropical humid highland climate in the northwest of South America. The not included Chinese collections were on hygric (angiosperm) branches of unidentified trees in subtropical humid southern China.

Specimens included. **ECUADOR**: **Pichincha**, Quito, ?30 km SW of San Jorge, Canzacoto, ?1940 m, stem of *Chusquea*, VII.1892, G. Lagerheim (FH, **lectotype**, H.B. 5748 ø).

Not included. **CHINA**: **Yunnan**, **Dali**, Yongping, ~25 km SSW of Yongping, Baotai Shan, ~1600 m, branch of indet. tree, 14.VI.2006, J.W. Guo (J.W.G. jgs-j-5, YMFT). – **Wenshan**, locality not stated, branch of indet. tree, 30.VI.2006, J.W. Guo (J.W.G. ws-j-5, YMFT). – **Jiangsu**, **Nanjing**, Zijinshan, ?200 m, branch of indet. angiosperm, IX.2009, J.W. Guo (J.W.G. zjs-3, zjs-32, YMFT). (Not specified by Guo et al. 2014a: fig. 1 which collection was illustrated.)

Hyalorbilia inflatula (P. Karst.) Baral & G. Marson, Micologia 2000: 44 (2001) — Pls 77–82, Map 7

≡ *Peziza inflatula* P. Karst., Not. Sällsk. Fauna Fl. Fenn. Förh. 10: 175 (1869)
≡ *Orbilia epipora* subsp. *inflatula* (P. Karst.) P. Karst., Not. Sällsk. Fauna Fl. Fenn. Förh. 11: 248 (1870)
≡ *Orbilia inflatula* (P. Karst.) Sacc., Syll. Fung. 8: 627 (1889)
≡ *Calloria inflatula* (P. Karst.) W. Phillips, Man. Brit. Discomyc.: 335 (1887)
≡ *Hyalinia inflatula* (P. Karst.) Boud., Hist. Class. Discom. Eur.: 104 (1907)
?= *Hirneola lancicula* Mont., Syll. Gen. Spec. Crypt.: 182 (1856)
≡ *Orbilia lancicula* (Mont.) Pat. & Gaillard, Bull. Soc. Mycol. Fr. 4: 99 (1889)
?= *Peziza vulgaris* var. *myceticola* Berk. & Curtis in Berkeley, Grevillea 3: 159 (1875)
≡ *Pezizella vulgaris* var. *myceticola* (Berk. & Curtis) Sacc., Syll. Fung. 8: 279 (1889)
≡ *Hyalinia vulgaris* var. *myceticola* (Berk. & Curtis) Boud., Hist. Class. Discom. Eur.: 103 (1907) (as *mycetophila*)
(?)= *Peziza succinea* Quél., Grevillea 8: 38 (1879) [non *Orbilia succinea* (Fr.) Quél., ?= *Pseudocenangium succineum* (Sprée) Dyko & Sutton]
≡ *Mollisia succinea* (Quél.) Quél., Compt. Rend. Associated Franç. Avancem. Sci. 9: 673, pl. 9 fig. 11 (1881) [non *Mollisia succinea* (Fr.) Gillet 1882]
≡ *Cistella succinea* (Quél.) Quél., Enchir. fung. (Paris): 319 (1886)
≡ *Pseudohelotium succineum* (Quél.) Sacc., Syll. Fung. 8: 299 (1889)
= *Peziza translucens* Gillet in Pat., Tab. anal. Fung. 5: 36 (1886)
≡ *Mollisia translucens* (Gillet in Pat.) Gillet, Champ. Fr., Discomyc., Suppl. (9° livraison) p. 212 (1887, '1886')
≡ *Pezizella translucens* (Gillet in Pat.) Sacc., Syll. Fung. 8: 287 (1889)
≡ *Hymenoscyphus translucens* (Gillet in Pat.) Kuntze, Revis. Gen. Pl. 3 (2): 486 (1898) [non *Hymenoscyphus translucens* (White) Arendholz, nom. illegit., ICN Art. 53.1, ≡ *H. whitei* Hengstm. 1985: 489]
≡ *Hyalinia translucens* (Gillet in Pat.) Boud., Hist. Class. Discom. Eur.: 104 (1907)
?= *Orbilia sinuosa* Penz. & Sacc., Malpighia 15: 219 (1902)
?= *Orbilia breviasca* Henn., Verh. Bot. Ver. Prov. Brandenburg 50: 132 (1909)
≡ *Hyalinia breviasca* (Henn.) Kanouse, Pap. Mich. Acad. Sci. 24: 27 (1939) (as '*breviascus*')
= *Orbilia cyathea* Velen., Monogr., Discom. Bohem.: 94, pl. 11 fig. 17 (1934)
?= *Orbilia linata* Velen., Monogr. Discom. Bohem.: 94, pl. 11 fig. 18 (1934)
(?)= *Dactylella passalopaga* Drechsler, J. Wash. Acad. Sci. 26: 403, fig. 1 (1936)
= *Orbilia pyrifera* Velen., Opera Bot. Čech. 4: 103 (1947)
= *Hyalinia rectispora* var. *majuscula* Grelet, Rev. Myc. (Paris) N. S. 13: 107 (1948b)

Etymology: *inflatula*: referring to the dry apothecia (inflated like a membranous swollen bladder); *myceticola*: from the substrate (unidentified polypore); *succinea*: amber-coloured; *lancicula*: a small dish; *sinuosa*: referring to the undulating margin; *translucens*: according to the translucid apothecia; *breviasca*: named after the short unstalked asci; *cyathea*: after the cup-shaped apothecia; *linata*: apparently after the apothecia being similar in colour as flax seeds; *passalopaga*: after the gag-like predacious cell; *pyrifera*: after the associated pyriform conidia; *majuscula*: apothecia larger than in *Hyalinia rectispora*.

Typification: Finland, Kanta-Häme, Mustiala and Pehkijärvi, bark and wood of angiosperm, especially *Populus*, IX.18[?67], P. Karsten (type of ***Peziza inflatula***, unlocated); Germany, Chemnitz, branch of *Salix*, 24.V.2010, B. Mühler (ex H.B. 9328, M-0276411, neotype, designated here, MBT202369; sq.: KT222346). — French Guiana, Cayenna, on unidentified wood (as 'lignum'), undated, [F.M.R.] (Leprieur, no. 1087, type of ***Hirneola lancicula***). — USA, South Carolina, Santee River, on pores of *Polyporus*, undated, H.W. Ravenel (herb. Ravenel 1571, K(M) 126131, lectotype of ***Peziza vulgaris* var**. ***myceticola***, designated by Dennis 1970: 70). — France, Haut Jura, on rotten wood, undated, L. Quélet (type of ***P. succinea***, not located). — France, Poligny, branch of *Fraxinus excelsior*, VII.1882, N. Patouillard (PC 0088499, syntype of ***P. translucens***). — Java, Bogor (Buitenzorg), branch of indet. angiosperm, 2.I.1897, A.J.O. Penzig (W 6467, lectotype of ***Orbilia sinuosa***, designated here, MBT202371). — Germany, Tamsel, on rotten wood, VIII.1904, P. Vogel n. 1712 (type of *O. breviasca*, not located). — Czechia, Liblice, branch of *Quercus* & old pyrenomycete, VII.1925, J. Velenovský (PRM 151694, lectotype of ***O. cyathea***, designated by Svrček 1954: 13). — Czechia, Mnichovice, branch of *Betula*, IV.1928, J. Velenovský (PRM 152443, lectotype of ***O. linata***, designated here, MBT382145). — USA, Beltsville, decaying plant material, undated, C. Drechsler (holotype of ***Dactylella passalopaga***: illustration in Drechsler 1936: fig. 1). — Czechia Klokočná, branch of *Quercus*, 4.IX.1941, J. Velenovský (PRM 152437, holotype of ***O. pyrifera***). — France, Savigné, branch of *Pinus*, VII.1925, L.J. Grelet (PC, herb. Grelet, lectotype of ***Hyalinia rectispora* var**. ***majuscula***, designated here, MBT202837).

Misapplied names: Dennis (1960a: 105, 1970: 352, 1978: 188, followed by most authors until 1987), as *O. auricolor*; Feltgen (1901: 35 p.p., on *Sorbus*), as *O. xanthostigma*; Korf (1992: 507 p.p. [CUP-MM 1537]), as *Orbilia epipora*; Nannfeldt (FES 2588, fide Spooner 1987), as *O. leucostigma*; Nylander (1869: 58 p.p.), as *Peziza epipora*; Rehm (1891: 455), as *O. luteorubella*.

Misinterpretation of *H. inflatula*: Korf (1992: 508), ?= *H. ulicicola*; Liu (2006, 35 p.p.), = *H. japonica*; Nannfeldt (1932: 254), ?= *Orbilia* sp.; Ekanayaka et al. (2018: 160), = *H. arcuata*; Otani (1990: fig. 7), = *O. ?epipora*; Guo et al. (2014b: fig. 8), ?= *H. juliae*.

Description: — **TELEOMORPH**: **Apothecia** fresh (0.2–)0.4–2(–4)((–5)) mm diam., 0.1–0.21(–0.4) mm high (receptacle 0.07–0.16 mm thick, at margin 0.04–0.06 mm), pale (yellowish-)chlorinaceous(-cream) to sometimes light yellow-chlorinaceous, rarely whitish or carneous when young, translucent, round or sometimes ± undulating to lobate when large, slightly gelatinous, scattered or often subgregarious, rarely densely aggregated; disc at first strongly concave, deeply to shallowly cupulate, then cyathiform to saucer-shaped and often with ± distinct concentric rings, also ± flat from the beginning, outermost margin not or up to 20 µm rising above disc, smooth; broadly sessile or with an indistinct to distinct, obconical stipe 0.05–0.3 × 0.1–0.7 mm, superficial; dry light to bright honey-yellow-chlorinaceous to ochre-amber or orange-brown, margin of larger apothecia incurved and covering the disc, often with a conspicuous white subiculum at apothecial base (invisible in hydrated state), senescent dirty reddish-brownish. **Asci** *((13–))(16–)20–27 {22} or 25–32(–38) {38} or (27–)32–38(–42)((–48)) {6} × (3.8–)4–5.3(–6) µm {~56}, †(17–)19–28(–30) × (2.8–)3.2–4.5(–5) µm {28}, 8-spored, spores *(3–)4(–5)-seriate, mostly in two superimposed bundles, pars sporifera *(11–)13–16(–17)((–20)) µm long; **apex** (†) hemispherical to slightly (rarely medium) truncate; **base** with or without very short, thick stalk arising from croziers {32} without or rarely with small round perforation. **Ascospores** *((4.5–))(5–)5.5–7.5(–8.5)((–9)) × (0.8–)0.9–1.2(–1.3)((–1.4)) µm {91}, †((4.2–))(5–)5.5–7(–8)((–9)) × (0.7–)0.8–1.1(–1.2) µm {~58}, narrowly (sub)cylindrical to fusoid, rarely very slightly heteropolar, ends rounded to obtuse, straight to very slightly curved, only exceptionally slightly helicoid; 1–2(–3) globose **SBs** ~0.3–0.4 µm diam. and 1–3 minute LBs at each end. **Paraphyses** apically uninflated or slightly clavate-capitate(-spathulate), terminal cells *15–30 × 2.5–4.5 µm {7}, †15–21(–28) {3} × (1.5–)1.8–3(–3.5) µm wide {6}, lower cells *5–11 × 2–3.5(–4) µm {3}, †4–8(–10) × 1.5–2 {3}; unbranched. **Medullary excipulum** ~20–110 µm thick in centre, of medium to very dense textura globulosa-prismatica(-intricata), (*) non–gelatinized, (†) slightly or partly medium to strongly gelatinized, towards margin 15–30 µm thick, of more horizontal t. prismatica-porrecta or t. intricata, only here medium to very sharply delimited. **Ectal excipulum** near base 50–160 µm thick, of (indistinctly) vertically oriented t. (prismatica-)angularis, cells *(10–)15–50(–60) × 10–27(–32) µm {6}, †27–43 × 10-19 {1}, not or slightly to medium gelatinized, common walls */†(0.2–)0.5–1(–1.5) µm thick, rarely †0.8–2(–3) µm {3}; from lower flanks up to margin of horizontal t. prismatica, 20–45(–

60) µm thick at flanks, cells */†10–30 × (5–)6–13 µm {6}, thin- to firm-walled, 10–20 µm thick at margin, marginal cortical cells in median section or surface view */†(7–)9–16(–22) {25} × ((2–))(3–)4–6(–7) {17} or (5–)6–12(–16) µm {16}, cylindrical to clavate or obovoid, ± thin-walled (0.2–0.5 µm), immersed in thin gel (wall 0.5–1.3 µm thick including gel). **Anchoring hyphae** sparse to usually abundant, radiating, ± straight, */†(2–)3–5(–6.5) µm wide {39}, near attachment up to 5–7 µm, walls 0.2–0.5(–0.8) {35} or (0.2–)0.5–1(–1.3) {8} µm thick, individual cells 8–22 µm long. **VBs** in terminal and often also lower cells of paraphyses (very) pale chlorinaceous (multiguttulate), medium-refractive, later low-refractive and fusing to angular or very elongate bodies. **Exudate** over paraphyses (0.2–)0.3–0.5(–1) µm thick, continuous, smooth or mostly strongly warted, very pale yellowish-chlorinaceous; over margin and flanks 0.3–1 µm thick, finely warted or sometimes smooth, hyaline to very pale chlorinaceous, very rarely brownish. — **ANAMORPH**: brachyphoris-like (from ascocarp in Petri dish {1} and from natural substrate {24}). **Conidiophores** *~12–23 × 2.5–3.7 µm, 2 µm at the tip, unbranched or sometimes branched, conidiogenous cell often sympodial (with a lateral scar). **Conidia** fusoid to fusiform, straight, *(33–)40–70(–83) × (3.5–)4–8(–9) µm {13}, †37–72 × 4–7 µm {7}, (3–)4–8(–12)-septate, living conidia with many minute, often peripheral guttules (LBs, KOH-resistant), usually also with some larger refractive globose **SCBs** (0.5–1.7 µm diam) {8} which disappear in KOH.

Habitat: lying on ± moist ground, rarely 0.5–2.5 m above the ground, corticated, more rarely decorticated, 14–40 mm thick branches, also logs or stumps, of *Abies alba* {2}, *A. nordmanniana* {1}, *Acacia* sp. {1}, *Acer* sp. {3/1}, *A. campestre* {1}, *A. pseudoplatanus* {2}, *Alnus* sp. {3}, *A. alnobetula* {1}, *A. glutinosa* {5}, *A. incana* {1}, *Betula* sp. {9/1}, *B. pubescens* subsp. *tortuosa* {2}, *Carpinus betulus* {2}, *Castanea sativa* {2}, *Cornus sanguinea* {1}, *Corylus avellana* {6}, *Cytisus scoparius* {1}, *Euonymus europaeus* {1}, *Fagus sylvatica* {27}, *F. sylvatica* var. *moesiaca* {1}, *Fagus orientalis* {1}, *Frangula alnus* {1}, *Fraxinus* sp. {1}, *F. excelsior* {15}, *Ilex aquifolium* {1}, *Juglans regia* {1}, *Malus domestica* {1}, *Ocotea foetens* {1}, *Picea abies* {1}, *Pinus* sp. {1}, *P. sylvestris* {2}, *Populus* sp. {4}, *P. alba* {1}, *P. ?canadensis* {1}, *P. tremula* {1}, *Prunus avium* {1}, *P. serotina* {1}, *P. spinosa* {3}, *Pyrus communis* {1}, *Quercus* sp. {14}, *Q. cerris* {1}, *Q. ilex* {3}, *Q. robur* {2}, *Rosa* sp. {1}, *Salix* sp. {4/5}, *S. ?atrocinerea* {1}, *Sorbus aria* {2}, *S. aucuparia* {1/3}, *Tilia* sp. {6}, *T. cordata* {1}, *T. platyphyllos* {3}, *Ulex europaeus* {5}, *U. minor* {2}, indet. angiosperms {17/2}, on 0.5–3 mm deep medium to strongly decayed bark {95} (bast and periderm) or wood {100}, on upper, lateral or mainly underside of logs, also on inner surface of bark, substrate partly dark brown to blackish, no green algae; on petiole of *Arecales* {1}; sometimes on ± old stromata of *Daldinia* sp. {1}, *Diatrype stigma* {2/3}, *Diatrypella favacea* {1}, *Eutypa ?lata* {1}, *Hypoxylon fragiforme* {4/1}, *Jackrogersella multiformis* {1}, *Menispora glauca* {1}, *Rosellinia* sp. {1}, or on basidiomata of indet. perennial basidiomycete {1}, *Cerioporus mollis* {1}, *Cyathus striatus* {1}, *Fomes fomentarius* {3}, *Ganoderma applanatum* {3}, *Schizopora paradoxa* {1}, *Trametes hirsuta* {1}, *T. versicolor* {1}. **Associated** *Ascocoryne cylichnium* {1}, *A. solitaria* {1}, *Astrosphaeriella* sp. {1}, *Brachysporium obovatum* {2}, *Cacumisporium capitulatum* {1}, *Calycellina* sp. {1}, *Calycina citrina* {1}, *Capronia* sp. {1}, *C. pilosella* {1}, *Claussenomyces atrovirens* {1}, *Cosmospora ?episphaeria* {1}, *Cryptadelphia brevior* {1}, *Dematioscypha delicata* {1}, *D. olivacea* {1}, *Endoxyla cirrhosa* {1}, *Flagelloscypha minutissima* {1}, *Glyphium elatum* {1}, *Hamatocanthoscypha laricionis* {1}, *Hymenoscyphus phiala* {1}, *Hyalorbilia berberidis* {2}, *H. fusispora* {1}, *H. juliae* {2}, *H. polypori* (1), *Hyaloscypha leucostigma* {1}, *H. quercicola* {1}, *Lachnum impudicum* {1}, *L. subvirgineum* {1}, *L. virgineum* {1}, *Menispora glauca* {1}, *Mollisia* sp. {2}, *M. cinerea* {1}, *M. ?oblonga* {1}, *M. prunicola* {1}, *Nectria* sp. {1}, *Orbilia auricolor* {1}, *O. crenatomarginata* {1}, *O. eucalypti* {4}, *O. naumburgensis* {4}, *O. subclavuliformis* {1}, *O. subsphaerospora* {1}, *O. ?tremulae* {1}, *O. xanthostigma* {1}, *Protounguicularia transiens* {1}, *Polydesmia pruinosa* {1}, *Resupinatus applicatus* {1}, *Rhizodiscina lignyota* {1}, *Scutellinia crinita* {1}, *Troposporella fumosa* {1}, *Tubeufia cerea* {2}, *Tulasnella cystidiophora* {1}. **Desiccation tolerance**: hymenial elements survive for 1 day or not even 2 hours in dry state, cells of medullary and ectal excipulum still viable after 4–7 days (narrow marginal cells), in specimens growing on still-attached branches even after 4 months; conidia sometimes viable after 4 months {H.B. 7623}. **Altitude**: 2–1620 m a.s.l. (Europe), 400–850 m (northeastern China), 1300–3500 m (western China), 180–1500 m (southern China), 5–270 m (eastern Australia). **Geology**: Ordovician, Devonian & Carboniferous sand-, silt- & mudstone, Permian (Rotliegend), Buntsandstein, Muschelkalk, Keuper (sand & marlstone), Jurassic & Cretaceous shale, sand-, lime- & marlstone, dolomite, Tertiary molasse, Pleistocene sand & gravel, loess, peat; granite, trachyte, basalt, dolerite, biotite-amphibolite, serpentinite, gneiss, mica schist. **Phenology**: throughout the year (especially from spring to autumn).

Phenology of *H. inflatula* (± temperate to boreal northern hemisphere)											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
4	5	11	27	30	33	26	19	19	12	12	0

Taxonomic remarks. *Hyalorbilia inflatula* is characterized by comparatively large, often cupulate but also flat, pale chlorinaceous or yellowish apothecia, more or less straight, rather small and narrow, cylindrical to narrowly fusoid ascospores, and a mostly hygric habitat. In the living mature asci the spores mostly form two characteristic parallel, superimposed bundles of four conglutinated spores.

H. andina can tentatively be separated by its wider, slightly curved spores. The more subtropical *H. japonica* differs in shorter asci and spores. The temperate *H. fagi* and *H. tortuosa* and the tropical *H. citrina* differ in ± helicoid spores, the latter also in narrower spores and thick-walled marginal cortical cells. Intermediate forms were now and then observed between most of these taxa, however.

Variation. Extraordinary variation among the many collections here referred to H. *inflatula* was particularly noted in width of marginal excipular cells, length of asci and spores, and apothecial shape. As an extreme example, the largest asci were observed in a specimen with narrow marginal cells on *Fomes* from Bad Reichenhall [H.B. 7758: *36–40(–42)((–48)) × 4.6–5.3 µm], and the smallest asci in one with broad marginal cells on *Sorbus* from Chemnitz [H.B. 8221: *(13–)16–21 × (3.8–)4.2–4.7(–5) µm]. In correlation with this huge difference in ascus volume, also the spores showed a very different size: *(5–)7.5–8.7 × 1.2–1.3(–1.4) µm and *(3.7–)4.5–5.5(–6) × 1(–1.1) µm, respectively. It is, therefore, well possible that the present concept of *H. inflatula* includes an aggregate of different taxa, a view which is confirmed by molecular data (see below). Yet, a separation based on morphological traits of either teleomorph or anamorph proved so far quite impracticable, since clear limits and correlations of the observed features could not be found.

In another collection on *Alnus* from Chemnitz (H.B. 8882a/b), two different variants of *H. inflatula* s.l. grew intermingled. One (a) shows wide marginal cells (mainly *7–11 µm) a smooth hymenial exudate, and rather small asci and spores (Pls 77: 9; 78: 2a–d; 80: 1), the other (b) narrow marginal cells (mainly *3–5 µm), a warted hymenial exudate, and slightly larger asci and larger, especially wider spores (Pls 77: 6: 78: 2a–c, e; 81: 12). The two variants are even macroscopically different: in (a) the apothecia are almost flat, watery-white, and 0.3–1 mm diam., while in (b) they are cupulate, pale chlorinaceous, and only 0.3–0.5 mm diam., but with a thicker flesh. In contrast to the above extreme example, ascus and spore size strongly

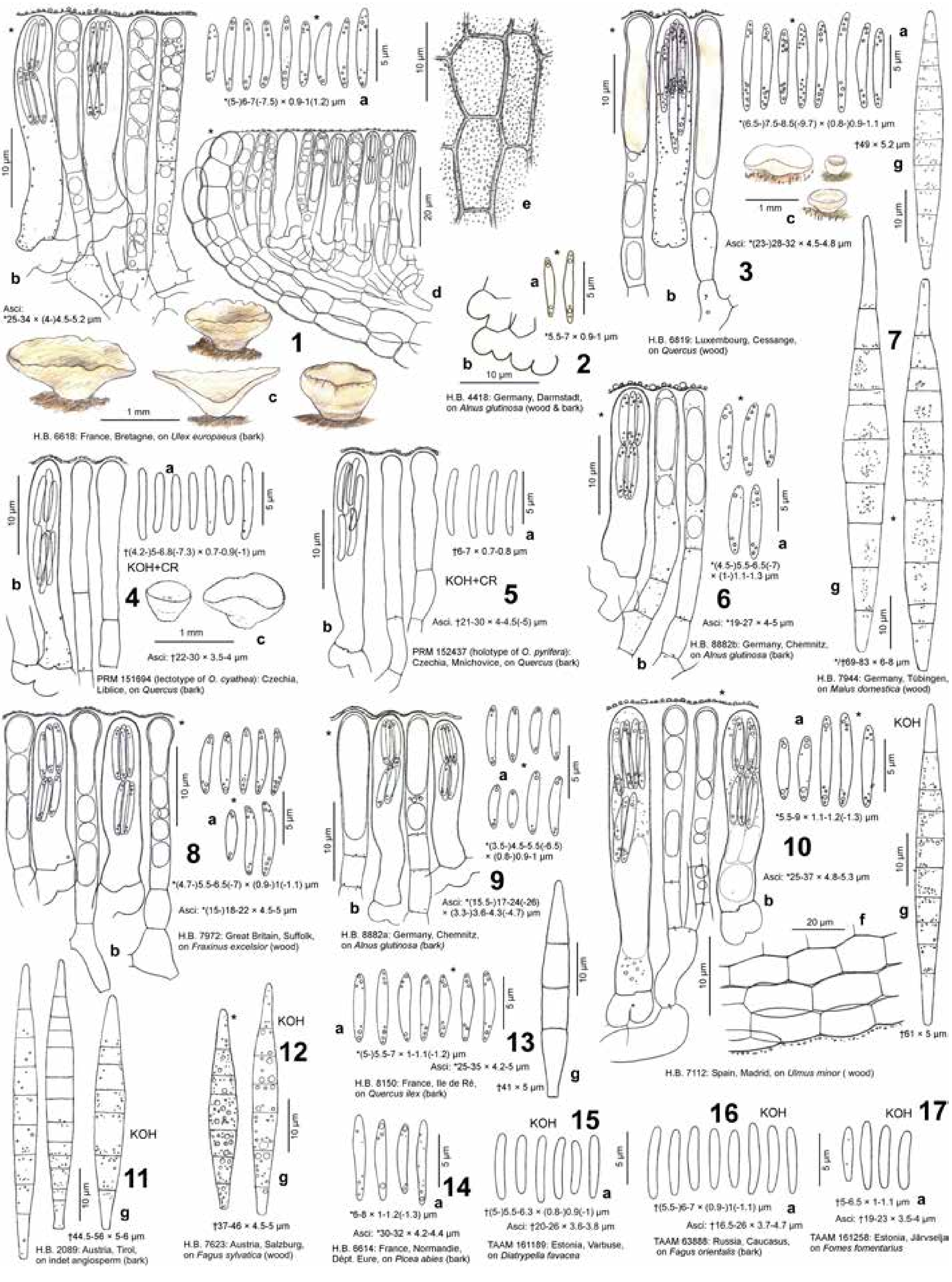


Plate 77. **1–2**, **4–17**: *Hyalorbilia inflatula*; **3**: *H.* cf. *inflatula*. – **a**. ascospores; **b**. asci and paraphyses (ascus bases with croziers); **c**. fresh or rehydrated apothecia; **d**. ectal excipulum with hymenium (margin and mid flanks, median section); **e**. id., at flanks, surface view; **f**. id., at lower flanks, in median section; **g**. conidia (**12**: large drops were partly LBs which resisted in KOH).

overlap here, except for spore width. Another population with broad marginal cells of *6–8 µm (on *Ulex* from Bretagne) has a warted hymenium, comparatively large asci, and spores intermediate between the two (Pl. 77: 1). Indeed, such broad spores as in H.B. 8882b were only rarely seen within *H. inflatula* s.l., for instance, in a sample on *Ulmus* from Madrid which has also narrow marginal cells (†3–5.5 µm, Pl. 77: 10).

The wide spores in H.B. 8882b are similar as in the type of *Orbilia abietina* (Pl. 78: 5), a collection with medium wide marginal cells [†(4–)5–7(–9) µm] and a warted hymenium. This sample is considered as possibly conspecific with *H. polypori*, but could instead, belong to the scope of the here proposed neotype of *H. inflatula* (Pl. 78: 1), which belongs to the variant with rather narrow marginal cells and cupulate apothecia.

Ellis & Ellis (1985: 11) separated between *O. cyathea* with distinctly cyathiform apothecia and *O. auricolor* (s.auct.) with non-cyathiform apothecia. This separation seems to have partly been based on material identified by Clark (1980b: 44) who distinguished between the two taxa in a collection list without diagnoses, and it seems to correspond to some rate with the present observation within *H. inflatula* s.l. of narrow marginal cortical cells in ± cupulate apothecia vs. broad cells in more flattened apothecia. However, broad marginal cells occur sometimes also in populations with cupulate apothecia, e. g., in a specimen from Bretagne and in the type of *O. cyathea* (Pl. 77: 1, 4). Adult apothecia of the cupulate form usually show rather typical concentric hymenial zones of slightly differing transparency when viewed from above, caused by a changing thickness of the receptacle. However, such concentric zones may also occur in *Orbilia leucostigma*, which may easily be confounded under the dissecting microscope with the present species (see Pl. 877: 2).

Cupulate apothecia with narrow marginal cells might display a certain desiccation tolerance, but such possible correlation requires further study.

Misapplications, **Nomenclature and type studies**. Great confusion occurred over the centuries regarding the epithets *inflatula* and *auricolor* (see Spooner, 1987: 164, 180), but also *epipora*. Whilst the epithet *inflatula* has rather consistently been applied in the here used wide concept, the epithets *auricolor* and *epipora* were misinterpreted for a long time as earlier synonyms of the former. *Peziza auricolor* was erected in 1865 almost without microscopic details (apart from 'narrow spores'), and it was only in 1987 when its rather long, distinctly curved, basally tapered spores were correctly described for the first time from the holotype (see p. 1527). When *Peziza epipora* was described in 1869, its description comprised already a mixture of two distinct species: *O. epipora* in the here lectotypified sense, and *H. inflatula*. A further name, *O. leucostigma* var. *xanthostigma*, was once applied by Feltgen (1901) without description to a sample here reidentified as *H. inflatula*.

In the 19th century the epithet *inflatula* has been used in the present sense, e. g., by Karsten (1869: 175, 1871: 100), Phillips (1887: 335), Saccardo (1889: 627), and Massee (1895: 149, figs 48–51). Descriptions of these authors include translucent, thin, flat, 1–1.5 mm large whitish apothecia with a tinge of yellowish-green when moist, but dirty-yellow and contracting angular to globose when dry, subsessile asci, and apparently straight (or slightly curved), short and narrow spores. Karsten wrote that the apothecia have quite a few whitish 'cilia' (anchoring hyphae) at their often stipe-like base, and also in Massee's description the apothecial base is 'furnished with a white down'. Karsten did not mention the paraphyses, and also Saccardo and Massee wrote not to have seen any. Massee even asserted their factual absence, and thought that would be characteristic of the species.

Particularly the microscopical data deviate somewhat in the descriptions provided by the older authors. Ascus and spore size as given by Karsten and Saccardo are rather concordant: 22–25 × 3 µm and 4–7 × ~0.5 µm vs. 18–24 × 2–3 µm and 5–8 × 0.5–0.7 or 0.5–1 µm, respectively. The spores are reported as acicular-filiform by Karsten, but cylindrical and slightly curved by Saccardo. It was Saccardo who emphasized the asci to be 'subsessile'. His illustration of a sample from Selva del Montello (Saccardo 1883: pl. 1290) shows slightly to medium allantoid spores and could instead refer to *H. fagi*. Phillips merely copied the description of Karsten. Massee described the spores as filiform, 6–10 × 0.5 µm, but his drawing shows much wider spores reminiscent of *H. polypori*.

Even more modern authors gave a rather incorrect spore width for *O. inflatula* or *O. auricolor* s.auct. Romero (1994: 113, fig. A–D) measured 5–6 × 0.5 µm, but judging from her scale the spores are 5–6 × 0.8–1 µm. Bride & Caillet (1975) gave the spores as 4–6 × 0.1 µm, probably in error for 1.0 µm. Svrček (1954: 8; 6–8 × 0.5 µm) and Baral (in Baral & Krieglsteiner 1985: 26; 5–8 × 0.3–0.5 µm) gave a too low spore width. The reason for such discrepancy lies at least partly in the fact that no oil immersion was applied. Too wide spores (5–7 × 1.5–2 µm) are stated by Bell (2005: 20, fig. 32 A–D) in her key, instead 4.8–5.3 × 0.8–1.1 µm can be evaluated according to her scale.

The epithet *auricolor* was adopted before 1900 by Cooke (1871: 700), Phillips (1887: 334), Saccardo (1889: 625), and Massee (1895: 148). Their diagnoses, except for Massee's, are purely based on the type collection of *O. auricolor* and lack microscopic data. The fresh apothecia are orange, flat with a raised margin, becoming dingy orange by hardly changing their shape when dry. Massee characterized the apothecia as surrounded by a delicate web of hyphae. He reported the spores as straight, 5–6 × 1.5 µm, although his drawing shows them much narrower. It seems possible that Massee described the spores from a specimen which belonged in the scope of *H. inflatula*.

O. epipora has been confused with *H. inflatula* starting with Nylander (1869), followed by Korf (1992), and apparently also by Dennis (1954) who followed Karsten (1870) in his believe that *Peziza inflatula*, which Karsten had erected 1 year before, was only a subspecies of Nylander's *O. epipora* (see also under that species, p. 1450). Rehm (1891) and Velenovský (1934, 1940, 1947) did not report either of the three epithets, but material referable to *H. inflatula* was found in their herbaria under the name *O. luteorubella*.

Type material of *Peziza inflatula* in Karsten's herbarium has never been found (Nannfeldt 1932: 254, Huhtinen pers. comm.). The original description in Karsten (1869) was based on a not stated number of collections on bark and wood of broad-leaved trees, especially *Populus*, made in September and originating from two sites (Mustiala and Pähkijärvi). The year was not stated but the record from Pehkijärvi, as this lake is now called, was perhaps made in 1867 because Karsten was very rarely in this area (S. Huhtinen pers. comm.) and collected there in 22.IX.1867 *Belonopsis excelsior* on *Phragmites* (Nannfeldt

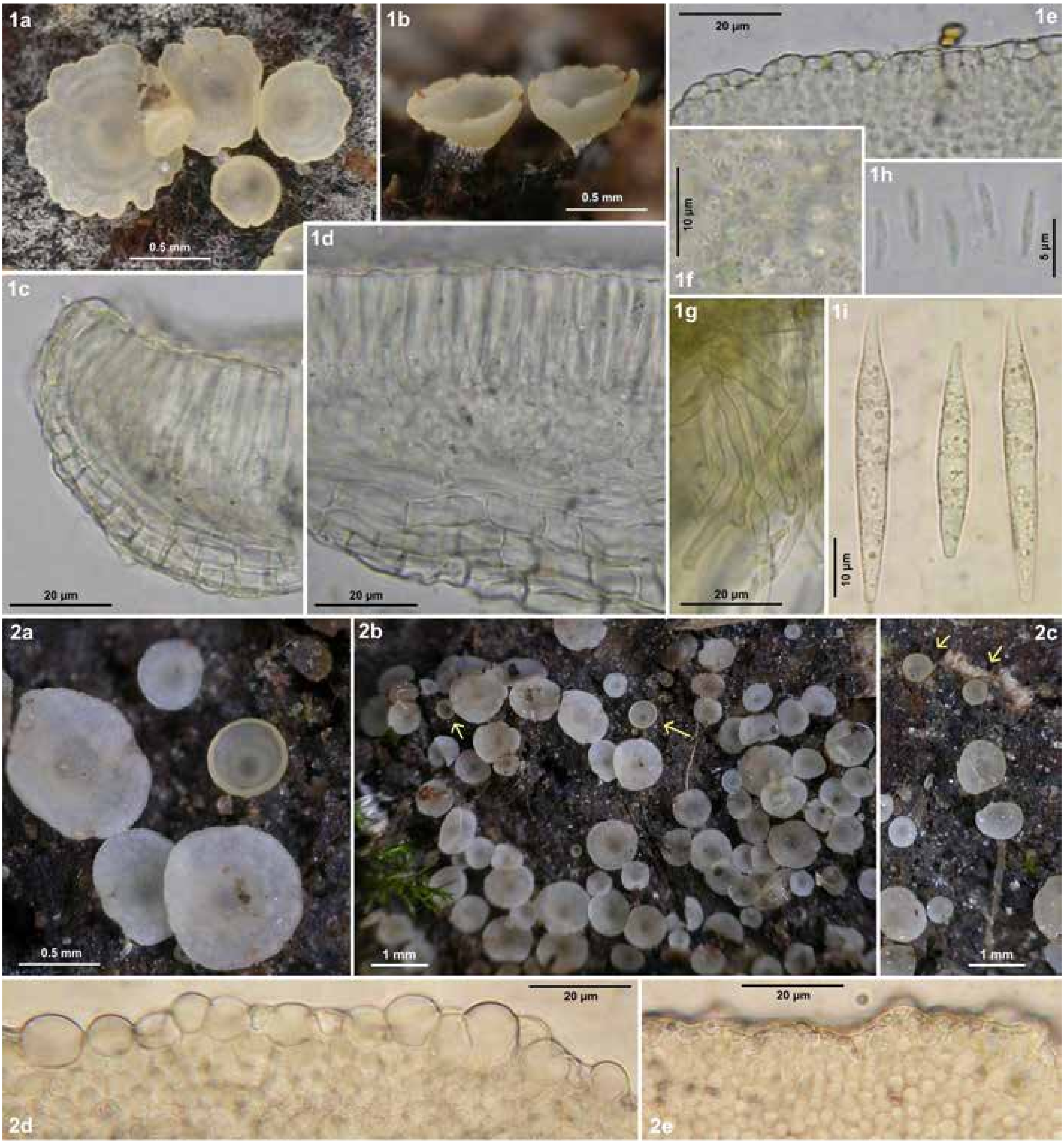


Plate 78. **1–2**: *Hyalorbilia inflatula*. – **1a–b**, **2a–c**. fresh apothecia; **1c–d**. apothecium in median section near margin (**c**) and lower flanks (**d**); **1e**, **2e**. margin in top view, with narrow marginal cells; **2d**. id., with broad marginal cells; **1f**. hymenium in top view, focused on warted-cloddy exudate; **1g**. anchoring hyphae at apothecial base; **1h**. ascospores; **1i**. conidia (from substrate). – Dead state in KOH (**1f** in H_2O), except for **1i** & **2d–e**. — **1a–i**. H.B. 9328 (neotype): Germany, Chemnitz, on *Salix*; **2a–e**. H.B. 8882a/b (**2b–c**: arrow = H.B. 8882b, **2d**: H.B. 8882a, **2e**: H.B. 8882b): ibid., on *Alnus*.

1986). Judging merely from the descriptions of Karsten, Massee, and Berkeley & Broome, Nannfeldt (l.c.) expressed severe doubts about whether *O. inflatula* is distinct from *O. auricolor*. Based on a reexamination of the type of *O. auricolor*, Nannfeldt (1939: 244) adopted the older epithet *auricolor* to replace *inflatula*, but did not mention any of its characteristics. Most workers followed this opinion and applied the name *auricolor* to the species with short straight spores and unstalked asci, e. g., Dennis (1960a: 105, 1970: 352, 1978: 188), Moser (1963: 68), Bride & Caillet (1975), Ahmad (1978: 210), Thind & Sharma (1980), Chmiel (1982), Baral (in Baral & Krieglsteiner 1985: 26), and Ellis & Ellis (1985: 11). Apparently only Seaver (1951: 154) and Svrček (1954: 8, 1962: 92) retained the epithet *inflatula* by neglecting the epithet *auricolor*.

Only 6 years after Nannfeldt had reintroduced the epithet *auricolor*, he revised his opinion about the synonymy of *O. auricolor* and *O. inflatula* (in Lundell & Nannfeldt 1946), but this change in mind obviously escaped notice of most later workers. When he issued there a specimen as *O. inflatula* (Småland, Kärda parish, ‘Kalkunda bokhult’, on heaped-up branches of *Fagus*, mainly on bark, 29.VII.1944, Fungi exsiccati Suecici 1388), he noted on the label: ‘On examining my microscopical slides I find that I made a bad mistake, when identifying this species with *Peziza auricolor* Berk. & Br.' (Spooner 1987: 180, pers. comm.). According to Spooner's revision of FES 1388, this actually represents *H. inflatula* in the sense adopted in the present work. Another collection briefly described by Nannfeldt (1932, fig. 40 d) under the name *O. inflatula* (Uppland, Ärentuna, Storvreta [substrate not indicated], 24.IX.1928, S. Lundell) shows isodiametrical excipular cells in surface view, suggestive of a species of *Orbilia* rather than *Hyalorbilia* (no asci and spores were described).

Spooner (1987) provided a detailed description of the type collection of *Peziza auricolor* and concluded that this represents an earlier synonym of *O. curvatispora* Boud. (see under *O. auricolor*, p. 1527). Consequently, Spooner followed Nannfeldt's (in Lundell & Nannfeldt 1946) concept when he applied the epithet *inflatula* to three north European collections and one from Victoria (Australia), which he described with sessile asci ('not greatly contracted at the base, not furcate') measuring 24–28 × 4 µm, and straight to slightly curved, 4.5–7 × 0.6–1 µm large spores being 'cylindric, sometimes slightly broader towards the proximal end'. Two of these European specimens were also seen by Nannfeldt (FES 1388, issued as *O. inflatula*; FES 2588 as *O. leucostigma*), the third was collected by Dennis (10.V.1981, Isle of Gigha, Scotland, as *O. auricolor*; see also Kirk & Spooner 1984: 529). The drawing in Spooner (1987, fig. 23) refers to the Australian collection which he assigned to *O. inflatula*.

Korf's (1992) report of *O. epipora* included *H. inflatula* and *O. dryadum*, and Ekanayaka et al.'s (2018) report of *H. inflatula* refers to *H. arcuata* based on the curved spores.

The brief descriptions of the older authors do not permit a clear recognition of the species treated, and not even the genus is very clear. Rehm appears never to have used the epithets *inflatula* and *auricolor*. Considering the frequency of *H. inflatula*, this species can hardly have escaped his notice. Rehm's (1891: 455) interpretation of *Orbilia luteorubella* shows a slight similarity with *H. inflatula*, although he described the spores as 6–10 × 1–1.5 µm, narrowly fusiform and the paraphyses with roundish, 3–5 µm wide apices. Rehm's ecological characterization (dry branches of *Pinus*, *Ulmus*, *Alnus*, *Fagus*) clearly excludes *O. luteorubella*. Actually, an exsiccatum in M and H (VII.1881, *Alnus* bark, M. Britzelmayr, Rehm Ascomyc. 621 = Karsten 4846, as '?*Calloria luteorubella* /Nyl./ Karsten') represents *H. inflatula* (yet, the number 621 is not cited in Rehm 1891). Seaver's (1951: 154) observation of curved spores (5–8 × 0.5–0.7 µm, asci 18–24 × 2–3 µm) might refer to *H. tortuosa* or *H. fagi* rather than *H. inflatula*.

Karsten's brief and unillustrated original description of *Peziza inflatula* more or less fits the interpretation of Spooner, but does not allow a final decision, even at the generic level. We here follow the application of the name in Spooner's sense. Since no authentic material in Karsten's herbarium could be located, a neotypification is necessary. However, our genetic results suggest that different closely related taxa are involved in our present concept of the species. This raises the question which specimen should be proposed as neotype. Karsten's protologue reports the dry apothecia to be inflated like a membranous swollen bladder, which seems to refer to cup-shaped apothecia. In those species with narrow marginal cells we have more often seen cup-shaped apothecia, therefore, it might be better to select a specimen of those, although this macroscopic feature is not strictly correlated with marginal cell size. We here designate a collection from Chemnitz, Germany (ex H.B. 9328, Pl. 78: 1) as **neotype** of *H. inflatula*. The apothecia are cup-shaped and have marginal cells of *10–12 × 4–5 µm in sectional view, asci with average length (*25–29 × 4–4.5 µm, †18–25 × 2.8–3.2 µm), with two superimposed bundles of four spores, and rather short, straight or only very slightly curved spores (†5–6 × 0.9–1 µm, not described in the living state). An ITS sequence was gained from its apothecia, which clusters in a clade with the sample from Madrid that was studied in more detail in the living state (Pl. 77: 10), though with ~4% distance (see below).

Type studies (European taxa). The type of ***Peziza translucens*** (Roumeguère, Fungi gallici exs. 2382) was described on '*Quercus*, *Fagus* etc.' from Poligny (Jura, VII.1882). The Kew syntype specimen was restudied by Dennis (1964: 69) and found to be a synonym of *O. auricolor* (s.auct., = *H. inflatula*), whereas the syntype studied by Höhnel (1926b: 95) was said to be completely immature. The here examined syntype (PC 0088499, IVV: H.B. 7750) confirms Dennis' result (apothecia 0.5–1.5 mm diam., honey-yellow, saucer-shaped, asci in KOH 23–28 × 4–4.2 µm, arising from croziers, ascospores 6.3–7.4 × 0.9–1 µm, straight, marginal cortical cells not measured). The substrate (rotten wood) belongs to *Fraxinus*, according to its microanatomy.

No type material of ***Orbilia breviasca*** (Brandenburg, Tamsel, Berganlagen, on rotten wood, VIII.1904, P. Vogel n. 1712) could be located in B, HBG, BPI, and S. The species was thought by Hennings (1909) to be close to *O. luteorubella*, differing in much shorter asci, uninflated paraphyses, and narrower spores. The asci are described as 'short-clavate, apically obtuse-truncate', 20–25 × 3–3.5 µm. The short asci point to a *Hyalorbilia*, and the gelatinous apothecia (1–1.5 mm diam.) and straight spores (6–7 × 0.5 µm) to *H. inflatula*. However, the possibility cannot be excluded that Hennings overlooked the stipe of the asci. The apothecial colour ('yellow-orange') is unusual for *H. inflatula*. Kanouse (1939) referred collections from USA (Michigan) and Canada to this taxon. Her brief description includes non-capitate paraphyses covered by exudate, which might refer to a *Hyalorbilia*.

The abundant lectotype of ***O. cyathea*** grew on fissured bark of obviously *Quercus* (often on very old black stromata of a pyrenomycete), contrary to Velenovský's statement on the label ('on rotten wood of *Quercus*'). Surprisingly, Velenovský's (1934) prolotogue mentions five different genera of broad-leaved trees as support of *O. cyathea*, but not *Quercus*. As the site 'Liblice' is mentioned in the protologue, Svrček's (1954: 13) choice of this collection as lectotype seems acceptable. At the flanks the ectal excipulum is composed of a horizontal textura prismatica (individual cells 12–28 × 8–12 µm), contrary to the author's statement in the protologue ['parenchym exceedingly large-celled (50 µm)']. On his manuscript sheet, which includes sketches of several collections (but none of the lectotype), he figures both a textura prismatica and a t. angularis (the latter with excipular cells 50 µm diam), but only the large-celled t. angularis is reproduced in Velenovský (1934 pl. 11 fig. 17). The origin of the different sketches on this plate is not very clear: the textura angularis was perhaps from *Fomes fomentarius*, Carpathians, VII.1933, and seems to belong to an *Orbilia*; the t. prismatica was apparently from *Carpinus*, Radotín, 20.V.1926, and undoubtedly refers to a *Hyalorbilia*. Svrček revised several of Velenovský's specimens, including that on *Fomes fomentarius*, and found them to concur 'perfectly' with *O. inflatula*.

The collection data of the lectotype (oak, Liblice, VII.1925) can be found on Velenovský's manuscript sheet and were added by him apparently rather late. No microscopic data of this specimen appear to have been noted by him. Nevertheless, ascus and spore size as here evaluated from the lectotype (Pl. 77: 4) fit well the protologue and also the present concept of *H. inflatula*, as do the cupulate, pale yellowish-chlorinaceous apothecia (rehydrated 0.5–1.5 mm diam.). The marginal excipulum is composed of rather large, thin-walled cells [9–11 × (4–)5–10 µm], and the minute warts over the hymenial gel are hardly perceptible. The name *O. cyathea* is thus available for the variant with wide marginal cells, if a split of *H. inflatula* will become necessary in the future.

The abundant lectotype of ***O. linata*** (on wood of *Betula* log) contains cupulate, rehydrated 0.4–1 mm large, yellowish-ochraceous apothecia which were found to be immature (asci 21–29 × 4–5 µm, with croziers, medullary excipulum strongly gelatinized, ectal excipulum slightly so, at margin thin, of thin-walled t. prismatica). Judging from apothecial shape and size, this could well belong to *H. inflatula* (with narrow marginal cells). Svrček (1954) stated that it is 'totally identical' with *O. inflatula*, but did not say whether he saw any asci and spores. Velenovský (1934), who compared the taxon with his *O. cyathea*, described asci of 25 × 5 µm and broadly ellipsoid, biguttulate, 4–5 µm long spores, though not from inside the asci. Such free spores of unclear origin (hyaline, ellipsoid-obovoid, very finely warted, 6–7 × 2.9–3.3 µm, with two large LBs) were abundantly found among the apothecia in the present reexamination. Also Svrček saw them and named them 'conidia', but did not report their warted surface. Undoubtedly, Velenovský mistook these as the ascospores of *O. linata*. He also described brown, 2-septate, pyriform conidia, which he seems to have considered as its anamorph, but they belong to the associated *Brachysporium obovatum*.

Svrček mentioned only this collection (as 'holotype'), although Velenovský based his new species on two different collections. On his manuscript sheet Velenovský named the *Carpinus* collection 'var. *carpinacea*', which he stated to deviate by almost colourless apothecia, but in his monograph he merged it with *O. linata*. Since the protologue largely refers to the *Betula* collection (PRM 152443), we here designate this as **lectotype** of *O. linata*. No material of the *Carpinus* collection could be located at PRM. The apothecia on *Betula* are described as honey-yellow (melina) in the protologue, and it is probably this colour after which Velenovský named the species *linata*.

For the abundant holotype of ***O. pyrifera*** (on bark of *Quercus*) Velenovský (1947) gave the spores much too small (2.5–3 × 0.5 µm). Svrček's (1954) conclusion that *O. pyrifera* represents *O. inflatula* is confirmed here (Pl. 77: 5). The apothecia were cyathiform, dry deeply cupulate, and the thin-walled marginal cortical cells measured 10–15 × 8–10 µm. The taxon grew among black setae of a hyphomycete. On the excipulum Velenovský found pyriform, 1-septate, hyaline 'corpuscules' of 25 µm length, from which the specific epithet is derived, and which might represent the conidia of this hyphomycete. The holotype contains many such setae though no conidia could be found in the present study. Only a much older collection (18.VI.1925, Mnichovice) is named *O. pyrifera* in Velenovský's unpublished manuscript, which is not mentioned in the protologue, and which obviously belongs to *O. auricolor*. Also this collection was named according to the presence of 2-celled conidia which here undoubtedly represent the *Arthrobotrys* anamorph of *O. auricolor*.

Hyalinia rectispora* var. *majuscula was placed in close vicinity of *Hyalinia rectispora* Boud. by Grelet (1948b) on account of a similar spore shape, and was segregated hereof by much larger apothecia and a ligneous substrate. Grelet overlooked the severe difference in ascus base and type of ectal excipulum between the two taxa. Five specimens that belong to four collections were received from PC and found to be conspecific with the present concept of *H. inflatula*. All were signed by Grelet as '*Hyalinia rectispora*'. For one of them (15. VI.1914, Savigné, on *Quercus* board) Grelet (in sched.) noted 'vidit Boudier'. Three are mentioned in the protologue and can, therefore, be considered as syntypes. Collection VII.1925 (Savigné, *Pinus* bark, PC) is designated here as **lectotype** of *Hyalinia rectispora* var. *majuscula*. In this specimen the apothecia measured rehydrated 0.5–1.8 mm diam. (Pl. 80: 6a–b), the asci 20–24 × 4 µm (with croziers), and the spores ~6–7 × 1 µm. The medullary excipulum is distinctly gelatinized; the marginal excipulum was not studied.

Type studies (extra-European taxa). The following three names belong to specimens with a subtropical to tropical origin. Reexamination of type or authentic material showed that all three have very similar spores which deviate from typical *H. inflatula* in being rather short and often very slightly curved, comparable to *H. japonica*, *H. citrina* p.p., *H. fagi*, or *H. andina*. Their possible identity with *H. inflatula* could not be resolved, nor do they fit very well any of the other accepted taxa (in ascus size they exceed slightly or distinctly the length of *H. japonica*). Therefore, we refrained from including them in either description.

Peziza vulgaris* var. *myceticola from South Carolina was published in Berkeley (1875) without diagnosis but only with the remark that the species deviates from typical *Peziza vulgaris* Fr. [≡ *Calycina vulgaris* (Fr.) Baral] in more concave discs. A syntype in K was designated as lectotype by Dennis (1964: 70, fig. 54 left) who believed that it might belong to *Orbilia epipora*. His drawing shows unstalked asci typical of *Hyalorbilia*, but deviates from the present examination of this material (Pl. 79: 5) in distinctly more capitate paraphyses. When rehydrated, the cyathiform apothecia measured 0.8–1.4 mm diam., the ectal excipulum at the flanks was a slightly gelatinized t. prismatica, and the thin-walled margin cortical cells measured 9–11 × 6–9 µm (in section). The other syntype specimen cited in the protologue (on oak, South Carolina, No. 2683) was not received from K.

No authentic material of ***Hirneola lancicula***, from French Guiana, Cayenna, on unidentified wood (as 'lignum'), [F.M.R.] Leprieur, no. 1087, could be located in PC and TCD. The species was described by Montagne (1856) without microscopic characters, with small, gregarious, plano-concave, umbilicate, gelatinous, amber-brown apothecia with undulating margins. When transferring this taxon to *Orbilia*, Patouillard & Gaillard (1889) included with hesitation a collection from Venezuela: V.1887, Haut-Orénoque, Mapire, on rotten bark [as 'wood'], A. Gaillard. Two specimens of this collection (PC 0001063, HBG) were examined (Pl. 79: 4). The ectal excipulum at the flanks is a thin- to thick-walled t. prismatica, but the margin was not studied.

Penzig & Saccardo (1902, 1904: 85, pl. 57 fig. 3) described ***O. sinuosa*** based on two collections from Java [12.I.1897, Tjampea;

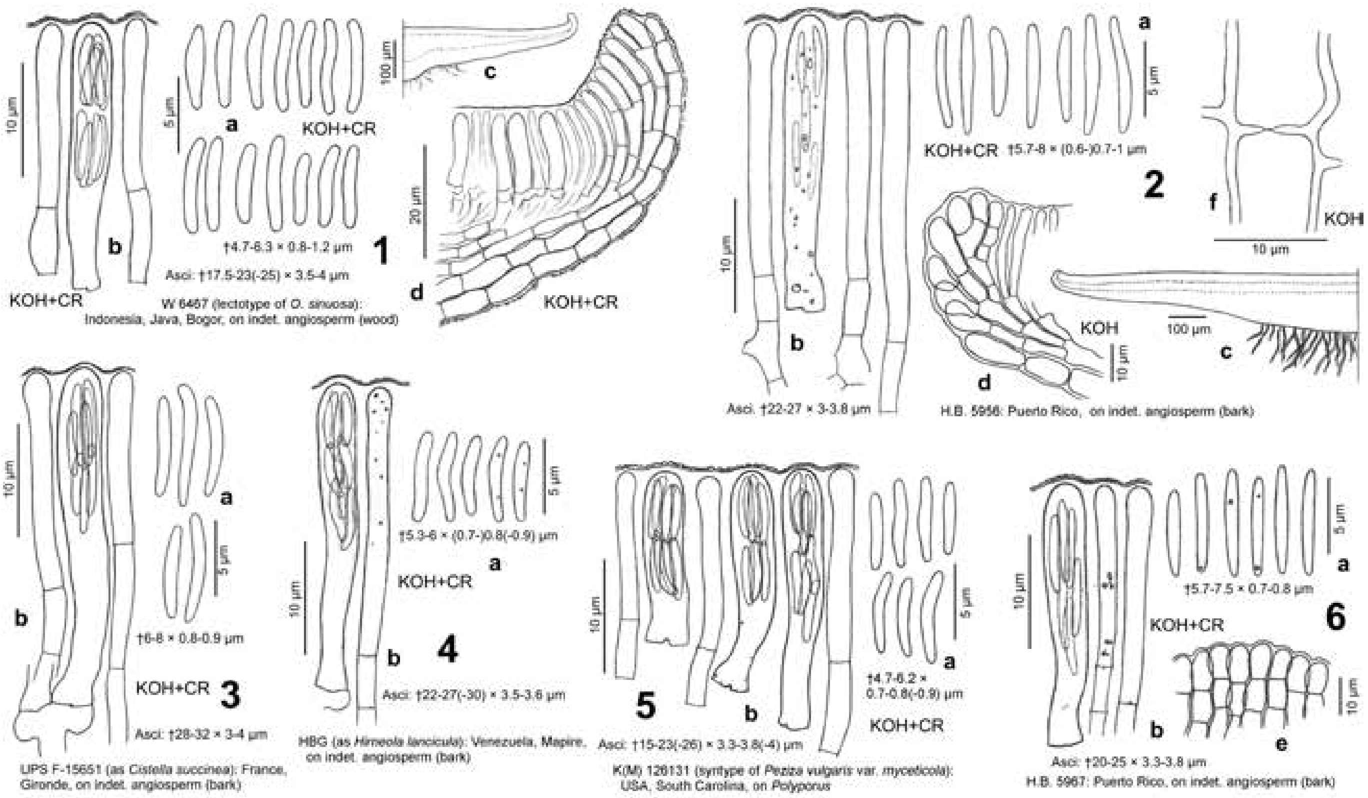


Plate 79. **2**, **6**: *Hyalorbilia inflatula*; **1**, **3–5**: *H.* cf. *inflatula*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. apothecia in median section; **d**. id., ectal excipulum and hymenium at margin and flanks; **e**. marginal ectal excipulum in surface view; **f**. id., near margin, showing thick walls.

2.I.1897, Bogor ('Buitenzorg') Botanical Gardens]. Only the specimen from Bogor could be located in W (Pl. 79: 1; 81: 7) and is designated here as **lectotype** of *O. sinuosa*. Although the apothecia were figured with a sinuous margin, from which the name derives, they showed in the studied specimen a roundish outline when rehydrated, with a rather even or only slightly undulating margin (0.25–1.4 mm diam). The other characters fit quite well the protologue. The spores are often slightly curved (allantoid) and sometimes even a bit helicoid (†4.7–6.3 × 0.8–1.2 µm, in the protologue '4–6 × 1 µm, slightly curved'). The asci were described much longer (28–35 × 4–5 µm) than found in the examined specimen (†17.5–25 × 3.5–4 µm). The merely slightly curved spores and the at most slightly gelatinized ectal excipulum with very narrow marginal cortical cells (4–10 × 3–3.5 µm) separate this tropical collection from *H. citrina*. Because of the rather short spores and their curvature some doubts remain whether *O. sinuosa* belongs in the scope of *H. inflatula* or perhaps *H. japonica*, for which the spores are too wide.

Ou (1936), copied by Teng (1939), reported under the name *O. sinuosa* the first record of *Orbiliomycetes* from China. The single sample (from Zhejiang) was considered by Liu (2006: 41) and Liu et al. (2006b: 109) to represent *H. inflatula*, though without reexamination (B. Liu pers. comm.). Judging from Ou's description of the slightly curved spores of 4–5 × 1 µm it could belong to *H. japonica*, but ascus size (35–45 × 5 µm) excludes that species and fits instead the upper range of *H. inflatula*.

Spooner's drawing of an Australian specimen (Victoria, on fallen log, 28.XII.1963, Beaton 176, see Fig. 171), referred by him to *O. inflatula*, should be compared with the above taxa, because the spores are figured predominantly slightly allantoid (6–7.3 × 0.7–1.1 µm as evaluated from scale).

A specimen in UPS collected by L. Quélet in France (Bordeaux, on bark, 25.VI.1884, L. Forquignon) and labelled '*Cistella* ~~*Mollisia*~~ *succinea* Q[uélet] 10 supp. t. 3 f. 11' represents authentic material of ***Peziza succinea***. The taxon was originally described from French Jura on rotten wood, but no holotype material came to our notice. Nannfeldt (1932: 266) found that the specimen from Bordeaux represents an *Orbilia* with a distinct hyaline subiculum at the base. Contrary to his statement of being 'hardly identical with *O. inflatula*', the present reexamination did not reveal any clear differences to that species worth mentioning. However, some of the spores are slightly curved (Pl. 79: 3), therefore this specimen appears to be intermediate to *H. fagi*. An illustration of the type is found in Quélet (1881, pl. 9 fig. 11) showing cupulate apothecia with radiating anchoring hyphae, and rod-shaped straight, 8 µm long, somewhat broad spores.

Not included collections. A specimen from Leipzig (on *Quercus*, IVV: H.B. 7408) deviates in exceptionally small apothecia, which measure rehydrated 0.25–0.35 mm diam. and are in addition distinctly stipitate. The exterior is covered by a very pale yellow-brown exudate, the marginal cortical cells are clavate but only †3–5 µm wide, the asci rather small (†14 × 3 µm), and the spores straight, *6–7 × 1 µm, with 1–2 small guttules at each end. The sample was collected with a crane 22 m above the ground on a dead, periodically dry, corticated, thin branch. The apothecia developed in a moist chamber in the laboratory, where the branch was brought after being collected. When received in the dry state and rehydrated, the excipular cells showed a certain drought tolerance. This sample is not included in the description. For the not included *Orbilia breviasca* and *O. linata* see under Type studies, and for *Dactylella passalopaga* under Anamorph.

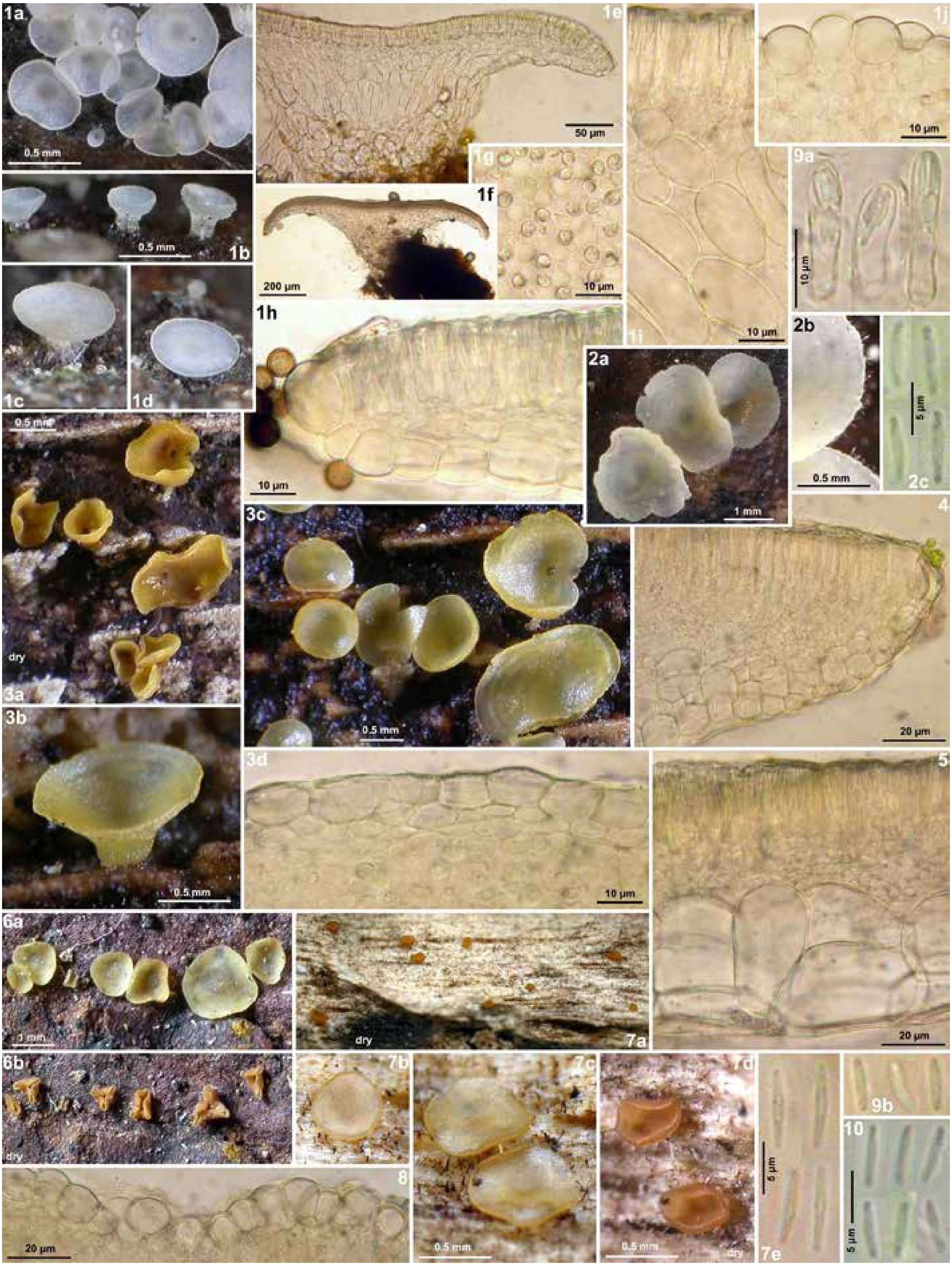


Plate 80. **1–10**: *Hyalorbilia inflatula* (with wide marginal cells). – **1a–d**, **2a–b**. fresh apothecia (**2**: margin hairy from conidiophores); **3b–c**, **6a**, **7b–c**. rehydrated apothecia (**3**: after 30 years, **6**: after 76 years); **3a**, **6b**, **7a**, **d**. dry apothecia; **1e–f**. apothecia in median section; **1h**, **4**. id., marginal part; **1j**, **5**. id., lower flanks; **1i**. id., medullary excipulum and hymenium in central part; **3d**, **8**. margin in top view; **1g**. hymenium in top view; **9a**. asci; **2c**, **7e**, **9b**, **10**. ascospores. – Living state, except for **3d**, **7e**, **8** (in KOH). – **10**: phot. P. Perz. — **1a–j**. H.B. 8882a: Germany, Chemnitz, on *Alnus*; **2a–c**. H.B. 8241a: Switzerland, Pilatus, on *Fagus*; **3a–d**. TAAM 63888: Russia, Caucasus, on *Fagus*; **4**. H.B. 7963a: Germany, Tübingen, on *Fagus*; **5**. H.B. 7972: Great Britain, Suffolk, on *Fraxinus*; **6a–b**. PC (lectotype of *Hyalinia rectispora* var. *majuscula*): France, Vienne, on *Pinus*; **7a–e**. H.B. 8406: Australia, Queensland, on *Acacia*; **8**. TAAM 161189: Estonia, Tartu, on *Diatrypella*; **9a–b**. H.B. 8221: Germany, Chemnitz, on *Sorbus*; **10**. P.P. 20070825: Poland, Srem, on *Prunus*.

Plate 81. **1–17**: *Hyalorbilia inflatula* (with rather narrow marginal cells). – **1a–d**, **2a**, **5a–b**, **9a**, **10**, **12c**, **14b**. fresh apothecia; **3a**, **4a**, **7a**, **8**, **11b**, **17b**. rehydrated apothecia (**3–4**, **8**, **11**: after 4–14 years, **7**: after 108 years); **4b**, **11a**, **17a**. dry apothecia; **14a**. apothecium in median section; **7b**, **15**. id., marginal ectal excipulum; **1f**, **4c**, **11c**, **13**. marginal cells in top view; **5e**. basal ectal excipulum with anchoring hyphae (median section); **3b**. anchoring hyphae; **12a**, **16**. exudate in surface view; **12b**. exudate in median section; **1e**, **5c–d**, **6**. asci and paraphyses; **1g**, **9b**. ascospores. – Living state, except for **3b**, **4c**, **7b**, **11c**, **13**, **16** (in KOH). – **6**: phot. M. Hairaud, **9a**: phot. W. Huth. — **1a–g**. H.B. 8885a: Germany, Chemnitz, on *Tilia*; **2**. H.B. 8885b: ibid., on *Salix*; **3a–b**. H.B. 5956: Puerto Rico, El Yunque, on

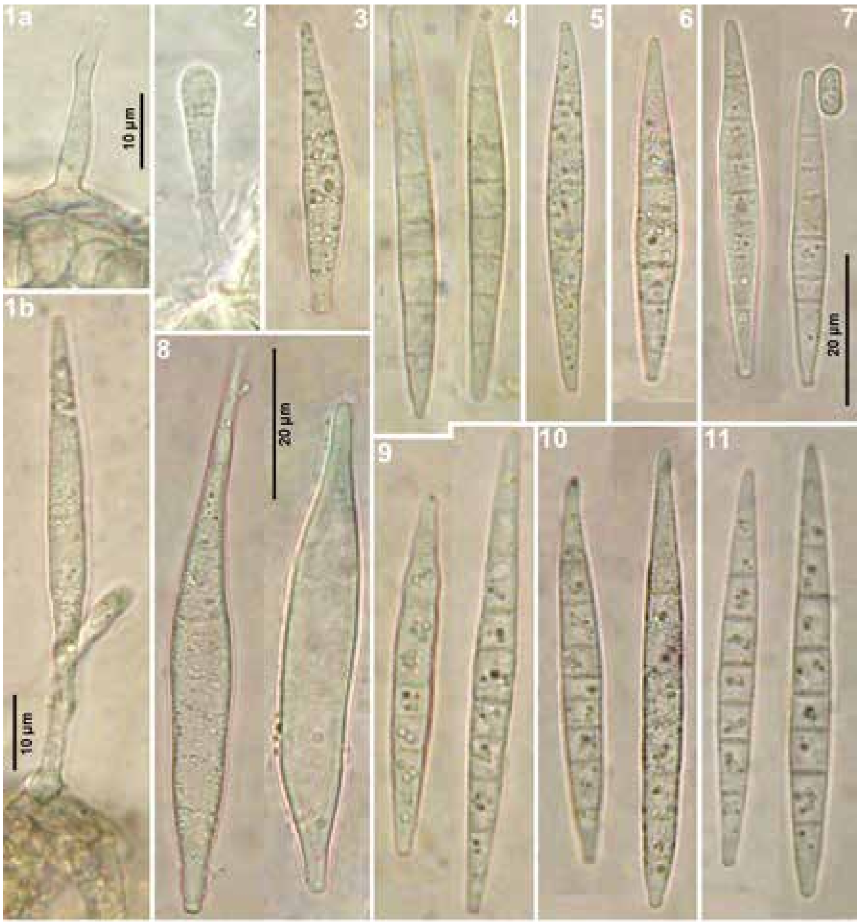


Plate 82. **1–11**: *Hyalorbilia inflatula* (anamorph). – Conidia (with refractive SCBs) and conidiophores [living state, except for **2** (in KOH); **8** (in H_2O); some cells in **1b**], from natural substrate, except for **10**: from lid of Petri dish. — **1a–b**. H.B. 8241a: Switzerland, Pilatus, on *Fagus*; **2**. H.B. 7746: France, Vienne, on *Pinus* (lectotype of *H. rectispora* var. *majuscula*); **3**. H.B. 7623: Austria, Salzburg, on *Fagus*; **4**. H.B. 8221: Germany, Chemnitz, on *Sorbus*; **5**. H.B. 8279b: Switzerland, Pilatus, on *Tilia*; **6**. H.B. 7972: Great Britain, Suffolk, on *Fraxinus*; **7**. H.B. 7879: Germany, Villingen, on *Carpinus*; **8**. H.B. 7944: Germany, Tübingen, on *Malus*; **9**. H.B. 8173: France, Forêt d'Aulnay, on *Fagus*; **10**. H.B. 8150: France, Ile de Ré, on *Quercus*; **11**. H.B. 9041a: Germany, Chemnitz, on *Acer*.

Four tropical collections examined in the present study (Pl. 79: 1–2, 4, 6) showed a stronger gelatinization of the excipulum. Two of them (*O. lancicula*, *O. sinuosa*) are not included because of slightly curved spores. These and two from warm-temperate Europe and USA (*Peziza succinea*, *P. vulgaris* var *myceticola*) are discussed under Type studies. A collection from Queensland (Australia), mentioned by Spooner (1987: 178) under *O. inflatula*, deviates by rather long asci (†28–31 × 4–4.5 µm) and long, apparently straight spores (†7–8.5 × 0.8–1 µm), also in smaller, orange apothecia (mostly less than 0.5 mm diam). Similarly, a collection from Luxembourg (Pl. 77: 3a) on an attached, 2 cm thick branch of *Quercus* 1 m above the ground was not included because of its extraordinarily long spores with often ~3–4 SBs near each end, also because of the generally more irregular spore arrangement which never showed the typical superimposed arrangement of 4+4 spores (Pl. 77: 3b). Also Guo et al. (2014b: fig. 8) reported under the name *H. inflatula* four Chinese collections with spores of *5.9–10.3 × 0.9–1.2 µm with 3–4 rather large SBs in each half, which certainly do not belong in the scope of *H. inflatula*. The samples from Australia, Luxembourg, and China approach short-spored collections of *H. juliae* which, however, differ in wider spores. On the other hand, Guo et al. (2014b: fig. 7) describe under the name *H.* aff. *inflatula* various samples which fit typical *H. inflatula* (fig. 7B showing narrow marginal cells).

Anamorph. Like D.H. Pfister (pers. comm.) we did not succeed in obtaining a pure culture from ascospores. However, a single time we obtained conidiophores and conidia growing out of the apothecia that were placed at the lid of a Petri dish (Pl. 82: 10). The same anamorph was repeatedly found on or around apothecia on the natural substrate in various further European samples (Pl. 77: 10–13 and Pl. 82).

The conidia of '*Dactylella*' *passalopaga* as described by Drechsler (1936) from eastern North America fit quite well in their size (*60–80 × 4.5–6 µm) and number of septa (6–8), though being comparatively long. Because of the worldwide frequency of *H. inflatula* especially in temperate regions, we assume that '*D.*' *passalopaga* is the anamorph of *H. inflatula*. Similarly large conidia were mainly observed in the rare *H. caucasica* and the frequent *H. fagi*. The conidia of *H. fagi* are too short and mainly 3–6-septate, however, in order to belong to the true '*D.*' *passalopaga*. The conidia of *H. lignatilis* are a bit smaller and with fewer septa than observed in '*D.*' *passalopaga*, and the same is true for a number of further anamorphs in *Hyalorbilia*.

Phylogeny. In five European collections of *H. inflatula* ITS sequences were gained from apothecia (in two also LSU and SSU: H.B. 9080, 9915). Three of them (Chemnitz, H.B. 9080; Schwarzwald, H.B. 9915; Luzern, H.B. 8279b) possess an ectal excipulum of broad marginal cortical cells, whereas two (Chemnitz, H.B. 9328, neotype; Madrid, H.B. 7112) feature narrow marginal cells. All have an ascus length in the middle range. Our ITS analysis of these five sequences supports the existence of different taxa within the present concept of *H. inflatula*: the five strains clustered with high support in a clade which contains two strongly supported subclades in correlation with the marginal cells (Phyl. 5).

European strains with broad marginal cells showed a distance of only 0.8–1 % to each other, whereby H.B. 9915 and 9080 are identical. Likewise, the two European strains with narrow marginal cells differed by 0.8 % (5 nt) from each other. However, H.B. 7112 contains various ambiguous nucleotides. The distance between the two subclades lies at 5–6.2 %.

The S1506 intron was available for two samples with broad cells (H.B. 9080, 9915) and one with narrow cells (H.B. 9328).

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indet. angiosperm; **4a–c**. H.B. 7360: France, La Tranche sur Mer, on *Fraxinus*; **5a–e**. H.B. 7758: Germany, Bad Reichenhall, on *Fomes*; **6**. 20.III.2007: France, Forêt de Chizé, on *Abies*; **7a–b**. W 6467 (lectotype of *O. sinuosa*): Java, Bogor, on indet. angiosperm; **8**. H.B. 5066: Luxembourg, Koedange, on *Populus*; **9a–b**. H.B. 8573: Germany, Naumburg, on *Tilia*; **10**. 14.III.2008: Germany, Tübingen, on *Hypoxylon*; **11a–c**. H.B. 4885a: Luxembourg, Dudelange, on *Prunus*; **12a–c**. H.B. 8882b: Germany, Chemnitz, on *Alnus*; **13**. H.B. 6391: Germany, Starnberg, on *Cyathus*; **14a–b**. H.B. 8127: France, Forêt de Chizé, on *Acer*; **15**. H.B. 8173: France, Forêt d'Aulnay, on *Fagus*; **16**. Rehm Ascom. 621: Germany, Oberstaufen, on *Alnus*; **17a–b**. H.B. 8150: France, Ile de Ré, on *Quercus*.

For H.B. 8279b and 7112 the intron was not available because the ITS1-primer was used. The two broad-celled samples are identical in the overlapping part of the intron, whereas the narrow-celled one differs hereof at 16 positions (6.5%) and a small and large indel region in the overlapping 295 nt. An intron (S943) with a length of 329 nt occurs in H.B. 9915, and was also observed in some other taxa of *Orbiliomycetes* (Tab. 27).

Liu et al. (2006a) gained ITS sequences from seven Chinese collections under the name *H. inflatula*, but LSU only for one of them (B.L. X076). Three of these stains (from Fujian and Guangxi) show a relationship to *H. arcuata* and *H. japonica* (see under these species), whereas three are associated with European *H. inflatula*: one from Xinjiang (B.L. 6564 = HMAS 139536) and two from Tibet (B.L. X034 = HMAS 96789; B.L. X076 = HMAS 96788). Two of them clustered with strong support as a sister group to the clade with broad marginal cells by showing a distance of 1.5–4% and 3–5% to them, respectively (6–11% and 11.5–14% to the clade with narrow cells), whilst B.L. X076 clustered with strong support as a sister clade of the three *H. inflatula* subclades, with a distance of 9–13% and 11–19%. For B.L. 6564 the marginal cells were examined and found to be broad (B. Liu pers. comm.). Finally, B.L. HB19 from Shennongjia Nature Reserve (Hubei) clustered, besides other subclades, within the *inflatula-polypori* clade. When including the LSU region (Phyl. 6), B.L. X076 (Tibet) clustered with medium support and with an LSU distance of 1.7% (547 nt) with the German H.B. 9080 and 9915 in a clade.

Near the 5'-end of the ITS1 region, H.B. 8279b and 9915 (with broad cells) possess an insert of roughly 180 nt, which exists with a similar length also in B.L. 6564 and X034, though only ~145 nt are available (the also incomplete ITS1 of H.B. 9080 did not cover this insert). The insert is much shorter (around 20 nt) in the two samples with narrow cells (H.B. 7112, 9328) and similarly short also in other *Hyalorbilia* sequences which cover the 5'-end of ITS1. However, the alignment is very complicated in this region. In the overlapping 125 nt of the long insert, H.B. 8279b and B.L. 6564 are identical and H.B. 9015 deviates merely by 1 nt. B.L. X034 concurs with H.B. 9015 at this position, but deviates at 5 further positions from the German strains.

All this illustrates the molecular variation in the *H. inflatula* aggregate. For the case that future studies confirm the here observed molecular correlation with the width of the marginal cortical cells, a split into two or more species might be required. In this case, names need to be selected among the here listed synonyms of *H. inflatula*. For instance, *Orbilia cyathea* matches morphologically those with broad marginal cells, while the neotype of *H. inflatula* proposed here refers to a population with narrow cells.

The here recognized *inflatula-polypori* clade comprises besides *H. inflatula* also *H. arcuata*, *H. citrina*, *H. fagi*, *H. helicospora, H. japonica*, *H. lignatilis*, *H. lunata*, and *H. polypori*. It received strong support only in our analyses of LSU or ITS+LSU (Phyls S5, 6). For *H. arcuata* and *H. japonica* only ITS was available, therefore, they are shown only in the ITS analysis. In the *inflatula-polypori* clade clustered also Ekanayaka et al.'s (2018) *H.* cf. *inflatula*, which showed in the LSU D1–D2 a distance of 2.5–2.7% to *H. inflatula* and 3–4.5% to *H. fagi*, *H. citrina*, and *H. polypori*.

Ecology. In temperate regions, *Hyalorbilia inflatula* is the most often collected species of the genus. Unquestionably, this frequency is partly due to the rather large, conspicuous apothecia. The species grows on rotten bark and wood, mainly on the underside of branches and logs fallen to the ground. Bark and wood are quite equally inhabited, but often a fungicolous growth was noted which includes pyrenomycetes as well as aphyllophoralean basidiomycetes. A single collection was on non-ligneous substrate (base of leaflets of *Licuala ramsayi*, a fan palm in northeastern Australia). A report by Massee & Crossland (1905: 301) on herbaceous stems of *Angelica* is without description and more probably refers to an *Orbilia*. An Australian collection on dung was reported by Bell (2005: 20, fig. 32 A–D) and fits well the present concept of *H. inflatula*.

The wide host range of *H. inflatula* includes a large number of genera of angiosperms, but also some of gymnosperms. The most preferred genera observed by us were *Fagus* {29}, *Quercus* {20}, and *Fraxinus* {16}. Host genera indicated in the literature but not seen by us are *Crataegus* (Velenovský 1934: 94, Svrček 1954: 13, Ellis & Ellis 1985: 12), *Cupressus* (Ellis & Ellis 1985: 11), *Eucalyptus* (Romero 1994: 113), and *Robinia* (Bride & Caillet 1975). Helfer (1991: 50) listed *Gloeophyllum odoratum* and Svrček (1962) *Xanthoporia nodulosa* as additional supports. Quijada et al. (2014a) reported collections from Tenerife on laurel forest trees such as *Apollonias barbujana*.

H. inflatula was found from planar to subalpine altitude, and from atlantic to continental regions. The species apparently occurs worldwide. Most collections are from cold-temperate humid to mediterranean (semihumid) but also hemi- to oroboreal and cold-continental zones, in various vegetation types, such as *Alnetum*, *Fraxino-Aceretum pseudoplatani*, *Salicetum*, *Fagetum* etc. Based on a biodiversity project in southeastern Norway, Raitviir & Huhtinen (2003) identified the species as one of the most common lignicolous discomycetes in Norway.

A few collections were made on dry, hanging, 15–25 mm thick branches in 1–22 m above the ground, in a xeric environment. Although the trees grew rather close to running water in some of these samples, the apothecia were completely dry when collected, and exhibited a desiccation tolerance of the vegetative cells of at least 1–3 months, whereas in populations growing on the ground this tolerance was very low. Mature apothecia were found throughout the year, though with a maximum in spring and summer (April–September).

H. inflatula is widely distributed across whole Europe, but we have also seen samples or documentations from other continents, including subtropical to tropical humid regions in America, Asia, and Australia, although their conspecificity is more or less questionable, e. g., in the types of *O. lancicula* from Venezuela and *H. sinuosa* from Indonesia. Collections from Macaronesia (Tenerife, La Gomera, Madeira) were made in the thermo- to meso(sub)mediterranean subhumid to humid laurel forest (*Lauro novocanariensis-Perseetum indicae*; see also Quijada et al. 2014a). D.H. Pfister (pers. comm.) found the species quite frequently in the northeastern United States. Also Seaver wrote that it occurs in eastern North America from 'Toronto to Louisiana'. A single report for South America is that by Romero (1994, Argentina), and from Middle America it was recorded by Medel et al. (2013, Guatemala) in cloud and *Cupressus* forests at 1800 m. Reports for Asia and Australia are those of Ahmad (1978, Pakistan), Thind & Sharma (1980, India, Northwestern Himalayas), Liu (2006: 35) and Liu et al. (2006b: 108, China including Tibet, at 180–3500 m a.s.l., but see under Phylogeny), Raitviir (1991:

Map 7: Known distribution of *H. inflatula* in Europe and Macaronesia (yellow = not included collections).

358, northeastern Asia), and Bell (2005, eastern Australia).

A list of numerous collections on various substrates exists for Belgium (B. Declercq pers. comm.). Two of them were included in the specimen list as there exist documentations for them. Also for the Netherlands the NMV distribution atlas (www.verspreidingsatlas.nl) shows numerous records, but only for one we saw a documentation (S. Helleman pers. comm.). Liu (2006) listed not less than 114 collections, but some of them were here reidentified as *H. japonica*.

Specimens included (marginal excipular cells nar = 4–6 µm wide, wide = 6–12 µm wide). **IRELAND**: **Kildare**, 2.5 km S of Newbridge, 1 km WNW of Curragh Edge, 105 m, branch of *Ulex europaeus*, on wood, 6.V.2016 J.P. Priou (nar, J.P.P. 16136, doc. vid.). — **GREAT BRITAIN**: **Yorkshire**, **South Yorkshire**, 3.5 km S of Barnsley, 1.3 km SW of Worsbrough, Worsbrough Country Park, 70 m, branch of *Fraxinus excelsior*, on wood, 20.V.2011, H.O. Baral (ø). – 18 km ESE of Sheffield, 2 km SE of South Anston, Anston Stones Wood, 70 m, branch of *Fraxinus excelsior*, on wood, 16.V.2011, T. Fleming (ø). – **East England**, **Suffolk**, 4 km NW of Southwold, 1 km ESE of Wangford, Reydon Wood, 25 m, log of *Fraxinus excelsior*, on wood, 4.XI.2005, E. Batten (E.B. 4641, H.B. 7972, anam. substr.). – 6.3 km SW of Southwold, 2 km NW of Dunwich, Dunwich Forest, 20 m, log of *Acer pseudoplatanus*, on wood, 14.IX.2005, E. Batten (E.B. 4626, K(M) 227422, anam. substr., doc. vid.). – ibid., log of *Acer pseudoplatanus*, on wood, 1.XI.2005, E. Batten (E.B. 4639, K(M) 200526, H.B. 7973, anam. substr.). – 12.5 km SSW of Southwold, 2.5 km NE of Leiston, NW of Sizewell, Kenton Hills, 4 m, branch of *Betula*, on bark, 27.IV.2005, S.M. Francis (E.B. 4603, doc. vid.). – **Wales**, **Powys**, 7.5 km W of Rhayader, Craig Goch reservoir, 324 m, branch of *Ulex europaeus*, on wood, 27.IX.2017, J.P. Priou (wide, J.P.P. 17211, doc. vid.). — **DENMARK**: **Sjælland**, 5.5 km NW of Sorø, SE of Bromme, Lillesø, 35 m, branch of *Fagus sylvatica*, on wood & bark, 27.V.2007, T. Læssøe (ø). – 8 km NNW of Ringsted, 1 km S of Allindelille, Fredskov, 65 m, branches of *Fagus sylvatica*, on wood, 26.V.2007, J. Vesterholt, M. Nauta & B.M. Spooner (H.B. 8518, S). – 1 km SE of Allindelille, Fredskov, 68 m, branch of *Quercus*, on wood, 20.VI.2006, J.G.B. Nielsen (nar, J.N. 06-106, as *Corylus*). – Falster, 11 km WNW of Nørre Alslev, 4 km W of Vålse, Resle Skov, 14 m, branch of *Corylus avellana*, on wood, 10.VII.2006, J.G.B. Nielsen (J.N. 06-120). – ibid., 30.X.2006 (J.N. 06-232). — **NORWAY**: **Nord-Trøndelag**, 35 km SW of Børgefjell, 110 km ENE of Namsos, Røyrvik, near church, 430 m, stump of *Betula*, on bark, 29.VII.2010, P. Perz (H.B. 9404 ø). – **Aust-Agder**, 13 km NNE of Arendal, 3 km NNE of Brekka, Landbø, 95 m, on pores of *Ganoderma applanatum*, 28.IX.2008, T.H. Dahl (ø, doc. vid.). — **SWEDEN**: **Jämtland**, 60 km WSW of Saxnäs, 3 km SW of Leipikvattnet, Bjurälven, Lillälven waterfall, 500 m, branch of *Betula pubescens*, on bark, 27.VII.2010, T. Læssøe & J.H. Petersen (ø). – **Västerbotten**, 4.5 km SW of Saxnäs, Satsfjället, Pojken, 715 m, branch of *Betula pubescens*, on wood, 24.VII.2010, T. Læssøe (nar, H.B. 9362 ø). –3.3 km SE of Umeå, Gran, 15 m, log of ?*Salix*, on wood, 22.VI.2010, N. & Z. Lipovac (Lipovac 1009). – **Skåne**, Söderåsen, 3.2 km NW of Röstånga, 1.2 km W of Härsnäs, Härsnäsdammen, 145 m, log of *Betula*, on bark, 5.VI.2006, F. Baral-Weber (ø). – ibid., branch of (?)*Sorbus aucuparia*, on wood, 5.VI.2006, H.O. Baral (ø). — **FINLAND**: **Northern Ostrobothnia**, 46 km NNE of Kuusamo, 4 km NE of Laitila, Oulanka, Ampumavaara, ~230 m, log of *Betula*, on pileus of *Fomes fomentarius*, 13.VIII.1995, K. Põldmaa (H.B. 8730, TAAM 161686). – **Pirkanmaa**, 57 km NNE of Tampere, around Ruovesi, ~130 m, on bark of (?)*Betula* & on resupinate basidiomycete, 4.VIII.1859, P.A. Karsten (Karsten 5281, H-6003830, as *O. epipora*). – **Kanta-Häme**, ~1 km N of Tammela, Mustiala, and ~8 km NE of Tammela, lake Pehkijärvi (as Pähkijärvi), also ~1 km N of Tammela, Mustiala, ~110–120 m, indet. angiosperms (especially *Populus*), on bark and wood, IX.18[?67], P. Karsten (**syntypes** of *Peziza inflatula*, non vid., unlocated). – **Varsinais-Suomi**, 15 km SE of Somero, NE of Halkjärvi, 87 m, angiosperm stump, on pores of *Ganoderma applanatum*, 16.VIII.2019, S. Jakobsson (wide, doc. vid.). — **ESTONIA**: **Tartumaa**, 6 km NNW of Tartu, ~2 km ENE of Vorbuse, 40 m, log of *Corylus avellana*, on *Diatrypella favacea*, 25.VIII.1994, K. Põldmaa (TAAM 161189, H.B. 7997, anam. substr.). – 15.5 km E of Võnnu, 1.4 km NNE of Järvselja, Järvselja primeval forest, 47 m, log of *Betula*, on *Fomes fomentarius*, 2.IX.1994, K. Põldmaa (TAAM 161258, H.B. 7998). — **POLAND**: **Greater Poland**, 9 km WSW of Śrem, 2 km ENE of Rąbiń, Uroszysko Rąbiń, 103 m, branch of *Prunus serotina*, 25.VIII.2007, A. Kujawa & P. Perz (P.P. 20070825-3, doc. vid.). – **Lower Silesia**, 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, stump of *Pinus sylvestris*, on bark, 21.XI.2006, P. Perz (P.P. 20070820-2, H.B. 8605c ø). – **West Pomerania**, ~18 km SE of Szczecin, ~3 km NW of Kołowo, Puszcza Bukowa, ~120 m, branch of *Fagus sylvatica*, on *Cerioporus mollis*, 16.I.2010, G. Domian, vid. P. Perz (nar, P.P. 20100116, doc. vid.). — **CZECHIA**: **Central Bohemia**, 28 km NNE of Praha, Liblice, 190 m, branch of *Quercus*, on bark & old pyrenomycete, VII.1925, J. Velenovský (PRM 151694, **lectotype** of *Orbilia cyathea*, H.B. 6133 ø). – ~2.5 km NE of Mnichovice, Plecháč hill ESE of Klokočná, ~480 m, branch of *Quercus*, on bark, 4.IX.1941, J. Velenovský (PRM 152437, **holotype** of *Orbilia pyrifera*, H.B. 6267 ø). — **HUNGARY**: **Pest**, 24 km NNW of Budapest, 10 km NW of Pomáz, ~1 km NE of Pilisszentkereszt, Duna-Ipoly Nemzeti Park, 200 m, branch of *Quercus cerris*, on bark & old *Diatrype stigma*, 11.X.1999, L. Beenken (ø). — **SERBIA**: **Vojvodina**, Fruška Gora, 8 km SSE of Novi Sad, 2.7 km WSW of Bukovac, 255 m, branch of *Tilia platyphyllos*, on bark, 6.VI.2014, D. Savić (doc. vid.). – 22.5 km WSW of Novi Sad, 2.3 km SW of Grabovo, Ravne, 200 m, log of *T. platyphyllos*, on wood, 10.VI.2014, D. Savić (doc. vid.). — **MONTENEGRO**: 12.5 km SW of Plav, 1.7 km S of Vusanje, N of Prokletije Mt., 1065 m, branch of *Fagus sylvatica* subsp. *moesiaca*, on wood, 18.V.2014, O. Perić, vid. B. Perić (B.P. Dgf/C7D-18-05-14, doc. vid.). — **GERMANY**: **Mecklenburg-Vorpommern**, ~9.5 km SW of Demmin, near Schönfeld, ~33 m, branch of *Populus*, on wood, 6.IX.1984, D. Benkert (BHU). – 9 km SW of Rehna, 1.8 km NE of Dechow, Röggeliner See, 40 m, on bark of *Fraxinus excelsior*, 6.VIII.1993, T. Richter (T.R.). – 2.2 km SSE of Rehna, ENE of Nesow, Benziner Tannen, 35 m, on wood of *F. excelsior*, 22.VIII.1992, T. Richter (T.R.). – **Brandenburg**, 11.5 km SW of Potsdam, 1 km SW of Petzow, Glindower Tongruben, 47 m, branch of indet. angiosperm, on bark, 16.VI.1969, D. Benkert (BHU). – **Sachsen-Anhalt**, 29.5 km NNW of Magdeburg, 7.3 km NNW of Colbitz, Colbitzer Heide, 86 m, log of *Tilia*, on wood, 1.XI.2018, T. Richter (wide, doc. vid.). – 3 km NNE of Naumburg, NW of Hotel Henne, Keilholz, 160 m, branch of *Tilia cordata*, on bark, 30.VI.2007, W. Huth (nar, H.B. 8573 ø). – **Sachsen**, 8 km NNW of Chemnitz, ~1.5 km WSW of Auerswalde, Schützwald, 320 m, branch of *Populus tremula*, on bark & old pyrenomycete, 14.V.2006, B. Mühler (H.B. 8169a ø). – 6 km NNE of Chemnitz, 1 km W of Glösa, Kinderwaldstätte, 330 m, branch of *Tilia*, on bark, 5.VII.2008, B. Mühler (wide, H.B. 8885a). – ibid., branch of *Salix*, on wood, 5.VII.2008, B. Mühler (H.B. 8885b). – 7.5 km NE of Chemnitz, N of Niederwiesa, Auen-/Zapfenbachtal, 280 m, branch of *Alnus glutinosa*, on bark, 30.VI.2008, B. Mühler (wide, H.B. 8882a, nar H.B. 8882b). – 4.5 km NE of Chemnitz, N of Dresdner Straße, railway museum, 330 m, branch of *Sorbus aucuparia*, on wood & in *Corticiaceae*, 10.VII.2006, B. Mühler (H.B. 8221, anam. substr.). – ibid., branch of indet. tree, on bark & *Diatrypaceae*, 10.VII.2006, B. Mühler (H.B. 8222 ø). – 4 km ENE of Chemnitz, Zeisigwald, 360 m, branch of *Quercus*, on bark & old *Diatrype* ?*stigma*, 13.V.2006, B. Mühler (ø). – ibid., branch of *Tilia*, on bark, 29.VI.2009, B. Mühler (H.B. 9080; sq.: KY463698, KT222442). – 9 km ESE of Chemnitz, 2.5 km W of Erdmannsdorf, Edelmannsbachtal, 375 m, branch of *Fraxinus excelsior*, on bark, 23.VI.2010, B. Mühler (H.B. 9352 ø). – S of Erdmannsdorf, Zschopau river bank, 290 m, branch of *Salix*, on bark, 24.V.2010, B. Mühler (nar, ex H.B. 9328, M-0276411, **neotype**; sq.: KT222346). – 7.5 km SE of Chemnitz, E of Einsiedel, Fischzuchtgrund, 390 m, branch of *Acer*, on wood, 20.IV.2009, B. Mühler (nar, H.B. 9041a). – 4 km SW of Chemnitz, Morgenleite, 360 m, branch of *Corylus avellana*, on bark, 20.V.2009, B. Mühler (ø). – 9 km SE of Zwickau, 2 km WNW of Wildenfels, 370 m, branch of *Abies nordmanniana*, on bark, 3. XI.2015, B. Mühler (H.B. 9973b, anam. substr.). – **Thüringen**, 43 km N of Erfurt, ~2 km NW of Bad Frankenhausen, gorge near Kattenburg, 220 m, branch or log of *Fagus sylvatica*, on bark, 9.X.1973, D. Benkert (BHU). – 17 km WNW of Sonneberg, NNW of Weitesfeld, 525 m, branch of *F. sylvatica*, on wood, 20.V.2013, I. Wagner (ø, doc. vid.). – **Hessen**, 3 km WSW of Gießen, 1.5 km SSE of Heuchelheim, Silbersee, 160 m, branch of *Salix*, on wood, 18.VI.2014, W. Schößler, vid. I. Wagner (doc. vid.). – 3.5 km SE of Gießen, Schiffenberger Wald, 197 m, 18.III.2016, branch of ?*Salix*, on wood, W. Schößler, vid. I. Wagner (nar, doc. vid.). – ~17 km WSW of Darmstadt, ~3 km SW of Erfelden, Kühkopf, 87 m, branch of *Alnus glutinosa*, on wood & bark, 5.V.1991, J. Haedeke (H.B. 4418 ø). – **Rheinland-Pfalz**, 8 km SW of Koblenz, 1 km S of Winningen, Kondertal, 110 m, on indet. angiosperm, 9.V.1974, H.O. Baral (H.B. 21 ø). – **Baden-Württemberg**, 7 km E of Heidelberg, 1.5 km ESE of Ziegelhausen, Bärenbach, 175 m, branch of *Corylus avellana*, on wood, 24.X.2010, M. Bemmann (ø). – ~3.5 km S of Bad Mergentheim, 350 m, branch of *Fagus sylvatica*, on wood & bark, 20.IX.1974, H.O. Baral (H.B. 22, anam. substr.). – 3.5 km SW of Gaildorf, 1.5 km ESE of Fichtenberg, Rot, 340 m, branch of *Populus* × *canadensis*, on wood, 28.VII.1992, K. Siepe (K.S., doc. vid.). – 2 km WNW of **Stuttgart**, 1 km ENE of Botnang, Kräherwald, 370 m, branch of *Fraxinus excelsior*, on wood, 13.V.1975, H.O. Baral (H.B. 271 ø). – ~ibid., 360 m, branch of *Quercus*, on bark, 7.XI.1975, H.O. Baral (ø). – 5 km NW of Stuttgart, 1.8 km W of Feuerbach, Triebweg, 320 m, branch of *Fraxinus excelsior*, on wood, 23.IV. & 7.V.1975, H.O. Baral (nar, H.B. 1234a & b ø). – 1.4 km SE of Weilimdorf, Rainweg NW, 350 m, branch of *Acer*, on wood, 12.VII.1989, O. Baral (ø). – 3.2 km S of Weilimdorf, E of Solitude, Pfaffenwald, 450 m, branch of *Alnus glutinosa*, 9.VI.1975, H.O. Baral (H.B. 85 ø). – 6 km WSW of Stuttgart, 1.2 km NE of Büsnau, Schattenseen, 410 m, on wood of *Alnus*, 23.VI.1976, H.O. Baral (ø). – 2 km E of Leonberg, NE of Ramtel, Gerlinger Heide, 470 m, indet. substrate, 4.IX.1976, H.O. Baral (ø). – 3 km NW of Göppingen, SE of Wangen, Reutgarten, 390 m, indet. branch, 15.IX.2012, F. Schumm (nar, doc. vid.). – 6.5 km NW of **Tübingen**, 1.5 km E of Entringen, NE of Burg Hohenentringen, 510 m, on *Hypoxylon fragiforme*, 25.XI.1975, R. Agerer (R.A. 6843, H.B. 1412 ø). – 3.5 km NNW of Tübingen, 1.7 km NE of Hagelloch, W of Heuberger Tor, 490 m, indet. substrate, 24.V.1977, H.O. Baral (ø). – 3.5 km NNE of Tübingen, 1.6 km SE of Bebenhausen, Kirnbachtal, 370 m, on bark of *Fraxinus excelsior*, 16.XI.1976, H.O. Baral (ø). – 6.5 km NNE of Tübingen, 3.2 km NNW of Pfrondorf, SE of Eichenfirst, 490 m, on *Fagus sylvatica*, 30.V.1978, H.O. Baral (ø). – NE of Pfrondorf, Gähklinge, 400 m, branch of *Quercus*, on wood & bark, 26.VII.2001, H.O. Baral, P. Zinth & N. Matočec (ø). – E of Pfrondorf, Tiefenbach, 410 m, branch of *Tilia*, on bark, 3.IV.1990, H.O. Baral (ø). – ibid., 385 m, *Quercus* branch, on pores of *Trametes hirsuta*, 1.II.1995, H.O. Baral (ø). – ESE of Pfrondorf, Hinterpfand, 420 m, branch of *Fagus sylvatica*, on wood, 23.VII.2005, E. Weber (H.B. 7850 ø). – ibid., 5.XI.2005 (H.B. 7963a ø). – SE of Pfrondorf, Höhberg, 400 m, branch of *Carpinus betulus*, on bark & *Hypoxylon fragiforme*, 14.III.2008, H.O. Baral (nar, ø). – S of Pfrondorf, Obere Mähder, 390 m, branch of *Malus domestica*, on wood, 23.X.2005, E. Weber (H.B. 7944 ø, anam. substr.). – **Schwarzwald**, 2 km SSE of Triberg, Geutsche, 930 m, branch of ?*Sorbus aucuparia*, on wood, 30.VIII.2014, S. Baireuther (H.B. 9915; sq.: KY419193). – 2 km SW of Schwenningen, ENE of Zollhaus, Kugelmoos, 710 m, branch of *Salix*, on wood, 26.VII.1988, H.O. Baral & G. Marson (ø). – 3.5 km WNW of Villingen, SW of Bahnhof Kirnach, Kapf, 750 m, branch of *Carpinus betulus*, on wood, 19.VIII.2005, E. Weber (H.B. 7879 ø, anam. substr.). – 19 km S of Freiburg, ~4.5 km SE of Münstertal, Belchen, ~1100 m, branch of *Fagus sylvatica*, on wood, 7.VI.1976, H.O. Baral (ø). – **Bodensee**, ~4.5 km NNE of Radolfzell, ~SE of Stahringen, Bodanrück, 500 m, branch of *F. sylvatica*, on wood, 27.VII.1975, H.O. Baral (ø). – **Bayern**, **Unterfranken**, 15 km SE of Schweinfurt, 1 km S of Alitzheim, Hörnauwald, 230 m, log of *Tilia*, on wood, 12.XI.1995, G. Wolf, L.G. Krieglsteiner & H.O. Baral (ø). – ibid., branch of *Betula*, on bark, 12.XI.1995, G. Wolf, L.G. Krieglsteiner & H.O. Baral (ø). – **Oberfranken**, 11 km ESE of Lichtenfels, 3 km SW of Burgkunstadt, Külmitzberg, 430 m, on *Schizopora paradoxa*, 5.VIII.1989, B. Hanff (B.H. 11719). – 21 km W of Bayreuth, 2.8 km NW of Hollfeld, ESE of Freienfels, Lindenallee, 430 m, branch of *Tilia*, on wood, 12.X.2000, W. Beyer (ø). – **Oberpfalz**, ~20 km ESE of Regensburg, Pfatter, 330 m, branch of ?*Salix*, on wood, 25.VIII.1918, S. Killermann (M, as *Helotium* ?*subtrabinellum*, *Alnus*; mixture with *Calycina* aff. *parilis* on *Ulmus*). – **Schwaben**, 3 km W of Günzburg, ~1.5 km NE of Leipheim, forest along Donau river, 460 m, indet. substrate, 14.VI.1979, M. Enderle (ø). – **Niederbayern**, 12 km SE of Zwiesel, 4.5 km NNE of Spiegelau, Lärchenberg, south-slope of Rachel, 890 m, branch of *Fagus sylvatica*, on bark & old *Hypoxylon fragiforme*, 19.VI.1989, N. Luschka (REG). – ibid., 910 m, on pores of *Ganoderma applanatum*, 25.V.1990, N. Luschka 1658 (M). – 3.5 km NNE of Spiegelau, Recherau, 824 m, branch of *Alnus*, on bark & *Menispora glauca* (= *Zignoella ovoidea*), 25.V.1989, N. Luschka (REG 304). – **Oberbayern**, 10.5 km ENE of München, Aschheim, fire brigade, 512 m, log of *Prunus avium*, on bark, 23.III.2019, B. Fellmann (nar, doc. vid.). – 4 km NE of Starnberg, 1 km SE of Leutstetten, Sonnenberg, 610 m, log of *Fagus*, on bark, mainly on *Cyathus striatus*, 13.VI.1999, L. Beenken (nar, H.B. 6391). – ~5 km SW of Starnberg, ~1 km SW of Maising, Maisinger See, 638 m, on bark of *Quercus*, 20.II.1976, A. Einhelliger (M, as *O. auricolor*). – ~9 km SW of Starnberg, forest W of Aschering, ~700 m, branch of ?*Acer*, on bark, VIII.1961, J. Poelt (M). – 8 km NW of Tutzing, 3.5 km S of Andechs, Goaslweide, 720 m, branch of *Fagus sylvatica*, on wood, 13.IV.2001, P. Karasch (P.K. G/20-01). – ibid., branch of *F. sylvatica*, on wood, 8.V.2004, P. Karasch (ø). – 8.5 km WSW of Weilheim, ~2.5 km S of Forst, Sinkgraben, branch of *F. sylvatica*, on old *Hypoxylon*, 17.V.1964, J. Poelt (M). – 24 km NNE of Garmisch-Partenkirchen, 4 km E of Murnau, S of Guglhör, Loisachtal, branch of indet. angiosperm, on bark, 3.VII.1960, J. Poelt (M, as '*Orbilia luteorubella*'). – 22 km S of Isny, 7.5 km SE of Oberstaufen, Hochgrat, 'in einem Tobel', 1400 m, stump of *Alnus*, on bark, VII.1881, M. Britzelmayr (Rehm Ascom. 621, Karsten 4846, M, H-7023174, as ?*Calloria luteorubella*). – 5.5 km NNW of Bad Reichenhall, 1 km SW of Aufham, Aufhamer Wald, 620 m, on pores of *Fomes fomentarius*, 30.IV.2005, I. Rößl (nar, H.B. 7758, anam. substr.). — **AUSTRIA**: **Salzburg**, 30 km E of Salzburg, 3.7 km N of St. Wolfgang, E of Schafberg, north-slope of Spinnerin, 1435 m, log of *Fagus sylvatica*, on wood, 31.VII.2004, R. Türk (R.Tü. 34808, H.B. 7623 ø, anam. substr.). – **Niederösterreich** (incl. Wien), ~10 km W of Wien, [~1.5 km N of Hadersdorf], Kolbeter Mt., ?350 m, branch of *Fraxinus excelsior*, on wood & bark, 1907, F. v. Höhnel (herb. Höhnel A 4947, M, as *Orbilia luteorubella*). – 21 km SW of Wien, 1.2 km W of Gaaden, Schlößlwald, Dürnbach, 348 m, log of *Alnus glutinosa*, on wood & old pyrenomycete, 10.IV.2012, M. Mann (nar, ø, doc. vid.). – 18 km SSW of Wien, S of Hinterbrühl, Stephanieweg, 290 m, branch of indet. angiosperm, on bark, 28.II.2016, M. Mann (nar, M.M. 160228-5, doc. vid.). – **Steiermark**, 22 km SSE of Graz, ~1 km S of Wildon, Buchkogel, ~500 m, indet. angiosperm, on wood, 18.IX.1996, W. Maurer, vid. G. Friebes (W.M., doc. vid., anam. substr.). – 41 km S of Graz, 1.8 km W of Kitzeck im Sausal, E of Höch, Demmerkogel, 640 m, branch of *Quercus*, on wood, 15.VI.2011, R. Burkard (ø, doc. vid.). – 50 km SSW of Graz, ~4 km SW of Eibiswald, Radlpassstraße, ~450 m, indet. angiosperm, on bark, 16.IX.1996, W. Jaklitsch & W. Maurer, vid. G. Friebes (W.M., doc. vid.). – 11 km NNW of Bruck a. d. Mur, 2 km SSW of Thörl, Strohsitzgraben, ?1150 m, on bark of indet. angiosperm, undated, W. Maurer (W.M., doc. vid.). – **Kärnten**, 12.5 km SE of Klagenfurt, N of St. Margareten im Rosental, 583 m, branch of indet. angiosperm, on wood & *Diatrype stigma*, 2.VII.1994, W. Jaklitsch (ø). – NNE of St. Margareten, Lexe Vrt, 590 m, stump of *Pyrus communis*, on bark, 18.X.1994, W. Jaklitsch (ø). – **Tirol**, ~26 km WNW of Innsbruck, ~3.3 km N of Telfs, ~2 km S of Hohe Munde, ~1400 m, of indet. angiosperm, on bark, 1.VII.1977, H. Neubert (H.B. 2089, anam. substr.). — **SWITZERLAND**: **Schaffhausen**, 7 km NE of Schaffhausen, 1 km ENE of Thayngen, Flüheweg, 530 m, branch of *Corylus avellana*, on wood, 11.I.1991, P. Blank & H.O. Baral (nar, P.B. 1010, H.B. 9436 ø). – **Nidwalden**, 8 km SSW of Luzern, 2.5 km WSW of Hergiswil, NW of Renggeli, Mülibach, 960 m, branch of *Fagus sylvatica*, on wood, 16.VIII.2006, H.O. Baral (H.B. 8241a, anam. substr.). – ibid., branch of *Fraxinus excelsior*, on wood, 16.VIII.2006, V. Baral (nar, H.B. 8242 ø). – E of Renggeli, 820 m, branch of *Betula*, on bark & *Jackrogersella multiformis*, 30.V.1985, H.O. Baral (ø). – 1 km NW of Hergiswil, Bruustried, 600 m, branch of *Tilia platyphyllos*, on wood, 22.VIII.2006, U. Graf & H.O. Baral (H.B. 8279b, anam. substr.; sq.: KT222375). – **Uri**, 9.7 km ESE of Altdorf, 1.7 km SSW of Unterschächen, N of Sittlisalp, 1620 m, branch of *Alnus alnobetula*, on wood, 21.VIII.2006, H.O. Baral (ø). – **Jura**, 13 km NW of Biel, 1.5 km SE of Tramelan, 1035 m, trunk of *Sorbus aria*, on bark, 17.VI.2018, H.O. Baral (wide, H.B. 10162 ø). — **NETHERLANDS**: **Noord-Brabant**, 1 km W of Boxmeer, Brestbos, 18 m, branch of *Quercus*, on wood, 13.X.2007, S. Helleman (ø, doc. vid.). — **BELGIUM**: **Vlaanderen**, **West-Vlaanderen**, 12 km SSE of Brugge, 6 km NNE of Wingene, Eenndekooien, 30 m, on *Hypoxylon fragiforme*, 21.III.2007, B. Declercq (B.D. 07/021, doc. vid.). – **Wallonie**, **Hainaut**, 20.5 km N of Mons, 1.6 km SE of Silly, 90 m, bark of *Fagus sylvatica*, on pyrenomycete, 25.IV.1994, B. Declercq (B.D. 94/044, doc. vid.). — **LUXEMBOURG**: **L'Oesling**, **Diekirch**, 3.3 km NNW of Diekirch, 2.2 km W of Tomm, NE of Fridhaff, Hooldaer, 365 m, log of *Fagus sylvatica*, on bark, 23.IV.1995, A. Müller (ø). – 9.5 km NE of Mersch, 2 km NW of Medernach, Seitert, 330 m, branch of indet. angiosperm, on wood, 24.IV.1994, M.T. Tholl (ø). – **Gutland**, **Echternach**, 7.5 km W of Echternach, 3.3 km SW of Berdorf, NNE of Müllerthal, Schnellert, 230 m, log of indet. tree, on bark, 28.IV.1994, E. Weber (ø, doc. vid.). – **Mersch**, 4.3 km S of Larochette, 1.2 km N of Koedange, Mäschpesch, 300 m, branch of *Populus* (?)× *canadensis*, on bark, 25.IV.1994, H.O. Baral, G. Marson & B. Declercq (nar, H.B. 5066). – **Esch-sur-Alzette**, ~7.5 km SW of Luxembourg, Leudelange, unlocalized, ~330 m, branch of *Fagus sylvatica*, on wood, 2.VI.1985, P. Collin (nar, H.B. 8166). – 9 km WNW of Esch-sur-Alzette, 2 km W of Differdange, Tillebierg, 412 m, branch of ?*Salix*, on wood, 5.V.1999, H.O. Baral (ø). – 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, branches of *Prunus spinosa*, on bark, 11.IV.1992, H.O. Baral, E. Weber & G. Marson (ø). – ibid., 13.III.1993, G. Marson (G.M. 4959). – ibid., 23.V.1993, G. Marson (nar, H.B. 4885a, G.M. 4989). – **Grevenmacher**, 3.5 km N of Grevenmacher, 1.5 km E of Manternach, valley of Syre, Kaleberg, 190 m, branch of *Fraxinus excelsior*, on bark, 4.V.2000, C. Lechat & H.O. Baral (ø). – 3.8 km NNE of Grevenmacher, 1.8 km NW of Mertert, Schlaufiels, 180 m, branch of *F. excelsior*, on *Diatrype* ?*stigma*, 24.IV.1995, A. Müller (ø). – ~3 km NNW of Grevenmacher, Manternach, unlocalized, ?220 m, log of *Sorbus aria*, on bark, 30.VI.1900, V. Noppeney, vid. J. Feltgen (LUX 42464, as *O. xanthostigma*, immature). — **FRANCE**: **Haute-Normandie**, **Eure**, 18 km SSE of Rouen, 1.8 km SSW of Pont-de-l'Arche, Forêt de Bord, 54 m, branch of *Picea abies*, on bark, 25.III.2000, A. Delannoy (H.B. 6614 ø). – **Bretagne**, **Morbihan**, 5 km W of La Gacilly, 1 km WNW of St. -André, 85 m, branch of *Malus* *domestica*, on bark, 29.I.2012, J.P. Priou (J.P.P. 12027, as *H. japonica*, doc. vid.). – 1 km WNW of La Gacilly, La Glouzie, 45 m, branch of *Ilex aquifolium*, on bark & wood, 11.VI.2003, J.P. Priou (nar, H.B. 7390). – 1 km SE of La Gacilly, 2 km NW of Cournon, Les Tablettes, 50 m, branch of *Cytisus scoparius*, on wood, 9. IV.2001, J.P. Priou (J.P.P. 21074). – 4 km SE of La Gacilly, 1.2 km ESE of Cournon, S of La Buissonaie, 73 m, branch of *Frangula alnus*, on bark, 9. II.2003, J.P. Priou (ø, non vid.). – 2.5 km SSE of La Gacilly, 2 km NNE of Glénac, Pré Naval, 8 m, branch of *Ulex europaeus*, on wood, 21.XI.2001, J.P. Priou (ø, non vid.). – 12 km S of Auray, 1.5 km SW of Locmariaquer, SE of St.-Pierre Lopérec, Breneguy, 2 m, branch of *Ulex europaeus*, on bark, 31.III.2000, J.P. Priou (H.B. 6618a, anam. substr.). – 15 km SE of Quiberon, Île d'Houat, SW of Houat, 25 m, branch of *U. europaeus*, on bark & mycelium of *Chaetosphaeria phaeostroma*, 19.V.2000, J.P. Priou (J.P.P. 20153). – **Ille-et-Vilaine**, parc de Fougeray (probably Grand-Fougeray, 28 km ENE of Redon, 50 m), branch of indet. tree, on bark, 15.IX.1937, R. Meslin (herb. Grelet, PC, as *Hyalinia rectispora*). – **Pays-de-la-Loire**, **Maine-et-Loire**, ~40 km E of Angers, ~6 km ESE of Bauge, Forêt de Chandelais, 90 m, on *Hypoxylon* (?)*fragiforme*, 13.X.1985, R. Péan (J.M. 85106A). – ~24 km ENE of Nantes, St.-Sauveur-de-Landemont, Vallée de la Divatte, ~50 m, log of *Quercus*, on wood, 16.V.1993, T.R. Lohmeyer (ø). – **Vendée**, 21 km SSW of La Roche-sur-Yon, 2.3 km NNW of Avrillé, Bois de la Garde, 35 m, branch of *Quercus robur*, on bark, 5.VI.2003, V. Baral (ø). – 33 km NW of La Rochelle, 1.5 km NW of La Tranche sur Mer, NE of La Savinière, 4 m, branch of *Fraxinus excelsior*, on wood & bark, 3.VI.2003, G. Ouvrard (nar, H.B. 7360). – **Poitou-Charentes**, **Charente-Maritime**, 25 km SSE of Niort, 2.5 km ESE of la Villedieu, Forêt d'Aulnay, 115 m, branch of *Fagus sylvatica*, on wood, 28.IV.2006, H.O. Baral (nar, H.B. 8173 ø, anam. substr.). – Île de Ré, 2 km SE of St.-Martin-de-Ré, 1.8 km W of La Flotte, Les Maraises, 19 m, branch of *Quercus ilex*, on bark, 26.IV.2006, C. Lechat (H.B. 8140). – 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, branch of *Q. ilex*, on bark & *Diatrype* ?*stigma*, 26.IV.2006, P. Tanchaud (nar, H.B. 8150, anam. apoth., anam. substr.). – ibid., branches of *Quercus ilex*, on bark, 16.IV.2008, A. Brissard (ø). – ibid., branch of *Populus*, on wood, 28. IV.2011, R. Pacaud (nar, ø). – **Deux-Sèvres**, 17 km SSE of Niort, 3 km N of Villiers-en-Bois, Forêt de Chizé, Les Essarts, 85 m, branch of *Cornus sanguinea*, on wood, 14.IV.2008, P. Tanchaud (ø). – ibid., 90 m, branch of *Abies alba*, on wood, 20.III.2007, M. Hairaud (nar, ø, doc. vid.). – 3 km E of Villiers en Chizé, Forêt de Chizé, SE of Puymardier, 78 m, branch of *Acer campestre*, on bark, 24.IV.2006, H.O. Baral (nar, H.B. 8127). – 14.5 km WSW of Niort, 1.5 km NNW of Amuré, Marais Poitevin, Port Goron, 5 m, branch of *Fraxinus excelsior*, on bark & wood, 26.IV.2011, E. Weber (ø). – **Vienne**, ~2 km NE of Civray, Savigné, ~120 m, board/plank of *Quercus*, on wood, 15.VI.1914, L.J. Grelet (PC, herb. Grelet, as *Hyalinia rectispora* var. *majuscula*, H.B. 7745 ø). – ibid., branch of *Pinus*, on bark, VII.1925, L.J. Grelet (PC, herb. Grelet, **lectotype** of *H. rectispora* var. *majuscula*, H.B. 7746 ø, anam. substr.). – **Lorraine**, **Vosges**, 4.5 km SE of Gérardmer, Auberge de Grouvelin, NE of Roche des Bioquets, 1025 m, branch of *Fagus sylvatica*, on bark & old ?*Diatrypella*, 20.VI.1993, J. Deny (ø). – 5.5 km E of Gérardmer, 1.7 km SE of Xonrupt-Longemer, Lac de Longemer, 740 m, branch of indet. angiosperm, on bark, 9.IX.1998, J. Deny (ø). – **Alsace**, **Haut-Rhin**, 13 km ENE of Gérardmer, 3.5 km NE of Col de la Schlucht, Tourbière du Tanet, 1225 m, branch of indet. angiosperm, on wood, 23.VI.1993, J. Deny (H.B. 4908a). – branch of *Fagus sylvatica*, on wood, 3.IX.1996, H.O. Baral (ø). – **Franche-Comté**, **Jura**, ~50 km SSW of Besançon, Poligny, ?400 m, branch of *Fraxinus excelsior*, on wood, VII.1882, N. Patouillard (PC 0088499, **syntype** of *Peziza translucens*, H.B. 7750 ø). – **Doubs**, 4.7 km ESE of Besançon, 1.4 km SE of Morre, marais de Saône, 388 m, on wood of indet. tree, 21.VI.2012, G. Moyne (ø) – **Bourgogne**, **Côte-d'Or**, 24 km NE of Dijon, N of Bèze, Les Combottes, 225 m, branch of *Euonymus europaeus*, on wood, 29.X.2009, J.P. Priou (ø, J.P.P. 29206b, doc. vid.). – 33 km NE of Dijon, NW of Fontaine-Française, Étang Pagosse, 230 m, on wood of *Populus*, 26.X.2009, J.P. Priou (J.P.P. 29204, doc. vid.). – **Auvergne**, **Cantal**, 9 km S of St.-Flour, 1.3 km SSE of Alleuze, Bois de la Bastide, 855 m, on wood of *Abies alba*, 8.IX.2009, J.P. Priou & G. Girod (J.P.P. 29173, non vid.). – **Rhône-Alpes**, **Loire**, 16 km W of Boën, 3.7 km S of St.-Jean-la-Vêtre, La Iverneaux, 1095 m, branch of *Sorbus* ?*aucuparia*, on wood, 4.V.2010, B. Declercq (ø). – **Haute-Savoie**, ~11 km SSW of Annecy, Viuz-la-Chiésaz, ?700 m, branch of *Fagus sylvatica*, on wood & pores of *Trametes versicolor*, VIII.1927, A.É. de Crozals (PC, herb. Grelet, as *Hyalinia rectispora*). – **Auvergne**, **Puy-de-Dôme**, 2.4 km ESE of Chastreix, 1198 m, branch of *Fagus sylvatica*, on wood, 30.IX.2016, J.P. Priou (J.P.P. 16208, doc. vid.). – **Languedoc-Roussillon**, **Aude**, 4.5 km ESE of Quérigut, Forêt du Carcanet, 1390 m, branch of *Corylus avellana*, on bark, 22.IX.2016, R. Pacaud, vid. J.P. Priou (J.P.P. 16201, doc. vid.). — **SPAIN**: **Asturias**, 3.2 km N of Pola de Somiedo, 1.4 km S of Castro, 770 m, branch of *Rosa*, on bark and old *Eutypa* ?*lata*, 6.VI.2013, H. Lotz-Winter (H.L.W. 20130606-1). – **País Vasco**, **Álava**, 25 km SE of Vitoria, Urturi, 800 m, on wood of *Salix* ?*atrocinerea*, 23.III.2003, C.E. Hermosilla (ø, doc. vid.). – **Navarra**, 37 km N of Pamplona, 1.5 km N of Oronoz, 195 m, branch of *Fagus sylvatica*, on wood, 26.V.2012, I. Olariaga (wide, doc. vid., anam. substr.). – 31 km N of Pamplona, 0.9 km E of Almándoz, Regata de Marin, 340 m, branch of ?*Salix*, on bark, 4.IV.2015, F.J. Balda (nar, F.J.B., doc. vid.). – **Aragón**, **Huesca**, 55 km NNW of Huesca, 3 km SW of Javierregay, 660 m, wood of *Quercus*, 4.VI.2014, R. Blasco (doc. vid.). – 70 km NE of Huesca, 1 km W of Revilla, 1275 m, branch of *Pinus sylvestris*, on wood, 3.V.2014, M.A. Ribes (nar, M.A.R. 030514 176, doc. vid.). – **Zaragoza**, 29.5 km SW of Catalayud, 1.9 km NNE of Calmarza, 807 m, branch of *Juglans regia*, on wood, 31.III.2018, R. Blasco (wide, anam. substr., doc. vid.). – **Madrid**, 5.7 km ENE of Guadarrama, 1.5 km SSE of Collado Mediano, Las Canalejas, 1005 m, log of *Ulmus minor*, on bark, 25.I.2004, F. Prieto (AH 7588). – 20 km WSW of Madrid, W of Villaviciosa de Odón, 600 m, branch of *U. minor*, on wood, 19.III.2002, F. Prieto (nar, AH 7430, as *Populus nigra*, H.B. 7112, anam. substr.; sq.: KT222376). – **Castilla-La Mancha**, **Guadalajara**, ~22 km ENE of Guadalajara, near Archilla, ~800 m, on wood of *Populus alba*, 4.VII.1992, A. Castillo (ø, AH 6744). – **Andalucía**, **Granada**, 17.5 km ESE of Granada, 3.5 km SE of Güéjar Sierra, Fuente Agrilla, 1230 m, on bark of *Castanea sativa*, 10.III.1982, M. Jiménez & R. Galán (AH 6335). – **Cádiz**, 16 km NW of Algeciras, 9.5 km NW of Los Barrios, 88 m, branch of *Fraxinus*, on bark & wood, 5.XI.1991, A. Raitviir & R. Galán (AH 6795). – **Jaén**, 75 km NNE of Jaén, 7 km NNE of Santa Elena, Sierra Morena, Barranco de Valdeazores, 790 m, on bark of *Quercus*, 28.XI.1984, A. Ortega & A. García Buendía (AH 6487). — **PORTUGAL**: **Guarda**, Beira Interior Norte, Sistema Central, Serra da Estrela, 37 km WSW of Guarda, 4 km ESE of Seia, 1100 m, on bark of *Castanea sativa*, VII.1982, R. Galán (AH 6053). — **MACARONESIA**: **Madeira**, ~7 km SW of Punta Delgada, S of Rosário, campground at km 14.5, ~450 m, branch of indet. tree, on bark, 15.I.1977, R.P. Korf, R. Fogel, G.L. Hennebert & L.M.Kohn (CUP-MM 1537, as *O. epipora*, in Korf 1992 erroneously as MM 1145). – 2.8 km WSW of Seixal, Fanal, 1190 m, branch of *Ocotea foetens*, on wood, 24.IX.2015 (J.P.P. 15167, doc. vid.). – **Canary Islands**, **Tenerife**, Santa Cruz de Tenerife, Anaga, 2.3 km SW of Taganana, NE of Casa Forestal, 825 m, branch of indet. angiosperm, on bark, 18.IV.1989, E. Weber (REG 291). — **UKRAINE**: **Ivano-Frankivsk**, Nadvirna, 55 km W of Kolomyya, 5 km SE of Maksymets, Gorgany forestry, 1020 m, branch of *Fagus sylvatica*, on bark, 18.VII.2012, A.Y. Akulov (ex CWU Myc 4907, H.B. 9719). – 51 km WSW of Kolomyya, 9.5 km NW of Palyanytsya, Chernigivske forestry, southwest-flank of Dovbushanka Mt., 1350 m, log of *Acer*, on wood, 22.VII.2012, A.Y. Akulov (ex CWU Myc 4908, H.B. 9732). — **RUSSIA (West)**: **Adygea**, Caucasus Mts., ~62 km NE of Sochi, NNE of Guzeripl, Kisha river, ~600 m, branch of *Fagus orientalis*, on bark, 10.IX.1975, M. Pallo (TAAM 63888, H.B. 7996 ø). — **RUSSIA (East)**: **Altay**, **Turochak**, near Kamga cordon, ~8.5 km ENE of Yaylyu, mouth of Malyj Miokok river N of Lake Telezkoje, 450 m, on *Daldinia*, 17.VIII.2008, E.S. Popov (LE 294843, doc. vid.). — **CHINA**: **Xinjiang**, **Xinyuan**, Tian Shan Mts., Nalati grasslands, 1600 m, on wood of *Betula* sp., 15.VIII.2003, B. Liu & X.Z. Liu (B.L. 6564, HMAS 139536; sq.: DQ656660, doc. vid.). – **Tibet**, **Nyingchi** (Linzhi), 36 km ESE of Bomê (Bomi), 1.3 km ENE of Songzong, 3100 m, indet. tree, on wood, B. Liu & X.Z. Liu, 16.VII.2004 (B.L. X034, HMAS 96789; sq.: DQ656661, doc. vid.). – ~90 km W of Bomê, Lulangzhen, 3200 m, on indet. bark, 17.VII.2004, B. Liu & X.Z. Liu (B.L. X076, HMAS 96788; sq.: DQ656659, non vid.). – For further 110 collections across China see Liu (2006). — **AUSTRALIA**: **Queensland**, Wet Tropics, 43 km N of Port Douglas, S of Cape Tribulation, Myall Beach Walk, 5 m, leaflets of *Licuala ramsayi*, 30.VIII.2006, G. Marson (nar, H.B. 8496a). – 7 km S of Port Douglas, SSE of Craiglie, 10 m, branch of *Acacia*, on wood, 31. VIII.2006, G. Marson (nar, H.B. 8406). – **Victoria**, South Eastern Highlands, 160 km SW of Melbourne, 9 km WNW of Marengo, Maits Rest, 270 m, on indet. tree, 28.XII.1963, G. Beaton (Beaton 176, Spooner 1987: 177 fig. 23, doc. vid.). — **PUERTO RICO**, El Yunque, ~6 km SW of Luquillo, El Verde, along Rte. 988, ~150 m, branch of indet. angiosperm, on bark, 17.I.1996, D.H. Pfister & F.A. Harrington (nar, PR 23, FH 00458176, H.B. 5967 ø). – ibid., ~7 km S of Rio Grande, Guzman Obajo, Camino Los Tapia, ~450 m, branch of indet. angiosperm, on bark, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (nar, PR 103, FH 00458346, H.B. 5956). — **UNLOCALIZED**: on ?bark of indet. tree, undated, C.H. Persoon (H.B. 8840, L 910.261-266, as *Peziza aurea*).

Not included. **FRANCE**: **Aquitaine**, **Gironde**, Bordeaux, unlocalized, ?30 m, branch of indet. angiosperm, on bark, 25.VI.1884, L. Forquignon (UPS:BOT:F-015651, authentic material of *Cistella succinea*, H.B. 7335 ø). — **LUXEMBOURG**: **Gutland**, **Luxembourg**, 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, branch of *Quercus*, on wood, 5.XI.2000, G. Marson (H.B. 6819, anam. substr.). — **GERMANY**: **Sachsen**, 6 km NW of Leipzig, 1 km SW of Wahren, Burgaue, 120 m, branch of *Quercus robur*, on bark, 22.IV.2003, M. Unterseher (nar, grown in moist chamber, LZ, H.B. 7408). – Brandenburg, Tamsel, Berganlagen, on rotten wood, VIII.1904, P. Vogel (n. 1712; **holotype** of *O. breviasca*). — **CZECHIA**: **Central Bohemia**, 27 km SE of Praha, Mnichovice, ~370 m, branch of *Betula*, on wood, IV.1928, J. Velenovský (PRM 152443, **lectotype** of *O. linata*, H.B. 6190 ø). — **CANADA**: **Ontario**, Ottawa, on indet. angiosperm wood, 23.VI.2018, J. Mack (anam. substr., doc. vid., with *Niesslia* parasite). — **USA**: **Maryland**, near Beltsville, indet. plant material, undated, C. Drechsler (**holotype** of *Dactylella passalopaga*, doc. vid.). – **South Carolina**, Santee River (possibly around Columbia), ~40 m, on pores of *Polyporus*, undated, H.W. Ravenel (wide, herb. Ravenel 1571, K(M) 126131, **lectotype** of *Peziza vulgaris* var. *myceticola*, H.B. 7608 ø). — **VENEZUELA**: **Anzoátegui**, ~135 km WSW of Ciudad Bolivar, Mapire, Orinoco river, ~50 m, branch of indet. ?angiosperm, on bark, V.1887, A. Gaillard (PC, herb. Gaillard No. 5, as *Orbilia* (?)*lancicula*, H.B. 7727 ø). — **INDONESIA**: **Java**, **West Java**, 43 km S of Jakarta, centre of Bogor (Buitenzorg), Botanical Gardens, 260 m, branch of indet. angiosperm, on wood, 2.I.1897, A.J.O. Penzig (W 6467, **lectotype** of *Orbilia sinuosa*, H.B. 7730 ø). — **AUSTRALIA**: **Queensland**, South Eastern Queensland, ~11 km WSW of Brisbane, Brookfield, ~80 m, on wood of indet. tree, 28.VIII.1981, B.C. Sutton & J.L. Alcorn (IMI 263330, Spooner 1987: 178, non vid.).

Hyalorbilia japonica Baral, M.L. Wu & Y.C. Su, **sp. nov.**, MB813470 — Pls 83–85, Map 8

?= *Orbilia epipora* subsp. *major* Speg., An. Soc. Cient. Argent. 12: 223, n. 225 (1881)

≡ *Orbilia major* (Speg.) Mussat, in Sacc., Syll. fung. 15: 233 (1901), nom. inval., ICN Art. 36.1a, b (cited as synonym of *O. epipora*)

Etymology: *japonica*: named after the origin of the holotype specimen, Japan; *major*: based on the rather large apothecia.

Typification: Japan, Suzaka, branch of indet. angiosperm, 24.VIII.1997, W. Gams (ex H.B. 5906, M-0276412, holotype of ***Hyalorbilia japonica***). — Argentina, Buenos Aires, San Benito de Palermo, IV.1880, log of *Populus nigra* '*italica*', C.L. Spegazzini (holotype of ***Orbilia epipora* subsp. *major***, unlocated).

Misapplied name: Liu (2006: 35 p.p.), as *H. inflatula*.

Latin diagnosis: *Differt ab* Hyalorbilia inflatula *ascis et ascosporis minoribus, ab* H. oreadum *sporis angustioribus.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–2.5 mm diam., 0.1–0.22(–0.3) mm high (receptacle 0.06–0.11 → 0.04–0.05 mm), whitish or (very) pale to light chlorinaceous to yellowish or cream(-ochraceous), ± strongly translucent (hygrophanous), round, margin smooth to finely rough, sometimes strongly undulating to lobate with age, slightly gelatinous, scattered to ± gregarious; disc medium concave (cyathiform) to flat, sometimes slightly convex, margin thin, not or slightly protruding, smooth; broadly appressed to substrate or with obconical to abrupt stipe 0.05–0.18 × 0.1–0.18 mm, superficial; dry with inrolled margin, light yellow-ochraceous to buff, old light fox-brown, without or with a distinct white subiculum. **Asci** *(15–)17.5–24(–27) × (3–)3.5–4.5(–5) µm {3}, †(11–)14–20(–22) × (2.8–)3–3.5(–3.8) µm {14}, 8-spored, spores *4-seriate in two superimposed bundles, (†) often irregularly arranged, pars sporifera *10–12 µm long, †9–12 µm; **apex** (†) hemispherical (to slightly truncate); **base** ± unstalked, arising from croziers {9}. **Ascospores** *(3.5–)4.5–6(–6.5) × 0.8–1.1(–1.2) µm {3}, †(3.5–)3.8–5.7(–6) × (0.6–)0.7–0.9(–1) µm {14}, cylindric or sometimes slightly fusoid, sometimes very slightly heteropolar, rounded to obtuse, straight to (very) slightly curved (never distinctly helicoid); **SBs** 0.2–0.5 µm diam. {4}, globose, 1–2 at each end; with 1–3 minute LBs. **Paraphyses** apically uninflated or slightly (rarely medium) capitate, terminal cells *2–3.5 µm wide {1}, †12–16(–23) × (1.5–)1.8–3(–4.2) µm {4}, lower cells †3.3–5 × 1.6–2.3 µm wide. **Medullary excipulum** overall 5–15(–30) µm thick, scarcely to often strongly gelatinized, sharply delimited at least at flanks. **Ectal excipulum** at base of not or slightly (rarely medium) gelatinized, 60–100(–200) µm thick textura angularis-prismatica, cells at base †(10–)15–30(–45) × (5–)10–20(–35) µm {3}, common walls 0.3–0.4 or 0.5–2 µm thick, at lower flanks 50–80 µm thick, of t. prismatica(-porrecta), cells *23–42 × 8–18.5 µm {2}, †7–22 × 5–18 {2} or 20–37(–45) × (6–)10–19(–25) {3} µm, rarely up to †62 µm long {1}; 7–12 µm thick near margin, marginal cortical cells *8–11 × 6–8.5 µm {1}, †(4–)6–12(–15) × (2–)3–6.5 {8} or × 5–10.5 {3} µm, not or slightly gelatinized (wall 0.2–1 µm thick). **Anchoring hyphae** abundant, †(2–)3–6 µm wide, at insertion 5.5–7.5 µm, walls (0.2–)0.3–0.8(–1)((–1.5)) µm thick {9}. **VBs** in terminal cells of paraphyses pale yellowish, elongate. **Exudate** 0.2–0.3 µm thick, continuous, finely rough to granular, pale yellowish. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate {3}). **Conidiophores** not observed. **Conidia** fusoid to fusiform, straight, *36–41 × 5.5–6 µm {1}, †48–51 × 3.5–4.8 µm {2}, 5–7-septate.

Habitat: collected on moist or wet ground, rarely 0.5 m above the ground, ± corticated or decorticated, 20–50 mm thick branches of *Alnus* sp. {3}, *Bambusoideae* {1}, *Fagus crenata* {1}, *Pinus* sp. {1}, *Quercus* sp. {1}, indet. angiosperm trees {12}, on up to 0.5 mm deep medium to strongly decayed wood {5} or mostly bark (periderm and bast) {14}; slightly greyed, with a few green algae. **Associated**: *Hyalorbilia arcuata* {1}, *H. multiguttulata* {1}, *H. tortuosa* {1}, *Orbilia binchuanensis* {1}, *O. renispora* {1}, *O. xanthostigma* {1}. **Desiccation tolerance**: dead in all parts when examined after 1 month, perhaps slightly desiccation-tolerant. **Altitude**: ~300–1325 m a.s.l. (Japan), 520–2700 m (southern China), 200–385 m (Caribbean belt). **Geology**: Asia: Paleozoic, Devonian-Carboniferous & Tertiary sedimentary and felsic plutonic & volcanic mafic rock; USA: granite. **Phenology**: I, IV, VI–X (N-hemisphere, at present with maxima in I and VIII–IX).

Taxonomic remarks. With its rather large apothecia and narrowly cylindrical, straight to slightly curved ascospores *H. japonica* closely resembles *H. inflatula*. It differs in distinctly smaller asci and ascospores, with a distinctly shorter pars sporifera. However, the limit between these two species is not very sharp, and also *H. oreadum* deviates from *H. japonica* only gradually in wider spores. Five Chinese collections assigned to *H. oreadum* by Guo et al. (2014a) appear to be intermediate to *H. japonica* (for details see under *H. oreadum*, Pl. 74: 3–4). Delimitation from *H. citrina* with helicoid spores is also not sharp due to collections in which spore curvature (compare Pl. 83: 7 and Pl. 87: 9) and the texture of the marginal excipulum are intermediate. *H. japonica* was only available to us from dead herbarium material. However, several fresh specimens from Taiwan were investigated by Y. C. Su and M. L. Wu, and some of their illustrations are reproduced here (Pl. 83: 9; 84: 6–7).

Some of the Chinese collections reported by Liu (2006) under the name *H. inflatula* belong to *H. japonica*. Two were reexamined: B.L. 6446 (HMAS 138524, Guangxi) has straight spores †4–4.5 × 0.8–1 µm, asci †(13–)15–17 × 3 µm, and gelatinized marginal cells 4–7 µm wide, which well fits *H. japonica*; in B.L. 6418 (HMAS 139580, Fujian) the asci measured †15–21(–23) × 3.3–3.6 µm and spores could not be found, nevertheless we have included it here in the scope of *H. japonica*.

Variation. The present concept of *H. japonica* is only tentative due to pronounced variation, especially in excipular characters and apothecial colour, also in molecular data. Highly variable is the excipular cell length at the lower flanks, being quite long in some specimens from eastern Asia (†30–62 × 10–25 µm, H.B. 7461a; †20–45 × 6–11 µm, holotype; †20–37 × 6–15 µm, Pl. 84: 4a) and North America (*23–42 × 8–18.5 µm), but rather short in others (Pl. 84: 3c, 7a, 8h), e. g., in material from Puerto Rico (8–22 × 6–18 µm). Also the marginal cortical cells are in a majority of samples rather narrow and slightly to medium gelatinized (e. g., Pl. 84: 2c, 8g; IVV: H.B. 5906 holotype), but in collections from Puerto Rico (Pl. 83: 7f), Japan (Pls 83: 5f; 84: 4b), and North America (IVV: X.2017) they are ± distinctly wider and partly non-gelatinized. The degree of gelatinization at the flanks also varies from rather low, with common walls 0.3–0.4 µm thick (e. g., Pl. 84: 4a), to distinctly gelatinized, with 0.5–2 µm thick common walls (Pl. 83: 7g, in the holotype 0.5–1 µm). The apothecial colour varies from whitish or pale chlorinaceous (eastern Asia, South Africa, North America) to more light to bright yellow (Puerto Rico).

Type studies. No material of *Orbilia epipora* subsp. *major* from Argentina (on rotten log of *Populus nigra* '*italica*' in a

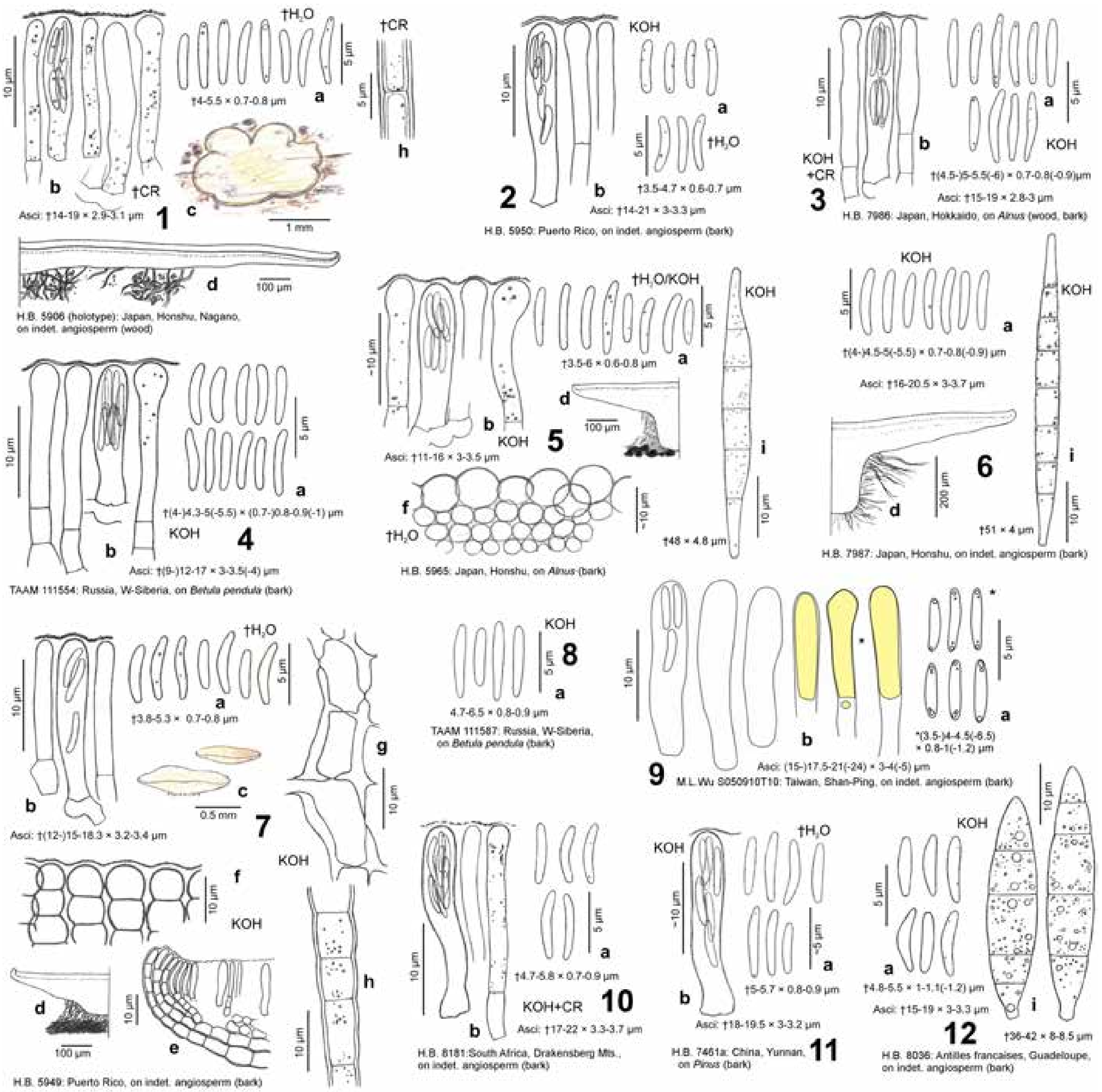


Plate 83. **1–3**, **5–7**, **9–11**: *Hyalorbilia japonica*; **4**, **8**, **12**: *H.* cf. *japonica*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. rehydrated apothecia; **d**. apothecia in median section; **e**. id., ectal excipulum at margin and flanks; **f**. marginal cells (**5f**: top view, **7f**: external view); **g**. cortical layer of ectal excipulum at lower flanks in external view; **h**. anchoring hyphae; **i**. conidia from substrate.

marsh) could be located in BAB and PAD. According to the original description by Spegazzini (1881), copied by Saccardo (1889: 626), the nearly unstalked asci (20–25 × 5 µm), uninflated paraphyses, and very large excipular cells (50–60 × 20 µm) point to a *Hyalorbilia*. The rather large apothecia (0.8–1.5 mm) together with small, cylindrical, curved spores (4–5 × 0.5–0.8 µm) are reminiscent of *H. japonica* or *H. arcuata*. Spegazzini considered the collection to be intermediate between *O. epipora* and *O. inflatula* (= *H. inflatula*).

Other not included collections. A collection from the Antilles (Pls 83: 12; 85: 2) is somewhat intermediate between *H. japonica* and *H. oreadum*. The often slightly curved spores are wider than in typical *H. japonica*, and the excipular cells a bit too thick-walled to be included in *H. oreadum*. Comparable is a collection from the Comoros with very similar, more straight spores (IVV: J.P.P. 14035). A very sparse collection from Azerbaijan (Pl. 84: 9, spores †5–6 × 0.9–1 µm) is more probably *H. japonica* than *H. inflatula* because of slightly (to medium) curved spores, but the presumed anamorph deviates (see below). An abundant sample from western Siberia (Tyumen, Pls 83: 4; 84: 10) differs in remarkably cyathiform, stipitate, yellow apothecia. The very short asci and the short, slightly curved spores would fit well *H. japonica*. A separate population in this collection (Pls 83: 8; 85: 1) has slightly longer spores and smaller, less stipitate apothecia, and is difficult to delimit from *H. inflatula*. The marginal cortical cells in the Siberian specimens are rather wide and thin-walled, with only sparse gel between. All these doubtful specimens differ from *H. fagi* in narrower, less curved spores.

Plate 84. **1–8**: *Hyalorbilia japonica*; **9–10**: *H.* cf. *japonica*. – **1**, **2a–b**, **5a–b**, **6**, **8a–c**, **10a–d**. rehydrated apothecia; **3a**, **10e**. dry apothecia; **3b**, **8d**. apothecia in median section; **4a**. id., ectal excipulum at flanks; **3c–d**, **7a**, **8h**, **9a–b**. id., marginal part of apothecia; **2c**, **4b**, **8g**, **10g–h**. margin in top view; **8e**. basal ectal excipulum with anchoring hyphae (median section); **8f**, **9c–d**. anchoring hyphae; **7b**, **10f**. asci and paraphyses; **4c**, **7c**. ascospores. – Dead state (**9a** in H_2O; **2c**, **3c–d**, **4a–c**, **8d–h**, **9b–d**, **10g–h** in KOH; **10f** in KOH+IKI) except for **7a–c**. – **6**, **7a–c**: phot. Y.C. Su. — **1**. H.B. 5906 (holotype): Japan, Sugadaira, on indet. angiosperm; **2a–c**. H.B. 7986: Japan, Hokkaido, on *Alnus*; **3a–d**. H.B. 7987: Japan, Sugadaira, on indet. angiosperm; **4a–c**. H.B. 5965: ibid., on *Alnus*; **5a–b**. H.B. 8181: South Africa, Nelspruit, on indet. angiosperm; **6**. TMUE S050910B2-1: Taiwan, Shan-Ping, on bamboo; **7a–c**. TMUE S050910T10: ibid., on indet. angiosperm; **8a–h**. H.B. 5949: Puerto Rico, Guajataca, on indet. angiosperm; **9a–d**. TAAM 68123: Azerbaijan, Zakataly, on *Tilia*; **10a–h**. TAAM 111554: Russia (East), Tyumen, Kanthy-Mansi, on *Betula*.

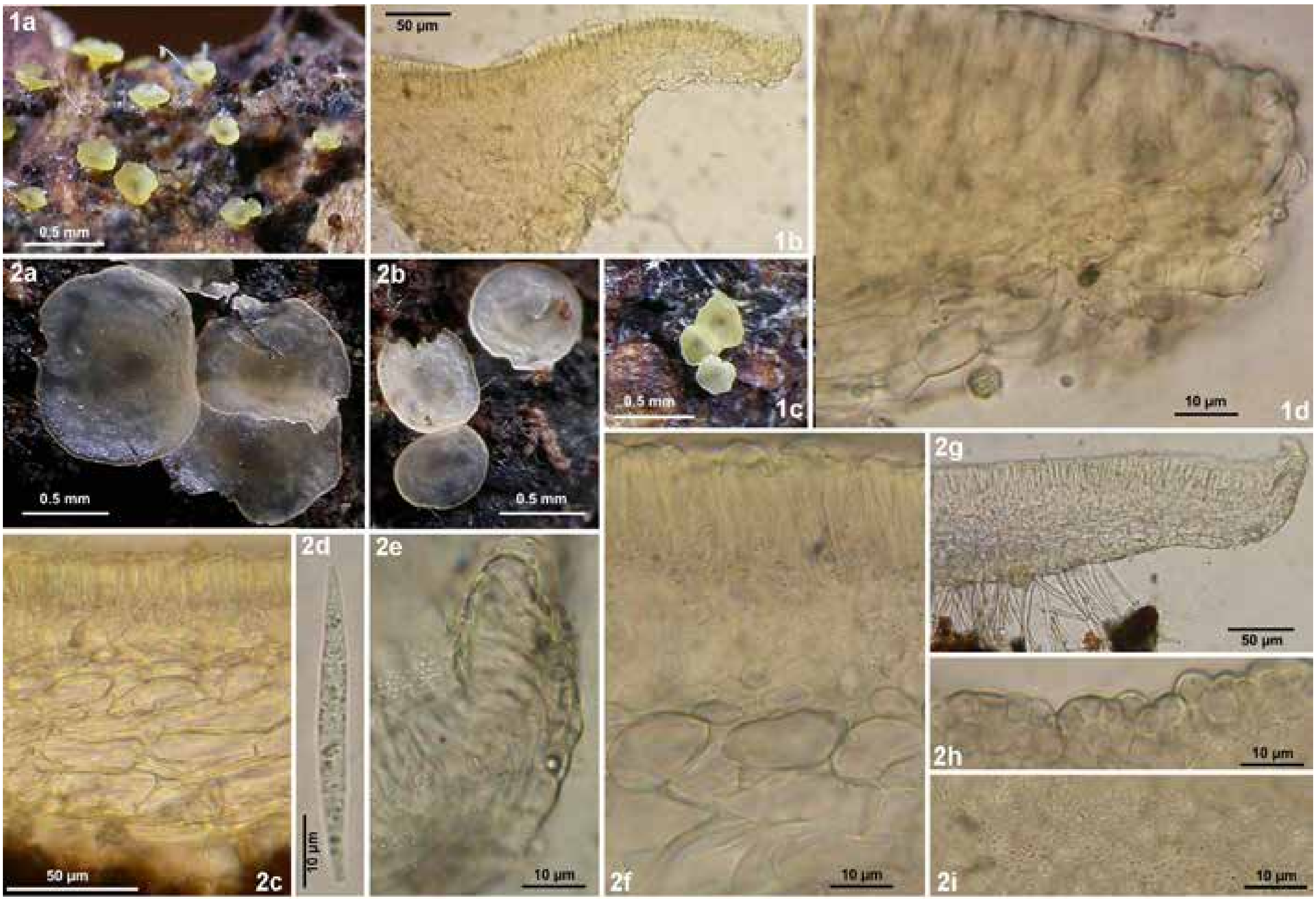


Plate 85. **1–2**: *Hyalorbilia* cf. *japonica*. – **1a**, **c**, **2a–b**. rehydrated apothecia (**1**: after 28 years, **2**: after 4 months); **1b**, **2g**. apothecia in median section; **1d**, **2e**. id., marginal ectal excipulum; **2c**, **f**. id., central part; **2h**. margin in top view; **2i**. exudate on hymenium; **2d**. conidium from substrate. – Dead state, except for **2d**. — **1a–d**. TAAM 111587: Russia, Tyumen, Kanthy-Mansi, on *Betula*; **2a–i**. H.B. 8036: Antilles, Guadeloupe, on indet. angiosperm.

Anamorph. Narrowly fusiform brachyphoris-like conidia were observed in three collections on the natural substrate (Pl. 83: 5–6; IVV: H.B. 8717). In a not included collection from Guadeloupe distinctly wider conidia were detected (Pl. 83: 12i), and a much shorter conidium occurred in the sample from Azerbaijan (IVV: TAAM 68123/H.B. 8725b). Conidiophores were not observed in any of these cases. The more slender conidia of *H. japonica* fit quite well those of *H. lignatilis*. However, conidia with this shape do not markedly differ from those known for *H. brevistipitata*, *H. oviparasitica*, and *H. inflatula* (?= '*Dactylella*' *passalopaga*).

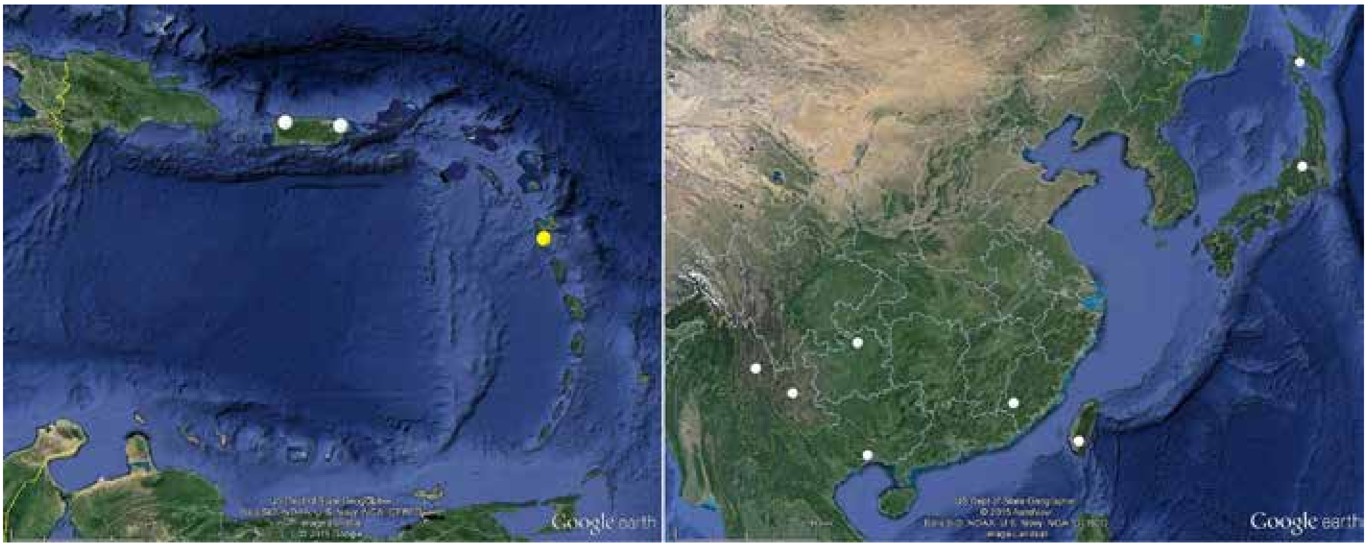
Phylogeny. ITS sequences from apothecia of the two here reexamined Chinese specimens, which Liu (2006) included in *H. inflatula*, were available: B.L. 6446 from Guangxi and B.L. 6418 from Fujian. However, no sequence from the type of *H. japonica* from Japan was gained. The two Chinese strains clustered in a clade in the analysis of Liu et al. (2006a). It seems that at least B.L. 6446 represents typical *H. japonica* (see above). In the ITS the two differ by 6.5 % and in our analysis they clustered in an unsupported (ML, strongly supported under NJ) subclade within the strongly supported *citrina-fagi* clade (Phyl. 5). Also for one of the samples from Massachusetts (bhi-F1000.1a) a sequence (S1506 intron, ITS) was available which clustered in our ITS analysis unresolved in the *citrina-fagi* clade (not shown), with a minimum distance of 5.5 % to *H.* cf. *fagi* from Massachusetts (bhi-F041), with which it also clustered when analysing the intron.

Other strains identified by Liu (2006) as *H. inflatula* clustered in our analyses with *H. arcuata* and *H. inflatula* (see under these species). The type of *H. lignatilis* differs by 22–23 % in the ITS region from the two Chinese *H. japonica* specimens.

Ecology. *Hyalorbilia japonica* was found on ± rotten bark and wood of hygric branches of angiosperm (rarely gymnosperm) trees, but also on a stem of bamboo. The collection with large thin-walled excipular cells (H.B. 5965) was from an air-protruding branch ~0.5 m above the ground, whereas all other samples appear to have grown on the moist or wet ground.

The collections are from eastern and southeastern Asia, southeastern Africa, and Middle America, with a cold-temperate to tropical humid (winter-dry), monsoon-influenced climate (in South Africa it was a savannah-like shrubland). According to M.L. Wu (pers. comm.) the species is frequent in southern Taiwan, being collected about 30 times throughout the year. The not included samples are, e. g., from oroboreal and suprasubmediterranean western Asia and cold-temperate central Europe.

Specimens included. **JAPAN**: **Hokkaido**, ~20 km NW of Tomakomai, Shikotsu lake, ~300 m, branch of *Alnus*, on wood & bark, 28.VII.1990, T. Hosoya (TRL 148, TNS-F-57477, H.B. 7986 ø). – **Honshu**, **Nagano**, Chiisagata-gun, 11 km SSE of Suzaka, 3 km NNE of Sugadaira, Hinotaki waterfall, 1380 m, branch of indet. angiosperm, on wood, 24.VIII.1997, W. Gams (ex H.B. 5906, M-0276412, **holotype**). – ibid., 1325 m, branch of *Alnus*, on wood, 21.VIII.1997, T. Hosoya (H.B. 5902c). – 16.5 km NE of Ueda, 1 km SE of Sugadaira, Arboretum in Sugadaira Montane Research Center, 1325 m, branch of *Alnus*, on bark, ~26.VIII.1997, W. Gams (H.B. 5965, anam. substr.). – ibid., branch of *Fagus crenata*, on bark, 30.IX.1991, collector unknown (TRL 410, TNS-F-57478. H.B. 7987 ø, anam. substr.). — **CHINA**: **Fujian**, **Longyan**, Shanghang, 25 km NW of Longyan, Buyun, Meihuashan, 800 m, branch of indet. angiosperm, on bark, 17.IV.2003, B. Liu (B.L. 6418, HMAS 139580 [erron. as 139532], as *H. inflatula*, H.B. 9109, immature; sq.:



Map 8: Known distribution of *H. japonica* in Middle America and eastern Asia (yellow = not included collection).

DQ656656). – **Yunnan**, **Dali**, Binchuan, 42 km NNE of Dali, Jizushan, 2700 m, branch of indet. angiosperm, on bark, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (H.Y.S. jz-3, CBCD, ex H.B. 8979a, M-0276443 [soc. *O. binchuanensis*]). – **Kunming**, Central Highlands, ~35 km W of Kunming, ~8 km WNW of Yiliang, Xiaobailong Mt., 1580 m, twig of *Pinus*, on bark, 10.IX.2003, M.H. Mo (M.M.H. 005 p.p., H.B. 7461a, mixture with *H. arcuata* & *H. lignatilis*). – **Guizhou**, **Zunyi**, Suiyang, ~62 km NNE of Zunyi, ~38 km ENE of Tongzi, Kuankuoshui, 1420 m, on bark of indet. angiosperm, 10.IX.2007, S.F. Li & J.W. Guo (J.W.G. gz-5, 57, YMFT, H.B. 8743 ø). – ibid. (J.W.G. gz-18, YMFT, H.B. 8717 ø, anam. substr.). – **Guangxi**, **Fangchenggang**, Shangsi, ~26 km S of Shangsi, Shiwandashan, 800 m, branch of indet. angiosperm, on bark, 20.VI.2003, B. Liu (B.L. 6446, HMAS 138524, H.B. 9110; sq.: DQ656649). – **Taiwan**, **Kaohsiung**, 54 km NE of Kaohsiung, 4.5 km SE of Liouguei, Shanping Natural Education Center, 520 m, stem of bamboo, 10.IX.2005, Y.C. Su (TMUE S050910B2-1, doc. vid.). – ibid., branch of indet. angiosperm, on bark, 10.IX.2005, Y.C. Su (TMUE S050910T10, TNM, doc. vid.). — **USA**: **Massachusetts**, Boston Harbor Islands, 19 km SE of Boston, 2.5 km NE of Hingham, World's End peninsula, 7 m, log of indet. angiosperm, on wood, 6.X.2017, D. Haelewaters, J.K. Mitchell & L. Quijada (bhi-F942, FH, doc. vid.). – 6.5 km SE of Boston, Thompson Island, 7 m, log of *Quercus*, on wood, 23.X.2017, D. Haelewaters, J.K. Mitchell & L. Quijada (bhi-F1000.1a, doc. vid.; sq.: MN339161). — **PUERTO RICO**, El Yunque, 6.3 km SSE of Rio Grande, El Verde, forest entrance trail before Oxcart Trail, 385 m, branch of indet. angiosperm, on bark, 24.I.1996, F.A. Harrington & M. Liftik (D.H.P. PR 132, FH 304912). – 10.5 km SE of Isabela, 1.7 km S of Pueblito de Ponce, Reserva Forestal Guajataca, 200 m, on pyrenomycete and bark of indet. angiosperm, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (D.H.P. PR 128, FH 304915, H.B. 5950 ø; D.H.P. PR 115, FH 304918). — **SOUTH AFRICA**: **Mpumalanga**, Drakensberg Mts., 11.5 km SSE of Mbombela (Nelspruit), WNW of Umhloti Lodge, 1055 m, branch of indet. angiosperm, on bark, 17.II.2006, V. Kummer (H.B. 8181).

Not included. **AZERBAIJAN**: **Shaki-Zaqatala**, Caucasus Mts., ?N of Zakatala, 'Kordon', 800 m, log of *Tilia*, on wood, 9.VIII.1974, B. Kullman (TAAM 68123, H.B. 8725b ø). — **RUSSIA (East)**: **Tyumen**, **Khanty-Mansi**, 45 km NNE of Beryozovsk, Tegi, 2 m, log of *Betula pendula*, on bark, 7.VII.1977, M. Saar (TAAM 111554, H.B. 7994a; TAAM 111587, H.B. 7994b). — **PUERTO RICO**: 10.5 km SE of Isabela, [1.7 km S of Pueblito de Ponce], Reserva Forestal Guajataca, 200 m, branch of indet. angiosperm, on bark, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (D.H.P. PR 131, FH 304903, H.B. 5949). — **LESSER ANTILLES**: **Guadeloupe**, 6.5 km WSW of Capesterre-Beolle-Eau, Le Grand Etang, 420 m, branch of indet. angiosperm, on bark, 6.IX.2005, C. Lechat (C.L.L. 5373, H.B. 8036, anam. substr.). — **ARGENTINA**: **Buenos Aires**, Buenos Aires, San Benito de Palermo, ~10 m, log of *Populus nigra* '*italica*', VIII.1880, C.L. Spegazzini (**holotype** of *Orbilia epipora* subsp. *major*, unlocated). — **COMOROS**: **Mayotte**, 4.5 km WNW of Mamoudzou, chemin de la convalescence, WNW of governor's house, 439 m, branch of indet. angiosperm, on bark, 11.I.2014, M. Pélissier, vid. J.P. Priou (J.P.P. 14035, doc. vid.).

Hyalorbilia lignatilis (M.H. Mo & K.Q. Zhang) E. Weber & Baral, **comb. nov.**, MB 829069 — Pl. 86

Basionym: *Dactylella lignatilis* M.H. Mo & K.Q. Zhang, Mycotaxon 91: 186 (2005)

Etymology: named after the growth on bark of a twig of *Pinus*.

Typification: China, Yunnan, Kunming, Xiaobailong Mt., twig of *Pinus*, 10.IX.2003, M.H. Mo (HT1.00596, holotype; YMF 1.00596, ex-type culture; sq.: KT215222).

Description: — **TELEOMORPH**: uncertain. – **ANAMORPH** (from Mo et al. 2005b, modified, see also Pl. 3: a): brachyphoris-like (from ascospore isolate {1}). **Conidiophores** 60–180(–270) µm long, 3.5–5 µm wide at base, 1.5–2.5 µm at the tip, strongly branched, side branches 7–35 µm long, conidiogenesis terminal, singly. **Conidia** unbranched, */†(25–)30–43(–51) × 3.5–5.2 µm, narrowly fusoid to fusiform, rounded at tip, truncate at base, straight, (1–)3–4(–6)-septate, (*) containing groups of refractive, globose to subangular droplets 0.7–1 µm diam. in centre of each cell. **Trapping organs** not observed.

Habitat: twig of *Pinus* lying on moist soil, on bark. **Associated**: *Hyalorbilia arcuata*, *H. japonica*. **Desiccation tolerance**: unknown. **Altitude**: 1580 m a.s.l. **Geology**: Paleozoic sedimentary rock.

Taxonomic remarks. Mo et al. (2005b) described the new species *Dactylella lignatilis* based on the anamorph which they obtained from an ascospore isolate of its teleomorph from *Pinus* bark collected in China. Under the name *Hyalorbilia* sp. they provided a description of the teleomorph. Our restudy

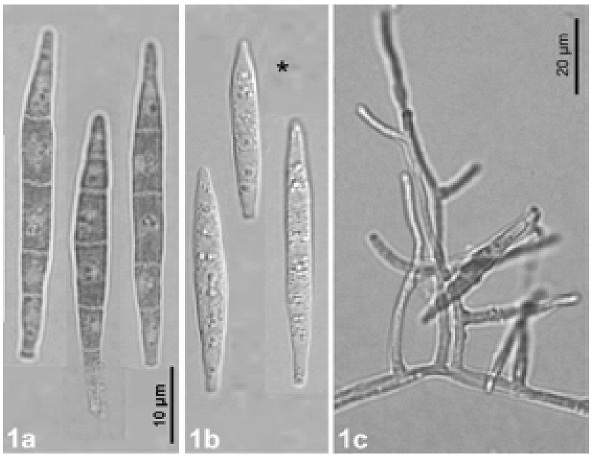


Plate 86. **1**: *Hyalorbilia lignatilis* (holotype). – **1a–b**. conidia from pure culture; **1c**. conidiophores. – Dead state, except for **1b**. — **1a–c**. from Mo et al. (2005b), YMF 1.00596: China, Yunnan, Kunming, on *Pinus*.

of a fragment of this collection revealed, however, a mixed population of at least two different *Hyalorbilia* species: whereas Mo et al. (l.c.: fig. 3) reported apothecia with consistently strongly curved, falcate ascospores and angular to prismatic cells of mostly 10–20 × 6.5–12 µm, which we here refer to *H. arcuata* (H.B. 7461b, Pl. 101: 2), our fragment surprisingly contained only apothecia with almost straight spores and ectal excipular cells at the flanks of 30–62 × 10–25 µm, which fit our concept of *H. japonica* (H.B. 7461a, Pl. 83: 11). Mo et al. appear to have overlooked this mixture of different species, and it might well be that their culture, which represents the type of *D. lignatilis*, derived from the straight-spored population, if not from a third taxon.

Chen et al. (2007b) examined an ex-type culture of *D. lignatilis* but could not observe any conidia. They obtained an ITS sequence from it, which 'showed a far distance from any species of *Dactylella*' (s.l., including *Brachyphoris*), but did not deposit it in GenBank. When we had the opportunity to study an ex-type culture of *H. lignatilis* in 2005, we observed a few of the characteristic brachyphoris-like conidia. Regrettably we did not document them. Molecular data gained by G. Hagedorn from this culture confirmed a relationship with *Hyalorbilia*, and we conclude that Chen et al.'s ex-type culture was contaminated.

Because of its high molecular distance to *H. arcuata* and *H. japonica* (see below), we here propose the new combination *H. lignatilis*, for which only the anamorph is known with certainty. The conidia of *H. lignatilis* hardly differ from other species of *Hyalorbilia*, such as *H. citrina*, *H. fagi*, *H. inflatula* etc. Mo et al. (2005b) gave a very wide range of conidial width (2.5–6.3 µm, mean value 4.8 µm), but from their scale we obtained 3.5–5.2 µm. The refractive droplets in the living conidia (Pl. 86: 1b) are suggestive of SCBs (cubical bodies), but in the dead conidia they are still visible (Pl. 86: 1a) which would, instead, point to lipid bodies.

Phylogeny. When analysing ITS (Phyl. 5), our sequence of the ex-type culture of *H. lignatilis* clustered in *Hyalorbilia* and here with strong support and a 6 % distance with a sample from Nanning under the name *H. inflatula* (B.L. 6193, Liu 2006). An illustration of B.L. 6193 was not available, and we can only assume from Liu's identification and from his general description of *H. inflatula* that it had ± straight ascospores. This might make it more probable that the type culture of *H. lignatilis* was obtained from a teleomorph with straight ascospores.

This is supported by the finding that our Australian collection of *H. arcuata* did not cluster with *H. lignatilis* but with another sample with arcuate spores identified by Liu (2006) as *H. andina* (B.L. 6408). However, an unillustrated sample identified by Liu as *H. inflatula* (B.L. 6426) clustered in the same clade, and another *H. andina* sample (B.L. 6184) clustered with one of '*H. juliae*, B.L. 6449' in a clade of its own (see Phyl. 5). The clade with *H. lignatilis* is also distant from *H. japonica* (B.L. 6446). Given that the ex-type culture of *H. lignatilis* derived from straight-spored apothecia, our description of *H. japonica* would be heterogeneous as it includes the straight-spored part of Mo et al.'s sample (H.B. 7461a). The same applies to the description of *H. arcuata* in which the curved-spored H.B. 7461b is incorporated, in case the apothecia from which *H. lignatilis* derived had curved spores. Because of this uncertainty and the very high ITS distance of 22–23 % between *H. lignatilis* and *H. japonica* (H.B. 9109, H.B. 9110), we here prefer for the time being to consider *H. lignatilis* as a species of its own.

G. Hagedorn's sequence of *H. lignatilis* comprises also SSU (S1506 intron absent) and LSU. When analysing ITS+LSU, *H. lignatilis* formed a medium supported subclade with *H. polypori* (Phyl. 6). When analysing LSU, (Phyl. S5), *H. lignatilis* clustered strongly supported with an environmental clone from Taiwan isolated from the rhizome of the orchid *Gastrodia*. This clone was identified by the authors as *Dactylella lignatilis* based on its short sequence of merely 201 nt of the D1 domain which, however, deviates from the type by 4 nt. Also an unidentified isolate from Michigan (LSU not shown in phylotree) deviates from *H. lignatilis* and from the Taiwan clone by only 4 nt in these 201 nt of LSU.

Ecology. The apothecia from which *Hyalorbilia lignatilis* was isolated grew on bark of a decayed twig of *Pinus*, being with one end submerged in the moist soil. The collection was made in a subtropical humid (winter-dry) mountain forest in southern China. The not included collection from Nanning was on unidentified bark in a lowland forest with a similar climate. This might also apply to the Taiwan clone, whereas the Michigan clone came from a cold-temperate humid climate.

Specimens included. **CHINA**: **Yunnan**, **Kunming**, ~35 km W of Kunming, ~8 km WNW of Jiliang, Xiaobailong Mt., 1580 m, twig of *Pinus*, on bark, 10.IX.2003, M.H. Mo (M.M.H. 005 p.p., HT 1.00596, H.B. 7461c ø, presumed mixture with *H. arcuata* & *H. japonica*; HT1.00596, **holotype**; YMF 1.00596, ex-type culture; doc. vid.; sq.: KT215222).

Not included. **CHINA**: **Guangxi**, **Nanning**, ~3 km SE of Nanning, Qingxiushan, 180 m, on indet. bark, 2.VII.2002, B. Liu (B.L. 6193, HMAS 138509, as *H. inflatula*, non vid.; sq.: DQ656655). – **Taiwan**, unlocalized, *Gastrodia* rhizome (G-jav2-LSU1_OTU-0-064_3, sq.: MF338616). — **USA**: **Michigan**, Pellston, forest soil (clone OTU512, sq.: MG927852).

Hyalorbilia citrina (A.L. Smith) Baral, **comb. nov.**, MB 813471 — Pls 87–88, Map 9

Basionym: *Calloria citrina* A.L. Smith, J. Linn. Soc., Bot. 35: 15 (1901)
= *Orbilia crenulatolobata* Höhnel, Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturw. Kl. 83: 31 (1907)
= *Orbilia andina* var. *lateritia* Pat., Bull. Soc. Mycol. Fr. 11: 218 (1895)

Etymology: *citrina*: named after the bright yellow colour of the apothecia; *crenulatolobata*: according to the roundish lobate protrusions of the apothecial margin; *lateritia*: named after the brick-red apothecia.

Typification: Dominica, Couliabon Mt., branch of indet. angiosperm, on bark, 1.III.1896, W.R. Elliott (K(M) 31762, lectotype of ***Calloria citrina***, designated here, MBT202652); Martinique, La Sérénité, Le St.-Esprit, log of *Swietenia macrophylla*, on *Ganoderma*, 29.VIII.2005, C. Lechat (ex C.L. 5247 & ex H.B. 8012, M-0291768, epitype, designated here, MBT385110; sq.: KT222377). — Brazil, São Paulo, branch of indet. tree, VII.1901, R. von Wettstein (FH, holotype of ***Orbilia crenulatolobata***). — Ecuador, Pululahua Mt., branch of indet. angiosperm, II.1892, collector unknown, (FH, herb. Patouillard, holotype of ***O. andina* var**. ***lateritia***).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.6–1.2 or 1–3.5(–4.5) mm diam., 0.1–0.25 mm high (receptacle 0.07–0.12 → 0.04–0.06 mm), pale or light chlorinaceous-yellow to bright yellow-ochraceous, also white, ± translucent, round, margin somewhat undulating when large, moderately gelatinous, scattered to subgregarious; disc shallowly cyathiform, finally flat, margin even {10} or crenulate-lobate to dentate {18}, lobes or teeth 6–30 up to 50–90 µm long, 30–100 µm wide; sessile on an obconical base or ill-defined stipe ~0.04–0.1 × 0.25–0.4 mm, superficial; dry cupulate to cyathiform, with strongly inrolled margin, pale to light cream or yellow-ochre(-orange), sometimes turning red-brown with age, very fragile. **Asci** *20–28 × 3.5–4 µm {1}, †(14–)15–22(–25) × (2.6–)2.8–3.6(–3.8) ((–4.5)) µm {17}, 8-spored, spores *~4-seriate, ± intertwined but often in two superimposed bundles, pars sporifera †10–15 µm long; **apex** (†) hemispherical to slightly subconical or subtruncate; **base** with or without short, thick stalk arising from croziers {9}. **Ascospores** *(5–)5.5–6(–6.5) × 0.8(–0.9) µm {1}, †(4–)4.5–6(–7) × (0.6–)0.7–0.8(–0.9) µm

{26}, (sub)cylindrical to sometimes slightly fusoid, slightly to medium helicoid (either stair-shaped or allantoid depending on the viewing direction), rarely some spores only very slightly curved; 1 **SB** at ?each end, ~0.4–0.6 × 0.4 µm {1}; often with 1–2 minute LBs. **Paraphyses** apically mostly cylindrical, rarely very slightly capitate or spathulate, terminal cells †(12–)14–20(–25) × (1.2–)1.7–2.5(–3.5) µm {6}, lower cells †3–7 × (1.2–)1.7–2.5(–3) µm {5}, a few paraphyses with rather long terminal cells, these appearing more firm-walled (possibly only by deposition of remnants of VBs) and arising deeply in the medullary excipulum {3}. **Medullary excipulum** hyaline to very pale yellowish, 10–20(–45) µm thick, of medium to very strongly gelatinized prismatic to angular cells, intercellular gel 1–3 µm thick, (very) sharply delimited. **Ectal excipulum** hyaline, of horizontal textura prismatica(-porrecta) from base to mid flanks, 40–130 µm thick near base, cells at lower flanks †(13–)20–60(–70)((–92)) × (6–)10–20(–25)((–32)) µm {12}, slightly to often strongly gelatinized: common walls 0.4–1.2 {6} or (0.7–)1–3(–5) {15} µm thick; 20–30 µm thick at mid flanks, towards margin of t. prismatica-angularis, upper margin or marginal teeth or lobes abruptly of t. globulosa of thick-walled cells, 25–30 µm thick in section, marginal cortical cells †(5–)7–17(–20) × (3–)6–12(–14) µm {6}, external wall 0.4–1 {8} or 1–3(–4) {14} µm thick, typically with a ± pronounced furrow between hymenium and margin. **Anchoring hyphae** sparse to abundant, long, radiating, †(2–)3–7(–10) µm wide (varying from 3–4 to rarely 7–9 µm), walls 0.3–1.2(–2) µm thick {11}. **Exudate** over paraphyses 0.2–0.8 µm thick, continuous, finely to strongly granular; over lower and upper surface of marginal teeth smooth or with scattered to dense fine warts, pale yellowish. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate {3}). **Conidiophores** not observed. **Conidia** narrowly fusoid to fusiform, straight, */†(36.5–)40–55(–61) × (3–)4–5(–5.5) µm {3}, 3–6-septate, containing some globose **SCBs** 0.9–1.2 µm diam. in centre of cells {2}.

Habitat: lying on the moist ground (rarely min. 0.5 m above the ground), on 1.3–5 or ~8–10 cm thick, corticated, rarely decorticated branches of *Cordia borinquensis* {1}, *Fraxinus* (*?mandshurica*) {1}, *Inga laurina* {1}, *Ormosia krugii* {1}, *Swietenia macrophylla* {1}, indet. angiosperm trees {20}, especially on the underside, on superficially or deeply (slightly to) medium (to strongly) decayed bark (partially detaching, usually on periderm) {21}, or wood {7}; on stem of *Bambusa* sp. {1}, petioles of *Oenocarpus* sp. {1}, fruit of *Hymenaea* sp. {1}; on hymeniophore (pores) of *Ganoderma* sp. {1}, *Phellinus* sp. {1}, *Trametes hydnoides* {1}, often on or close to old black pyrenomycetes {8}; no algae. **Further associated**: *Ascocoryne sarcoides* {Dennis 1954}, *Catinella olivacea* {1}, *Monodictys* sp. {1}, *Nectriaceae* {1}, *Ombrophila pura* {Dennis 1954, as '*O. microspora*'}, *Orbilia bambusina* {1}, *O. ?tremulae* {1}, *O. subuliformis* {1}, ?*Parmelia* sp. {1}. **Desiccation tolerance**: presumably desiccation-sensitive (dead in all parts when examined after 3 months), but in 2 collections apparently slightly desiccation-tolerant; conidia survived for 6.5 months in the herbarium. **Altitude**: 3–1165 or up to min. 1600 m a.s.l. (Middle & South America), 20–210 m (Japan). **Geology**: Japan: marine Tertiary sedimentary & volcanic pyroclastic rock. **Phenology**: in tropical belt almost throughout the year, in Japan in spring and summer.

Taxonomic remarks. *Hyalorbilia citrina* is characterized by subcylindrical, narrow ascospores which typically show a distinct helicoid curvature (appearing somewhat stair-shaped in profile view), and by a gelatinized medullary and ectal excipulum. *H. citrina* could only be studied in the dead state, therefore, no data on the SBs are available, except for a single observation by J.P. Priou (pers. comm.). Similar helicoid spores occur in the temperate taxa *H. helicospora*, *H. tortuosa* and *H. fagi*. These differ either in much smaller, more whitish apothecia, or in the constant absence of a gelatinized ectal excipulum and a dentate margin, or slightly longer or wider spores with more tapered ends. The more tropical *H. japonica* differs in shorter, never helicoid spores and a usually less gelatinized excipulum which never forms teeth at the margin.

Variation. The rehydrated apothecia vary in colour between pale and (e. g., in the lectotype of *H. citrina*) bright yellow-chlorinaceous. Typically, the margin is distinctly crenulate or dentate. The teeth consist of globose cells with often extraordinarily thick walls, and have a rounded to obtuse rather than acute shape. However, in 9 out of 30 collections the margin was smooth or only very slightly and irregularly crenulate (e. g., in the type of *O. andina* var. *lateritia*). 15 collections from Puerto Rico were examined, but only nine of them showed a ± toothed margin. All four specimens from Brazil were toothed, whereas all three Japanese collections showed smooth margins, and only one of them [from (sub)tropical Ogasawara islands, H.B. 7983a, Pl. 88: 5c] very thick-walled excipular cells. The degree of gelatinization, i. e., the thickness of the common walls, actually varies considerably among the collections. The collection from Hokkaido (on *Fraxinus*, H.B. 7984) is the only specimen from a temperate climate here referred to *H. citrina*. It differs from *H. tortuosa* only tentatively in a stronger gelatinization of the ectal excipulum, and resembles closely a collection from more southern Japan (H.B. 7985).

More constant proved ascus and spore size, and spore shape. Yet, in some specimens included here the characteristic helicoid shape of the spores is less pronounced (e. g., Pl. 87: 9a). This causes problems in separating *H. citrina* from species with straight or only slightly curved but never distinctly helicoid spores. Collections with such spores and with the marginal ectal excipulum medium gelatinized are tentatively assigned here to *H. japonica* (e. g., Pl. 83: 7) and *H.* cf. *inflatula* (Pl. 79: 1, 3–5), and a sharp limit to *H. citrina* is difficult to draw. Moreover, some collections here included in *H. citrina* with distinctly helicoid spores show an only very slightly gelatinized margin (IVV: e. g. D.H.P. PR 120 & PR 134), thus causing problems in delimitation from *H. tortuosa* or *H. fagi*. Furthermore, the flanks may sometimes be only slightly gelatinized though the margin is strongly gelatinized, and vice versa, which was the case in, e. g., a sample on fruit of *Hymenaea* (Pl. 87: 9). Here the margin shows deep incisions typical of *H. citrina*, yet the spores were often only very slightly curved. In this collection some of the paraphyses have extraordinarily long and firm-walled terminal cells, a character also noted in the type of *H. citrina*, but not seen in most other collections examined and referred to *H. citrina*.

Not included collection. A sample from Puerto Rico (IVV: D.H.P. PR 134) deviates by the excipulum being rather thin-walled at flanks and margin, although the spores fit *H. citrina*.

Type studies. The brief protologue of ***Calloria citrina*** in Smith (1901) and Saccardo & Saccardo (1906: 143) includes lemon-yellow apothecia up to 4 mm diam., turning fuscous with age, externally with enlarged angular cells. The spores are described as ellipsoid, eventually 1-septate (no size indicated), the asci cylindrical, 50 × 6 µm, spores obliquely uniseriate, and the paraphyses as filiform. The species was based on two collections from Dominica (Elliott No. 1476: on wood, head of Castle Bruce River, II.1896; Elliott No. 1581: Morne Couliabon, III.1896). No. 1581 exists in K and bears W.R. Elliott's handwriting, but No. 1476 could not be located there. Dennis (1954: 297) apparently reexamined authentic material when stating that 'the name *Calloria citrina* A.L. Smith appears to have originated in confusion from a mixture of a bright yellow *Orbilia* with *Coryne sarcoides* [≡ *Ascocoryne sarcoides*] and *Ombrophila microspora* [= *Ombrophila pura*]'.

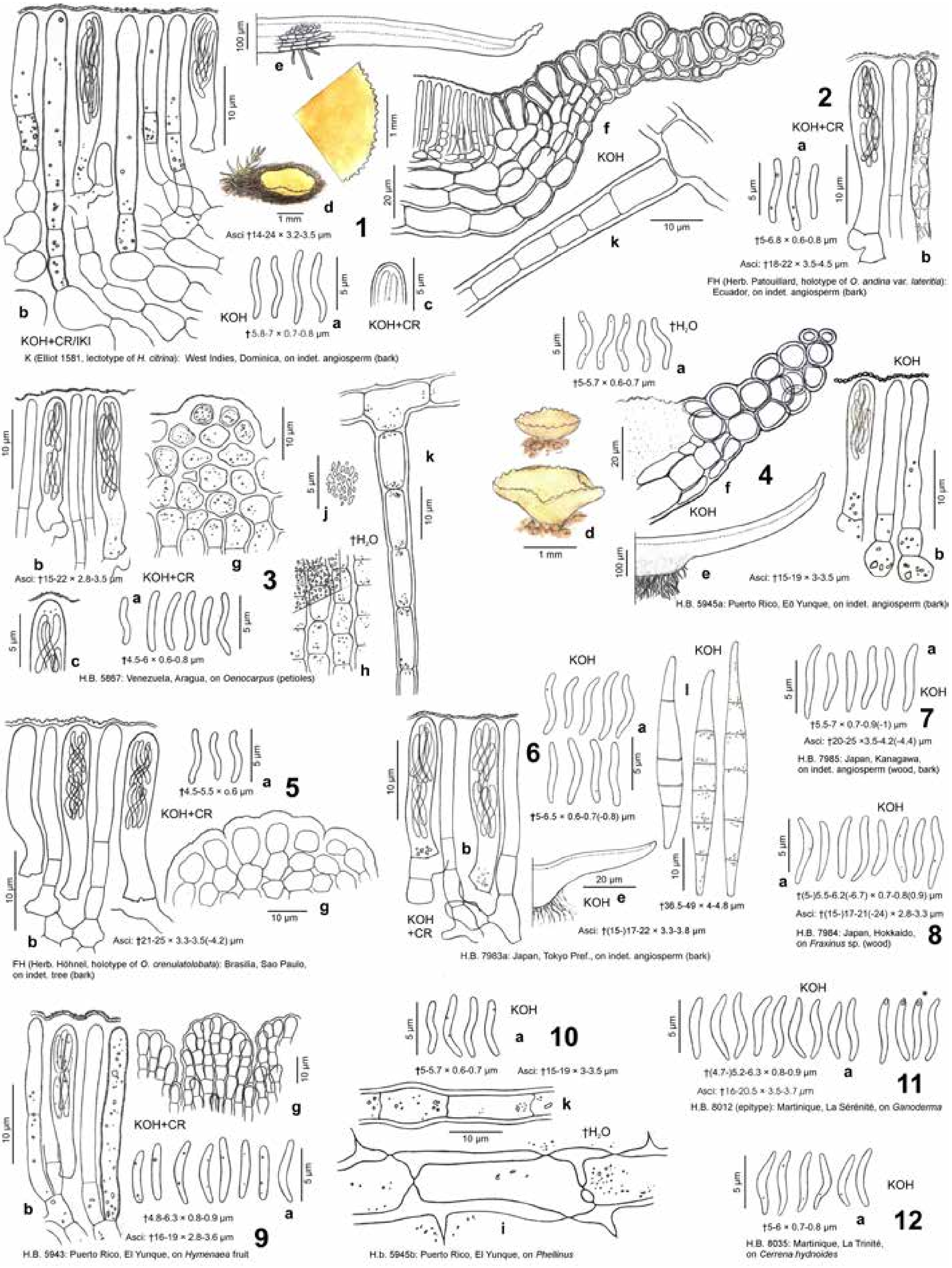


Plate 87. **1–12**: *Hyalorbilia citrina*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. ascus apices; **d**. apothecia with dentate margin; **e**. apothecia in median section; **f**. id., ectal excipulum at margin and mid flanks; **g**. marginal ectal excipulum in external view; **h**. id., at flanks, with warted exudate; **i**. lower flanks in median section, ectal excipular cells with thick gelatinized walls and thin septa; **j**. warted-cloddy exudate on ectal excipulum; **k**. anchoring hyphae; **l**. conidia from substrate.

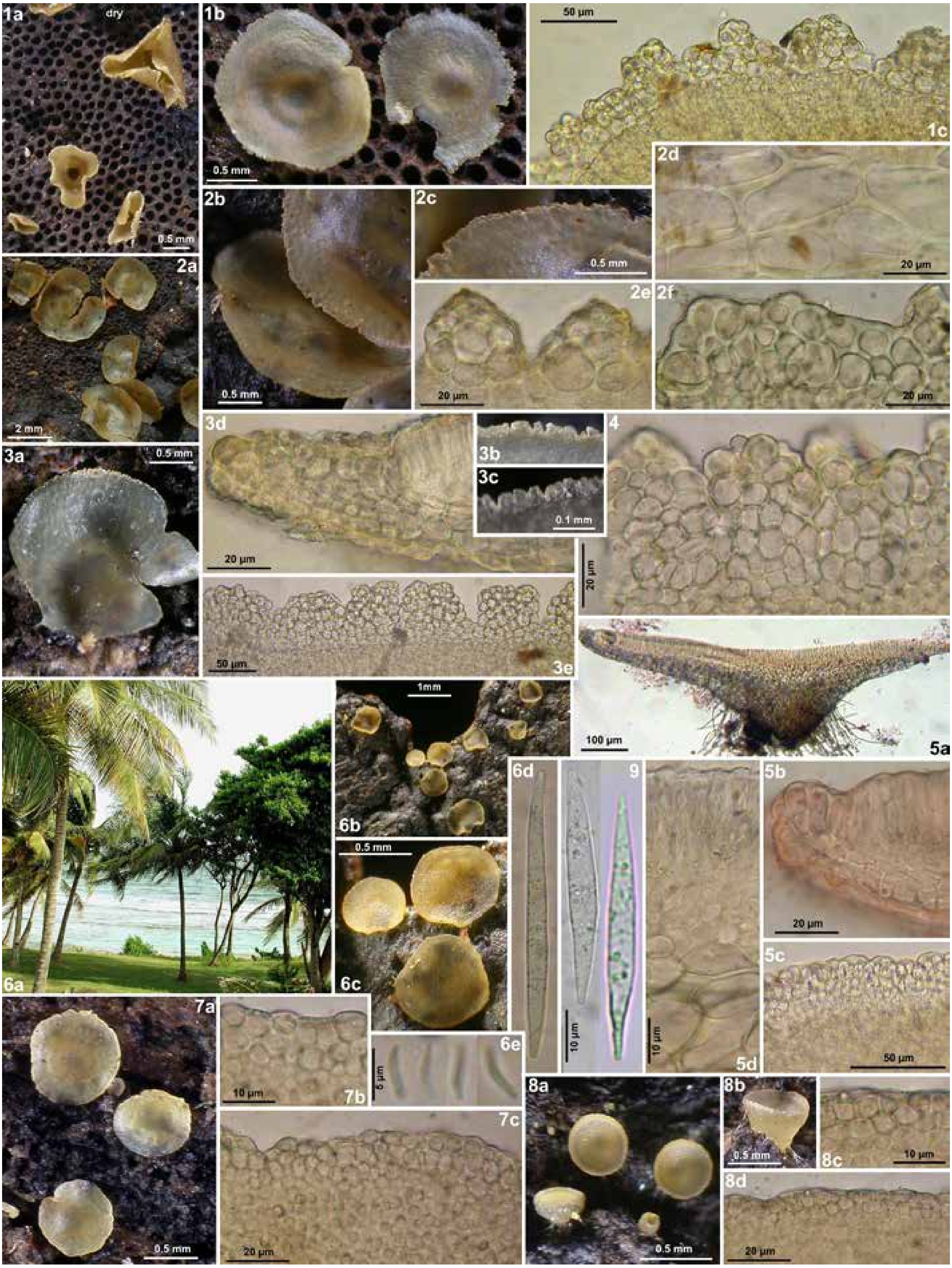


Plate 88. **1–9**: *Hyalorbilia citrina*. – **6a**. tropical beach on Lesser Antilles (near collection site); **1b**, **2a–c**, **3a**, **6b–c**, **7a**, **8a–b**. rehydrated apothecia; **3b–c**. closeup of crenulate margin; **1a**. dry apothecia; **5a**. apothecia in median section; **3d**, **5b**. id., marginal region; **5e**. id., central part of apothecium; **2d**. ectal excipulum at flanks (squash mount); **1c**, **2e**, **2f**, **3e**, **4**, **5c**, **7b–c**, **8c–d**. margin in top or external view, showing shallow to prominent marginal lobes or teeth; **6e**. ascospores; **6d**, **9**. conidia from substrate. – Dead state (**2e** in H_2O; **1c**, **2d**, **f**, **3d–e**, **4**, **5c–d**, **7b–c**, **8c–d** in KOH; **5a–b** in KOH+CR), except for **6d** & **9**. – **6a**: phot. C. Lechat. — **1a–c**. H.B. 8035: Martinique, La Trinité, on *Hexagonia*; **2a–f**. H.B. 8012 (epitype): Martinique, La Sérénité, on *Ganoderma*; **3a–e**. H.B. 8454: French Guiana, Cayenne, on indet. angiosperm; **4**. H.B. 5945a: Puerto Rico, El Yunque, on indet. angiosperm; **5a–d**. H.B. 7983a: Japan, Tokyo, on indet. angiosperm; **6a–e**. H.B. 8409a: Martinique, La Trinité, on indet. angiosperm; **7a–c**. H.B. 7984: Japan, Hokkaido, on *Fraxinus*; **8a–d**. H.B. 7985: Japan, Kanagawa, on indet. angiosperm; **9**. H.B. 9671: Brazil, Itatiai, on indet. angiosperm.

No. 1581 contains fragments of bark and wood. The bark fragments bear yellow apothecia of the *Hyalorbilia* redescribed here (Pl. 87: 1). The wood fragments bear dark apothecia which were not examined in the present study and which probably represent the *Ombrophila* mentioned by Dennis. The microscopic data as well as the fuscous colour mentioned in the protologue appear to be based on the dark apothecia. Apparently, Smith did not find any spores in the yellow apothecia. Because the specific epithet clearly refers to the *Hyalorbilia*, we here designate the yellow apothecia in Elliott No. 1581 (K) as **lectotype** of *Calloria citrina*. A specimen from Martinique (on *Ganoderma*, ex H.B. 8012, Pls 87: 11; 88: 2), for which a sequence was gained, is designated here as **epitype** of *H. citrina*.

Examination of the holotype of ***O. crenulatolobata*** (Pl. 71: 5) revealed conspecificity with *H. citrina*. The taxon was described by Höhnel (1907b) as having 'white' apothecia, but now they are light yellowish-ochraceous when dry. Höhnel based his new taxon on the deeply notched margin of roundish lobes composed of cartilaginous, thick-walled cells. He considered the hymenia to be immature and described the spores as 'probably sausage-like curved, very small'. No doubt, Höhnel's statement it due to the frequent difficulty to find free spores in *Hyalorbilia*. In fact, mature asci occur abundantly in the holotype, but the spores could only be seen inside the asci. Höhnel compared his taxon with *O. sinuosa* Penz. & Sacc. [?= *H. inflatula*], apparently because of the undulating margin reported for that species. He found the ectal excipulum to be composed of radially (horizontally) arranged cells measuring 60–100 × 25–35 µm, an extraordinary size which was approximately observed in the present study in the type of *O. andina* var. *lateritia* (40–92 × 10–23 µm).

The very brief protologue of ***Orbilia andina*** **var.** ***lateritia*** in Patouillard (1895) simply reads 'brick-red, spores 5 × 1 µm', and 'close to *Orbilia lancicula*'. Revision of the holotype at FH revealed helicoid spores of about that size, an ectal excipulum of very thick-walled cells (common walls 1–3 µm), and a smooth gelatinized margin (Pl. 87: 2). Contrary to the protologue, the colour of the dry apothecia was light ochre-yellowish-amber. The label bears Patouillard's handwritten notes and sketches that show, e.g., the margin made up of thick-walled cells, and asci 20–22 × 4 µm. Dennis (1954: 294) assumed *O. andina* var. *lateritia* to be a possible synonym of *O. juruensis* Henn. However, the latter is not a *Hyalorbilia* but belongs to *Orbilia* section *Helicoon.*

Anamorph. The fusoid conidia observed in *H. citrina* on the natural substrate (Pls 87: 6l; 88: 6d, 9) resemble those of *H. arcuata*, *H. japonica*, *H. fagi*, and others.

Phylogeny. Sequences taken from apothecia of two samples of *H. citrina* were available, one comprising the ITS region (Martinique, H.B. 8012), the other SSU, half of 5.8S, ITS2, and LSU (Rio de Janeiro, H.B. 9661). The S1506 intron is absent in H.B. 9661 (unclear in H.B. 8012). A high distance of 16% is observed when comparing the two sequences in the available ITS2 region. Nevertheless, a large gappy region is characteristic for *H. citrina* in the alignment of ITS2, where the other sequences of the *citrina-fagi* clade have about 20–25 nt more.

S1506 intron, ITS1, and LSU D1–D2 exists for a sample from Florida in GenBank (not shown in phylograms). In the ITS1 5 nt & 1 gap differ from H.B. 8012, suggesting conspecificity, while in the LSU it clustered supported with H.B. 9661, with a likewise 5 nt & 1 gap difference. The intron region is closest to *H. fagi* but differs here in over 40 nt.

When analysing the entire ITS region (Phyl. 5), the two sequences formed a weakly supported subclade within the strongly supported *citrina-fagi* clade, which is part of the large *inflatula-polypori* clade. The complete ITS sequence of the Martinique strain shows in an alignment of all members of the *citrina-fagi* clade an 8–11% distance to *H. japonica*, *H. lunata*, *H. fagi*, and *H.* '*polypori*' (B.L. 288), while in the ITS2 alone the distance lies for *H. citrina* in the range of 15–20% (13% between the two *H. citrina* strains). Also when analysing LSU (Phyl. S5), *H. citrina* clustered with medium support in the *citrina-fagi* clade. In our combined analysis (Phyl. 6), *H. citrina* clustered with strong support with B.L. 288 and *H. fagi*, with a 2.5% and 2% LSU distance, respectively (1.5% between B.L. 288 and *H. fagi*).

Ecology. *Hyalorbilia citrina* is a plurivorous species and appears to occur widespread in the Neotropis in tropical humid rain or cloud forests in the Caribbean belt and in tropical northeastern parts of South America. It also occurs in subtropical humid eastern (Serra da Mantiqueira and Sao Paolo) and western parts of South America (Ecuadorian Andes), in (sub)tropical to cold-temperate humid, continental to oceanic eastern Asia (Japan), in the tropical wet & dry rainforest of the Comoros, and in tropical humid northeastern Australia. *H. citrina* inhabits a wide range of substrates of angiosperm trees, predominantly periderm of rotten bark and less often wood of hygric branches and logs, sometimes also petioles and fruits, xeric stems of *Bambusa*, or polypores. Judging from the associated discomycetes, the species appears to be desiccation-sensitive. However, the presence of a foliose lichen in one of the Japanese collections (H.B. 7983a) and the occurrence on standing stems of *Bambusa* in Australia seem to indicate a certain desiccation tolerance. Florida wetland in a *Quercus-Acer-Liquidambar* dominated forest.

Specimens included. **USA**: **Florida**, 6.3 km E of Melrose, E of Ashley Lake, 33 m, indet. tree, 8.VIII.2017, B. Kaminsky & M.E. Smith (FLAS-F-60759, as *Orbilia* sp., non vid.; sq.: MH281853, MH620243). — **PUERTO RICO**: 10.5 km SE of Isabela, 1.7 km S of Pueblito de Ponce, Reserva Forestal Guajataca, 200 m, branch of indet. angiosperm, on bark & wood, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (D.H.P. PR 118, FH 00304917; PR 120, FH 00304911). – El Yunque, ~9.5 km SW of Luquillo, trail to falls of Rio de la Mina, 500 m, branch of *Inga laurina*, on bark, 5.VI.1970, R.P. Korf, J.B. Benson, J.B. Dixon etc. (CUP-PR 3841). – trail to El Toro, 750 m, on wood of *Cordia borinquensis*, 5.VI.1970, R.P. Korf, J.B. Benson, J.B. Dixon etc. (CUP-PR 3835). – 30 km ESE of St. Juan, Rio Grande, El Verde Field Station, 15 m, on *Phellinus*, 20.I.1996, D.H. Pfister, F.A. Harrington & M. Liftik (D.H.P. PR 74, FH 00304905, H.B. 5945b ø). – ibid., branch of indet. angiosperm, on wood, 20.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik & D. Potter (D.H.P. PR 79, FH 00304904). – ibid., log of indet. angiosperm, on bark, 20.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik & D. Potter (D.H.P. PR 77, FH 304907, H.B. 5945a). – 2.5 km SSW of Luquillo, near Rio Sabana, hill above chicken farm, 20 m, log of indet. angiosperm, on wood, 17.I.1996, D.H. Pfister, F.A. Harrington, D.J. Lodge & S. Hundorf (D.H.P. PR 32, FH 304913). – ibid., seeds of *Hymenaea*, 17.I.1996, S.M. Hundorf (D.H.P. PR 36, FH 304914, H.B. 5943 ø). – ~7 km S of Rio Grande, Guzman Obajo, Camino Los Tapia, ~450 m, branch of indet. angiosperm, on bark, 23.I.1996, D.H. Pfister, F.A. Harrington, M. Liftik, S. Hundorf & D.J. Lodge (D.H.P. PR 105, FH 304909; PR 109, FH 304906). – 6.3 km SSE of Rio Grande, El Verde, forest entrance trail before Oxcart Trail, 385 m, branch of indet. angiosperm, on bark, 24.I.1996, F.A. Harrington & M. Liftik (D.H.P. PR 136, FH 304910). – ibid., log of *Ormosia krugii*, on bark, 24.I.1996, F.A. Harrington & M. Liftik (D.H.P. PR 138, FH 304908, H.B. 5958 ø). – trail from Sierra Palm to Mt. Britton, ~650 m, branch of indet. angiosperm, on bark, 18.I.1996, D.H. Pfister & F.A. Harrington (D.H.P. PR 43 [mixture with *Orbilia subuliformis*], FH 00304919). — **LESSER ANTILLES**: **Dominica**, ESE of Roseau, Couliabon Mt. (Morne Anglais), ?1000 m (as 1100 m), branch of indet. angiosperm, on bark, 1.III.1896, W.R. Elliott (No. 1581, K(M) 31762, **lectotype** of *H. citrina*, H.B. 5756 ø). – **Martinique**, 8 km SE of La Trinité, 5 km NE of Le Robert, Pointe Rouge, 3 m, on *Trametes hydnoides*, 27.VIII.2005, C. Lechat (C.L. 5208, H.B. 8035). – 6 km SE of La Trinité, 4.5 km NE of Le Robert, Pointe Bateau, ~30 m, branch of indet. angiosperm, on bark, 3.XII.2006, C. Lechat (C.L. 6169, H.B. 8409a, anam. substr.). – 5 km SE of La Sérénité, 3 km ENE of Petit-

Map 9. Known distribution of *H. citrina* in America and Japan.

Bourg, Le St.-Esprit, Le Bois La Charles, 100 m, log of *Swietenia macrophylla*, on *Ganoderma*, 29.VIII.2005, C. Lechat (ex C.L. 5247 & ex H.B. 8012, M-0291768, **epitype** of *H. citrina*; sq.: KT222377). — **VENEZUELA**: **Aragua**, Cordillera de la Costa, Henri Pittier, 15 km NW of Maracay, 6.5 km NNE of Aguas Calientes, Rancho Grande, 1150 m, on petioles of *Oenocarpus*, 26.VIII.1970, D.H. Pfister, H.E. Moore, J.D. Ambrose & R.E.Dietz (CUP-Venezuela 4494, H.B. 5867 ø). — **FRENCH GUIANA**: 11 km SE of Sinnamary, Paracou, 40 m, branch of indet. angiosperm, on bark, 26.II.2007, C. Lechat (C.L. 7057, H.B. 8454). — **ECUADOR**: **Pichincha**, Región Andina: ~30 km N of Quito, La Sierra, Pululahua Mt., ~1600–2900 m, branch of indet. angiosperm, on bark, II.1892, collector unknown, (FH, herb. Patouillard, **holotype** of *Orbilia andina* var. *lateritia*, H.B. 7591 ø). — **BRAZIL**: **Rio de Janeiro**, ~145 km WNW of Rio de Janeiro, Serra da Mantiqueira, 9.5 km N of Itatiai, N of Penedo, 660 m, branch of indet. angiosperm, on bark, 2.X.2011, M. Mann (H.B. 9661; sq.: KY463700, KT222443). – ibid., branch of indet. angiosperm, on bark & wood, 5.X.2011, M. Mann (H.B. 9662). – ibid., branch of indet. angiosperm, on bark, 24.X.2011, M. Mann (H.B. 9660 ø). – **Minas Gerais**, ~145 km WNW of Rio de Janeiro, 20 km N of Itatiai, Maringa, 1165 m, branch of indet. angiosperm, on bark, 10.X.2011, M. Mann (H.B. 9671, anam. substr.). – **São Paulo**, 50 km S of São Paulo, [24 km NE of Itanhaém,] 'near Conceição', Rio Branco, ~100 m, branch of indet. tree, on bark, VII.1901, R. von Wettstein (FH, **holotype** of *O. crenulatolobata*, H.B. 6288 ø). — **JAPAN**: **Hokkaido**, 4.8 km N of Tomakomai, Experimental Forest, 25 m, branch of *Fraxinus* (?*mandshurica*), on wood, 27.VII.1990, T. Hosoya (TRL 128, TNS-F-57476, H.B. 7984 ø). – ~980 km SSE of Tokyo, Ogasawara Island, unlocalized, ?20 m, branch of indet. angiosperm, on bark, VII.1996, I. Tanaka (TRL 1429, TNS-F-57118, H.B. 7983a ø, anam. substr.). – **Honshu**, **Kanagawa**, Miura peninsula, 23 km S of Yokohama, 2 km SW of Kinugasa, Ogusu-yama Mt., 210 m, branch of indet. angiosperm, on bark & wood, 16.IV.1994, T. Hosoya & Y. Otani (TRL 943, TNS-F-57480, H.B. 7985 ø). — **AUSTRALIA**: **Queensland**, Wet Tropics, 43 km N of Port Douglas, Cape Tribulation, 14 m, stem of *Bambusa*, 30.VIII.2006, G. Marson (H.B. 8497c). — **COMOROS**: **Mayotte**, 11.5 km SW of Mamoudzou, 2.2 km E of Chiconi, 98 m, branch of indet. angiosperm, on bark, 22.I.2013, M. Pélissier (J.P.P. 12023, doc. vid.).

Not included. **PUERTO RICO**: El Yunque, 6.3 km SSE of Rio Grande, El Verde, forest entrance trail before Oxcart Trail, 385 m, branch of indet. angiosperm, on bark, 24.I.1996, F.A. Harrington & M. Liftik (D.H.P. PR 134, FH 304916).

Hyalorbilia tortuosa Baral, E. Weber, Y.C. Su & M.L. Wu, **sp. nov**., MB 813472 — Pls 89–90, Map 10

Etymology: named after the helicoid (tortuous) ascospores.

Typification: France, Reims, on *Fuscoporia* (?)*ferruginosa* on branch of *Fraxinus excelsior*, 11.IX.2004, F. Valade (ex H.B. 7576, M-0276420, holotype).

Latin diagnosis: *Ab* Hyalorbilia fagi *ascosporis paulo longioribus et angustioribus*, *magis helicoideis*, *conidiis cylindrico-ellipsoideis*, *brevioribus et latioribus differt*, *ab* H. helicospora *ascosporis angustioribus*, *habitat in ramis et truncis uvidis differt.*

Description: — **TELEOMORPH**: **Apothecia** fresh (0.09–)0.15–0.42(–0.47) {7} or (0.2–)0.5–1.5(–2.2) {5} mm diam., 0.07–0.25 mm high (receptacle 0.06–0.07 → 0.03–0.055 mm), whitish to pale cream-chlorinaceous or light yellowish-ochraceous, translucent, round, ± lobate when large, scarcely to medium gelatinous, gregarious; disc slightly concave to flat, finally medium convex, margin thin, smooth to finely rough, not or only slightly raised; with indistinct obconical or often distinct cylindrical stipe 0.03–0.1 × 0.05–0.2 mm, superficial; turning reddish-ochraceous when senescent, dry cupulate when large, with inrolled margin. **Asci** *(15–)18–28(–31) {10} × 3–3.8 {1} or (3.7–)4–5(–6) {9} µm, †(13–)16–23(–25) × (3–)3.2–4.2(–4.5) µm {6}, 8-spored, spores *4-seriate, intertwined, often in two superimposed bundles but also in one bundle, (†) arrangement more irregular, pars sporifera *(9–)11–14(–15) µm long; **apex** (†) hemispherical; **base** with or without short, thick stalk, with croziers {8}. **Ascospores** *((4–))(5–)6–7.5(–8)((–8.5)) × (0.7–)0.8–1.2 µm {13}, †(4.5–)5–7(–7.5) × 0.7–0.9(–1.1) µm {7}, subcylindric to mostly narrowly fusoid, ± homopolar, both ends rounded to obtuse (rarely subacute), (slightly to) medium to rather strongly helicoid (looking S- or C-shaped depending on the viewing direction); **SBs** *0.2–0.3(–0.5) µm {5}, ± globose, 1–2(–4) near each end. **Paraphyses** apically uninflated to slightly, rarely medium clavate-capitate, terminal cells *12–24 × 2.5–5.5 µm {2}, †12–22 × 2–5 µm {3}, lower cells *5–12 × 2–3 µm {1}, †5–6 × 1.7–2.5 µm {2}. **Medullary excipulum** 5–20 µm thick, of textura prismatica-globulosa-intricata, not or only slightly, also strongly gelatinized, scarcely to sharply delimited. **Ectal excipulum** of thin-walled to slightly gelatinized, horizontally oriented t. prismatica(-globulosa) from lower flanks up to margin, 50–210 µm thick near base, of t. globulosa-angularis, cells at lower flanks */†(10–)20–45(–60)((–83)) × (5–)10–25(–30)((–40)) µm {5}, common walls 0.4–1(–1.3) µm thick {3}; 5–15 µm thick near margin, marginal cortical cells *8–17(–23) × (4–)5–12(–15) µm {4}, †5–11 × 2.5–4.5 {2}, × 6–7.5 {1} or × 7–10 µm {1}, wall */†0.2–0.3 µm thick. **Anchoring hyphae** sparse to medium abundant, radiating, †(1.5–)2.5–5(–6) µm wide, at insertion 4–11 µm, walls 0.2–0.6(–0.9) µm thick {8}. **VBs** in terminal cells of paraphyses globose to elongate, hyaline to very pale yellowish, slightly refractive. **Exudate** over paraphyses and excipulum 0.2–0.4(–1) µm thick, granular-cloddy to rough or even smooth, continuous. **— ANAMORPH**: brachyphoris-like (from ascocarp in Petri dish {1} and natural substrate {4}). **Conidiophores** ~150–200 µm long, frequently branched, side branches ~18–45 µm long, conidia formed terminally or on short lateral denticles (sympodial). **Conidia** cylindric-ellipsoidal, straight, from pure culture *22–35.3 × 6–7.3 µm {1}, 3-septate; from natural substrate *15.5–19 × (4–)4.7–5.2(–5.8) {1} or *18.5–21.5 × 5.8–6.5 µm {2}, †15.5–22(–25) × 4.3–5.3 µm {Japan}, 1–3(–4)-septate, with small peripheral LBs (KOH-resistant) and several large SCBs 1–1.7 µm diam. (KOH-sensitive).

Habitat: collected on or close to moist ground, corticated or decorticated, 2–20 cm thick branches and logs of *Alnus* sp. {1}, *Carpinus betulus* {1}, *Castanea sativa* {1}, *Erica arborea* {1}, *Fagus sylvatica* {2}, *Myrica faya* {2}, *Quercus* sp. {3/2}, *Salix* sp. {1}, indet. angiosperm {4}, stem of *Bambusa* sp. {1}, on 2–10 mm deep strongly decayed wood {10} or bark {5} (periderm), on upper or lower side, with or without algae; on pores of slightly to strongly rotten *Fuscoporia*

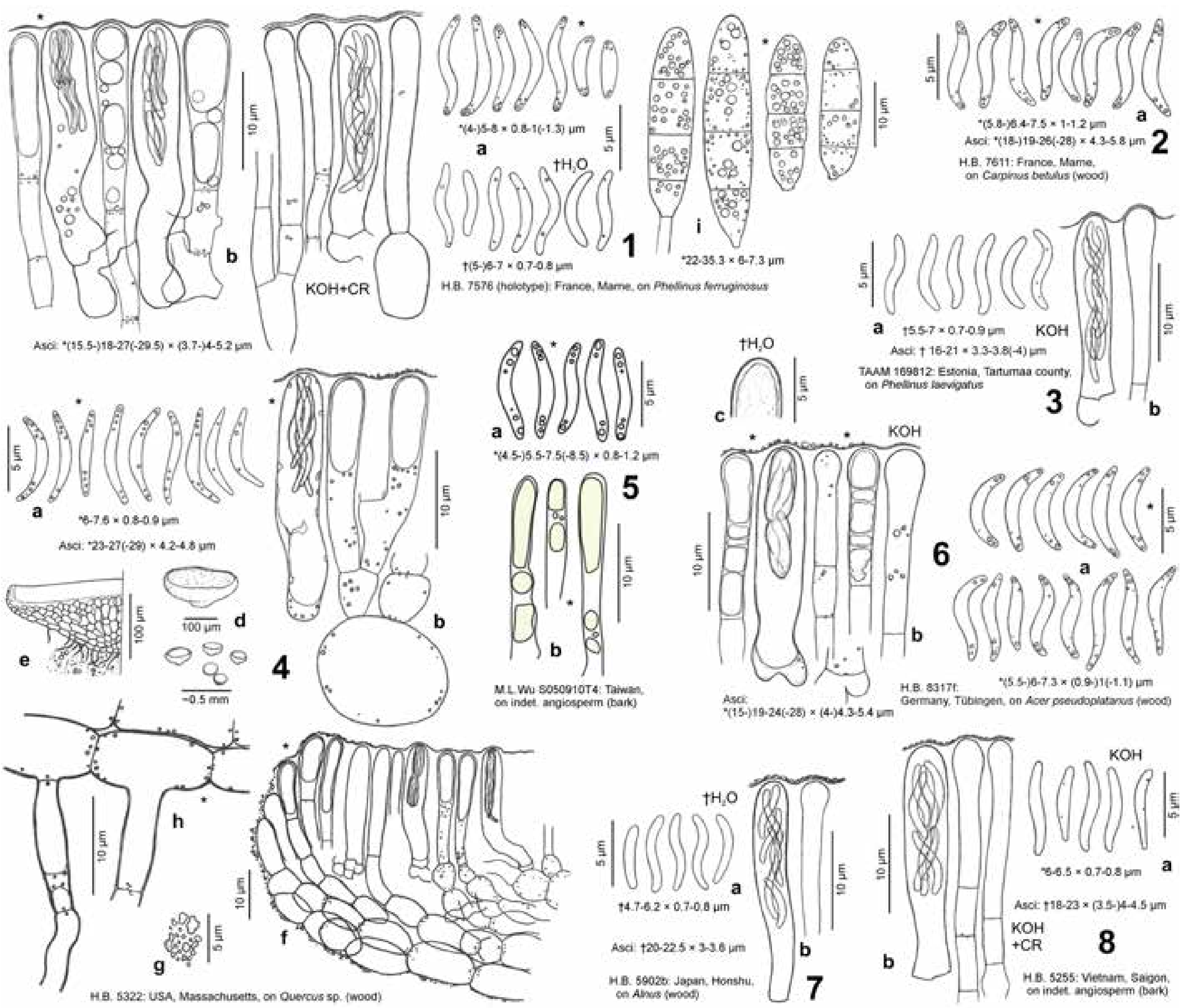


Plate 89. **1–7**: *Hyalorbilia tortuosa*. – **a**. ascospores; **b**. asci and paraphyses (bases with croziers); **c**. ascus apex; **d**. fresh apothecia; **e**. apothecium in median section; **f**. id., ectal excipulum and hymenium near margin; **g**. warted-cloddy exudate on ectal excipulum; **h**. anchoring hyphae; **i**. conidia. – **5**: del. Y.C. Su.

?*ferruginosa* {1}, *P. laevigatus* {1}, *Trametes gibbosa* {1}, rarely jumping on living *Hypnum cupressiforme* or *Lasiosphaeria hirsuta* {H.B. 8317f}. **Further associated**: *Brachysporium* sp. {1}, *Calycina citrina* {1}, *Cirrenalia lignicola* {1}, *Dematioscypha olivacea* {1}, *Hyalorbilia japonica* {1}, *Lasiosphaeria hirsuta* {1}, *Leptodontidium trabinellum* {1}, *Mollisia* ?*oblonga* {2}, *Orbilia leucostigma* {1}, *O. orientalis* {1}, *O. polybrocha* {1}, *O. xanthostigma* {1}, *Tubeufia* sp. {1}. **Desiccation tolerance**: dead in all parts when examined after 1 hour dry on slide. **Altitude**: 0–485 m a.s.l. (Europe), 665–895 m (Macaronesia), 40–2000 m (southeastern Asia). **Geology**: Ordovician & Devonian clay & sandstone, Lower & Upper Jurassic and Tertiary clay, sand- & limestone, Pleistocene loess & silt; volcanic sedimentary deposits, tephritic & phonolitic mafic flows, basalt. **Phenology**: I, IV, VI, VIII–XI (throughout the year?).

Taxonomic remarks. *Hyalorbilia tortuosa* is very similar to the tropical *H. citrina* in its helicoid ascospores, but differs in somewhat longer spores, a thin-walled ectal excipulum (especially at the always ± smooth margin), and in usually lacking any chlorinaceous colour typical of *H. citrina*. *H. helicospora* closely resembles *H. tortuosa* in the spores which are, however, slightly wider and contain more SBs. Contrary to *H. tortuosa* the apothecia of *H. helicospora* usually grow on xeric branches. The also similar *H. fagi* deviates from *H. tortuosa* in slightly shorter and wider, less curved spores, but a remarkable difference is found in the anamorph (see below).

Variation. Among the European collections, the two on *Phellinus* formed much larger apothecia (0.6–1.6 mm) than those on rotten wood and bark (0.15–0.4 mm). Apothecia from Macaronesia on wood were also small (0.2–0.5 mm), whereas southeastern Asian samples from wood and bark had quite a large size (0.5–1.5 mm). All of them were mature, and the microscopic features very similar. The medullary excipulum was usually slightly gelatinized, but in some of the eastern Asian collections it was strongly gelatinized. The excipular cells at the margin varied in size among the collections from Europe as well as eastern Asia, also apothecia colour varied between whitish and distinctly yellowish. Ascospores varied especially in width from *0.8–1 up to *1.1–1.2 µm. The collection from cold-temperate North America (Pl. 89: 4) deviates from European specimens in apparently 2–4 rather small instead of 1–2 SBs near each spore end, though the other characters fit well (apothecial size was here 0.2–0.35 mm). In

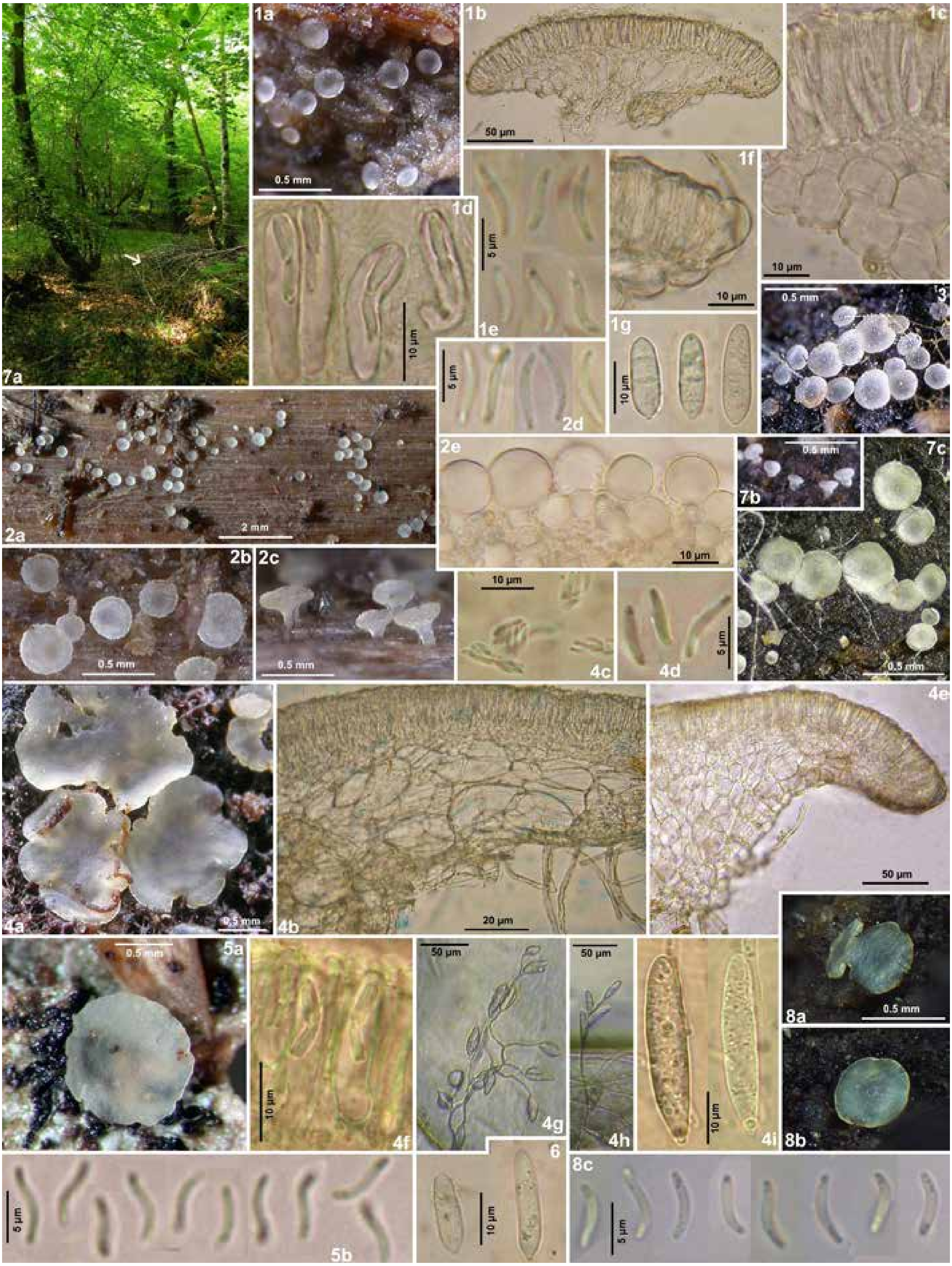


Plate 90. **1–8**: *Hyalorbilia tortuosa*. – **7a**. mixed mesosubmediterranean (mesotemperate?) *Fagus* forest; **1a**, **2a–c**, **3**, **5a**, **7b–c**, **8a–b**. fresh apothecia; **4a**. rehydrated apothecia; **1b**, **4e**. apothecia in median section; **1c**, **g**. marginal part of apothecium in median section; **2e**. margin in top view; **4b**. apothecium at lower flanks (median section); **1d**, **4f**. asci and paraphyses; **1e**, **2d**, **4c–d**, **5b**, **8c**. ascospores; **4g–h**. conidiophores; **1g**, **6**. conidia from substrate; **4i**. conidia from culture. – Living state, except for **4i** right & **6** (in KOH, **4i** right: same conidium as left, SCBs disappeared). – **5a–b**: phot. Y.C. Su; **7a**: phot. N. Matočec, **7c**: phot. J.P. Priou; **8a–c**: phot. L. Quijada. — **1a–g**. H.B. 8317f: Germany, Tübingen, on *Fagus*; **2a–e**. H.B. 8939b: France, Deux-Sèvres, on *Acer*; **3**. H.B. 7611a: France, Marne, on *Carpinus*; **4a–i**. H.B. 7576 (holotype): France, Marne, on *Phellinus*; **5a–b**. TMUE S050910T4: Taiwan, on indet. angiosperm; **6**. H.B. 5902b: Japan, Honshu, on *Alnus*; **7a–c**. H.B. 9485: France, Deux-Sèvres, on *Fagus*; **8a–c**. TFC Mic. 23527: Tenerife, on *Myrica faya*.

subtropical specimens studied in the living state, the spores contained 2–3 not or slightly larger SBs near each end (Pls 89: 5; 90: 5b, 8c).

A sample from Germany on *Populus* wood (IVV: H.B. 10202) is not included because of rather short and only sometimes helicoid spores of *4.7–6.2 × (0.8–)0.9 µm and rather short asci of *16–23 × 4–5 µm. *H. oreadum* and *H. japonica* differ from it in never helicoid spores, *H. oreadum* also in much wider spores and narrower marginal cortical cells.

Anamorph. The conidia are cylindric-ellipsoid, with obtuse ends and (1–)3(–4) septa, whereas those of the similar *H. citrina*, *H. fagi*, and *H. helicospora* are distinctly longer and narrower, fusoid to fusiform, with tapered ends and 3–5 or more septa. The observed conidiophores of *H. tortuosa* grew out of the ascocarps placed at the lid of a Petri dish. Conidia from natural substrate (wood and *Trametes*, Pl. 90: 1g, 6) showed a similar shape and number of septa as those from culture (holotype on *Phellinus*, Pls 89: 1i; 90: 4i), but were distinctly smaller. However, a single conidium found in the holotype near apothecia had the large size seen in the culture. No anamorph was so far observed in specimens from subtropical to tropical evergreen forests in southeastern Asia and from the laurel forest in Macaronesia.

Dactylella zhongdianensis resembles the anamorph of *H. tortuosa* quite well with its 17.5–35 × 5–10 µm large, mainly 3-septate conidia borne on branched conidiophores. Yet, a molecular analysis placed this species in *Dactylella*, distant from *Brachyphoris* (Chen et al 2007a/b, see also under *Orbilia zhongdianensis*, p. 1472). *H. polypori* has a very similar anamorph which differs from that of *H. tortuosa* in larger, especially wider conidia.

Phylogeny. A sequence was gained from apothecia of a sample from the Netherlands (on *Quercus* bark, IVV: S.H. 868, apothecia small, spores *6.5–7.5 × 1.1–1.2 µm), comprising SSU (without S1506 intron), ITS, and LSU. The strain clustered in our combined analysis (Phyl. 6) weakly supported with *H. berberidis*. It shows a minimum ITS distance of 15% to *H. berberidis* (8.3% in LSU D1–D2) and ~20% to *H. helicospora* and *H. inflatula* (8–9% in LSU). Various environmental strains clustered in the ITS analysis unsupported and with high distance with *H. tortuosa* (H6–H12), the closest being that from Minnesota (H7, ITS distance 18.5%).

In the SSU V7–V9 *H. tortuosa* fully concurs with *H. berberidis*, while other available *Hyalorbilia* sequences differ in the V8–V9 region by 1–5 nt, the closest being *H. inflatula* (H.B. 9080 & 9915). *H. tortuosa* is unique within *Hyalorbilia* in the Orb5.8s3F primer region, but concurs here with some groups of *Orbilia* (Tab. 18). Also in the first 4 nt of ITS2 (ATTA) it is unique within *Hyalorbilia* but concurs with *Lilapila* and various *Orbilia* species (Tab. 20).

Ecology. *Hyalorbilia tortuosa* was found on rotten wood and bark of hygric branches of angiosperm trees but also on perennial polypores. Collection sites are scattered in atlantic to subcontinental, hemiboreal to mesotemperate or mesosubmediterranean humid, planar to colline central Europe, cold-temperate humid lowlands of eastern North America, cold-temperate humid continental highland of Japan (central island), and thermo- to lower mesomediterranean subhumid to humid laurel forests (*Lauro novocanariensis-Perseetum indicae*) of Macaronesia. The collection on *Castanea* was in a degraded woodland with *Erica arborea* in the lower laurel forest zone (Monte de la Esperanza). Collections from southeastern Asia are from subtropical to tropical humid (winter-dry) evergreen forests (China) and tropical rainforests in northern Thailand and southern Vietnam.

Specimens included. **NETHERLANDS**: **Utrecht**, 6 km SSE of Utrecht, 2 km N of Houten, Nieuw Wulven, 0 m, branch of *Quercus*, on bark, 28.VI.2016, E. Osieck, vid. S. Helleman (S.H. 868, doc. vid., sq.: KY419192). —**FRANCE**: **Champagne-Ardenne**, **Marne**, 8 km E of Reims, 1 km SW of Berru, Bois de Berru, 220 m, on *Fuscoporia* (?)*ferruginosa* on branch of *Fraxinus excelsior*, 11.IX.2004, F. Valade (ex H.B. 7576, M-0276420, **holotype**, anam. apoth., anam. substr.). – 19 km SSW of Reims, 5.5 km N of Epernay, Forêt de La Montagne de Reims, 250 m, on ?*Quercus*, 14.IX.1999, R. Collot (doc. vid.). – ibid., log of *Carpinus betulus*, on wood, 7.XI.2004, R. Collot (H.B. 7611a). – **Poitou-Charentes**, **Deux-Sèvres**, 17 km E of Melle, 0.8 km WSW of Le Breuillac, Bois de Fontadam, 150 m, log of *Salix*, on wood, 7.X.2008, B. Coué (H.B. 8939b). – 4.5 km NW of Chizé, 1.3 km SSE of Villiers-en-Bois, Forêt de Chizé, 77 m, branch of *Fagus sylvatica*, on wood, 27.IV.2011, N. Van Vooren (H.B. 9485). — **GERMANY**: **Baden-Württemberg**, Schönbuch, 8 km NE of Tübingen, 4 km N of Pfrondorf, Eisenbachhain, 485 m, log of *Fagus sylvatica*, on wood, 3.X.2006, H.O. Baral (H.B. 8317f, anam. substr.). — **POLAND**: **West Pomerania**, 20 km SE of Szczecin, ~2 km E of Dobropole Gryfiński, Osetno, ~80 m, on *Trametes gibbosa*, 3.VIII.2008, G. Domian, vid. P. Perz (P.P. 20080803-GD-Osetno-3, doc. vid., anam. substr.). — **ESTONIA**: **Tartumaa**, 33 km WNW of Tartu, Alam-Pedja, Tõllassaare, 40 m, on *Phellinus laevigatus*, 28.VIII.1997, K. Põldmaa (TAAM 169812, H.B. 5981 ø). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Tegueste, 5 km NNW of San Cristóbal de La Laguna, 1.5 km NE of Tegueste, La Hoya del Palomo, 665 m, branch of *Myrica faya*, on wood, 16.VI.2012, L. Quijada, C. Quijada & E.V. Rodríguez (TFC Mic. 23527, doc. vid.). – La Matanza de Ajentejo, 10.5 km ENE of Puerto de la Cruz, 2.4 km SSE of La Matanza de Acentejo, SW of La Vica, Los Canarios, 855 m, branch of *Castanea sativa*, on wood, 10.XI.2008, E. Beltrán-Tejera, J. Díaz Armas & J. Guttiérrez Peraza (TFC Mic. 20657, doc. vid.). – Santa Cruz de Tenerife, Anaga, 3.3 km ESE of Taganana, El Pijaral, 775 m, on wood of *Erica arborea*, 24.X.2012, L. Quijada, C. Quijada & E.V. Rodríguez (TFC Mic. 23691, doc. vid.). – 4.3 km E of Taganana, 2 km SW of Chamorga, Chinobre, 895 m, on wood of *Myrica faya*, 7.IV.2013, L. & C. Quijada (TFC Mic. 24019, doc. vid.). — **USA**: **Massachusetts**, Middlesex, 28.5 km NW of Boston, 4.3 km N of Concord, Estabrook Woods, 65 m, branch of ?*Quercus*, on wood, 15.VIII.1995, D.H. Pfister & S.H. Goldbarg (H.B. 5322). — **JAPAN**: **Honshu**, **Nagano**, Chiisagata-gun, 19 km SE of Nagano, 16.5 km NE of Ueda, 1 km SE of Sugadaira, Arboretum in Sugadaira Montane Research Center, 1325 m, branch of *Alnus*, on wood, 21.VIII.1997, T. Hosoya (H.B. 5902b, anam. substr.). — **CHINA**: **Yunnan**, **Kunming**, 8 km NE of Kunming, Jindian, ~2000 m, branch of indet. angiosperm, 13.VI.2006, J.W. Guo (J.W.G. jd-j-4, YMFT, doc. vid.). – **Taiwan**, **Kaohsiung**, 54 km NE of Kaohsiung, 4.5 km SE of Liouguei, Shanping Natural Education Center, 520 m, branch of indet. angiosperm, on bark, 10.IX.2005, Y.C. Su (TMUE S050910T4, TNM, doc. vid.). – ?ibid. (TMUE S051030T6, S051010T4, S050924T2, S060124T4). — **THAILAND**: **Northern Thailand**, **Chiang Mai**, 125 km WNW of Chiang Mai, 10.5 km SW of Mae Hong San, Huay Pu Keng, 185 m, on stem of *Bambusa*, 13.XI.2012, J.P. Priou (J.P.P. 12170 ø, doc. vid.). — **VIETNAM**: **Phú Quốc island**, 14.5 km NNE of Dương Đông, 5.5 km ESE of Rạch Vẹm, 40 m, branch of indet. angiosperm, on bark, I.1995, N. Petit (H.B. 5255).

Not included. **GERMANY**: **Niedersachsen**, 5.5 km S of Mönchengladbach, E of Wickrath, 64 m, branch of *Populus*, on wood, 12.VII.2019, H. Bender (H.B. 10202).

Map 10. Known distribution of *H. tortuosa* in Europe and Macaronesia (yellow = not included collection).

Hyalorbilia fagi E. Weber, Baral & J.W. Guo, **sp. nov.**, MB 813473 — Pls 91–93, Map 11

?= *Calloria chrysocoma* var. *microspora* Sacc., Michelia 2 (8): 571 (1882)
  ≡ *Orbilia chrysocoma* var. *microspora* (Sacc.) Sacc., Syll. Fung. 8: 624 (1889)
?= *Hyalinia inflatula* var. *lonicerae* Rehm in Straßer [as '*inflata*'], Verh. K. K. Zool.-Bot. Ges. Wien 60: 472 (1910)
  ≡ *Orbilia inflatula* var. *lonicerae* (Rehm in Straßer) Sacc. & Trotter, Syll. Fung. 22: 723 (1913)

Etymology: *fagi*, *lonicerae*: named after the substrate of the type; *microspora*: small spored.

Typification: Germany, Tübingen, branch of *Fagus sylvatica*, 23.VII.2005, E. Weber & H.O. Baral (ex H.B. 7847a, M-0276407, holotype of ***Hyalorbilia fagi***). — USA, New Jersey, Newfield, on wood and bark, undated, J.B. Ellis (Ellis n. 64 et 3547, type of ***Calloria chrysocoma* var. *microspora***, not located). — Austria, Ybbsitz, on decorticated branch of *Lonicera*, undated, P. Lambert (type of ***Hyalinia inflatula* var. *lonicerae***, not located).

Latin diagnosis: Hyalorbiliae inflatulae *similis sed ascosporae distincte curvatae, plerumque helicoideae.*

Description: — **TELEOMORPH**: **Apothecia** fresh (0.15–)0.3–0.8(–1) {5} or (0.5–)1–2.5(–4) {16} mm diam., 0.12–0.25(–0.32) mm high [receptacle 0.07–0.15 → 0.03–0.06(–0.1) mm], whitish or pale to light cream-chlorinaceous-yellowish, ± translucent, round, slightly to strongly lobate when large, somewhat gelatinous, scattered to sub- or densely gregarious; disc young cupulate, remaining slightly to medium concave or often becoming flat, margin thin, smooth; with ± distinct obconical stipe 0.05–0.17 × 0.1–0.5 mm, superficial; dry light to bright yellow-chlorinaceous-ochraceous, sometimes turning sulphur-yellow or red-brown. **Asci** *18–29(–36) × (3.8–)4–4.8(–5) µm {8}, †(13–)15–22(–26) × (2.8–)3.2–4(–4.7) µm {15}, 8-spored, spores mostly *4-seriate in two superimposed bundles, pars sporifera *10–13 µm long; **apex** (†) hemispherical; **base** unstalked, with croziers {11}. **Ascospores** *((3.5–))(4.3–)4.7–6.5(–7)((–8)) × (0.8–)1–1.2((–1.5)) µm {12}, †((4–))4.5–6.5(–7.5) × (0.7–)0.8–1.1(–1.2) µm {12}, (sub)cylindric to narrowly fusoid, sometimes fusoid-clavate, slightly to medium helicoid, sometimes only slightly inequilateral, rarely sickle-shaped; **SBs** *0.2–0.3(–0.4) µm {4}, globose, 1(–2) at each end. **Paraphyses** apically uninflated, rarely slightly capitate, terminal cells *14.5–24 × (2–)2.5–3.5(–4.3) µm {5}, lower cells *(3–)4–7(–9) × 2–3.5(–4) µm {5}. **Medullary excipulum** 15–30 µm thick, of medium dense to dense textura globulosa-angularis-prismatica, not or usually slightly to medium, sometimes strongly gelatinized, ± sharply delimited. **Ectal excipulum** of thin-walled to slightly gelatinized [common walls †1–1.5(–2) µm], horizontally oriented t. prismatica or t. globulosa-angularis from base to margin, 30–60 or up to 150–250 µm thick near base, cells */†(15–)25–60(–80) × (8–)15–30(–40) µm {4}; 25–40 µm thick at flanks, 10–20 µm near margin, marginal cortical cells */†(5–)7–15(–23) × (2.5–)4–8 µm {11}, in surface view (2.5–)4–10(–12) {11} or 10–18 µm wide {2}, ± thin-walled (†0.2–0.5 µm). **Anchoring hyphae** ± abundant, long radiating, */†3–6 µm wide (up to 6–8.5 µm at insertion), walls 0.3–1(–2) µm thick {13}. **SCBs** rarely present in ectal excipular cells from lower flanks up to margin (Pl. 76: 1d), strongly refractive, ring-shaped, ~1.5–2 µm diam.; **VBs** in paraphyses subhyaline to chlorinaceous, low- to rather high-refractive, globose to elongate. **Exudate** over paraphyses and excipulum 0.2–0.4(–1) µm thick, finely granular-cloddy, also nearly smooth. — **ANAMORPH**: brachyphoris-like (from ascocarp in Petri dish {2} and from natural substrate {8}). **Conidiophores** *13–50 × 3.3–3.7 µm when unbranched, 1–2-septate in lower part, up to ~110 µm long when repeatedly branched, *(1–)1.3–1.7 µm wide at the tip, conidia formed terminally. **Conidia** fusoid to fusiform, *((24–))(30–)35–55(–67) × (4–)4.5–5.5(–6) µm {6}, †(32–)37–54(–58) × 4–5.3(–5.7) µm {4}, (1–)3–6(–8)((–10))-septate {9}, with many small peripheral LBs, in centre often with groups of 0.4–1.4(–1.7) µm large, globose, strongly refractive **SCBs** {7} (living state); also a few small 1-septate conidia seen (*13–17 × 3–3.5 µm {2}).

Habitat: collected on the moist ground, mostly decorticated, 1.5–15 cm thick branches and logs of *Aesculus hippocastanum* {1}, *Alnus incana* {1}, *Betula* sp. {1}, *B. pubescens* {1}, *Carpinus* sp. {1}, *Fagus sylvatica* {9}, *Fraxinus* sp. {1}, *Picea abies* {1/1}, *Populus* sp. {1}, *Quercus cerris* {1}, *Robinia pseudoacacia* {2}, *Rosa canina* {1}, *Sorbus domestica* {1}, ?*Ulmus* sp. {1}, indet. resupinate basidiomycete {2}, *Ischnoderma benzoinum* {1}, *Jackrogersella* ?*multiformis* {1}, old pyrenomycete {2}, on 0.5 mm or much deeper medium to usually strongly decayed wood {17} or bark (periderm and bast) {8}, on underside and laterally. **Associated**: *Calycina citrina* {1}, *Ceriporia* sp. {2}, *Chaetosphaeria* sp. {1}, *Hyaloscypha leucostigma* {1}, *Lasiosphaeria hirsuta* {2}, *L. ovina* {1}, *Mollisia rosae* {1}, *Nectria* sp. {1}, *Nemania chestersii* {1}, *Orbilia dryadum* {1}, *O. eucalypti* {1}, *O. nemaspora* {1}, *O. oxyspora* {1}, *Psilocistella quercina* {1}, *Rhizodiscina lignyota* {1}, *Scutellinia* sp. {1}, *Tubeufia cerea* {2}, *Trichoderma* ?*sinuosum* {1}, *Trichosphaeria notabilis* {1}. **Desiccation tolerance**: only excipular cells viable after 12 days. **Altitude**: 50–1350 m a.s.l. (Europe), 5–900 m (Caucasus). **Geology**: Keuper (marl and sandstone), Jurassic-Cretaceous sandstone and dolomite, Tertiary molasse, Miocene lime- and marlstone, Pleistocene calcareous till. **Phenology**: (II–)VI–X.

Phenology of *H. fagi*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
0	1	0	1	0	2	9	6	1	4	0	0

Taxonomic remarks. *Hyalorbilia fagi* resembles the variant of *H. inflatula* with flatter apothecia in macroscopical appearance, but is rather easily recognized in most cases, at least within Europe, by its distinctly curved, somewhat helicoid ascospores. The similar *H. tortuosa* differs in slightly longer and narrower, more distinctly helicoid spores and particularly in ellipsoid-oblong conidia, often also in much smaller apothecia. *H. helicospora* differs in longer spores containing 2–4 SBs in each half, and smaller, desiccation-tolerant apothecia. The tropical *H. citrina* differs in thick-walled excipular cells forming often teeth or lobes at the margin, and in narrower asci and spores, and *H. arcuata* in sickle-shaped, only exceptionally slightly helicoid spores.

Variation. Considerable variation among the collections of *H. fagi* was noted in width of the marginal cortical cells. Most included collections had a medium width of about 4–8 µm, but in two samples the cells were extraordinarily inflated (10–18 µm wide in surface view, Pls 92: 6b; 93: 3d, f–g). As an exception, one of these samples (Pl. 93: 3) showed truncate teeth-like protrusions at the margin of some apothecia, formed by rather large cells similar as in *H. citrina* but thin-walled. The medullary excipulum was usually not or only slightly to medium gelatinized in the collections from central Europe, but strongly so in that from Italy (Pl. 92: 7) and in one from Caucasus (TAAM 109518).

A collection on wood of *Fagus* from Tübingen (Pl. 92: 8) deviates by more concave apothecia with an incurved margin composed of a textura porrecta of very narrow cells (†2.5–4 µm, surface view 2.5–5 µm), in combination with rather long asci (*25–36 × 4.2–4.8 µm) and spores (*6–8 × 1–1.1 µm). It resembles the cupulate variant of *H. inflatula* with narrow marginal cells, from which it deviates in its distinctly helicoid spores. It is included in the description because a sequence of it falls to a typical collection of *H. fagi* from the same area and substrate (Pl. 92: 3). Cupulate apothecia occurred also in specimens from Bretagne and Canada, but the marginal cells seem to be broader here. The spores were sometimes only slightly curved in the latter two samples. Nevertheless, we have also included the Bretagne sample in the scope of *H. fagi*.

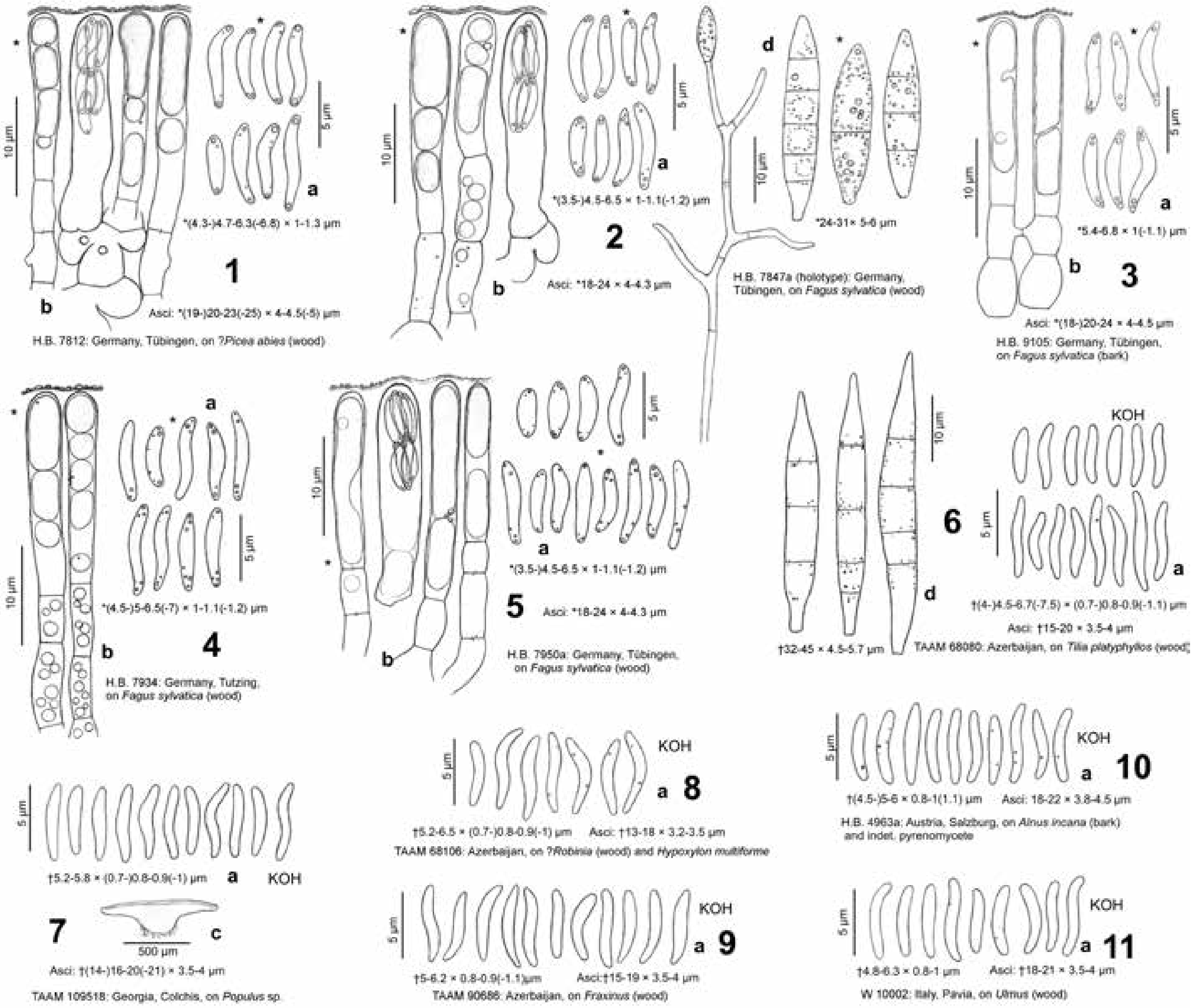


Plate 91. **1–11**: *Hyalorbilia fagi*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. apothecium in median section; **2d**. conidiophore and conidia from culture, **6d**. conidia from substrate.

Not included collections. The four North American samples closely concur with European *H. fagi*, based on the available morphology. However, because of strongly deviating molecular data in two of them (see below) we have excluded also those from eastern Asia and restricted the above description on samples from Europe. Yet, also a Slovakian sample (IVV: A.P. 19/27) is genetically very distant, although its ± strongly helicoid spores of *5.8–7(–7.7) × 1–1.1 µm resemble those of *H. fagi* or *H. tortuosa*, while the associated conidia exclude the latter and resemble with its 6–10 septa more those of *H. inflatula*.

In China, J.W. Guo (pers. comm.) often found the ectal excipulum at the flanks to be composed of rather globose cells. He believed this to be a character separating *H. fagi* from *H. tortuosa* (for photos of his sections showing globose excipular cells see IVV: th4b-28 & zcw-j-3). We have actually also sometimes seen European *H. fagi* with quite isodiametric excipular cells at the flanks (Pl. 92: 1c, 2b), but our specimens of *H. tortuosa* had likewise rather broad, sometimes almost isodiametric cells. One of these Chinese collections of *H.* cf. *fagi* (zcw-j-3, Pl. 93: 4) seems to concur well with European *H. fagi* and was even said to grow on a branch of *Fagus*. Two others for which J.W. Guo provided us photos deviate in wider spores with a falcate instead of helicoid shape (*5–6.5 × 1.1–1.5 µm, Pl. 93: 5–6). Although a few falcate spores were seen in European samples (see Pl. 91), these refer at least in part to helicoid spores seen in profile view. Predominantly falcate but narrower spores were noted in some other south Chinese samples which are, therefore, tentatively assigned to *H. arcuata* (Pl. 101: 7–8).

Type studies. Type material of ***O. chrysocoma* var. *microspora*** (USA, New Jersey, Newfield, on wood and bark, J.B. Ellis n. 64 & 3547) could not be located in PAD, PAL, W (no response from TO). The yellow, membranaceous apothecia and the nearly unstalked asci (20–26 × 5 µm) with cylindrical, curved spores of 5–6 × 0.5 µm point to a *Hyalorbilia*. A specimen in W under that name ([Italy, Pavia,] in horto botanico ticinensi, on ring-pored wood, F. Cavara, possibly authentic) was studied and found to be conspecific with *H. fagi* (Pls 91: 11; 92: 7). Rehm (1891: 456) referred a specimen with much shorter spores (3–3.5 × 0.5 µm) to this variety (Ostpreußen, Cladow, log of *Fagus*, H. Sydow). '*O. chrysocoma* var. *macrospora*' in McNabb (1973: 501) is a misspelling for *microspora*.

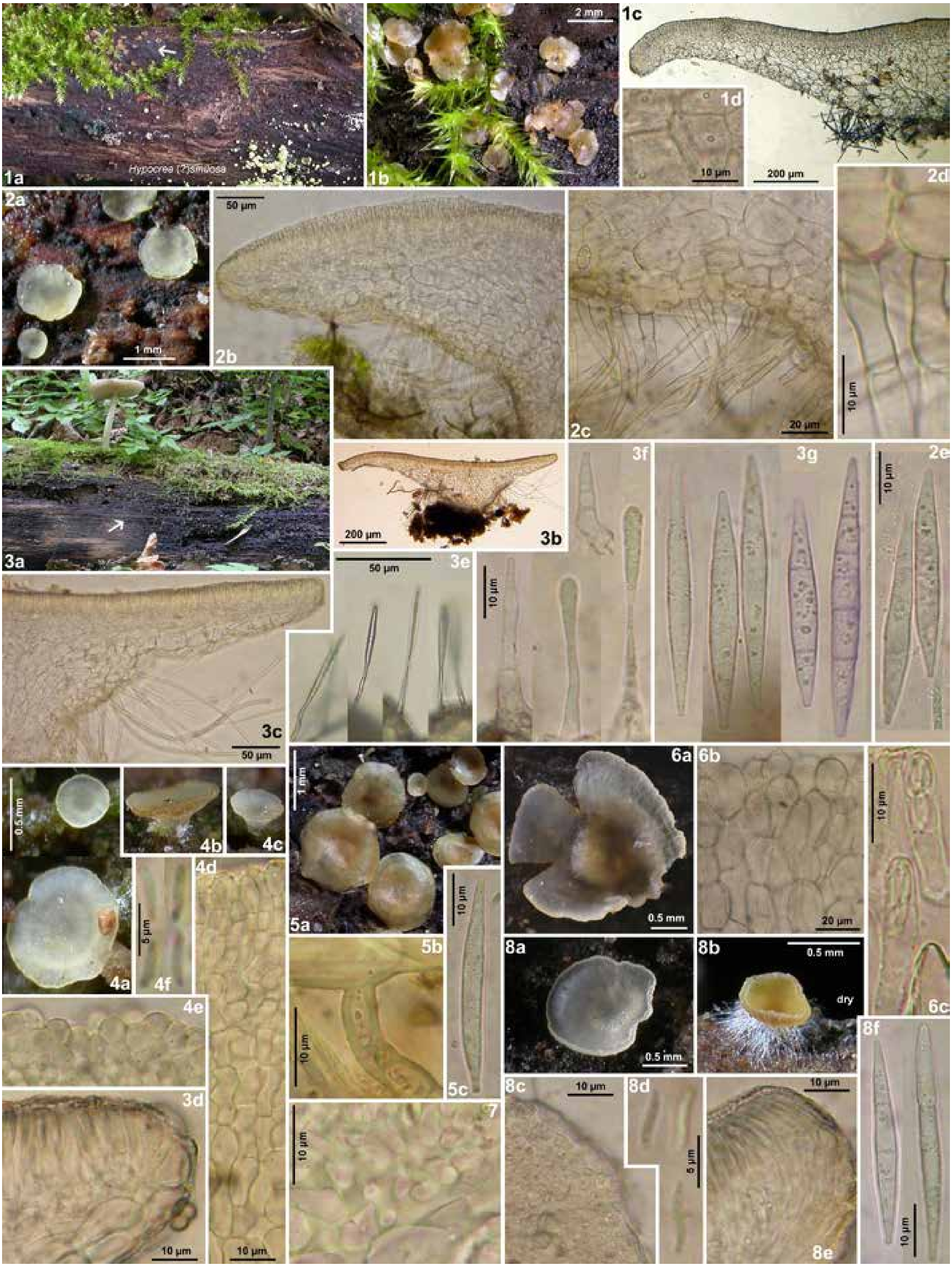


Plate 92. **1–8**: *Hyalorbilia fagi*. – **1a**, **3a**. decorticated branch/log of *Fagus sylvatica*; **1a–b**, **2a**, **4a–c**, **6a**, **8a**. fresh apothecia; **5a**. rehydrated apothecia; **8b**. dry apothecium; **1c**, **2b**, **3b–c**. apothecia in median section; **3d**, **8e**. id., marginal ectal excipulum; **4d–e**, **6b**, **8c**. id., in external or top view; **2c**. median section of basal ectal excipulum, with anchoring hyphae; **7**. gelatinized medullary excipulum; **1d**. ring-shaped SCBs in excipular cells; **2d**, **5b**. anchoring hyphae; **6c**. asci; **4f**, **8d**. ascospores; **3e–f**. conidiophores with mature/young conidia; **2e**, **3g**, **5c**, **8f**. mature conidia. – Living state, except for **8d** (in H_2O), **5b–c**, **7**, **8c** (in KOH). — **1a–d**. H.B. 7847a (holotype): Germany, Tübingen, on *Fagus*; **2a–e**. H.B. 7934: Germany, Tutzing, on *Fagus*; **3a–g**. H.B. 9105a: Germany, Tübingen, on *Fagus*; **4a–f**. H.B. 7812: ibid., on ?*Picea*; **5a–c**. H.B. 4963a: Austria, Salzburg, on *Alnus*; **6a–c**. H.B. 7950a: Germany, Tübingen, on *Fagus*; **7**. W 10002: Italy, Pavia, on *Ulmus*; **8a–f**. H.B. 8224b (topotype): Germany, Tübingen, on *Fagus*.

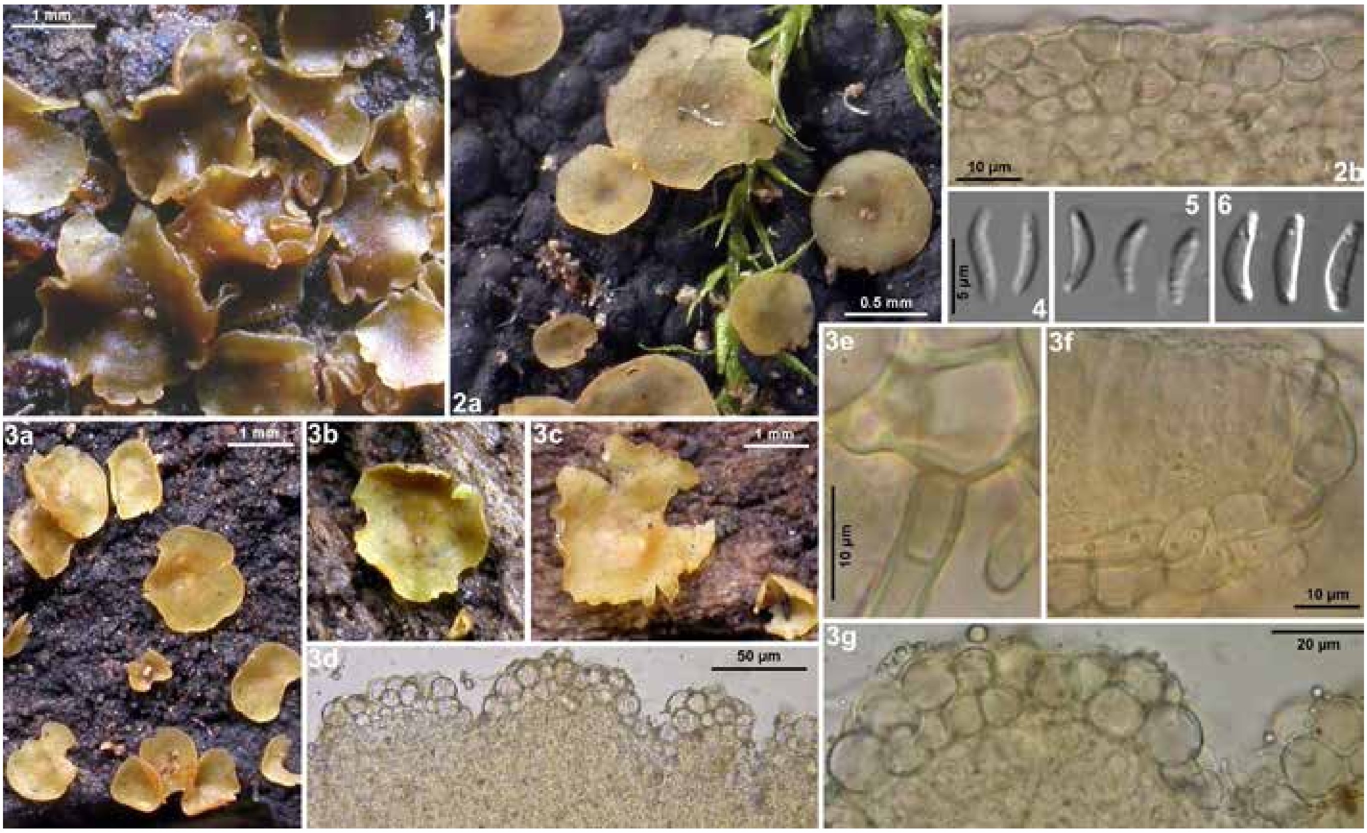


Plate 93. **1–4**: *Hyalorbilia fagi*; **4–6**: *H.* cf. *fagi*. – **1**, **2a**, **3a–c**. rehydrated apothecia; **3f**. marginal part of apothecium (median section); **2b**, **3d**, **g**. margin in top view; **3e**. anchoring hypha; **4–6**. ascospores. – Dead state (in KOH, **4** in H_2O) except for **5–6**; **3b** illuminated with Luxeon-LED. – **4–6**: phot. J.W. Guo (DIC). — **1**. TAAM 68080: Azerbaijan, on *Tilia*; **2a–b**. TAAM 68106: ibid., on *Hypoxylon*; **3a–g**. TAAM 90686: ibid., on *Fraxinus*; **4**. J.W.G. zcw-j-3: China, Sichuan, on *Fagus*; **5**. J.W.G. jzh-2: ibid., on indet. angiosperm; **6**. J.W.G. th4b–28: China, Yunnan, on indet. angiosperm.

Type material could also not be located for ***Hyalinia inflatula* var. *lonicerae*** in PAD and S (on decorticated branch of *Lonicera*, Ybbsitz, Niederösterreich, leg. P. Lambert). The original description obviously refers to a *Hyalorbilia*, perhaps *H. fagi*: apothecia yellowish-hyaline, with thin acute margin, ectal excipulum prosoplectenchymatous, subgelatinous, asci 20–25 × 4 µm, with rounded apex, spores 5–7 × 1–1.2 µm, subcurvate, 1-guttulate at each end, paraphyses scarcely inflated.

Anamorph. In H.B. 7847a and H.B. 9105 we obtained unbranched or branched conidiophores forming conidia, growing out of the ascocarps that hung at the lid of a Petri dish, and in a total of seven further collections fusoid conidia occurred on the natural substrate. The anamorph closely resembles that observed in *H. inflatula*, but the conidia tend to be shorter and to have fewer septa, although the values strongly overlap. This appears to exclude conspecificity with '*Dactylella*' *passalopaga*. In *H. lignatilis* the conidia are a bit shorter and narrower than in *H. fagi*. However, conidial size varied rather strongly among the collections of *H. fagi*, being shortest in H.B. 7847a (holotype, Pl. 91: 2d), longest in H.B. 9105a (Pl. 92: 3g), and rather narrow in H.B. 8224b (topotype, Pl. 92: 8f) (all from Tübingen).

Phylogeny. Three sequences gained from apothecia of central European *H. fagi* were available: H.B. 9105a (SSU, ITS, LSU), H.B. 8224b (ITS), and H.B. 9724 (ITS+LSU). In the ITS region they differ by only 1 nt in H.B. 8224b (but the ITS of H.B. 9105a lacks over 200 nt, especially in ITS1), while a collection from Boston (North America, H.B. 9995) differs by 7–7.5% from them, suggesting a different species. A recent sample under the name *H. lunata* from Florida in GenBank (MH211887, ITS) coincides with *H. fagi* from Boston with a 0.5% distance (not shown in phylograms), but both differ from *H. lunata* H.B. 9113 from China by 5.2–5.5%. H.B. 9724 and the Boston sample include the S1506 intron, in which the distance is even 14.3% in the overlapping ~280 of 339 nt (the other two sequences do not cover the intron region). In the LSU the two central European samples differ in the overlapping 403 nt of the D1 domain by 1 nt, but also *H. citrina* (H.B. 9661) and *H.* '*polypori*' (B.L. 288) differ from them by only 1–2 nt in that region. In the entire LSU (D1–D2) the distance between these three taxa is around 1.5% (4 nt, the formation of two subclades for the two *H. fagi* samples in Phyl. S5 is due to incomplete D2 in H.B. 9105a).

When analysing ITS (Phyl. 5) or ITS+LSU (Phyl. 6), *H. fagi* clustered with *H. citrina*, *H. japonica* and *H. lunata* (B.L. 6416) in a strongly supported clade, which is referred here to as *citrina-fagi* clade and forms a subclade within the *inflatula-polypori* clade. The distances within the *citrina-fagi* clade range at 4.5–10.5%, whereas the distance to *H. inflatula* is much higher. The not included *H.* aff. *fagi* from Slovakia (S1506 intron, ITS) shows a high ITS distance of 22% to *H. fagi*. When analysing ITS or the intron (both not shown) it clustered with a 16–20% ITS distance more near *H. inflatula* s.l.

Ecology. *Hyalorbilia fagi* was found on rotten wood (rarely bark) of hygric branches and logs of angio-, rarely gymnosperm trees, often on *Fagus*, exceptionally on perennial basidiomycetes or pyrenomycetes. The species was mainly found from June to October, but sometimes in spring. European collections derive from atlantic to subcontinental, warm- to cold-temperate and hemiboreal humid regions, but also from mesotemperate to suprasubmediterranean humid Caucasus at border to Asia. The not included eastern Asian samples were on branches of mostly unidentified trees in orotemperate to subtropical humid (winter-dry) broad-leaved, mainly evergreen forests of southern China (J.W. Guo pers. comm., once on a deciduous Asian species of *Fagus*), that from central Asia (Irkutsk) in a continental, boreal humid forest, and those from northeastern North America in continental, hemiboreal to cold-temperate humid forests.

Specimens included. **POLAND**: **Greater Poland**, 9 km WSW of Śrem, 2 km ENE of Rąbiń, Uroszysko Rąbiń, 100 m, stump of *Betula*, on wood, 25.VIII.2007, A. Kujawa & P. Perz (P.P. 20070825-2, H.B. 8674). — **GERMANY**: **Baden-Württemberg**, 3.5 km NNE of Tübingen, 1.6 km SE of Bebenhausen, Kirnbach, 370 m, log of ?*Picea abies*, on wood, 12.VI.2005, H.O. Baral & E. Weber (H.B. 7812). – 6 km ENE of Tübingen, 1 km ESE of Pfrondorf, Hinterpfand, 420 m, branch of *Fagus sylvatica*, on wood, 23.VII.2005, E. Weber & H.O. Baral (ex H.B. 7847a, M-0276407, **holotype**, anam. apoth.). – ibid., log of *F. sylvatica*, on wood, 16.VII.2006, E. Weber (H.B. 8224b, anam. substr.; sq.: KT222378). – 1.4 km SE of Pfrondorf, Poppelesloch, 335 m, branch of *F. sylvatica*, on wood, 30.X.2005, E. Weber (H.B. 7950a, anam. substr.). – ESE of Pfrondorf, Tiefenbach, Schützenhaus, 385 m, log of *F. sylvatica*, on bark, 26.VII.2009, E. Weber, H.O. Baral & B. Liu (H.B. 9105a; sq.: KT222453, KT222449, MK503675). – ibid., on wood, 23.VIII.2009 (H.B. 9105b). – **Bayern**, **Oberbayern**, Fünfseenland, 8 km NW of Tutzing, 3.5 km S of Andechs, ENE of Hartschimmel, Goaslweide, 720 m, branch of *F. sylvatica*, on wood, 15.X.2005, P. Welt, F. Dämmrich & N. Heine (H.B. 7934, anam. substr.). — **AUSTRIA**: **Niederösterreich**, Wienerwald, 22 km SW of Wien, 2.5 km W of Gaaden, Sandriegel, 400 m, branch of *F. sylvatica*, on bark and pyrenomycete, 2.IX.2012, M. Mann (M.M. 160220-5, H.B. 9724, anam. substr.; sq.: MK493133). – 2 km NE of Gaaden, 305 m, branch of *F. sylvatica*, on bark, 20.II.2016, M. Mann (doc. vid.). – 1.6 km SSW of Gaaden, Zweieichen, 395 m, branch of *Quercus cerris*, on wood, 12.VII.2016, M. Mann (M.M. 160712-4, doc. vid.). – **Salzburg**, 7.5 km WSW of Salzburg, 1 km SW of Wals, Saalach, 437 m, branch of *Alnus incana*, on bark & pyrenomycete, 13.X.1993, W. Dämon (H.B. 4963a, anam. substr.). – **Steiermark**, 13 km SE of Leibnitz, S of Unterschwarza, 240 m, bark of indet. angiosperm, on old resupinate basidiomycete, 10.IV.2014, A. Draxler, H. Kahr, W. Maurer, vid. G. Friebes (W.M., doc. vid.). – 3 km NNW of Graz, Reinerkogel, 470 m, branch of *Aesculus hippocastanum*, on wood, 22.VII.2014, I. Wendelin, vid. G. Friebes (G.F. 20140053, anam. substr., doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 17 km S of Novi Sad, 1 km SE of Irig, 180 m, branch of *Rosa canina*, on bark, 13. & 26.VI.2014, D. Savić (FG-153, H.B. 9896 ø). — **FRANCE**: **Bretagne**, **Morbihan**, 2.7 km SSW of La Gacilly, 1.7 km NNW of Glénac, N of Launay, 52 m, branch of *Sorbus domestica*, on wood, 17.X.2011, J.P. Priou (J.P.P. 11142 ø, doc. vid.). — **SPAIN**: **País Vasco**, **Vizcaya**, 11 km SE of Bilbao, 3.5 km SSW of Usansolo, SW of Lekubaso Embalse, 130 m, branch of *Robinia pseudoacacia*, on bark, 13. & 20.VII.2017, R. Ibarretxe (R.I. 170720, doc. vid.). – **Navarra**, 31 km N of Pamplona, 1 km E of Almándoz, 350 m, branch of *Fagus sylvatica*, on wood, 16.VII.2014, F.J. Balda (F.J.B. 16714, doc. vid.). — **ITALY**: **Lombardia**, **Pavia**, Pavia, Hortus Botanicus Ticinensis, 78 m, branch of (?)*Ulmus*, on wood, undated, F. Cavara (W 10002, as *Orbilia chrysocoma* var. *microspora*, H.B. 7731 ø). — **RUSSIA (West)**: **Pskov**, **Sebezh**, 10 km SW of Sebezh, Lake Midino, 136 m, on bark of *Betula pubescens*, 21.VII.2002, E.S. Popov (LE 222223, 402-7-Seb, as *O. inflatula*, doc. vid.). — **UKRAINE**: **Ivano-Frankivsk**, Nadvirna, 55 km W of Kolomyya, 5 km SE of Maksymets, Gorgany forestry, 1020 m, log of *Picea abies*, on *Ischnoderma benzoinum*, 19.VII.2012, A.Y. Akulov (ex CWU Myc 4904, H.B. 9714). — **GEORGIA**: **Samegrelo-Zemo Svaneti**, Caucasus region, Kolkheti (as Colchis), Poti, ?5 m, branch of *Populus*, on wood, 7.VIII.1977, V. Puusepp (TAAM 109518, H.B. 8010 ø). — **AZERBAIJAN**: **Shaki-Zaqatala**, Caucasus Mts., ?N of Zaqatala, 'Kordon', ?800 m, log of *Fraxinus*, on wood, 12.VIII.1974, E. Parmasto (TAAM 90686, as *Corylus avellana*, H.B. 8021 ø). – ibid., 900 m, log of *Robinia pseudoacacia*, on wood and *Jackrogersella* (?)*multiformis*, 8.VIII.1974, B. Kullman (TAAM 68106, as *Orbilia epipora*, H.B. 8020 ø). – ibid., 700 m, log of ?*Carpinus*, on wood and resupinate basidiomycete, 8.VIII.1974, B. Kullman (TAAM 68080, as *Tilia platyphyllos*, H.B. 7988 ø, anam. substr.).

Map 11. Known distribution of *H. fagi* in Europe (yellow = not included collection).

Not included. **SLOVAKIA**: **Bratislava**, 10 km SE of Bratislava, 4.8 km S of Podunajské Biskupice, Topoľové hony, 132 m, branch of *Acer campestre*, on wood & bark, 5.VI.2019, A. Polhorský (A.P. 19/27, BRA-CR31731, anam. substr., doc. vid., sq.: MN611702). — **CANADA**: **Québec**, 16 km NNW of Québec, Lac Beauport, Chemin du Rouet, 206 m, log of indet. (?)angiosperm, on wood, 10.VII.2012, J. Cimon (J.C. 50466, CMMF, doc. vid.). — **USA**: **Massachusetts**, Boston Harbor Islands, 19 km SE of Boston, 2.5 km NE of Hingham, World's End peninsula, 7 m, log of *Acer*, on wood, 13.IX.2013, D. Haelewaters, K. & R. Healy, S. Verhaeghen (bhi-F041, FH, H.B. 9995, sq.: MF161167). – 12.5 km SE of Boston, Peddocks Island, East Head, 10 m, log of *Acer*, on wood, 29.VIII.2015, D. Haelewaters, L. Millman & J. Warfel (bhi-F457b, FH, H.B. 10000). – **Florida**, Putnam, 5 km ESE of Melrose, SW border of Ross Lake, 38 m, wood of indet. tree, 15.VIII.2017, B. Kaminsky & D. Borland (FLAS-F-61330, as *H. lunata*, sq.: MH211887). — **RUSSIA (East)**: **Irkutsk**, Sayan Mts., SW of Baykalsk, south-end of lake Baykal, ~1000 m, branch of *Alnus alnobetula* subsp. *fruticosa*, on wood, 17.VIII.1975, E. Parmasto (TAAM 96057, H.B. 8710b ø). — **CHINA**: **Sichuan**, **Ngawa** (Aba), Jiuzhaigou, 2000–2500 m, branch of *Fagus*, 8.X.2006, J.W. Guo (J.W.G. zcw-j-3, YMFT, doc. vid.). – ibid., ?2500 m, branch of indet. angiosperm, 6.VIII.2007, J.W. Guo & S.F. Li (J.W.G. jzh-2, YMFT, doc. vid.). – **Yunnan**, **Yuxi**, Tonghai, ~35 km SE of Yuxi, ~S of Tonghai, Xiushan Forest Park, ~2000 m, indet. angiosperm, on bark, 17.IX.2007, J.W. Guo & S.F. Li, (J.W.G. th4b-28/th2-34, YMFT, doc. vid.).

Hyalorbilia helicospora Baral & G. Marson, **sp. nov.**, MB 813474 — Pls 94–95, Map 12

Etymology: named according to the helicoid shape of ascospores.

Typification: Luxembourg, Alzingen, branch of *Quercus*, 22.VII.1993, G. Marson (ex H.B. 4923a, M-0276409, holotype).

Latin diagnosis: *Differt ab* Hyalorbilia fagi *ascosporis longioribus*, *ab* H. tortuosa *ascosporis latioribus*; *habitat in ramis siccis in aere prominentibus differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.12–0.8(–1.4) mm diam., in total 0.06–0.17 mm high (receptacle 0.05–0.09 → 0.03–0.05 mm), whitish-greyish to pale (or light) cream-chlorinaceous, turning light reddish-brown with age, translucent, round, slightly gelatinous, subgregarious to gregarious in swarms; disc slightly concave to flat, finally slightly convex, margin thin, scarcely protruding, smooth to finely rough, exterior glabrous; subsessile or with distinct, glassy stipe 0.03–0.1 × 0.08–0.15 mm, superficial; dry light ochre-amber. **Asci** *(16–)20–30(–33) × (4–)4.2–5.2(–6) µm {7}, †(16–)18–24(–26) × 3.4–4.3(–4.7) µm {6}, 8-spored, spores *±4-seriate, sometimes forming two superimposed bundles, pars sporifera *(11–)13–15 µm long, **apex** (†) hemispherical; **base** unstalked, with croziers {5} with or without small to large perforation. **Ascospores** *(5.5–)6–7.5(–8) × 1–1.3(–1.4) µm {12}, †5.3–7.3(–7.8) × (0.8–)0.9–1.2(–1.3) µm {7}, subcylindrical to narrowly fusoid, rarely slightly fusoid-clavate, both ends obtuse (sometimes subacute), slightly to medium helicoid (looking very slightly S-shaped or falcate depending on the viewing direction), with 2–4 globose **SBs** 0.3–0.5(–0.6) µm diam. {8} and 1–2 minute LBs in each spore half. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cells *17–27 × (2.5–)3–4(–5.5) µm {2}, †13–20 {2} × 2–3.7 {4} µm, lower cells †4–6 × 1.4–2 µm {1}. **Medullary excipulum** 10–30 µm thick, of medium dense textura intricata-angularis, (very) slightly gelatinized, rather sharply delimited. **Ectal excipulum** of thin-walled, horizontally oriented t. prismatica-angularis from base to margin, 25–70(–120) µm thick near base, cells */†(8–)10–40(–55) × (4–)8–22(–26) µm {4}, common walls †0.3–1.2 µm thick, at flanks 10–25 µm thick, at margin 8–15 µm, marginal cortical cells */†7–20 × (4–)5–9(–11) µm {7}, external wall †0.2–0.3 µm thick. **Anchoring hyphae** sparse to abundant, */†(1.5–)2.5–4.5(–6.5) µm wide, wall *0.2–0.3 µm thick

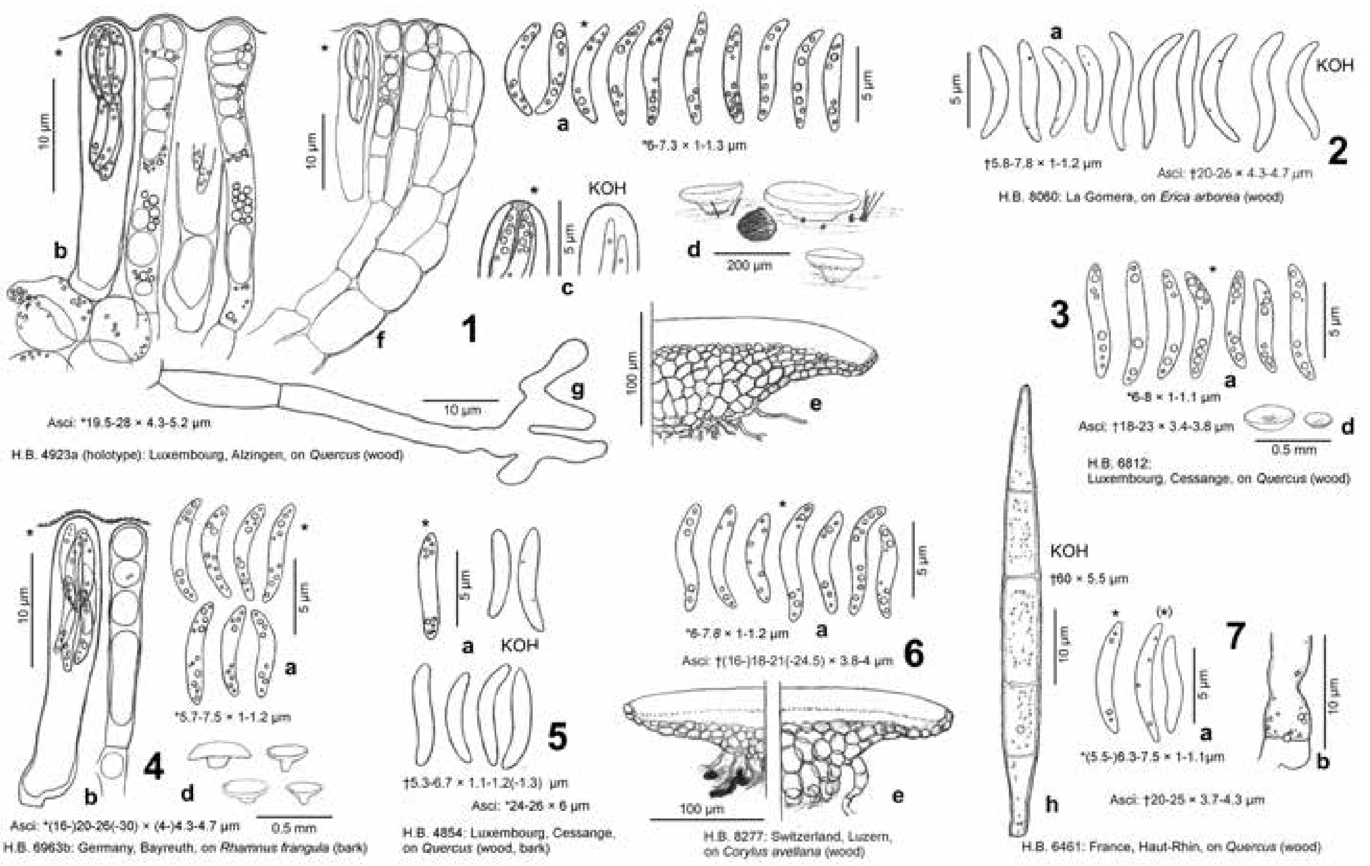


Plate 94. **1–7**: *Hyalorbilia helicospora*. – **a**. ascospores; **b**. asci and paraphyses (**7b**: ascus base with croziers); **c**. ascus apices; **d**. apothecia (moist or rehydrated); **e**. apothecia in median section; **f**. ectal excipulum in median section (margin and mid flanks); **g**. terminally branched anchoring hypha; **h**. conidium from substrate.

{6}. **VBs** in terminal cells of paraphyses slightly to strongly refractive, large, subhyaline to pale chlorinaceous. **Exudate** over paraphyses and excipulum 0.2(–0.3) µm thick, smooth to finely warted or granular. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate {1}). **Conidiophores** not observed. A single observed **conidium** fusiform, straight, †60 × 5.5 µm, 4-septate.

Habitat: 1–4 m above the ground, also on moist ground (on underside with close contact to soil), corticated or ± decorticated, 15–50 mm thick branches of *Corylus avellana* {2}, *Erica arborea* {1}, *Fagus sylvatica* {1}, *Frangula alnus* {1}, *Ilex aquifolium* {1}, *Quercus* sp. {11}, *Sorbus aucuparia* {2}, on partly very deeply medium to usually strongly decayed wood {17} and bark {4} (periderm {1} & bast {2}), on senescent resupinate basidiomycete {1}, often greyed and with abundant green algae. **Associated**: *Calocera cornea* {1}, ?*Chaetosphaerella* sp. {1}, *Colpoma quercinum* {1}, *Dothiorina tulasnei* {1}, *Mollisia* ?*oblonga* {2}, *M. albogrisea* {1}, *Orbilia arachnovinosa* {1}, *O. cejpii* {1}, *O. eucalypti* {1}, *O. pleistoeuonymi* {1}, *O. tremulae* {1}, *O. vinosa* {1}, *Proliferodiscus pulveraceus* {1}, *Propolis farinosa* {1}, *Resupinatus* sp. {1}, *Rutstroemia firma* {1}. **Desiccation tolerance**: mature asci tolerate desiccation for min. 1 week. **Altitude**: 75–1145 m a.s.l. (temperate Europe). **Geology**: Lower Carboniferous sediment, Buntsandstein, Keuper (Knollenmergel), Lower Jurassic sandstone, Pleistocene calcareous till & loess; granite, gneiss. mica schist, volcanic rock. **Phenology**: III–IV, VII–XII (apparenty throughout the year).

Taxonomic remarks. *Hyalorbilia helicospora* is characterized by more or less distinctly helicoid ascospores with 2–4 SBs near each end, and comparatively small, ± desiccation-tolerant apothecia. *H. sibirica* is only tentatively separated (see p. 375). Four species with more desiccation-sensitive apothecia resemble *H. helicospora* in spore shape: *H. tortuosa* and *H. citrina* differ in narrower spores (*H. citrina* also in shorter spores), *H. fagi* in larger apothecia and shorter spores with only 1(–2) SBs at each end, and *H. arcuata* in falcate spores. *H. juliae* occurs in similar habitats as *H. helicospora* but differs in longer, straight spores. However, the limits between all these species are not always clear.

Variation. The collection from Macaronesia (Pls 94: 2; 95: 4, on *Erica arborea*, with *Proliferodiscus pulveraceus*) deviates from the European samples in larger (0.4–0.8 mm), more intensely pigmented apothecia. It was only studied in the dead state, therefore, no information on the SBs in the spores is available.

Anamorph. A single brachyphoris-like fusoid conidium was observed (Pl. 94: 7h), which concurs with anamorphs of similar *Hyalorbilia* species with curved ascospores, except for *H. tortuosa* which has cylindric-ellipsoid conidia.

Phylogeny. Sequences of *H. helicospora* were taken from apothecia of two samples from Sonneberg (Germany), one from Berchem (Luxembourg), and one from Ardèche (France), all on wood of *Quercus*, comprising S1506 intron, ITS, and LSU (one also S943-intron and SSU V6–V9). In the ITS and LSU (D1–D6), the four strains are identical, and also in the intron only 1 nt deviates in H.B. 9897 (one of the Sonneberg samples) from the other three.

In analyses of ITS, ITS+LSU, and LSU, *H. helicospora* clustered in a strongly (Phyls 5, 6) or weakly (S5) supported clade with the *H. lunata* strain from England, with a distance of 2.1 % in the ITS and 2 nt difference in the D2 domain of LSU. Moreover, the S1506 intron is absent in *H. lunata*, while both possess the S943 intron (for differences see p. 382). A minimum distance of ~14–16 % is observed in the ITS region to any other sequence of a *Hyalorbilia*. In the ITS

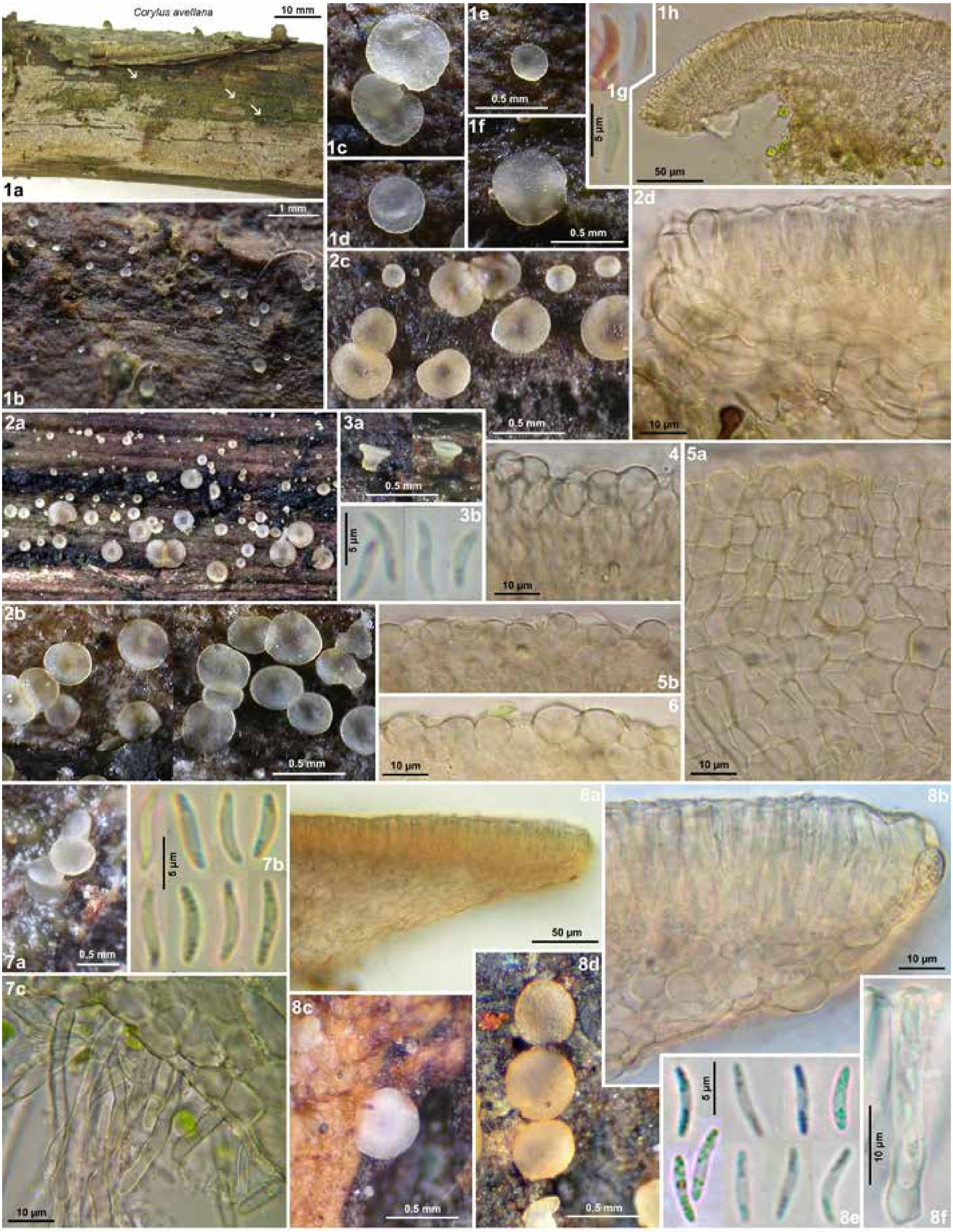


Plate 95. **1–8**: *Hyalorbilia helicospora*. – **1a**. decorticated xeric branch with remnants of bark; **1b–f**, **2a–c**. rehydrated apothecia; **3a**, **7a**, **8c–d**. fresh apothecia; **1h**, **8a**. apothecium in median section; **2d**, **8b**. id., near margin; **5a**. marginal ectal excipulum in surface view; **4**, **5b**, **6**. id., in top view; **1g**, **3b**, **7b**, **8e**. ascospores; **8f**. ascus; **7c**. anchoring hyphae. – Living state (**8e** partly in CRB) except for **2d**, **4**, **5a–b**, **6** (in KOH), **1g** (in KOH+CR). – **3a** right, **3b**: phot. I. Wagner; **7a–c**: phot. P. Perz; **8a–f**: phot. M. Bemmann. — **1a–h**. H.B. 8277: Switzerland, Luzern, on *Corylus*; **2a–d**. H.B. 6812: Luxembourg, Cessange, on *Quercus*; **3a–b**. H.B. 9897: Germany, Sonneberg, on *Quercus*; **4**. H.B. 8060: La Gomera, on *Erica*; **5a–b**. H.B. 6816: Luxembourg, Cessange, on *Quercus*; **6**. H.B. 4854: ibid.; **7a–c**. P.P. 20080713: Poland, substrate unknown; **8a–f**. 17.10.2010: Germany, Heidelberg, on *Fagus*.

analysis, the two species clustered strongly supported with two environmental strains from the Netherlands (H3). This clade falls unsupported in the *inflatula-polypori* clade, whereas in the LSU analysis they fall with strong support in this clade, and in the combined analysis in a strongly supported subclade with *H. citrina* and *H. inflatula.*

Ecology. *Hyalorbilia helicospora* was found on ± rotten wood and bark of both xeric and hygric branches of various angiosperm trees and shrubs, predominantly *Quercus*. The species does not appear to be rare. It was so far recorded from cold-temperate humid atlantic western and subcontinental central Europe. Vegetation types include rather moist (*Fagus*-) *Quercus* forests. The Macaronesian collection was from thermomediterranean semihumid fayal-brezal ridge crest forest (*Myrico fayae-Ericetum arboreae* or *Ilici canariensis-Ericetum platycodonis*).

Specimens included. **FRANCE**: **Bretagne**, **Morbihan**, Bretagne, 3 km S of Baud, 1.2 km W of Camors, Etang du Petit Bois, 75 m, branch of *Ilex aquifolium*, on wood, 23.X.2004, J.P. Priou (J.P.P. 24170, doc. vid.). – **Alsace**, **Haut-Rhin**, 25 km W of Basel, 2 km E of Bisel, Rehhof, 425 m, branch of *Quercus*, on wood, 19.IX.1999, H.O. Baral (H.B. 6461a, anam. substr.). – **Rhône-Alpes**, **Loire**, 12 km ESE of St.-Étienne, 1.9 km NNE of Le Bessat, 1145 m, branch of *Sorbus aucuparia*, on wood, 13.IX.2018, G. Marson (G.M. 2018-09-13.4). – **Ardèche**, 30 km W of Valence, 1.2 km N of St.-Julien-Labrousse, 842 m, branch of *Quercus*, on wood, 12.X.2016, G. Marson (G.M. 2016-10-12.3, sq.: MK493159). — **LUXEMBOURG**: **Gutland**, **Luxembourg**, 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 300 m, branch of *Quercus*, on bark & wood, 28.III.1993, G. Marson (H.B. 4854, G.M. 4964). – ibid., branch of *Quercus*, on wood, 7.X.2000, G. Marson (G.M. 2000-10-07.3, H.B. 6812). – ibid., branch of *Quercus*, on wood, 5.XI.2000, G. Marson (H.B. 6816). – 5 km SSW of Luxembourg, NNW of Kockelscheier, 305 m, branch of *Corylus avellana*, on wood, 23.X.1999, G. Marson (ø). – 6.5 km SE of Luxembourg, 2 km ESE of Alzingen, Héid, 290 m, branch of *Quercus*, on wood, 22.VII.1993, G. Marson (ex H.B. 4923a, M-0276409, **holotype**). – 8 km S of Luxembourg, 1.2 km W of Berchem, Aire-de-Berchem, 293 m, branches of *Quercus*, on wood & bark, 9.XI.2015, G. Marson (G.M. 2015-11-09.1; sq.: MK493150). — **POLAND**: locality and host unknown, on wood, 13.VII.2008, vid. P. Perz (P.P. 20080713-1, doc. vid.). — **SLOVAKIA**: **Bratislava**, 6.5 km SE of Bratislava, 5 km SW of Podunajské Biskupice, Kopáč, 133 m, branch of *Quercus*, on wood, 10.IX.2019, A. Polhorský (A.P. 19/35, doc. vid.). — **GERMANY**: **Thüringen**, 3 km W of Sonneberg, 1.5 km W of Bettelhecken, Mürschnitzer Sack, 355 m, branch of *Sorbus aucuparia*, on bark, 8.VIII.2016, I. Wagner (ø, doc. vid.). – 1.3 km N of Bettelhecken, Wehd, branch of *Quercus*, on wood, 30.VII.2016, I. Wagner (doc. vid.). – 5 km SE of Sonneberg, SW of Rottmar, 358 m, branch of *Quercus*, on wood, 17.VII.2014, I. Wagner (H.B. 9897; sq.: KY419175). – 5.5 km SE of Sonneberg, WNW of Mark, Marker Hang, 397 m, branch of *Quercus*, on wood, 29.X.2015, I. Wagner (G.M. 2015-10-29.1, doc. vid.; sq.: KY419176). – **Bayern**, **Oberfranken**, 6 km WNW of Bayreuth, 3 km WSW of Heinersreuth, Dühlbach, 350 m, branch of *Frangula alnus*, on bark, 29.IV.2001, W. Beyer (H.B. 6963b). – **Baden-Württemberg**, 7 km E of Heidelberg, 1.5 km SE of Ziegelhausen, Bärenbach, 150 m, branch of *Fagus sylvatica*, on wood, 17.X.2010, M. Bemmann (ø, doc. vid.). — **SWITZERLAND**: **Nidwalden**, 6 km S of Luzern, 1 km NW of Hergiswil, Bruustried, 600 m, branch of *Corylus avellana*, on wood, 22.VIII.2006, H.O. Baral (H.B. 8277). — **MACARONESIA**: **Canary islands**, **Gomera**, 8.5 km NW of San Sebastián de la Gomera, 2.5 km NW of Chejelipes, Garajonay, 720 m, branch of *Erica arborea*, on wood, 9.XII.2000, E. Beltrán-Tejera (TFC Mic. 14413 ø, H.B. 8060a).

Map 12. Known distribution of *H. helicospora* in Europe and Macaronesia.

Hyalorbilia sibirica E. Weber & Baral, **sp. nov.**,
MB 813475 — Pls 96–97

Etymology: from the type locality (Tuva, Siberia).

Typification: Russia (East), Tuva, Tannu-Ola Mts., log of *Larix*, 19.VII.1972, A. Raitviir (TAAM 62289, holotype).

Latin diagnosis: Hyalorbiliae helicosporae *similis sed ascosporae paulo latiores*, *apothecia majora*, *asci majores*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.4–1 mm diam., 0.13–0.15 mm high (receptacle 0.1 → 0.065 mm), light chlorinaceous-cream, medium translucent, round, slightly gelatinous, scattered to gregarious in small groups; disc flat, margin thin, not protruding, smooth; sessile on a narrow obconical base, superficial; dry light honey-brown, ± cupulate. **Asci** †(22–)24–30(–33) × 4–4.7 µm, 8-spored, spores 3–4-seriate, intertwined; **apex** (†) hemispherical; **base** unstalked, with croziers. **Ascospores** †(5.5–)6–7(–7.7) × (1.1–)1.2–1.3(–1.4) µm, subcylindrical, homopolar, both ends obtuse, consistently rather strongly helicoid; **SBs** not seen in dead state. **Paraphyses** apically uninflated to slightly capitate, terminal cells †12–17 × 2–2.5(–3) µm, lower cells †6–8 × 2–2.5 µm wide. **Medullary excipulum** 10–20 µm thick, slightly gelatinous, of medium dense textura prismatica-globulosa, rather sharply delimited. **Ectal excipulum** of slightly gelatinized, horizontally oriented t. prismatica-globulosa from base to margin, 90–100 µm thick near base, cells †(10–)15–25(–30) × (7–)10–13(–20) µm, at flanks 10–20 × 6–20 µm, common walls 0.8–1.7 µm thick, cortical wall 1–2 µm; 15 µm thick near margin, marginal cortical cells †9.5–16 × 3.7–7 µm, external wall 0.2–0.4 µm thick. **Anchoring hyphae** medium abundant, †2–5 µm wide (at insertion sometimes up to 7 µm), walls (0.2–)0.3–0.5(–0.7) µm thick. **Exudate** over paraphyses and margin yellowish-ochraceous, 0.2–0.3 µm thick, smooth to finely warted. **— ANAMORPH**: unknown.

Habitat: decorticated surface of over 10 cm thick log of *Larix* sp., on 0.1 mm deep medium decayed wood, strongly greyed, with some green algae, with old black fructifications of ?pyrenomycete below apothecia **Associated**: *Coccocarpia* sp. (or *Pannariaceae*?), indet. foliose lichen. **Desiccation tolerance**: unknown, probably somewhat desiccation-tolerant because of the associated lichens. **Altitude**: ~1000 m a.s.l. **Phenology**: VII.

Taxonomic remarks. *Hyalorbilia sibirica* is very similar to *H. helicospora* from which it is tentatively separated by larger apothecia, slightly wider ascospores, larger asci, and more thick-walled anchoring hyphae, also by substrate and geographical origin. *H. tortuosa* and *H. fagi* likewise differ from *H. sibirica*

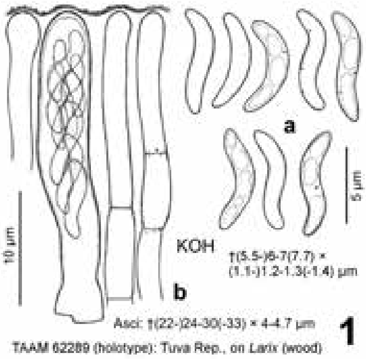


Plate 96. **1**: *Hyalorbilia sibirica*. – **a**. ascospores; **b**. ascus and paraphyses.

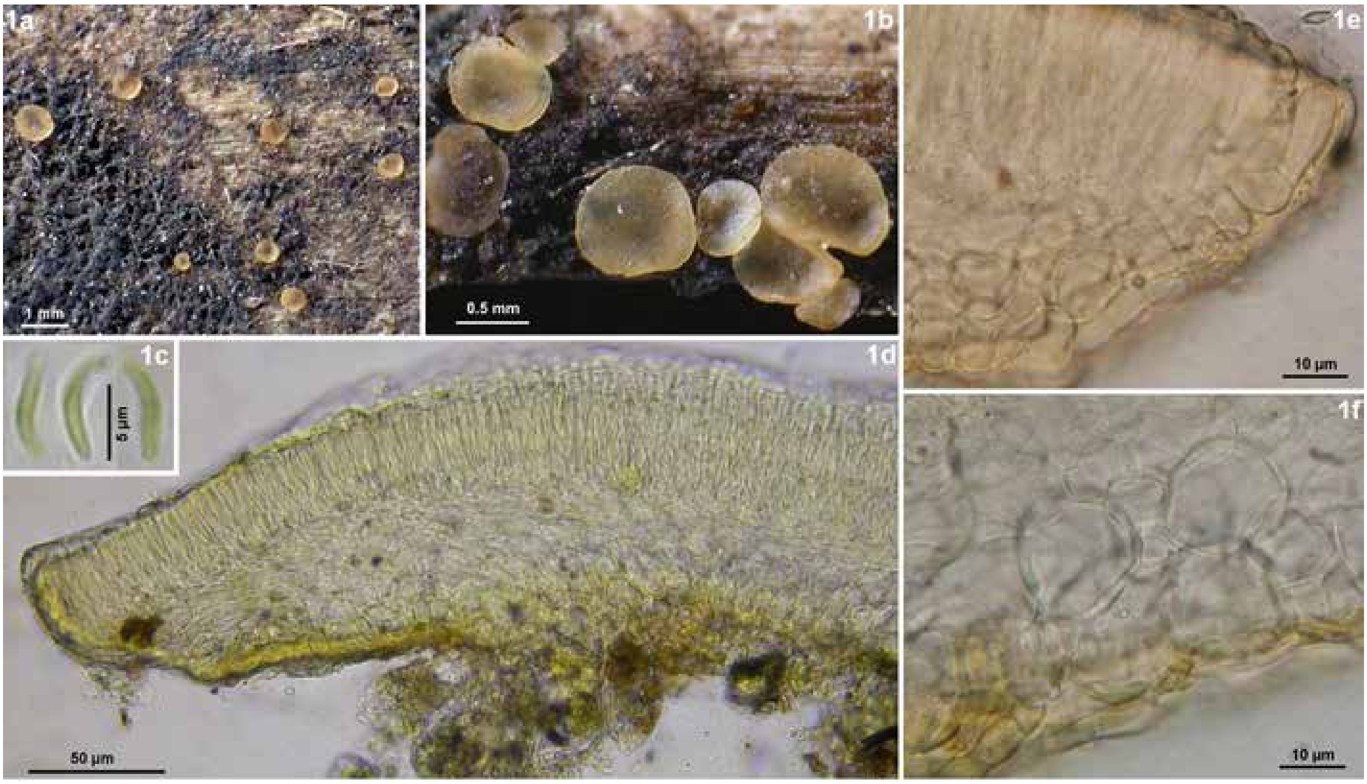


Plate 97. **1**: *Hyalorbilia sibirica*. – **1a–b**. rehydrated apothecia; **1c**. ascospores; **1d**. median section of apothecium; **1e**. id., marginal ectal excipulum; **1f**. id., basal ectal excipulum in median section. – Dead state (in KOH, **1c** KOH+IKI). — **1a–f**. TAAM 62289 (holotype): Russia, Tuva, on *Larix*.

in narrower spores, smaller asci, and perhaps in their more desiccation-sensitive apothecia.

Ecology. *H. sibirica* was found on medium rotten wood of a log of *Larix* in the continental, cold-temperate humid Sayan Mountains of central Asia.

Specimens included. **RUSSIA (East)**: **Tuva**, Sayan Mts., Tannu-Ola Mts., ~70 km S of Kycyl, Durgenj river, ~1000 m, log of *Larix*, on wood, 19.VII.1972, A. Raitviir (TAAM 62289, **holotype**, as *Orbilia oreadum*, H.B. 7993a ø)

Hyalorbilia macrohelicospora Baral & Hong Y. Su, **sp. nov.**, MB 813476 — Pls 98–99

Etymology: named after the comparatively large, strongly helicoid ascospores.
Typification: China, Yunnan, Jizushan, log of indet. angiosperm, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (ex H.B. 8956, M-0276414, holotype).

Latin diagnosis: Hyalorbiliae helicosporae *et* H. sibiricae *similis sed ascosporae multo majores, valde helicoideae, asci latiores, paraphyses ad apicem magis inflatae.*

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated 0.22–0.45 mm diam., 0.11 mm high (receptacle 0.06 → 0.04 mm), whitish-cream to pale chlorinaceous, translucent, round, non-gelatinous, scattered; disc flat to medium convex, margin finely rough, not protruding; with a hidden 0.05 mm high stipe, superficial. **Asci** *22–28 × 6.2–6.7 µm, †20–25 × 5–6 µm, 8-spored, spores *3–4-seriate, strongly intertwined, pars sporifera *14–19 µm long; **apex** (†) hemispherical to slightly conical; **base** sessile or with short, thick stalk, arising from croziers (with or without slit). **Ascospores** *9.5–12 × 1.4–1.7 µm, †9.5–11(–13) × 1.3–1.5 µm, cylindrical, ends very slightly tapered, rounded to obtuse, consistently very strongly helicoid (like a right-hand thread); **SBs** *0.7–1.1 µm diam., globose, about 3–4 in each spore half together with a few small LBs. **Paraphyses** apically (slightly to) medium to strongly clavate-capitate, terminal cells †19–23 × 4–5.5 µm, lower cells †4–7 × 1.5–2 µm. **Medullary excipulum** non-gelatinized. **Ectal excipulum** of ± thin-walled, horizontally oriented textura prismatica from base to margin, cells at flanks †15–23 × 7–12 µm (up to 18 µm wide near base); marginal cortical cells †17–23 × 5–9 µm, clavate, thin-walled. **Anchoring hyphae** sparse, †2–3(–3.5) µm wide, walls 0.2 µm thick. **VBs** in living paraphyses low-refractive, elongate. **Exudate** over paraphyses and marginal excipulum absent or as scattered, 0.1–0.2 µm thick, granular. **— ANAMORPH**: unknown.

Habitat: 15 cm thick log of unidentified angiosperm tree lying on moist ground, decorticated, on eroded, deeply medium decayed wood, ± strongly blackened, no algae. **Associated**: closely associated with an old black pyrenomycete and a yellow ?*Orbilia* (later not rediscovered). **Desiccation tolerance**: apparently intolerant (dead in all parts when examined after 1 month). **Altitude**: 2700 m a.s.l. **Geology**: mafic volcanic rock. **Phenology**: X.

Taxonomic remarks. *Hyalorbilia macrohelicospora* resembles *H. helicospora* and *H. sibirica* in the helicoid shape of its ascospores, but differs from these species in much larger and much more strongly curved spores, wider asci, and more inflated apices of paraphyses.

Ecology. The sparse collection was made on rotten wood of a hygric log of an unidentified angiosperm tree in a subtropical humid, winter-dry evergreen broad-leaved forest in southeastern Asia.

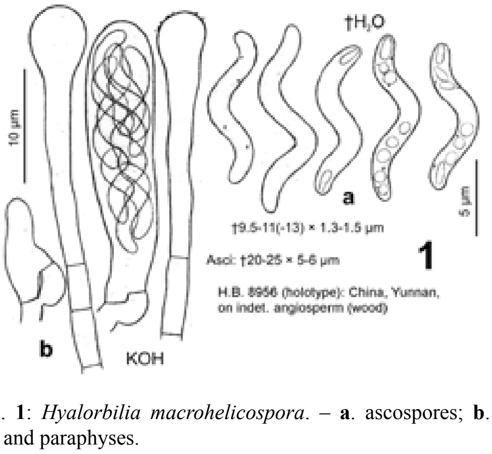


Plate 98. **1**: *Hyalorbilia macrohelicospora*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses.

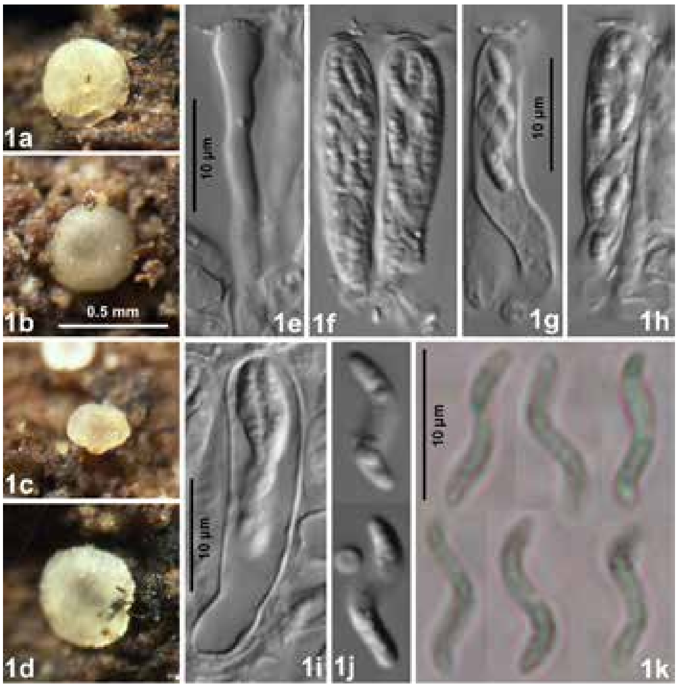


Plate 99. **1**: *Hyalorbilia macrohelicospora*. – **1a–d**. fresh apothecia; **1e**. paraphysis; **1f–i**. asci; **1j–k**. ascospores. – Living state, except for **1k** (in H_2O), asci in **1f–h**. – **1a–j**: phot. H.Y. Su (DIC). — **1a–k**. H.Y.S. jz-7 (holo-/isotype): China, Yunnan, on indet. angiosperm.

Specimens included. **CHINA**: **Yunnan**, **Dali**, Binchuan, 42 km NNE of Dali, Jizushan, 2700 m, log of indet. angiosperm, on wood, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (ex H.B. 8956, M-0276414, **holotype**; H.Y.S. jz-7, CBCD, **isotype**).

Hyalorbilia arcuata Baral, M.L. Wu & Y.C. Su, in Wu et al., Fungal Diversity 25: 235, figs 5–15 (2007) — Pls 100–101, Map 13

Etymology: named according to the strongly curved, bow-shaped ascospores.
Typification: Taiwan, Tengjhih, indet. angiosperm, 30.X.2005, Y.C. Su (TNM F20072, holotype).
Misapplied name: Liu (2006: 26), as *H. andina* (HMAS 139538); Liu (2006: 36), as *H. inflatula* (HMAS 139537); Ekanayaka et al. (2018: 160), as *H.* cf. *inflatula*.

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated (0.2–)0.4–1.8 mm diam., 0.09–0.19 mm high (receptacle 0.075–0.12 → 0.04–0.06 mm), watery-whitish to pale or light yellowish-chlorinaceous(-orange), translucent, round to somewhat undulating, membranaceous, slightly gelatinous, scattered to gregarious; disc slightly concave to flat, margin thin, not protruding, smooth; sessile on a broad base, sometimes with a stipe 0.06 × 0.15 mm, superficial; dry light yellowish-buff, with distinct whitish subiculum. **Asci** *20–27(–32.5) × 4–4.8 µm {1}, †18–26(–29) × 3.2–4.3(–4.8) µm {4}, 8-spored spores *3–4-seriate, pars sporifera *13–16 µm long; **apex** (†) hemispherical to slightly conical; **base** unstalked or only slightly narrowed, with croziers {5}. **Ascospores** *5.8–7(–8) × (0.8–)0.9–1.2(–1.4) µm {1}, †5–7 {4} × 0.8–1 {3} or 1.1–1.2 {1} µm, (sub)cylindrical, sometimes narrowly fusoid when dead (then sometimes distinctly heteropolar), both ends obtuse (also subacute or rounded), (slightly to) medium to (very) strongly curved (falcate), not or sometimes very slightly helicoid, in dead state less curved; **SBs** *0.2–0.4(–0.5) µm diam. {1}, globose, (1–)2–3(–4) near each end. **Paraphyses** apically uninflated or slightly capitate, terminal cells *2–3.5 µm wide {1}, †13–20 × 1.8–2.5 µm {2}, lower cells †4–5 × 1.6–1.8 µm {1}, strongly agglutinated with asci. **Medullary excipulum** 10–30 µm thick, of slightly to strongly gelatinized textura angularis-prismatica-intricata, medium to very sharply delimited. **Ectal excipulum** thin-walled, in cortex slightly to rather strongly gelatinized (common walls †0.3–1 µm thick), at base of t. angularis to t. prismatica, 25–60 µm thick, cells *20–28 × 13–17 µm {1}; at lower flanks of horizontally oriented t. prismatica, 15–25 µm thick, cells †(10–)15–40(–48) {4} × 5–7 {1} or (6–)8–15(–22) {3} µm; 5–20 µm thick at margin, of t. prismatica to t. porrecta, marginal cortical cells †6–11 {2} or 11–15 {T} × 2.5–4 {2} or 7–10 {T} µm, thin-walled to slightly gelatinized. **Anchoring hyphae** abundant, radiating, */†(2.5–)3–5(–6) µm wide, at insertion also *7–10 µm, walls (0.2–)0.3–0.5(–1) µm thick {3}. **Exudate** over paraphyses and marginal excipulum 0.2–0.5 µm thick, rough-warted to granular. **VBs** in terminal cells of paraphyses and marginal cortical cells globose to elongate, hyaline or pale yellow, slightly to medium refractive. — **ANAMORPH**: unknown (but see below).

Habitat: collected on moist ground, also 0.5–1.5 m above the ground, on corticated (to almost decorticated), 7–28 mm thick twigs and branches of *Barringtonia racemosa* {1}, *Pinus* sp. {1}, *Prunus persica* {1}, indet. angiosperm {4}, indet. tree {6}, on slightly to strongly decayed bark (outer surface of periderm, sometimes bast) {9} or wood {4}, ± greyed, no algae, also on stroma of immature ?*Hypoxylon* {1}. **Associated**: *Hyalorbilia japonica* {1}, *Orbilia cejpii* {1}, *O.* ?*fusiformis* {1}. **Desiccation tolerance**: immature asci and excipular cells still viable after 11 months (Australia). **Altitude**: 460–?2000 m a.s.l. (Asia), 5 m (northeastern Australia). **Geology**: Australia: Devonian sedimentary rock; Asia: Paleozoic & Tertiary sedimentary and felsic plutonic rock. **Phenology**: I, III, V–VII, IX–X (Asia).

Taxonomic remarks. *Hyalorbilia arcuata* is characterized by falcate ascospores with mostly 2–3 spore bodies near each end. It herein resembles *H. berberidis*, from which it differs in much shorter but also narower spores and in fewer and smaller SBs. For the similar *H. nodulosa* see below. *H. fagi*, *H. helicospora* and *H. tortuosa* mainly differ in their helicoid spores.

Variation (***H. arcuata*** s.l.). *H. arcuata* varies in the strength of spore curvature, often even within a collection. Typically, the spores are moderately to strongly curved (Pls 100: 1–3; 101: 1d). In the dead state the strength of curvature slightly decreases (Pl. 100: 1a, 2a). A slightly helicoid curvature is sometimes seen in dorsal view (Pl. 100: 2a upper right spore). Such spores resemble those of the temperate species *H. fagi*.

The spores are usually homopolar, but some slightly heteropolar spores were observed (particularly in the dead state) in those specimens with strongly curved spores (Pl. 100: $1a_2$, 3a). The spores in the Australian specimen contain a fewer number of SBs Pl. 100: 2a compared to the holotype, and the asci and spores are wider. This specimen is also extraordinary in growing on xeric substrate. Great variation was noted in the marginal cortical cells, which are very narrow in the specimens from Australia (Pl. 101: 4l) and in one of the not included Chinese samples (H.B. 8716), and widest in the holotype of *H. arcuata* (Pl. 101: 1f). Further collections are needed to clarify the taxonomic value of these morphological traits. The falcate ascospores illustrated as the teleomorph of *Dactylella lignatilis* by Mo et al. (2005b, Pl. 101: 2) fit rather well the holotype of *H. arcuata* (Pl. 100: $1a_2$) when compared in the dead state, also the large (2–3 mm diam.), pale orange apothecia concur (the size of the marginal cortical cells was not stated). In the type of *H. arcuata* the apothecia were described as 0.8–1.8 mm diam. and whitish to pale chlorinaceous.

Literature reports and misapplications. Liu (2006: 25, fig. 2) reported six south Chinese collections under the name *H. andina*, with apothecia 0.5–3 mm diam. and medium curved spores 5.4–7.2 × 0.8–1.3 µm (figured in the dead state). The illustrated collection (HMAS 139533, Pl. 101: 5a–c) and another which was reexamined here (HMAS 139632, Pls 100: 3; 101: 3)

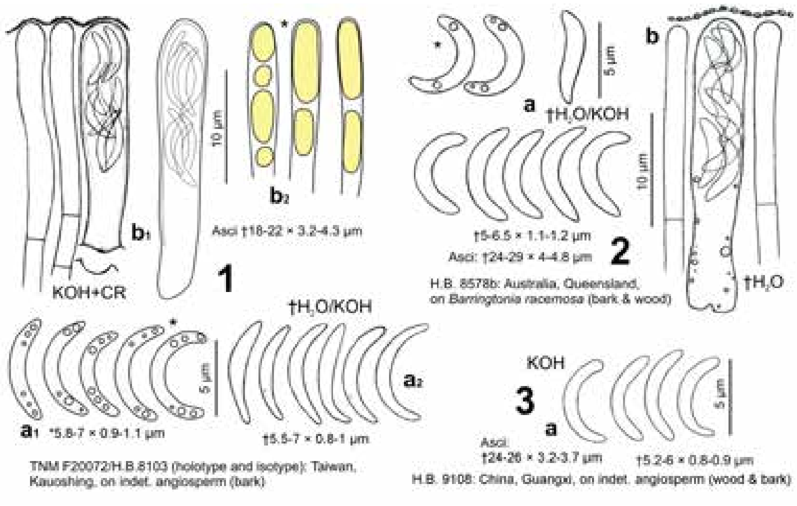


Plate 100. **1–3**: *Hyalorbilia arcuata*. – **a**. ascospores; **b**. asci and paraphyses. – **1a**$_1$ and **1b**$_2$: from Wu et al. (2007).

appear to fit well *H. arcuata*. Guo et al. (2014b) reported 11 south Chinese collections under the name *H. arcuata*, one of which was illustrated on their fig. 5 (details in Pl. 101: 6). Guo et al. did not specify which collection was illustrated, but when J.W. Guo (pers. comm.) earlier sent us the plate he referred it to th-j-21, a code which does not appear in his publication. The given spore size lies with (4.6–)5.8–7.4(–9) × 0.8–1.3 µm at the upper range regarding the length, while the illustrated spores measure only about †4.5–5 × 1 µm. A sample from Northern Thailand on indet. wood was reported by Ekanayaka et al. (2018) as *H.* cf. *inflatula*. It has slightly to medium, sometimes strongly curved spores of †4.5–5.5 × 0.5–1.3 µm (average 5.2 × 1.1 µm, but ~0.6–0.8 µm wide according to scale). The authors believed that their sample was conspecific with *H. inflatula* as described by Quijada et al. (2014a) although the spores are reported there as straight to very slightly curved.

Not included collections. Three Chinese collections from Guizhou (Pls 101: 7–8) and Yunnan (IVV: H.B. 8718) deviate by somewhat shorter, less curved spores.

Anamorph. The anamorph in the sample on *Pinus* bark from Kunming described from an ascospore isolate as *Dactylella lignatilis* by Mo et al. (2005b) is regarded here to represent a species different from *H. arcuata* (see under *H. lignatilis*, p. 359).

Phylogeny. An ITS sequence was gained from apothecia of the Australian sample (H.B. 8578b), while no sequence was available from the type of *H. arcuata*. Among the six Chinese specimens named *H. andina* by Liu (2006), three were sequenced by him regarding the ITS region: B.L. 6184 and 6185 from Guangxi and B. L. 6408 from Fujian. Another ITS sequence from Fujian (B.L. 6426, without microscopic data, B. Liu pers. comm.) was treated in Liu (2006) as *H. inflatula*, and both Fujian sequences were uploaded as *H. inflatula* in GenBank. Our drawing of B.L. 6185 (Pl. 100: 3) and photos of B.L. 6184 and 6408 kindly provided by B. Liu (pers. comm., see IVV) show the typical spores of *H. arcuata*. For the Thailand sample (as *H.* cf. *inflatula*), sequences of S1506 intron, ITS, and LSU exist.

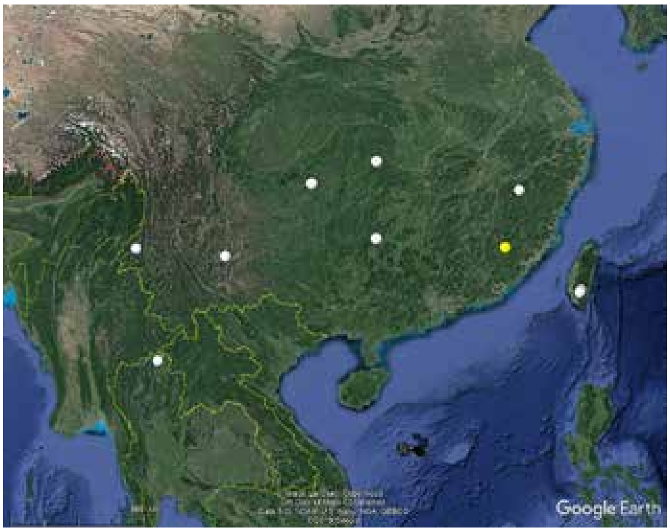
Our Australian *H. arcuata* clustered highly supported but with a 9% ITS distance in a clade with the two strains from Fujian (Phyl. 5). The latter show a 2.5% distance between each other, so they might be conspecific, whereas the Australian sample appears to belong to a different taxon. A distant, likewise strongly supported clade is formed by the two Guangxi strains and that from Thailand (the latter not shown in phylogram). The Guangxi strains show a 10.5% distance between each other, while that from Thailand differs by 4.5% from B.L. 6184 and 12% from B.L. 6185. The type of *H. lignatilis* differs by 22–23% from all these strains and is, therefore, not conspecific with any sequenced *H. arcuata* strain.

There was some confusion of numbers in Liu's unpublished list of strains regarding B.L. 6185 (HMAS 139632, as *H. andina*) and B.L. 6449 (HMAS 139535, as *H. juliae*), a strain not included in Liu (2006), if not confused with HMAS 139553, listed in Liu (2006) under *H. juliae*. B.L. 6449 appears in GenBank (DQ656650), but this sequence is tentatively assumed here to belong to B.L. 6185, because it was labelled '*H. andina*' in Liu et al.'s (2006a) phylogenetic analysis and Liu's unpublished list of strains. Yet, B. Liu (pers. comm.) expressed some doubts about the correctness of this attribution. Sample B.L. 6449 is morphologically very deviant from *H. arcuata*, in having long straight spores as in the long-spored variant of *H. juliae* in spore shape (see under *H. juliae*, p. 389). It appears unlikely that a species with such long and straight spores clusters in a clade with one with short and curved spores, whereas our sequences of European *H. juliae* clustered very distant from DQ656650.

Because we cannot see morphological differences between Australian and Taiwanese *H. arcuata* in comparison with Liu's concept of *H. andina* based on the samples from Guangxi and Fujian and a photo plate of the unsequenced HMAS 139533, we have included all illustrated *Hyalorbilia* samples from China with similar falcate spores in the description of *H. arcuata*.

Ecology. *Hyalorbilia arcuata* was found on rotten bark and wood of hygric or sometimes xeric (Australia) branches of both angio- and gymnosperm trees and shrubs in evergreen broad-leaved rainforests of subtropical to tropical humid (winter-dry) southeastern Asia and tropical northeastern Australia.

Specimens included. **CHINA**: **Yunnan**, **Kunming**, ~35 km W of Kunming, ~8 km WNW of Jiliang, Xiaobailong Mt., 1580 m, twig of *Pinus*, on bark, 10.IX.2003, M.H. Mo (M.M.H. 005 p.p., H.B. 7461b ø, doc. vid., mixture with *H. japonica*



Map 13: Known distribution of *H. arcuata* in eastern Asia (yellow = not included collection).

Plate 101. **1–6**: *Hyalorbilia arcuata*; **7–8**: *H.* cf. *arcuata*. – **4a**. border of small tropical forest, with *Barringtonia racemosa*; **1a**. fresh apothecia; **4b–i**, **7a–c**. rehydrated apothecia; **4j**. apothecium in median section; **1f**, **4l**. id., marginal ectal excipulum; **1e**. id., heavily gelatinized medullary excipulum; **3**, **4k**. id., ectal excipulum near base with anchoring hyphae; **1b**. anchoring hyphae; **1c**, **5a–b**, **6a**. asci and paraphyses; **1d**, **2**, **5c**, **6b**, **7d**, **8**. ascospores; – Living state, except for **2**, **5c**, **6a–b**, **7d** (in H_2O), **1e–f** (in KOH+CR), **3** (in KOH). – **1a–d**: from Wu et al. (2007); **2**: from Mo et al. (2005b); **5a–c**: from Liu (2006, fig. 2, as *H. andina*, DIC); **6a–b**, **8**: phot. J.W. Guo (DIC, **6**: from Guo et al. 2014b). — **1a–f**. TNM F20072, H.B. 8103 (type of *H. arcuata*): Taiwan, on indet. angiosperm; **2**. M.M.H. 005, H.B. 7461b: China, Yunnan, on *Pinus*; **3**. B.L. 6185: China, Guangxi, on indet. angiosperm; **4a–l**. H.B. 8578b: Australia, Queensland, on *Barringtonia*; **5a–c**. HMAS 139533: China, Hunan, on *Prunus*; **6a–b**. J.W.G. th-j-21: China, Yunnan, on indet. tree; **7a–d**. J.W.G. gz-34, H.B. 8716: China, Guizhou, on indet. angiosperm; **8**. J.W.G. gz-22: ibid., on indet. angiosperm.

& *H. lignatilis*). – Shuanglong, ?1800 m, branch of indet. tree, 19.V.2006, J.W.G. Guo (J.W.G. sl-j-9). – Jindian, ?2000 m, branch of indet. tree, 13.VI.2006, J.W. Guo (J.W.G. jd-j-16). (Not specified by Guo et al. 2014b: fig. 5 which collection was illustrated [originally as th-j-21].). – **Guangxi**, **Guilin**, Xing'an, ~65 km NNE of Guilin, ~30 km NW of Xing'an, Mao'er Shan, 1500 m, branch of indet. angiosperm, on wood, 26.VII.2002, B. Liu (B.L. 6185, HMAS 139632, as *H. andina*, H.B. 9108, sq.: ?DQ656650 [as B.L. 6449, *H. juliae*]). – ibid., indet. tree, on bark & wood, 26.VII.2002, B. Liu (B.L. 6184, HMAS 139534, as *H. andina*, doc. vid.; sq.: DQ656645). – **Hunan**, **Zhangjiajie**, Jinbian Xi (Golden Whip), 600 m, *Prunus persica*, indet. tree, on bark, 16.IX.2005, B. Liu & X.Z. Liu (HMAS 139533, doc. vid.). – **Fujian**, **Nanping**, Wuyishan, ?Huanggangshan 1500 m, indet. tree, on bark, 14.IV.2003, B. Liu & L.M. Zhang (B.L. 6408, HMAS 139538, as *H. andina* in Liu 2006, doc. vid.; sq.: DQ656657 as *H. inflatula*). – **Longyan**, Shanghang, Buyun, Meihuashan, 700 m, indet. tree, on bark, 17.IV.2003, B. Liu (B.L. 6426, HMAS 139537, non vid., as *H. inflatula*; sq.: DQ656658). – **Taiwan**, **Kaohsiung**, Tengjhih, 1500 m, branch of indet. angiosperm, on bark, 30.X.2005, Y.C. Su (M.W. T051030T9, TNM F20072, **holotype**; H.B. 8103, **isotype**). – ibid., 24.I.2006, Y.C. Su (M.W. T060124T4, TNM, non vid.). – 54 km NE of Kaohsiung, 4.5 km SE of Liouguei, Shanping, 800 m, branch of indet. angiosperm, on bark, 13.I.2005, Y.C. Su (TMUE S050113T4, TNM, non vid.). – ibid., 14.III. & 10.X.2005. — **THAILAND**: **Northern Thailand**, **Chiang Rai**, 16 km NNE of Chiang Rai, Mae Fah Luang University, ~460 m, branch of indet. tree, on bark (as 'wood'), 15.I.2015, A.H. Ekanayaka (hd007, MFLU 15-0167, doc. vid., sq.: MG599270). — **AUSTRALIA**: **Queensland**, Wet Tropics, 21 km N of Mossman, 8 km ESE of Daintree, Cape Tribulation Road, Daintree Swamp, 5 m, branch of *Barringtonia racemosa*, on bark & wood, 29.VIII.2006, G. Marson (H.B. 8578b; sq.: KT222447).

Not included. **CHINA**: **Yunnan**, **Baoshan**, Tengchong, 2 km SE of Tengchong, Laifengshan, ~1800 m, branch of indet. ?gymnosperm, on bark, VIII.2004, Z.F. Yu, (Z.F.Y. tc-51, H.B. 8718). – **Guizhou**, **Zunyi**, Suiyang, ~62 km NNE of Zunyi, ~38 km ENE of Tongzi, Kuankuoshui, 1420 m, branch of indet. angiosperm, on bark, 10.IX.2007, S.F. Li & J.W. Guo (J.W.G. gz-34, YMFT, H.B. 8716). – ibid. (J.W.G. gz-22, YMFT, doc. vid.).

Hyalorbilia nodulosa Baral, Hong Y. Su & X.J. Su, in Su et al., Mycol. Progress 10: 380, fig. 5 (2011) — Pls 102–103

Etymology: named after the knob-like glassy processes on the marginal cortical cells.

Typification: China, Yunnan, Yongping, branch of indet. angiosperm, 8.XII.2007, R.X. Bi, X.M. Gao & H.Y. Su (ex H.Y.S. jgs-1, CBCD, holotype).

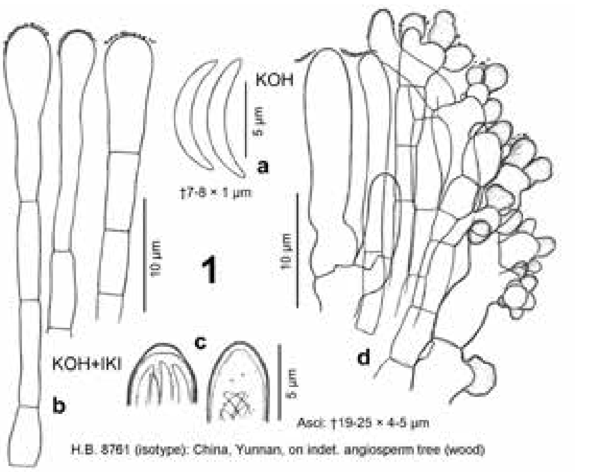


Plate 102. **1**: *Hyalorbilia nodulosa*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. ectal excipulum in median section at margin.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.14–0.24 mm diam., 0.08 mm high (receptacle 0.06 → 0.035 mm), whitish when fresh, rehydrated whitish to light brownish, slightly translucent, round, gregarious in small groups; disc flat, margin thin, 5 µm protruding, finely crenulate; with a short stipe 0.02 × 0.05 mm, superficial; dry pale reddish-brownish. **Asci** *20–24 × 5–5.5 µm, †19–25 × 4–5 µm, 8-spored, spores *~4-seriate, pars sporifera *15–16.5 µm long; **apex** (†) obtuse to submammiform; **base** unstalked, arising from croziers (without distinct slit). **Ascospores** *6.8–8 × 1–1.1 µm, †7–8 × 1 µm, fusoid, sometimes slightly heteropolar, ends *obtuse or †subacute to acute, consistently medium curved; **SBs** globose, *0.2–0.5 µm diam., ~3–4 in each half. **Paraphyses** apically uninflated to medium clavate-capitate, terminal cells †10–19 × 2.5–4.2 µm, lower cells †6–9.5(–13) × 1.8–2.5 µm; unbranched at upper septum. **Medullary excipulum** 10–15 µm thick, non-gelatinized, of medium dense textura prismatica-porrecta, upwards oriented in centre, horizontally at flanks, indistinctly delimited. **Ectal excipulum** at lower flanks of thin-walled (to medium gelatinized), irregularly horizontally oriented t. prismatica, 20 µm thick, cells †10–15 × 5–8 µm; 10 µm thick near margin, marginal cortical cells †5–12 × 2–4 µm, thin-walled; cells at mid flanks and margin with short protuberances which bear one or mostly several knob-like, strongly refractive **glassy processes** (1–)1.5–3 × (1.3–)2–2.5 µm, these KOH-

Plate 103. **1**: *Hyalorbilia nodulosa*. – **1b**. fresh apothecia; **1a**, **c**. rehydrated apothecia; **1d**. apothecium in median section; **1h**. id., marginal ectal excipulum, with glassy processes; **1i**. margin in surface view, with glassy processes; **1e**. asci; **1f**. ascospores; **1g**. paraphyses. – Living state: **1e** (four asci with clearly visible spores), **1f** (left spore); dead state: **1f–g** (in H_2O), **1d**, **h–i** (in KOH). – **1b**, **e–g**: phot. H.Y. Su (p.p. from Su et al. 2011c, DIC). — **1a**, **c–d**, **h–i**. H.B. 8761 (isotype), **b**, **e–g** (holotype): China, Yunnan, on indet. angiosperm.

resistant, IKI-. **Anchoring hyphae** sparse at base, †2–3.5 µm wide, walls 0.2–0.4 µm thick. **VBs** in paraphyses: no data available. **Exudate** over paraphyses 0.2–0.5 µm thick, granular to continuous, over margin as sparse minute granules. **— ANAMORPH**: unknown.

Habitat: collected on moist ground, decorticated, ~5–10 cm thick branch of unidentified angiosperm tree, on strongly decayed wood, somewhat blackened, no algae. **Associated**: none observed. **Desiccation tolerance**: unknown (dead in all parts when examined after 2 months). **Altitude**: 2730 m a.s.l. **Geology**: Jurassic sedimentary rock. **Phenology**: XII.

Taxonomic remarks. *Hyalorbilia nodulosa* deviates from *H. arcuata* in small, knob-like glassy processes resting in groups on short protuberances of the marginal cortical cells, also in slightly longer ascospores, wider paraphyses with longer lower cells, smaller excipular cells at lower flanks, and in distinctly smaller apothecia. The presence of glassy processes is so far unique within the genus *Hyalorbilia*. Similar protuberances were occasionally seen in *H. juliae* and *H. resinae*, but they never carried glassy caps.

Ecology. *H. nodulosa* was found on rotten wood of an unidentified angiosperm tree lying near a ditch in a subtropical humid (winter-dry) evergreen virgin mountain forest (with *Castanopsis orthacantha*, *Cinnamomum glanduliferum*, *Magnolia campbellii* etc.) in southeastern Asia.

Specimens included. **CHINA**: **Yunnan**, **Dali**, Yongping, 35 km ENE of Baoshan, Jinguangsi virgin forest, 2730 m (as 2850 m), branch of indet. angiosperm, on wood, 8.XII.2007, R.X. Bi, X.M. Gao & H.Y. Su (H.Y.S. jgs-1, CBCD, **holotype**, doc. vid.; H.B. 8761, **isotype**).

Hyalorbilia lunata (Korf) Baral, Micologia 2000: 44 (2001) — Pls 104–105, Map 14

≡ *Orbilia lunata* Korf, Mycotaxon 45: 508 (1992)

Etymology: named according to the spore shape that resembles a half-moon in profile view.

Typification: Macaronesia, Tenerife, Las Mercedes, branch of indet. angiosperm, 7.I.1976, R.P. Korf, W.C. Denison, L.M. Kohn & M.A. Sherwood (CUP-MM 247, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.23–)0.35–1.5(–3) mm diam., (0.08–)0.1–0.17(–0.22) mm high (receptacle 0.05–0.1 → 0.035–0.05 mm), pale to light yellowish-chlorinaceous(-ochraceous), ± translucent with darker centre, round, somewhat lobate when large, not or moderately gelatinous, medium scattered to gegarious; disc slightly concave, soon flat, centre sometimes with a slight depression, margin distinct, 0–8 µm rising above disc, smooth to finely rough or crenulate; broadly sessile or with an obconical to abruptly cylindrical stipe somewhat hidden in biofilm, 0.03–0.13 × 0.1–0.25(–0.4) mm, superficial; dry flat to cupulate, light yellowish-ochre, reddish-brown with age. **Asci** *(23–)27–35(–40) × (4.5–)4.8–5.5(–6) µm {4}, †(21–)24–32(–35) × (3.5–)4–5(–6) µm {4} [Quijada: *(25–)30–34(–41) × (4.8–)5–5.5(–6) µm, †(20–)24–30(–32) × 3.2–4 µm {6}], 8-spored, spores (*) obliquely biseriate, often intertwined, pars sporifera *13–20 µm long → 10.5 µm (†22–25 µm, irregularly arranged; or †14–17 µm long if still intertwined); **apex** (†) hemispherical to slightly truncate; **base** with a very short, thick stalk arising from croziers {6}. **Ascospores** *((4.1–))(4.5–)5–7(–8) × (1.5–)1.6–2(–2.1) ((–2.3)) µm {5}, †(4.3–)5–6.5(–7) × (1.3–)1.5–1.8(–2) µm {4} [L. Quijada: *(4.8–)5–5.5(–6) × 1.7–2.1 µm, †4.3–4.9 × 1.5–1.7 µm {6}], fusoid to fusiform, sometimes fusoid-clavate, both ends obtuse to subacute († subacute to acute), slightly or usually medium to strongly curved, partly or consistently helicoid (like a right-hand thread), in profile view looking like a half-moon; **SBs** globose, *0.4–0.8(–1) ((–1.3)) µm diam. {3}, 1–4 in each half, sometimes laterally attached; LBs absent or sparse, minute. **Paraphyses** apically uninflated to medium clavate-capitate, terminal cells *(16–)19–25(–31) × (2.5–)3–4(–4.5) µm {3}, †(11–)18–24(–27) × (2–)2.3–3.5(–4) µm {4}, lower cells *6–8.5 × 2.7–3.3 µm {1}, †4–8 × 1.4–2 µm {1}; unbranched. **Medullary excipulum** hyaline, 10–30 µm thick, of dense textura intricata-epidermoidea–globulosa, slightly horizontally oriented, cells

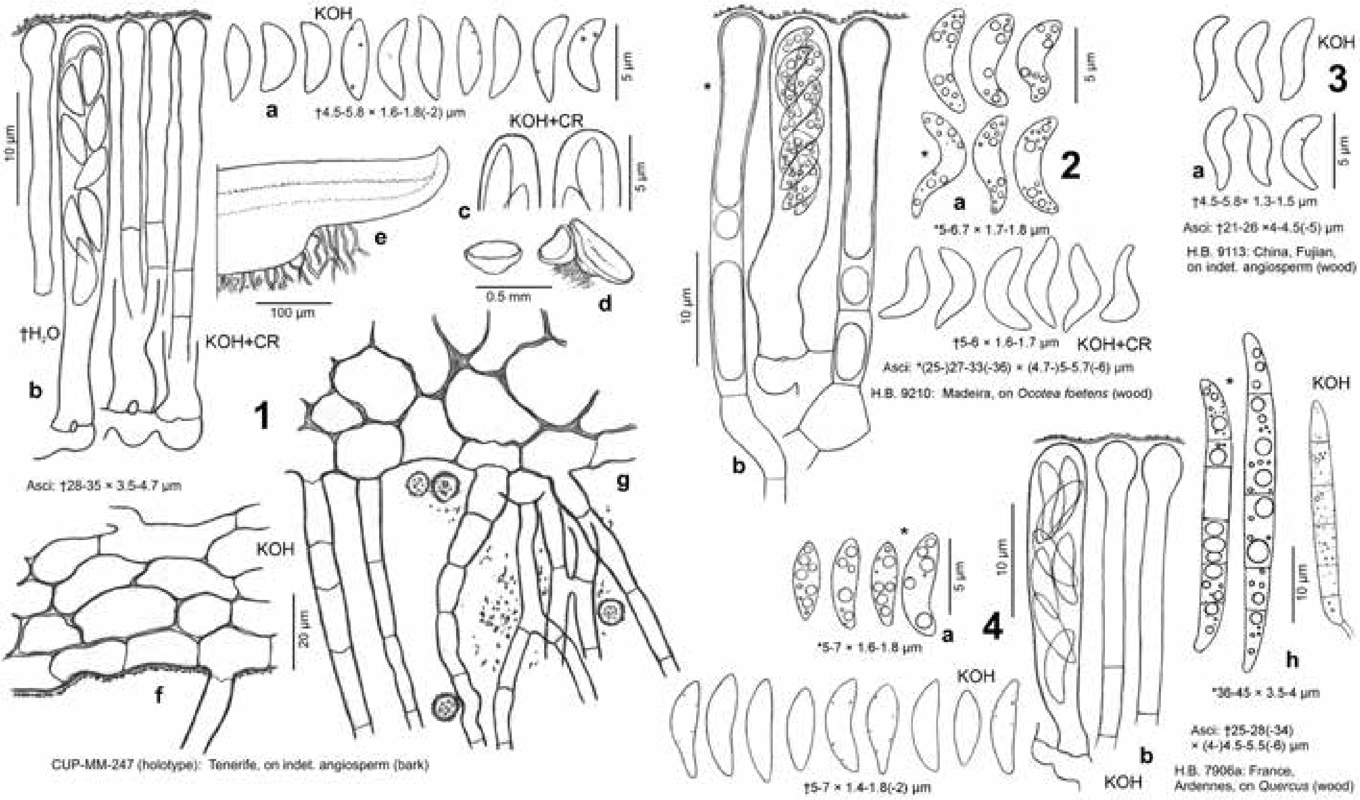


Plate 104. **1–4**: *Hyalorbilia lunata*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., ectal excipulum at lower flanks; **g**. id., basal ectal excipulum and anchoring hyphae; **h**. conidia from substrate.

10–17 × 2–4.2 µm, not or slightly to strongly gelatinized, not or rather sharply delimited. **Ectal excipulum** hyaline, at base of vertically oriented t. angularis-prismatica, (40–)60–120(–180) µm thick, cells *(12–)15–25(–30) × (7–)12–20(–24) µm {2}, †12–25 × 10–20 µm {1} or †7–20 × 5–10 {T+1}, ± gelatinized near exterior [common walls †0.5–1.5(–3) µm], sometimes with a unicellular cortical layer of horizontal prismatic cells; 20–70 µm thick at lower flanks, of horizontal t. prismatica, cells */†(15–)20–35(–42) × 10–17(–23) µm {3} or †8–17 × 5–9 {T+1}, 10–20 µm thick at margin, marginal cortical cells *8–11 × 6–7 µm {1} or *12–16(–20) × 7–11 µm {1}, †8–11 × 5–8(–9) µm {T+1}, in surface view up to 10–12(–15) µm wide. **Anchoring hyphae** medium to very abundant, hyaline, long and straight (radiating) or undulating, */†2–4(–7) µm wide, near insertion 3–6(–8) µm, walls 0.2–0.3 {4} or sometimes 0.5–1 µm thick {2}, anastomoses and branches rare. **Exudate** over paraphyses continuous, 0.2–0.5(–1.2) µm thick, slightly to strongly granular; over margin and flanks a thin layer of fine warts and clods. **VBs** pale chlorinaceous, medium refractive; large **LBs** in ectal excipulum absent. **— ANAMORPH**: brachyphoris-like (presumed, from natural substrate {3}). **Conidiophores** not observed. **Conidia** unbranched, elongate fusoid, slightly curved at both ends, *36–45 × 3.5–4 µm {1}, †29–41 × 3–3.1 µm {1}, ~4–5-septate, with some large LBs and many small ones (both KOH-resistant) {H.B. 7906a}; or ± straight, *50–65 × 4.5–6 µm, 6–11-septate, with some large or many small or only a few minute LBs {N.A. 342}.

Habitat: collected on moist ground, corticated or decorticated, 16–200 mm thick, entirely decayed branches and logs of *Acer campestre* {1}, *Erica arborea* {2}, *Eucalyptus gunnii* {1}, *Ilex canariensis* {1}, *Laurus novocanariensis* {1}, *Myrica faya* {1}, *Ocotea foetens* {3}, *Picconia excelsa* {1}, *Quercus* sp. {1}, ?*Salix* sp. {1}, indet. angiosperm {3}, on lower, lateral or upper side, on 0.3 mm to deeply very rotten wood {8} or bark {8}, partly blackened, sometimes on old pyrenomycete, green algae absent or abundant among anchoring hyphae. **Associated**: *Capronia pilosella* {1}, *Coenogonium pineti* {1}, *Coprinellus* sp. {1}, *Mollisia* ?*cinerea* {1}, *Pluteus salicinus* {1}, *P. umbrosus* {1}, *Rhizodiscina lignyota* {1}, ?*Ruzenia spermoides* {1}, *Simocybe centunculus* {1}, small foliose liverwort. **Desiccation tolerance**: many mature asci and excipular cells survived for about 1 hour dry on slide, after ~½ day in the herbarium only some immature asci viable, after a few days only ascospores survived. **Altitude**: 15–210 m a.s.l. (Europe), 665–1136 m (Macaronesia), ~1400–2500 m (southern China). **Geology**: Macaronesia: volcanic sedimentary deposits, tephritic and phonolitic mafic and basaltic flows; England: Triassic & Lower Cretaceous mud-, silt- & sandstone; Pleistocene loess & silt. China: Jurassic sedimentary rock; felsic plutonic rock. **Phenology**: I–VI, VIII–X (apparently throughout the year).

Taxonomic remarks. Korf (1992) characterized the species by lunate ascospores (looking like a half-moon) which are in fact often slightly to distinctly helicoid. *H. lunata* closely resembles *H. fusispora* and *H. subfusispora*, which mainly differ in wider and predominantly straight spores with a somewhat higher in situ length, also in smaller, more desiccation-tolerant apothecia. Yet, a few slightly curved spores were encountered in a few collections of *H. fusispora* and *H. subfusispora*. A French sample on *Robinia* (J.P.P. 11179) with ± distinctly curved spores mentioned under *H. subfusispora* is not included in *H. lunata* because of smaller apothecia growing on xeric wood.

Variation. Spore shape in *H. lunata* is in fact often helicoid, which is evident when seeing the spores in dorsal view (looking S-shaped), while in profile view such spores look lunate (C-shaped). A few spores look ± straight (Pl. 104: 1a, 4a), but such are probably seen from their dorsal side, and are in fact falcate by lacking the helicoid curvature.

The collection from France referred to *H. lunata* (Pls 104: 4; 105: 1) corresponds rather well to the Macaronesian samples. It differs from the holotype (Pl. 104: 1) in slightly longer, sometimes heteropolar (fusoid-clavate) spores, slightly shorter asci, apically slightly more enlarged paraphyses, larger excipular cells at flanks, and occurrence on wood. That these differences lie in the scope of variation of this species is supported by a collection from Madeira (Pls 104: 2; 105: 2) in which most of these features also occur. However, in this sample the often distinctly heteropolar spores are always medium to strongly helicoid, contrary to the holotype and the French specimen.

In a specimen from Fujian (China) reported under the name *H. lunata* by Liu (2006: 42) the spores are also distinctly helicoid, though slightly smaller (Pls 104: 3; 105: 3). The cortical excipular cells at the flanks are more strongly gelatinized, and the anchoring hyphae thicker-walled. In two further Chinese specimens (from Sichuan and Yunnan) reported by Guo et al. (2014a) the spores are distinctly lunate though not helicoid; they measure *3.2–4.6 × 1.4–1.7 µm (but 4.5–5 × 1.5–1.6 µm according to scale) and contain rather large SBs (Pl. 105: 4). The apothecia are described in Guo et al. as 0.1–0.3 mm, with a 85 µm long stipe and a hairy margin, but in the median section no hair-like projections are seen.

Although the spores of *H. lunata* do not lose their helicoid curvature in the dead state, their intertwined arrangement was often only seen inside the living asci, due to a more condensed arrangement of the spores. In the sample from Fujian, however, the spores were consistently intertwined also in the dead asci.

Type studies. The holotype consists of ~40 well-preserved apothecia and fairly concurs with the protologue, except for the substrate being bark, not wood as originally stated. The anchoring hyphae were found to be narrower than indicated by Korf (1992) who reported them as 3.7–10.2 µm wide and ± moniliform, even in their middle part. The here gained ascus length slightly exceeds that given in the protologue while spore size fits well [data given by Korf: asci 26–30 × 3.7–4.4 µm, spores (4.1–)4.4–5.1(–5.9) × (1.1–)1.5–1.9 µm]. Korf mentions two paratypes from the same laurel forest in Tenerife, which were not examined in the present study.

Anamorph. A few conidia were observed on the substrate in three collections, sometimes emerging from the base or margin of an apothecium. In the French collection the conidia were somewhat curved at both ends (Pl. 104: 4h), but in the sample from southern England they were straight and larger, with more septa (Pl. 105: 5f). Also in the sample from Madeira (H.B. 9210) J.P. Priou (pers. comm.) observed ± straight conidia. In culture no conidia were formed (Liu 2006).

Phylogeny. Sequences of two strains included in *H. lunata* were available which, however, are very distant. An ITS sequence was gained by B. Liu from the Chinese culture (B.L. 6416, HMAS 139531), and a sequence with S943-intron and SSU V6–V9 (without S1506 intron), ITS, and LSU (D1–D5) by us from apothecia of a British sample (N.A. 342). The Chinese strain clustered with *H. citrina*, *H. fagi*, and *H. japonica* in the strongly supported *citrina-fagi* clade (Phyl. 5) which is part of the supported *inflatula-polypori* clade (Phyls 6, S5; see also Liu et al. 2006a). The lowest ITS distance was 7–8 % to *H. fagi*. In the 5.8S region, this sequence fully matches *H. arcuata* (H.B. 8578b), *H. inflatula*, and *H. citrina*. The British strain clustered also in the *inflatula-polypori* clade, but strongly supported with two strains of *H. helicospora*, with a 2.1 % distance in the ITS, 2 nt in the LSU (D2), and 3 nt and 2 gaps in the S943 intron, which is surprising considering the much broader spores. The 100 % identity of the four *H. helicospora* ITS sequences supports the

Plate 105. **1–5**: *Hyalorbilia lunata*. – **2a**. laurel forest in Madeira (at Fanal, with *Ocotea foetens*, ~1 km away from site of H.B. 9210); **5a**. inhabited log of *Acer campestre* in *Quercus*-*Fraxinus* forest with *Salix* etc.; **1a–b**, **2c–e**. rehydrated apothecia (all one week later); **5b–c**. fresh apothecia; **1c**, **2b**. apothecia in median section; **2g**, **3a**. id., marginal ectal excipulum; **2f**. id., near base; **2i**, **4a**, **5e**. mature asci, paraphyses; **1d**, **2h**, **3c**, **4b**, **5d**. ascospores; **3b**. anchoring hyphae; **5f**. conidia formed on and around apothecia. – Living state, except for **1d**, **3c** (in H_2O); **1c**, **3a–b** (in KOH). – **2a**, **d**: phot. J.P. Priou; **3c**: from Liu (2006, fig. 9, DIC); **4a–b**: from Guo et al. 2014a (DIC); **5a**: phot. P. Clabburn; **5b–e**: phot. N. Aplin. — **1a–d**. H.B. 7906a: France, Ardennes, on *Quercus*; **2a–i**. H.B. 9210: Madeira, on *Ocotea*; **3a–c**. H.B. 9113: China, Fujian, on *Salix*; **4a–b**. J.W.G. ch-9: China, Sichuan, on indet. angiosperm; **5a–f**. N.A. 342: Great Britain, West Sussex, Plaistow, on *Acer*.

H. lunata sample being not conspecific. The morphologically similar *H. subfusispora* and *H. fusispora* show to *H. lunata* s.l. an ITS distance of 19–23.5 % and 23–24 %, respectively. More sequences of *H. lunata* from different regions, especially from Macaronesian samples are necessary to elucidate the boundaries of this species.

Ecology. *Hyalorbilia lunata* was found on rotten wood and bark of hygric branches and logs of different trees and shrubs in Madeira and especially in different regions of Tenerife (Teno, Monte de las Mercedes, Anaga). It occurs mainly in the thermo- to meso- or mesosubmediterranean subhumid to humid laurel forest (*Lauro novocanariensis-Perseetum indicae*) and fayal-brezal (*Ilici canariensis-Ericetum platycodonis*), but also in the thermomediterranean semihumid Monteverde seco (*Visneo mocanerae-Arbutetum canariensis*) adjacent to *Sideritido solutae-Pinetum canariensis* in the Valle de Güímar in eastern Tenerife. In the laurel forest *H. lunata* seems to be among the most common species of *Hyalorbilia* (L. Quijada pers. comm.). The French sample grew on *Quercus* in a supratemperate subatlantic *Quercetum* in the region of Argonne Ardennaise (France), and those from England in the supratemperate East Midlands and mesotemperate Southeast. The Chinese collections came from orotemperate to subtropical humid (winter-dry) evergreen broad-leaf forests.

Specimens included. **GREAT BRITAIN**: **East Midlands**, **Nottinghamshire**, 5 km NW of Retford, 2 km NE of Barnby Moor, Daneshill Energy Forest, 15 m, trunk of *Eucalyptus gunnii*, on ?bark, 26.V.2011, C. Hobart (ø, doc. vid.). – **South East England**, **West Sussex**, 9.5 km WNW of Billingshurst, 2 km SSW of Plaistow, 60 m, log of *Acer campestre*, on wood & old pyrenomycete, 2.X.2016, N. Aplin (N.A. 342, anam. substr., doc. vid.; sq.: KY419195). — **FRANCE**: **Champagne-Ardenne**, **Ardennes**, 11 km ESE of Vouziers, 4 km SE of La-Croix-aux-Bois, Forêt Domaniale de la Croix-aux-Bois, 210 m, branch of *Quercus*, on wood, 25.IX.2005, R. Jouan (H.B. 7906a, anam. substr.). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Los Silos, Teno, 6.5 km SSE of Buenavista del Norte, 1.9 km ESE of Las Portelas, La Rife, 1098 m, branch of *Picconia excelsa*, on wood & bark, 4.V.2012, L. Quijada, I. Pérez-Vargas, J. Díaz-Armas (TFC Mic. 23490, doc. vid.). – San Cristóbal de La Laguna, Anaga, 8 km NNW of Santa Cruz, 1.8 km NE of Las Mercedes, Cruz del Carmen, ~930 m, branch of indet. angiosperm, on bark, 7.I.1976, R.P. Korf, W.C. Denison, L.M. Kohn & M.A. Sherwood (CUP-MM 247, **holotype**, H.B. 5150 ø). – ibid. (CUP-MM 241, paratype, non vid.). – 1.5 km NE of Las Mercedes, Hoya del Llano los Viejos, 895 m, on indet. angiosperm, 5.I.1976, R.P. Korf, W.C. Denison, L.M. Kohn, M.A. Sherwood (CUP-MM 92 paratype, doc. vid.). – ibid., branch of *Ocotea foetens*, on bark, 18.IV.2013, L. & C. Quijada (TFC Mic. 24119, doc. vid.). – Santa Cruz de Tenerife, 3.3 km ESE of Taganana, El Pijaral, 775 m, branch of *Myrica faya*, on bark, 14.II.2012, L. & C. Quijada (TFC Mic. 23377, doc. vid.). – ibid., branch of *Ocotea foetens*, on wood & bark, 24.X.2012, L. & C. Quijada (TFC Mic. 23682, doc. vid.). – ibid., branch of *Laurus novocanariensis*, on bark, 24.X.2012, L. & C. Quijada (TFC Mic. 23684, doc. vid.). – ibid., branch of *Erica arborea*, on wood, 24.X.2012, L. & C. Quijada (TFC Mic. 23679, doc. vid.). – Tegueste, 5 km NNW of San Cristóbal de La Laguna, 1.5 km NE of Tegueste, La Hoya del Palomo, 665 m, branch of *Ilex canariensis*, on wood, 2.V.2012, L. Quijada & E.V. Rodríguez (TFC Mic. 23473, doc. vid.). –ibid., branch of *Myrica faya*, on bark, 16.VI.2012, L. Quijada & E.V. Rodríguez (TFC Mic. 23561, doc. vid.). – Güímar, 3.5 km W of Güímar, Higueras Salvajes, 927 m, branch of *Erica arborea*, on bark, 23.III.2013, L. Quijada, I. Pérez-Vargas & J. Díaz-Armas (TFC Mic. 24235, doc. vid.). – **Madeira**, 4.7 km SSE of Ribeira da Janela, 3.5 km SW of Seixal, 1136 m, branch of *Ocotea foetens*, on wood, 15.X.2009, J.P. Priou (J.P.P. 29179 ø, H.B. 9210, anam. substr.). — **CHINA**: **Fujian**, **Nanping**, ~135 km NNE of Nanping, ~25 km NW of Wuyishan, Huanggangshan, 1800 m, branch of ?*Salix*, on wood, 14.IV.2003, B. Liu (B.L. 6416, HMAS 139531, H.B. 9113, sq.: DQ656654). – **Sichuan**, **Ngawa** (Aba), Jiuzhaigou, 2000–2500 m, branch of indet. angiosperm, 5.VIII.2007, J.W. Guo & S.F. Li (J.W.G. ch-9, YMFT). – **Yunnan**, **Yuxi**, Xinping, ?18 km S of Xinping, Mopanshan, ?1850 m, branch of indet tree, V.2009, J.W. Guo (J.W.G. mp2-60, mp2-63). (Not specified by Guo et al. 2014a: fig. 3 which collection was illustrated.)

Map 14. Known distribution of *H. lunata* in Tenerife (Macaronesia).

Hyalorbilia juliae (Velen.) Baral, Priou & G. Marson, *in* Priou, Bull. Mens. Soc. Linn. Lyon 74 (num. spécial): 55 (2005) — Pls 106–109, Map 15

Basionym: *Orbilia juliae* Velen., Monogr. Discom. Bohem.: 95, pl. 11 fig. 39 (1934)

= *Orbilia fusispora* var. *microscopica* Velen., Monogr. Discom. Bohem.: 96 (1934)

Etymology: *juliae*: named after Julie (perhaps a student of Velenovský who was with him at the type locality, Z. Pouzar pers comm.); *microscopica*: referring to the minute apothecia.

Typification: Czechia, Central Bohemia, Zvánovice, branch of *Fagus sylvatica*, VII.1929, J. Velenovský (PRM 151740, holotype of ***Orbilia juliae***). — Czechia, Central Bohemia, Mnichovice, branch of *Lonicera tatarica*, VII.1926, J. Velenovský (PRM 152442, holotype of ***O. fusispora* var. *microscopica***).

Misapplied name: Guo et al. (2014b: fig. 8), as *H. inflatula* (?= *H. juliae*).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.13–0.4 or 0.3–0.7(–0.9) mm diam., 0.065–0.17 mm high (receptacle 0.05–0.09 → 0.04–0.045 mm), whitish to pale to light chlorinaceous(-greyish) or yellowish-cream-amber, translucent, round, scarcely to medium gelatinous, very scattered or ± gregarious; disc slightly concave to flat, sometimes slightly convex, immarginate or mostly with thin, slightly protruding, ± smooth, sometimes finely rough margin, rarely crenulate; subsessile or with a short obconical or abrupt stipe 0.01–0.12 × 0.05–0.2 mm, superficial, rarely ± immersed in algal layer; turning reddish-amber with age. **Asci** *(21–)24–36(–45) × (5–)5.3–6.5(–7)((–8.5)) µm {19}, †(18–)20–30(–35) × 4–5.2(–5.5) µm {12}, 8-spored, spores *(4–)8-seriate, in a parallel bundle or some lower spores separated from the bundle, also irregularly distibuted, rarely in two superimposed bundles of four spores, pars sporifera *12–18 (8-seriate) or 17–28 µm long, †16–23 µm, a few asci with 1–2 LBs at the base; **apex** (†) hemispherical(-subconical) to slightly truncate; **base** unstalked or slightly constricted, arising from croziers {23} with or without small, roundish or slit-like perforation. **Ascospores** *(7–)8–10(–11.5) {8} or (8.5–)10–13(–15) {43} × (1–)1.2–1.6(–1.9) µm {46}, †(6.5–)7–9(–10) {5} or (6.5–)8–12(–15) {17} × (0.9–)1–1.5(–1.7) µm {21}, narrowly cylindric-fusoid to fusoid (rarely narrowly fusiform), sometimes slightly to distinctly heteropolar (fusoid-clavate), ends obtuse, sometimes rounded or subacute, straight to (very) slightly curved; with (2–)3–6(–10) globose **SBs** (0.2–)0.3–0.6(–0.9) µm diam. and some slightly smaller LBs near each end. **Paraphyses** apically uninflated or mostly slightly to medium, rarely strongly clavate-capitate, terminal cells *11–22 × (2.3–)3–5(–7) µm {3}, †10–20 × (2–)2.5–4.3(–5) µm {7}, lower cells *5–8 × 2.5–3.5 µm {1}, †3–8 × 1.7–2.5(–3.3) µm {5}; frequently branched near base. **Medullary excipulum** 10–50 µm thick, of scarcely to medium gelatinized, upwards or irregularly oriented prismatic to hyphoid cells *8–16 × 4–7.5 µm, indistinctly to sharply delimited. **Ectal excipulum** from base to margin of thin-walled, nearly non-gelatinized, horizontal textura prismatica(-globulosa), 20–55 µm thick, cells at lower flanks */†(5–)9–20(–28)((–37)) × (3.5–)6–12(–14) µm {11}; 8–20 µm thick near margin, marginal cortical cells ± clavate,

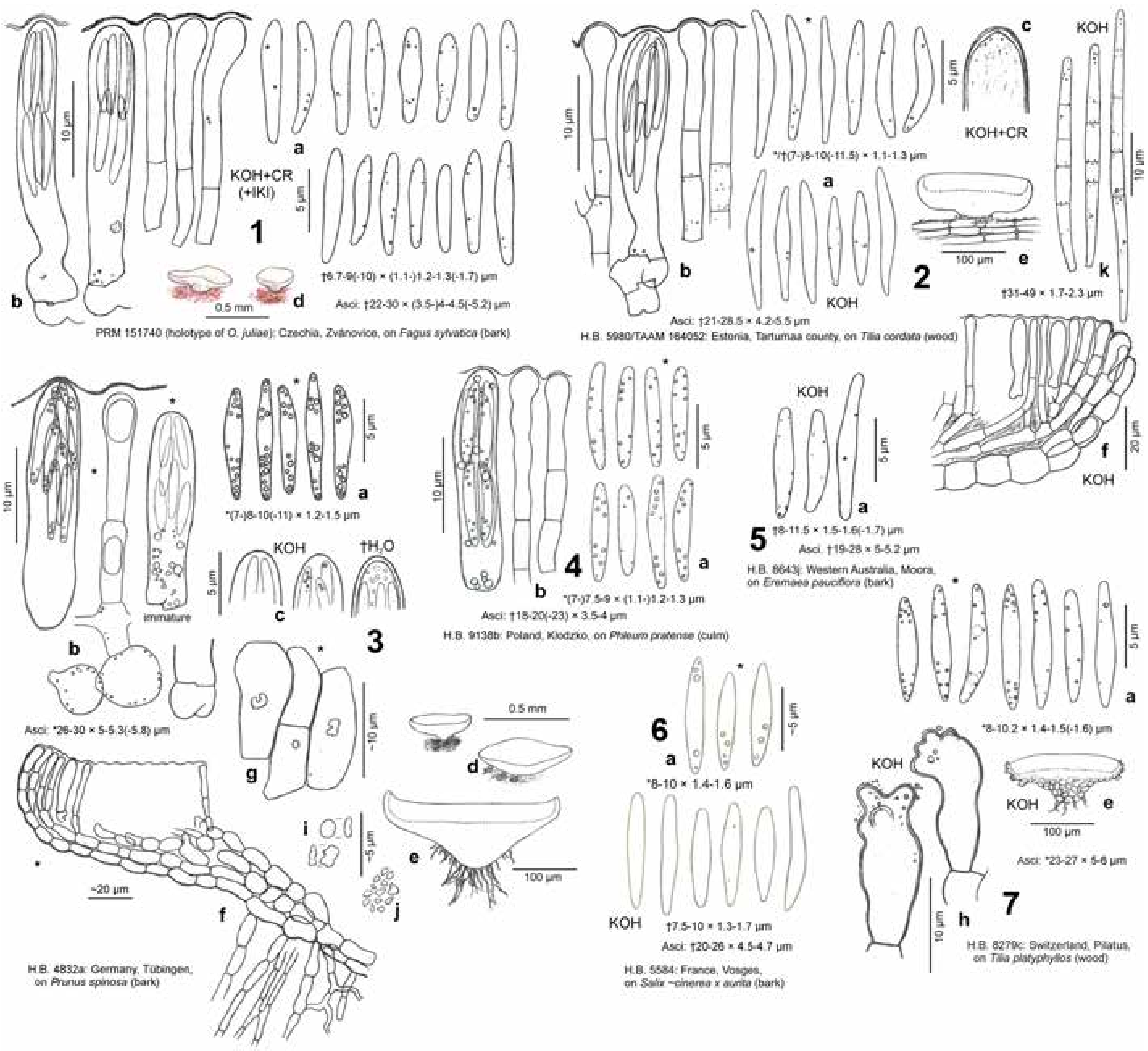


Plate 106. **1–3**, **5–7**: *Hyalorbilia juliae*; **4**: *H.* cf. *juliae*: – **a**. ascospores; **b**. asci and paraphyses (ascus bases with croziers); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., ectal excipulum from base to margin; **g**. excipular cells at flanks (with SCBs, squash mount); **h**. hair-like cortical cells with outgrowths (at flanks and margin); **i**. SCBs in ectal excipular cells; **j**. warted exudate on surface; **k**. conidia from substrate.

*/†(6–)9–23(–28) {15} × 2.5–4 {5} or (4–)5–9(–11)((–13)) {17} µm (in section or external view), very rarely with denticulate, ± protruding apical protuberances {1}. **Anchoring hyphae** sparse to abundant, */†2–3.5(–4.5)((–5.5)) µm wide, sometimes moniliform, walls 0.2–0.3(–0.4) µm thick {7}. **SCBs** globose to irregularly shaped, 0.5–2.3 µm diam., medium refractive, in centre of cells of ectal excipulum at flanks or margin {2}, but usually absent; **VBs** in terminal (and lower) cells of paraphyses and in marginal cortical cells large, low to medium refractive, pale chlorinaceous; **LBs** in ectal excipular cells at base and lower flanks usually absent or with some minute ones, rarely with large LBs 1–2 µm diam. {1}. **Exudate** (0.1–)0.2–0.4(–1) µm thick, continuous, pale yellowish-amber, very finely to roughly warted, sometimes with loose granules; margin and flanks densely covered by ± fine, cloddy, pale chlorinaceous warts. — **ANAMORPH**: unknown (but see below).

Habitat: Collected 0.1–5 m above the ground, rarely lying on moist ground, ± corticated (rarely decorticated), often completely rotten, (5–)10–50 mm thick branches, also 10–80 cm thick, sometimes living trunks of *Acer* sp. {1}, *A. campestre* {1}, *A. platanoides* {1}, *Aesculus hippocastanum* {1}, *Alnus alnobetula* {1}, *A. incana* {1}, *Carpinus betulus* {2}, *Clematis vitalba* {3}, *Cornus sanguinea* {1/1}, *Corylus cornuta* {1}, *Crataegus laevigata* {1}, *Eremaea pauciflora* {1}, *Fagus sylvatica* {10}, *Fraxinus excelsior* {2}, *Hedera helix* {1}, *Hippophae rhamnoides* {1}, *Juglans regia* {1}, *Larix decidua* {1}, *Ligustrum vulgare* {1}, *Lonicera tatarica* {1/1}, *L. ?xylosteum* {1}, *Malus domestica* {2}, *Pinus* sp. {1}, *Platanus* × *acerifolia* {3}, *Populus* sp. {1}, *P. ?× canadensis* {1}, *P. tremula* {2}, ?*Prunus* sp. {1}, *P. domestica* {1}, *P. spinosa* {3}, *Pyrus communis* {1}, *Quercus* sp. {1}, *Q. ilex* {1}, *Robinia pseudoacacia* {2}, *Salix* sp. {7}, *S. caprea* {2}, *S. ?cinerea* × *aurita* {1}, *S. ?viminalis* {1}, *Tamarix anglica* {1}, *Tilia* sp. {2}, *T. cordata* {1}, *T. platyphyllos* {2}, *Ulex* sp. {1}, *U. europaeus* {3}, *Ulmus* sp. {5}, *U. laevis* {2}, *U. minor* {1}, on (slightly to) medium to strongly decayed bark {61} (bast and periderm), on inner and outer surface of detached bark, often at edges of bark, sometimes on detritus, less often on wood {28}, 1–2 mm deep medium to often strongly rotten, often on smaller or larger decorticated spots, sometimes below bark, or in larger cavities, sometimes greyed, often with abundant green algae, rarely on blackened resin; on *Fomitiporia hippophaeicola* {1}, hymenophore of *Hymenochaetopsis tabacina* {1}, *Trametes ?hirsuta* {1}, *Xanthoporia radiata* {1}, stromata or perithecia of *Bertia moriformis* {1}, *Diaporthe* sp. {1}, *Hypoxylon* *fragiforme* {1}, indet. {1}. **Further associated**: *Calycina claroflava* {1}, *Capitotricha bicolor* {1}, *Capronia* sp. {2}, *Ciliolarina laricina* {1}, *Coenogonium pineti* {1}, *Corticiaceae* {3}, *Crepidotus cesatii* {1}, *Cryptocoryneum condensatum* {1}, *Cryptodiscus foveolaris* {1}, *Diatrype bullata* {1}, *Durella connivens* {1}, *Entoloma alliodorum* {1}, *Episphaeria fraxinicola* {1}, *Gloniopsis praelonga* {1}, *Glyphium elatum* {1}, '*Helotium*' *uvidulum* {1}, *Hyalorbilia fusispora* {4}, *H. inflatula* {2}, *H. rotifera* {2}, *H. subfusispora* {4}, *H. ulicicola* {1}, *Hyaloscypha minuta* {1}, *Hymenochaete* sp. {1}, *Hysteropatella prostii* {1}, *Karstenia rhopaloides* {6}, *Lachnum virgineum* {1}, *Lasiobelonium corticale* {1}, *L. lonicerae* {1}, *L. variegatum* {1}, *Lasiosphaeria* sp. {1}, *L. hirsuta* {1}, *L. ovina* {1}, *Licea castanea* {1}, *Lophiostoma compressum* {1}, *L. subcorticale* {1}, *Lophium mytilinum* {1}, *Lophocolea* sp. {1}, *Mollisia ?oblonga* {2}, *M. prunicola* {1}, *Mycoceros antennatissimus* {1}, *Nectria pseudopeziza* {1}, *Octospora affinis* {1}, *Olla scrupulosa* {2}, *Orbilia amberina* {1}, *O. aprilis* {2}, *O. arachnovinosa* {1}, *O. aradi* {1}, *O. aristata* {1}, *O. auricolor* {1}, *O. austrocylindrica* {1}, *O. clavispora* {1/1}, *O. curvativitalbae* {1}, *O. eucalypti* {6}, *O. euonymi* {1}, *O. filiformis* {1}, *O. microserpens* {1}, *O. multicurvula* {1}, *O. obtusispora* {1}, *O. orientalis* {1}, *O. pilifera* {1}, *O. pleistovitalbae* {1}, *O. plurililacina* {1}, *O. sarraziniana* {1}, *O. subclavuliformis* {1}, *O. trapeziformis* {1}, *O. tremulae* {1}, *O. vinosa* {2}, *O. vitalbae* {1}, *O. xanthoguttulata* {1}, *Orthotrichum* sp. {1}, *Parmelia* sp. {1}, *Patellaria atrata* {1}, *Physcia* sp. {1}, *Proliferodiscus pulveraceus* {2}, *P. olivaceoviridis* {1}, *Propolis farinosa* {1}, *Pseudohelotium sordidulum* {1}, *Resupinatus* sp. {1}, *Rosellinia aquila* {1}, *R. britannica* {1}, *Stictis* sp. {1}, *Thelonectria discophora* {1}, *Tubeufia cerea* {1}, *Unguiculariopsis* sp. {2}, *Vibrissea filisporia* {1}, *Xanthoria parietina* {2}, crustose lichens, further apo- and pleurocarpous mosses. **Desiccation tolerance**: asci survive for min. 2 days, excipular cells for at least 9 days, ascospores for 13.5 months. **Altitude**: 0–1310 m a.s.l. (Europe), ?2500 m (eastern China). **Geology**: Neoproterozoic, Cambrian & Ordovician shale, silt, greywacke & sandstone, Buntsandstein, Keuper (marl & limestone), Lower & Upper Jurassic and Cretaceous sand-, clay-, marl- & limestone, Tertiary molasse, Pleistocene loess, marl & till, peat; granite, quartz diorite, gneiss, mica schist, phyllite, biotite-amphibolite, serpentinite. **Phenology**: throughout the year (long-lived).

Phenology of *H. juliae* (N-hemisphere)											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
6	5	7	7	8	2	6	9	8	13	8	11

Taxonomic remarks. *Hyalorbilia juliae* is characterized by more or less straight, narrowly subcylindrical to fusoid ascospores containing mostly 3–6 SBs near each end. The species comes close to *H. subfusispora*, but spore width in *H. juliae* is only very exceptionally up to *1.7(–1.9) µm whereas *H. subfusispora* has mostly *1.8–2.4 µm wide spores. Those collections of *H. juliae* with long, sometimes very slightly curved spores resemble *H. berberidis*, a very close taxon which can merely be separated by its consistently more or less distinctly falcate spores. *H. berberidis* shows a tendency to slightly longer spores but the values strongly overlap with those of *H. juliae*. *H. juliae* differs from *H. inflatula* in distinctly larger ascospores containing a higher number of SBs, and in smaller, never cup-shaped, more desiccation-tolerant apothecia. The asci have a similar length as in *H. inflatula* but are wider.

The spores of *H. polypori* are similar as in short-spored specimens of *H. juliae*, but they are slightly wider and contain only 1–2 SBs at each end. The excipular cells of *H. polypori* are much larger, and the apothecia desiccation-sensitive. Although the two species rather sharply differ in spore guttulation and desiccation tolerance, delimitation of their holotypes is less clear, mainly because Velenovský neglected spore guttules in most of his orbiliaceous taxa. The protologue of *H. juliae* says 'on damp bark of *Fagus*' but this does not exclude a desiccation-tolerant fungus. The small excipular cells at the lower flanks in the type of *H. juliae* (10–14 × 6–9 µm) clearly exclude conspecificity with *H. polypori*. A distinction based on the medullary excipulum (strongly gelatinized in the type of *H. polypori*, nearly non-gelatinized in the type of *H. juliae*) seems irrelevant because the degree of gelatinization was found to be variable at the species level: collections here included in *H. juliae* varied from non- to medium gelatinized. The holotype of *Orbilia cryptocarpa* seems to be intermediate between *H. juliae* and *H. polypori*, but fits better *H. polypori* with its large apothecia growing on hygric substrate, and its spores with just one SB at each end.

Variation. In the present circumscription of the species, *H. juliae* is very variable, especially in spore length, but also in spore width and shape, ascus length, and apothecial size, colour, and shape. Although ranges in spore length do not even overlap in many of the ~90 measured samples, trials to split the species based on morphology alone failed because of the frequent occurrence of collections with intermediate spore length.

About 50 samples lie within the range of 10–14(–15) µm, with mean values of 11–12 µm in ~40 of them (including the type of *O. fusispora* var. *microscopica*) and 12.2–13.5 µm in ~13 samples. About 12 collections (including the type of *H. juliae*) show a spore length of only (6.5–)7.5–10(–11) µm, with mean values of 8–9 µm. However, about 26 intermediate samples occur, with spores around 8–11 µm (mean values 9.2–9.8 µm) in six samples (e.g., Pl. 106: 2, 5) and around 9–12 µm (mean values 10–10.8 µm) in the remaining ~20 samples (Pl. 108: 2, 4) (measurements mostly in living state). Also spore width varied somewhat, within the long-spored group between *1.1–1.4 µm (Pl. 108: 2, 4–5) and *1.3–1.5(–1.7) µm (Pl. 108: 3, 6), and to a similar rate in the short-spored group.

Spore shape varied from ± cylindrical (mainly in the long-spored specimens) to distinctly narrowly fusoid or fusiform (more often seen in the short-spored and intermediate collections but also in the long-spored ones). Hence, no clear cut between short- and long-spored collections, or between those with subcylindric and fusoid spores could be established, nor any correlation with other features, besides a tendency of the short-spored specimens to occur at a more montane altitude. The type of *H. juliae* is, therefore, rather marginal in comparison with the majority of collections here assigned to that species.

Spore arrangement within the asci appears to be more or less correlated with spore length. If short-spored, the 8 spores are sometimes found in two superimposed bundles of four spores (Pl. 106: 4b), a feature being very typical of *H. inflatula*, whereas in the long-spored specimens the spores often form a single parallel bundle (Pl. 108: 3b, 5b). However, a less regular arrangement is frequently observed, especially in those specimens with an intermediate spore length, also the arrangement may change to some degree in dead asci. Specimens with short spores tend to have short asci of ca. *(21–)25–30(–35) µm, whereas those with long spores often measured *(25–)30–35(–45) µm in length.

Rather great variability was observed in the width of the marginal cortical cells. They are frequently rather strongly inflated to 4–10 µm [in the type of *H. juliae* (6–)7–10(–12) µm] and show a ± clavate shape. However, in at least four specimens with ± long spores (H.B. 8447a, 8797a, 8894a, 13.X.1983) they were 2.5–4 µm wide, and in only one (H.B. 8067a) they were intermediate: (2–)3–6(–8) µm. This striking difference

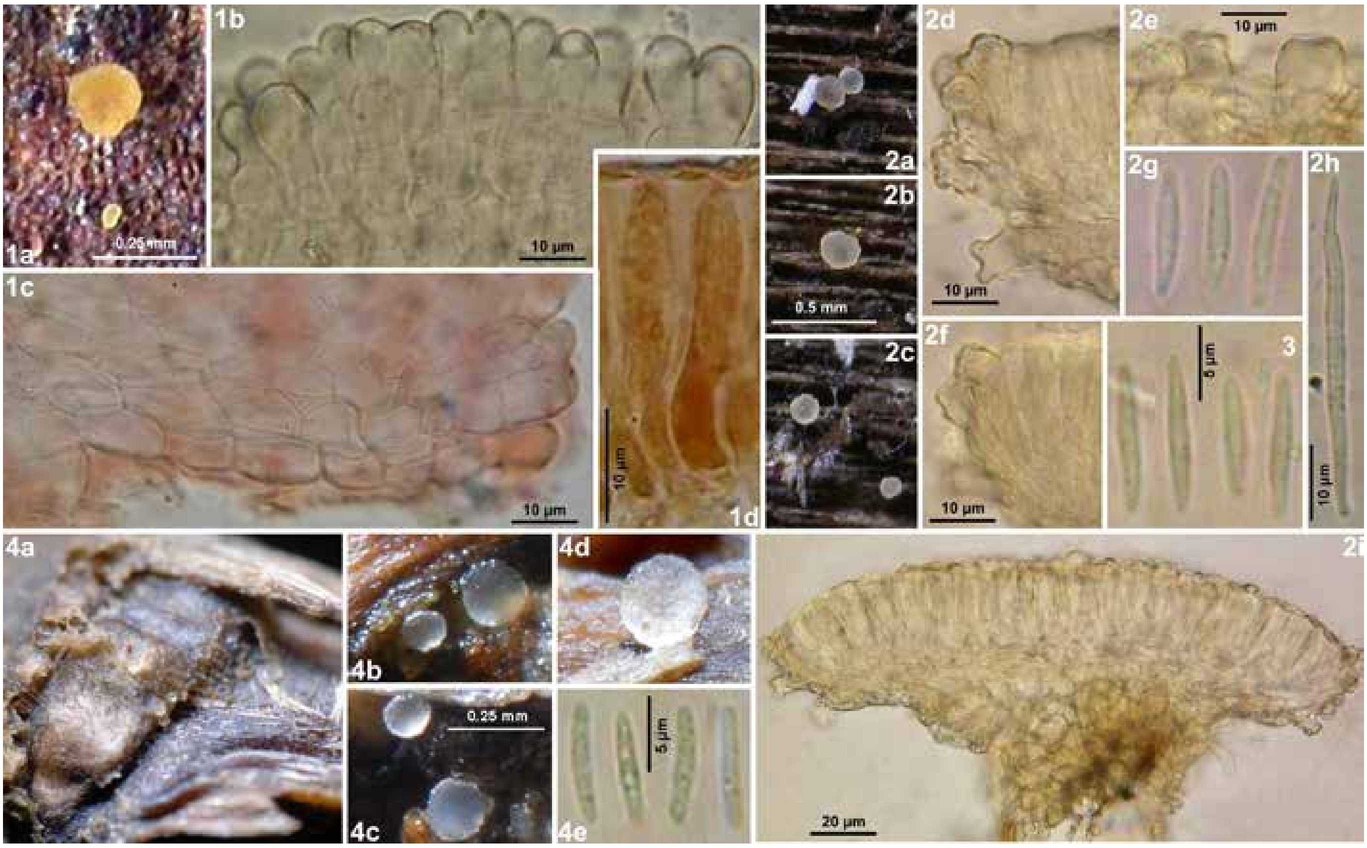


Plate 107. **1–3**: *Hyalorbilia juliae*; **4**: *H.* cf. *juliae*. – **4a**. node of *Phleum* culm with apothecia; **4b–d**. fresh apothecia; **1a**, **2a–c**. rehydrated apothecia; **2i**. apothecium in median section; **1c**, **2d**, **f**. marginal ectal excipulum in median section; **1b**, **2e**. id., in surface view; **1d**. asci; **2g**, **3**, **4e**. ascospores; **2h**. conidia from substrate. – Living state, except for **1b**, **2d**, **f**, **i**, **3** (in KOH), **1c** (in KOH+CR), **1d** (in KOH+IKI). – **4a–d**: phot. P. Perz. — **1a–d**. PRM 151740 (holotype of *O. juliae*): Czechia, Zvánovice, on *Fagus*; **2a–i**. H.B. 8279c: Switzerland, Pilatus, on *Tilia*; **3**. H.B. 5584: France, Vosges, on *Salix*; **4a–e**. H.B. 9138b: Poland, Kłodzko, on *Phleum*.

represents one of the separating characteristics between *H. subfusispora* and *H. fusispora*, and it may well be that *H. juliae* is heterogeneous in the present circumscription. In any case, a correlation with spore length was not observed: many of the long-spored collections possessed very wide marginal cells, and these were often seen in rather small apothecia. Macroscopically, some of the specimens with narrow marginal cells closely resemble *H. fusispora* in their ochraceous colour (Pl. 109: 3a–c), whereas others are quite hyaline (Pl. 109: 14a–c).

Apothecia varied in diameter between (0.1–)0.15–0.4 and 0.3–0.7(–0.9) mm, and in colour between whitish and light yellowish-amber. In two collections the margin was distinctly crenulate (H.B. 9494, Pl. 109: 17; J.P.P. 13121). In H.B. 9494 the first inspection revealed curved spores reminiscent of *H. berberidis* (T. Læssøe pers. comm.), nevertheless the few documented spores look ± straight (see IVV). In another collection assigned to *H. juliae* the cortical cells formed striking denticulate protuberances (Pls 106: 7; 107: 2a–i). In its other features it concurs with the short-spored samples, therefore this specimen is not believed to represent a separate taxon. The single very sparse Australian collection (on xeric bark of *Eremaea*, Pl. 107: 5) with a medium spore length seems to be conspecific with *H. juliae*. It differs from *H. texensis* from subtropical humid North America in much longer spores.

Richter (in Montag & Richter 2017: 62) described and illustrated the long-spored form of *H. juliae* from a collection on branches of *Ligustrum* from northern Germany, with small apothecia of 0.2–0.4 mm diam. and spores of *(8.5–)10–12.5 × 1.2–1.3 µm.

Type studies. The holotype of ***H. juliae*** now contains three scattered apothecia. Velenovský (1934) gave a spore length of 6–10 µm which is confirmed here, whereas ascus size (25 × 6–8 µm) exceeds our measurements of living asci in width. Yet, on his uncalibrated manuscript sketch the asci are drawn distinctly narrower, which corresponds to the here evaluated width of the dead asci of mainly 4–4.5 µm (Pl. 106: 1). Svrček (1954) found the spores only 6–7 × 1 µm and referred the taxon to synonymy with *O. inflatula*. Spore width as evaluated in the present study corresponds to Velenovský's sketch and clearly segregates *H. juliae* from *H. inflatula*. Velenovský found the apothecia 0.5–1 mm diam. but they are now rehydrated only 0.3–0.5 mm.

Although the holotype of ***O. fusispora* var. *microscopica*** (PRM 152442, a mixture with the holotype of var. *fusispora*) was said to contain no longer any apothecia (Svrček, 1954), a total of nine were detected (see under *H. fusispora*, p. 400). One out of three very small whitish apothecia that grew on a single chip of bark was examined and found to belong to this taxon, whereas two of the six larger ones on separate bark chips represent *H. fusispora*. Velenovský's description is very brief ('apothecia 0.1 mm diam., hyaline, glassy, spores linear-acicular'). The differences to var. *fusispora* were seen by him merely in the spores which he gave on his illustrated manuscript sheet as 12 µm long. Though the spores of var. *fusispora* and var. *microscopica* greatly differ in Velenovský's drawings, the author apparently could not believe that the two closely associated populations belong to two separate species. Besides the very different spores, the type of var. *microscopica* differs from that of var. *fusispora* also in ascus size and in the length

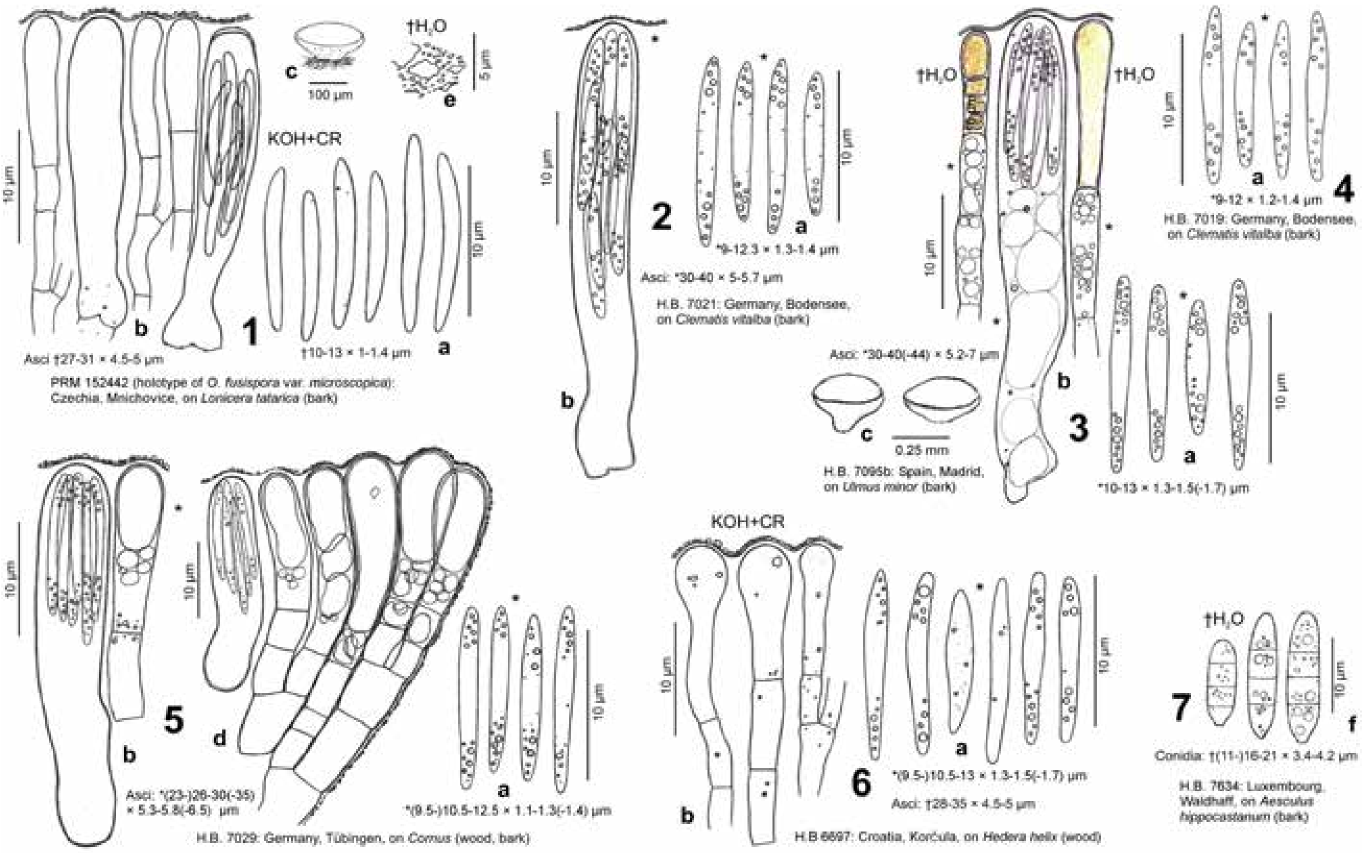


Plate 108. **1–7**: *Hyalorbilia juliae*. – **a**. ascospores; **b**. asci and paraphyses (**3**: VBs in dead cells with secondary pigmentation, **5**: living cells with hyaline VBs); **c**. rehydrated apothecia; **d**. marginal ectal excipulum (median section); **e**. warted-cloddy exudate on ectal excipulum; **f**. conidia from substrate.

of the terminal cells of paraphyses (10–13 vs. 18–27 µm, see Pl. 108: 1 and Pl. 114: 1).

Not included collections: A collection from Poland, on culms of *Phleum pratense* lying on the moist ground (Pls 106: 4; 107: 4a–e), has very small apothecia (0.12–0.2 mm diam.), which are easily overlooked and do not tolerate drying, spores of the short type as in the type of *H. juliae*, but rather short asci. Similarly, a tropical collection from the Comoros was on a hygric log of *Albizia*, with very small apothecia (around 0.12 mm), very short asci (*17–20.5 × 5.3–6.2 µm, †16.5–18 × 4.7–5 µm) but spores as in the type of var. *microscopica*: *11–14(–15) × 1.1–1.3 µm. In the apothecia on *Phleum* the marginal cells were *(4.5–)6–10(–12.5) µm wide and without VBs, while in those on *Albizia* they were *5–6 µm wide and each contained a single globose VB (IVV: J.P.P. 13004). Due to the extraordinary habitat and short asci we refrained from including the two samples in the description.

Among records from China, Liu (2006: 41, pl. 8; 2007b) reported under the name *H. juliae* three and Guo et al. (2014b) five Chinese collections (provinces of Beijing, Zhejiang, Anhui, Yunnan, Sichuan, on wood of *Quercus* etc.). Liu's description of the spores (*7.2–11.8 × 1.2–1.7 µm) with many small SBs would very well fit *H. juliae*, but the larger apothecia (0.5–3 mm) point to a different species. Also Guo et al. gave rather large apothecia (0.6–1 mm) and very similar spores (*7.4–12.8 × 1.2–1.7 µm) with 4–7 large globose SBs of 0.6–0.9 µm diam. in each half. Because of the large apothecia we preferred not to include any eastern Asian records in the description. A unpublished sample from Sichuan (IVV: zcw-j-4, J.W. Guo pers. comm., not mentioned in Guo et al. 2014b, originally referred to *O. fusispora* var. *microscopica*) has small apothecia of 0.5 mm diam., but the straight spores measure only *6–8 × 1–1.2 µm according to the scale and contain, unlike *H. inflatula*, several rather large SBs near each end. A similar collection (IVV: ys-j-8) was included in *H. juliae* by Guo et al.; it has the very same collection data and same spore size of *6–7.5 × 1–1.2 µm (from scale), according to its unpublished plate, but the spores are sometimes curved and with less SBs. Longer spores occurred in four samples which Guo et al. (2014b: fig. 8) referred to *H. inflatula*, with spores of *5.9–10.3 × 0.9–1.2 µm with 3–4 rather large SBs in each half. Apothecial size (0.2–0.55 mm diam. from scale) would fit *H. juliae*, but spores are also too narrow to belong to short-spored *H. juliae*.

Anamorph. In one collection ellipsoid-cylindrical, 3-septate conidia were observed on the natural substrate (Pls 108: 7; 109: 9), which resemble those of the brachyphoris-like anamorphs of *H. polypori* and *H. tortuosa*, but differ in a smaller size: *(11–)16–21 × 3.4–4.2 µm. Their cells contained some large low-refractive guttules and many small LBs. In another sample (IVV: H.B. 8279c) two ± cylindrical, 3-septate conidia of *40–42 × 7.5–8 µm were seen. In addition, in H.B. 5980 (Pl. 106: 2k) and H.B. 8279c (Pl. 107: 2h) narrower conidia (†31–49 × 1.7–2.3 µm) were found similar to those observed near apothecia of *H. rotifera* and *H. subfusispora*. However, it is unclear which of these conidial types represent the anamorph of *H. juliae*.

Phylogeny. Sequences of four long-spored strains of *H. juliae* were available (France: *Ulmus* [from apothecia]; Luxembourg: *Clematis* [from culture], *Populus* and *Fagus* [from apothecia]). Two comprise only ITS, the other two ITS and LSU D1–D3. The S1506 intron is present in three of them (for the *Ulmus* sequence the ITS1 primer was used). Spore size varied among these collections: *(10–)11.5–14.5 × 1.3–1.4 µm on *Ulmus*, *10–

13.5 × (1.2–)1.4–1.6(–1.8) µm on *Clematis*, *9–12.5 × 1–1.2 µm on *Populus*, *(10.5–)12–13 × 1.2 µm on *Fagus*.

The *Fagus* sequence differs from the other three in a 1.5–2.1 % ITS distance (2.5 % in the intron). The other three differ among each other in the ITS at 4 positions and 2 gaps (when neglecting untrustworthy 14 nt at the 5'-end in the *Ulmus* sample), resulting in a 0.4–0.5 % distance between each of them. Also in the intron these differ by only 2 nt and 1 gap in the overlapping 339 nt (0.6 %), while their LSU is identical.

When analysing ITS, *H. juliae* clustered with *H. tenuifusaria* and *H. fusispora* (H.B. 8447b) in an unsupported clade (Phyl. 5) by showing a very high distance of 20 and 25 %, respectively. In the 5.8S region, *H. juliae* fully matches *H. tenuifusaria* and *H. subfusispora* but deviates from *H. fusispora* by 1 nt (pos. 142). When analysing ITS+LSU, *H. juliae* clustered with high support in a clade with *H. tenuifusaria* and various uncultured DNA soil and leaf litter isolates (*juliae-tenuifusaria* clade, Phyl. 6, H18–H19, H21–H23, H26), with a minimum distance of 2 % in the LSU (D1–D2) to EF446004 from California, while the ITS distance to uncultured strains was very high. When analysing the S1506 intron, a high distance is found to all *Hyalorbilia* species that possess the intron (see Phyl. S4).

An ITS sequence in GenBank under the name *H. juliae* (DQ656650, strain [B.L.] 6449) was gained by B. Liu from apothecia of HMAS 139535 (IVV), with spores strongly reminiscent of *H. juliae*, but collection data and spore size were unavailable to him (B. Liu pers. comm.). Surprisingly, the distance of this sequence to European *H. juliae* lies at over 25 %. Instead, it clustered highly supported and with a 10.5 % distance with a strain identified as *H. andina* (B.L. 6184, HMAS 139534, from Guangxi) in the *inflatula-polypori* clade (Phyl. 5). Possibly a confusion is the reason for this mismatch (see under *H. arcuata*, p. 378). Note that the very similar number HMAS 139553 is among the three *H. juliae* samples listed in Liu (2006, see also under *H. arcuata*).

Ecology. *Hyalorbilia juliae* was found on rotten bark (more rarely wood) of xeric branches and trunks of various angiosperm trees, shrubs and climbers. Sometimes it occurred on aphyllophoralean fungi or pyrenomycetes, and a single very sparse collection was on blackened resin (large wound of a *Larix* branch). *H. juliae* is quite a common species, being recorded from various parts of atlantic to subcontinental Europe, including hemi- to mesoboreal, meso- to orotemperate, and suprasub- to thermomediterranean, humid to semihumid regions. The vegetation includes sun-exposed or shady borders of forests, old hedges, also rather moist woodlands, shrubs, ditches such as *Aceri-Fraxinetum*, *Salicetum* or *Alnetum viridis*, and in mediterranean regions (*Quercetum ilicis*). *H. juliae* does not seem to differ markedly in its ecological preferences from *H. subfusispora* (see p. 403). Both occur almost exclusively on xeric branches, nearly always of angiosperm trees, whereas *H. inflatula* is predominantly found on hygric substrate. Also the not included samples from China are from (oro)temperate as well as subtropical humid (winter-dry) regions, and a collection from the island of Mayotte (Comoros) was in a tropical wet & dry rainforest on a log of *Albizia* lying on the moist ground, where the apothecia grew intermingled with the desiccation-sensitive *Orbilia blumenaviensis*.

Map 15. Known distribution of *H. juliae* in Europe: white = spores *8–10 µm long, yellow = spores *10–13 µm long.

Specimens included (shsp = short-spored: average 8–9 µm, med1: average 9.2–9.8 µm, med2: average 10–10.8 µm; lgsp1 = long-spored, average 11–11.8 µm, lgsp2 = long-spored, average 12–13 µm).

SWEDEN: **Västerbotten**, 12 km WNW of Umeå, 1 km NE of Sörfors, 40 m, trunk of *Populus tremula*, on bark, 5.X.2014, O.E. Eriksson (lgsp1, ø). — **DENMARK**: **Sjælland**, 4.5 km NNW of centre of København, Strødamvej, Ramløsevej, 12 m, trunk of *Tilia*, on bark, 9.II.2011, T. Læssøe (lgsp1, H.B. 9494, J.H.P. 11.003 ø, T.L. 2011-14, DMS-143464). — **GREAT BRITAIN**: **East England**, **Suffolk**, 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Ulex europaeus*, on bark, 21.XII.2004, S.M. Francis, vid. E. Batten (shsp, E.B. 4574 ø, doc. vid.). — **NETHERLANDS**: **Flevoland**, 17 km SE of Lelystad, 5 km N of Harderwijk, Broekbos, 2 m, branch of *Fraxinus excelsior*, on bark, 20.III.2005, H.O. Baral (med2, ø). – 6 km SW of Kampen, 9 km E of Dronten, Revebos, 9 m, branch & branch of *Salix*, on bark, 20.III.2005, H.O. Baral (lgsp1, ø). – **Utrecht**, 6 km SSE of Utrecht, 2 km N of Houten, Nieuw Wulven, 0 m, branch of *Quercus*, on old pyrenomycete, 16.XII.2016, E. Osieck, vid. S. Helleman (lgsp1, S.H. 893, non vid.) – **Zeeland**, Schouwen-Duiveland, 10.5 km NNE of Zierikzee, 3.5 km ENE of Brouwershaven, Stampersplaat island, 1 m, *Hippophae rhamnoides*, on *Fomitiporia hippophaeicola*, 26.X.2010, S. Helleman (med1, S.H. 674, doc. vid.). — **BELGIUM**: **Wallonie**, **Luxembourg**, 8 km SE of Arlon, SE of Sterpenich, 325 m, branch of *Salix*, on bark, 23.IV.2001, H.O. Baral & G. Marson (med2, H.B. 6932). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 10.5 km W of Ettelbruck, 1.8 km NW of Grosbous, Bruch, 385 m, branch of *Salix*, on *Hymenochaetopsis tabacina*, 27.V.2001, G. Marson (med2, H.B. 7007). – **Gutland**, **Capellen**, 6.7 km ESE of Arlon, 1.3 km NW of Steinfort, quarry at Aechels, 330 m, branch of *Carpinus betulus*, on bark, 5.V.1998, H.O. Baral (med2, ø). – **Grevenmacher**, 13.5 km NE of Luxembourg, 1.7 km WNW of Junglinster, south-end of Bierger, 350 m, trunks of *Fagus sylvatica*, on bark, 21.VIII.2005, G. Marson (med2, ø). – **Luxembourg**, 6 km NE of Luxembourg, SE of Waldhaff, Gréngewald, Arboretum, 410 m, branches of *Aesculus hippocastanum*, on bark, 27.XI.2004, G. Marson (lgsp1, H.B. 7634 ø, anam. substr.). – NE of Waldhaff, 417 m, branch of *Larix decidua*, on resin, 12.II.2006, G. Marson (med1, H.B. 8067a ø). – ibid., trunk of *Fagus sylvatica*, on bark, 3.I.2010, G. Marson (lgsp2, ø). – 1.5 km WSW of Luxembourg, Parc de Merl, 290 m, trunk of *Ulmus laevis*, on bark, 23.V.2004, G. Marson (med2, ø). – 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, branch of *Fraxinus excelsior*, on wood, 14.X.2011, G. Marson (med2, ø). – 5 km S of Luxembourg, 1 km W of Hesperange, Géisselbierg 290 m, trunk of *Fagus sylvatica*, on bark, 7.IV.2005, G. Marson (lgsp1, H.B. 7718b). – **Esch-sur-Alzette**, 3.3 km NNW of Bettembourg, 1.2 km N of Abweiler, trunk of *Fagus sylvatica*, on bark, 2.X.2019, G. Marson (lgsp2, G.M. 2019-10-02.2, doc. vid., sq.: MN626470). – 2 km S of Bettembourg, 1.8 km W of Berchem, 280 m, trunk of *Populus*, on bark, 17.XII.2014, G. Marson (lgsp1, G.M. 2014-12-17.1, sq.: MK493152). – 4.2 km S of Bettembourg, 2.8 km NW of Zoufftgen, along railway, 295 m, branches of *Clematis vitalba*, on wood & bark, 14.XII.2013, G. Marson (lgsp1, G.M. 2013-12-14.2; sq.: KY419178). – 6.5 km ESE of Esch-sur-Alzette, 1.5 km SW of Dudelange, Haard, 375 m, branch of *Populus tremula*, on wood, 2.I.2005, G. Marson (lgsp2, H.B. 7649a). – 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, branch of *Robinia pseudoacacia*, on wood, 31.X.1993, G. Marson (lgsp1, H.B. 4983). – 2.2 km S of Esch-sur-Alzette, 1.5 km ENE of Audun-le-Tiche, Ellergronn, 345 m, branch of *Crataegus laevigata*, on wood, 26.IV.2001, G. Marson & H.O. Baral (lgsp1, H.B. 6923b). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 7 km E of

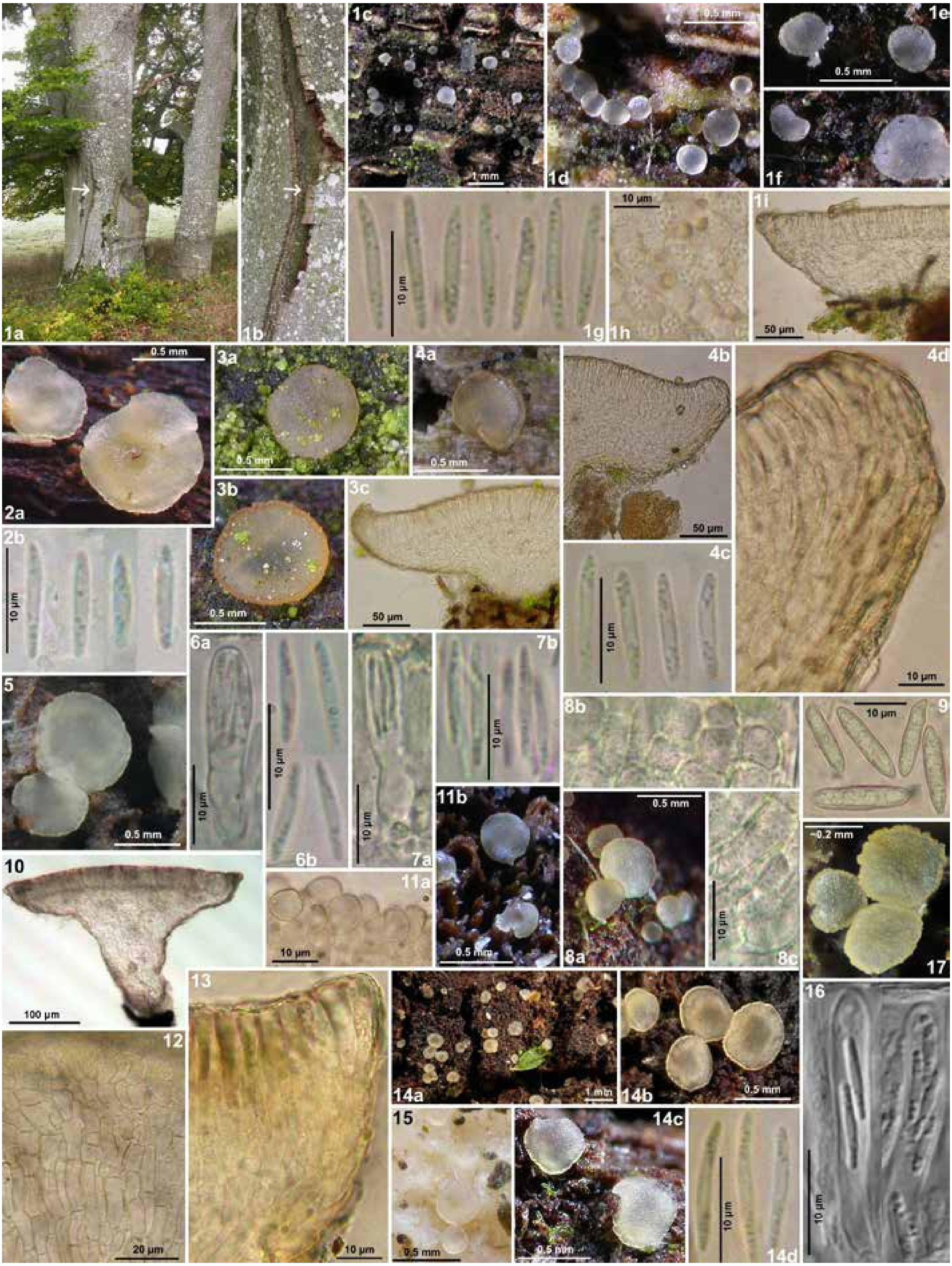


Plate 109. **1–17**: *Hyalorbilia juliae*. – **1a**. pasture with free-standing living beech trees; **1b**. closeup of *Fagus* trunk with wound, on inner surface of detaching bark; **14a–c**, **17**. fresh apothecia; **1c–f**, **2a**, **3a–b**, **4a**, **5**, **8a**, **11b**, **15**. rehydrated apothecia; **1i**, **3c**, **4b**, **10**. apothecia in median section; **4d**, **13**. marginal ectal excipulum in median section; **11a**, **12**. id., in top and surface view; **8b–c**. exudate on ectal excipulum (surface view); **1h**. hymenium in top view; **6a**, **7a**, **16**. asci and paraphyses; **1g**, **2b**, **4c**, **6b**, **7b**, **14d**. ascospores; **9**. conidia. – Living state, except for **9** (in H_2O); **11a** (in KOH), asci in **16**. – **2a–b**, **5**, **6a–b**, **7a–b**, **8a–c**, **10**, **15**: phot. P. Perz; **16**: phot. J.W. Guo (DIC). — **1a–i**. H.B. 7930: Germany, Tutzing, on *Fagus*; **2a–b**. P.P. 20061213-1: Poland, Kłodzko, on *Prunus*; **3a–c**. H.B. 8797a: France, Eure-et-Loire, on *Ulmus*; **4a–d**. H.B. 8894a: Germany, Tübingen, on *Ulmus*; **5**. P.P. 20071006: Poland, Kłodzko, on *Tilia*; **6a–b**. P.P. 20070827: ibid., on

Rennes, 2.2 km SE of Cesson-Sévigné, Forgé, 47 m, branch of *Ulmus*, on wood, 24.V.2013, J.P. Priou (lgsp1, J.P.P. 13121, doc. vid.). – **Morbihan**, 4.5 km SW of Guer, 2 km NE of Monteneuf, Les Pierres Droites, 140 m, branch of *Ulex europaeus*, on bark, 4.XII.2009, J.P. Priou (lgsp1, J.P.P. 29234, ø, doc. vid.). – 7.5 km NNE of La Gacilly, 3 km ENE of Carentoir, Le Gouta, 87 m, branch of *U. europaeus*, on bark, 14.III.2004, J.P. Priou (med1, J.P.P. 24095, doc. vid.). – 8.5 km WNW of Redon, 2 km E of St.-Jacut-les-Pins, Moulin de Calléon, 19 m, branch of *Salix*, on bark, 5.II.2006, J.P. Priou (lgsp2, J.P.P. 26037, doc. vid.). – 12 km S of Auray, 1.5 km SW of Locmariaquer, Breneguy, 2 m, branch of *Tamarix anglica*, on bark, 29.XII.2003, J.P. Priou & A. Delannoy (?lgsp, J.P.P. 23152, non vid.). – **Poitou-Charentes**, **Deux-Sèvres**, 16 km ESE of Melle, 2 km ENE of Clussais-la-Pommeraie, E of Clussais, 130 m, trunk of *Ulmus*, on bark, 13.V.2006, B. Coué (lgsp1, H.B. 8171 ø). – 9.5 km SSE of Niort, 1.7 km NNE of Fors, 37 m, trunk of *Ulmus*, on bark, 2.III.2007, M. Hairaud (lgsp2, M.H. 40307, H.B. 8447a; sq.: KT222380). – **Centre**, **Eure-et-Loire**, 23 km NNW of Orleans, 1.3 km NE of Poupry, Le Aire Héron Cendré, 125 m, branch of *Ulmus*, on wood, 12.IV.2008, S. Helleman & H.O. Baral (lgsp1, H.B. 8797a ø). – **Champagne-Ardenne**, **Ardennes**, MEN 2909 D, 14.5 km WSW of Charleville-Mézières, ~2 km E of Thin-le-Moutier, Forêt de Froidmont, 210 m, on branch of *Fagus sylvatica*, on bark and *Hypoxylon fragiforme*, 20.X.2003, R. Collot (?lgsp, ø). – **Lorraine**, **Vosges**, 10 km WNW of Gérardmer, 1.8 km ESE of Rehaupal, SE of Varinfête, 630 m, branch of *Salix* (?)*aurita* × *cinerea*, on bark, 7.IX.1996, H.O. Baral & G. Marson (shsp, H.B. 5584). – **Bourgogne**, **Côte-d'Or**, 24 km NE of Dijon, N of Bèze, Les Combottes, 225 m, branch of *Euonymus europaeus*, on wood and *Diaporthe*, 29.X.2009, J.P. Priou (lgsp1, J.P.P. 29207, doc. vid.). – **Languedoc-Roussillon**, **Hérault**, Haut-Languedoc, 23 km WSW of Bédarieux, E of St.-Vincent-d'Olargues, Les Boires, 295 m, branch of *Prunus domestica*, on bark, 10.XII.2006, G. Garcia (lgsp1, G.G., doc. vid.). – **Provence-Alpes-Côte d'Azur**, **Var**, Îles d'Hyères, Île de Port-Cros, 14 km S of Le Lavandou, E of La Palud, 16 m, trunk of *Quercus ilex*, on bark, 13.X.1983, C. Roux (med2, ø). — **GERMANY**: **Mecklenburg-Vorpommern**: 4.3 km WNW of Rehna, 1 km WNW of Löwitz, 45 m, branch of *Ligustrum vulgare*, on wood, 13.I.2017, T. Richter (lgsp1, doc. vid.). – **Sachsen**, 3.5 km W of Döbeln, WNW of Stockhausen, branch of *Salix*, on bark & wood, 16.II.2013, S. Pohlers (lgsp1, ø). – 7 km SSW of Freiberg, 2 km SW of Brand-Erbisdorf, Himmelsfürst, 480 m, branch of indet. angiosperm, on bark, 19.V.2014, B. Mühler (lgsp1, ø). – **Baden-Württemberg**, 12.5 km E of Heidelberg, 1 km SE of Neckarsteinach, 128 m, branch of *Malus domestica*, on wood, 25.XII.2011, M. Bemmann (lgsp1, doc. vid.). – 6 km NW of Stuttgart, S of Weilimdorf, Raiffeisenstraße, 330 m, branch of *Lonicera* ?*tatarica*, on bark, 7.IV.2002, H.O. Baral (med2, ø). – 4 km N of **Tübingen**, W of Bebenhausen, Goldersbach, 380 m, branches of *Prunus spinosa*, on bark, 20.IV.1993, H.O. Baral (shsp, ø). – ibid., 20.V.2001, H.O. Baral (med2, ø). – 1.5 km NE of Tübingen, W of Lustnau, Wilhelmstraße, 325 m, trunk of *Corylus cornuta*, on bark, 24.IV.2005, H.O. Baral (lgsp1, ø). – 3 km NE of Tübingen, 1 km NE of Lustnau, Stauden, 400 m, branch of *Cornus* ?*sanguinea*, on bark & wood, 15.IX.2001, H.O. Baral (lgsp1, H.B. 7029). – ibid., 380 m, branch of *Lonicera* (?)*xylosteum*, on bark & wood, 15.IX.2001, H.O. Baral (lgsp1, H.B. 7030). – 5 km NNE of Tübingen, 1.5 km NW of Pfrondorf, N of Sophienpflege, 460 m, branch of *Prunus spinosa*, on bark, 23.I.1993, H.O. Baral (shsp, H.B. 4832a). – 2 km NNE of Pfrondorf, NW of Einsiedel, 460 m, branch of *Ulmus*, on wood, 13.VII.2008, H.O. Baral (lgsp1, H.B. 8894a ø). – N of Pfrondorf, Brandklinge, 410 m, trunk of *Acer platanoides*, on bark, 9.I.2005, H.O. Baral (lgsp2, ø). – Pfrondorf, Blaihofstraße, 430 m, branch of *Juglans regia*, on wood & bark, 29.VI.1994, H.O. Baral (med2, H.B. 5109). – ibid., branch of *Pyrus communis*, on wood, 27.VIII.2002, H.O. Baral (lgsp1, ø). – ibid., branches of *Robinia pseudoacacia*, on bark, 9.IX.2003, H.O. Baral (med2, H.B. 7414). – ibid., branch of *Tilia platyphyllos*, on bark & wood, 27.VII.2007, H.O. Baral (lgsp2, H.B. 8587a). – E of Pfrondorf, Tiefenbach, 385 m, branch of *Acer campestre*, on bark, 16.XII.2005, H.O. Baral (lgsp2, H.B. 8017b ø). – ibid., 430 m, branch of *Salix caprea*, on bark, 22.X.2005, H.O. Baral (lgsp1, ø). – S of Pfrondorf, Obere Mähder, 390 m, branch of *Malus domestica*, on bark, 9.II.2003, H.O. Baral (lgsp1, ø). – 1 km SE of Pfrondorf, SE of Rauhalde, 345 m, branch of *Tilia*, on wood, 18.XI.2001, H.O. Baral (lgsp1, ø). – 1.3 km SW of Pfrondorf, quarry near Bitzle, 420 m, branch of *Salix caprea*, on bark, 16.XI.2003, H.O. Baral (lgsp1, H.B. 7434a). – ibid., branch of *Cornus sanguinea*, on wood, 19.XI.2006, H.O. Baral (lgsp1, ø). – 6.7 km SSE of Tübingen, 2 km WNW of Gomaringen, Wiesaz SSE of Pulvermühle, 370 m, branch of *Salix* ?*viminalis*, on bark, 19.III.2009, H.O. Baral (lgsp1, H.B. 9026a ø). – 7 km E of Metzingen, 2.2 km S of Neuffen, Winnender Berg, 660 m, stump of *Fagus sylvatica*, on bark, 25.V.2005, H.O. Baral (lgsp2 H.B. 7789 ø). – 7.5 km NE of Radolfzell, SW of Bodman, E of graveyard, 450 m, branch of *Clematis vitalba*, on bark, 31.VIII.2001, H.O. Baral (med2, H.B. 7021 ø). – 4.5 km SE of Bodman, NW of Marienschlucht, 405 m, branch of *C. vitalba*, on bark, 30.VIII.2001, H.O. Baral (med2, H.B. 7019). – **Bayern**, **Oberbayern**, 8 km NW of Tutzing, 3.5 km S of Andechs, Goaslweide, 720 m, trunk of *Fagus sylvatica*, on bark, 15.X.2005, H.O. Baral (lgsp2, H.B. 7930). — **SWITZERLAND**: **Nidwalden**, 6 km S of Luzern, 1 km NW of Hergiswil, Bruustried, 600 m, branch of *Tilia platyphyllos*, on wood, 22.VIII.2006, U. Graf & H.O. Baral (shsp, H.B. 8279c, anam. substr.). — **LIECHTENSTEIN**: 6 km SE of Vaduz, SSE of Steg, Saminatal, Im Grund, 1310 m, twig of *Alnus alnobetula*, on bark, 7.VII.1997, H.O. Baral (shsp, ø). — **AUSTRIA**: **Wien**, 5.5 km SSE of Wien, 1.3 km E of Favoriten, Laaer Wald, 248 m, branch of *Acer*, on wood, 8.XI.2013, R. Moosbeckhofer, vid. B. Wergen (lgsp1, H.B. 9856 ø). – **Steiermark**, 11 km NW of Deutschlandsberg, 3 km W of Rachling, E of Rosenkogel, 1160 m, branch of *Fagus sylvatica*, 24.III.2012, G. Friebes (lgsp1, ø, non vid.). – 8 km WNW of Bad Radkersburg, 4 km W of Halbenrain, SW of Unterpurkla, Donnersdorfer Au, 218 m, branch of *Ulmus laevis*, on wood, 30.X.2011, G. Friebes (lgsp1, G.F. 20110196, doc. vid.). — **RUSSIA (West)**: **Leningrad**, **Vyborg**, Gulf of Finland, 46 km S of Vyborg, 7 km SSE of Primorsk, Bolshoy Berezovy Island, 0.5 km NW of Krasnoostrovsk, 30 m, branch of *Salix* on wood, partly on *Bertia moriformis*, 10.IX.2004, E.S. Popov (lgsp1, LE, doc. vid.). — **ESTONIA**: **Tartumaa**, 20.5 km WSW of Tartu, 3 km E of Puhja, SE of Mõisanurme, valley of Kavilda, 40 m, branch of *Populus*, on wood, 19.VIII.1997, A. Raitviir & K. Pärtel (sh, TAAM 164052, H.B. 5980, anam. substr.). – **Pärnumaa**, 4.8 km NW of Varbla, 1.5 km SSW of Nõmme, E of Mereäärse, 20 m, on hymenophore of *Xanthoporia radiata*, 27.IX.1994, K. Põldmaa (med1, TAAM 161510, H.B. 5360 ø). — **POLAND**: **Lower Silesia**, 6 km SW of Kłodzko, 1 km W of Krosnowice, 450 m, branch of ?*Prunus*, on wood & bark, 13.XII.2006, P. Perz (lgsp1, P.P. 20061213-1, doc. vid.). – 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, branch of *Salix*, on bark, 9.XI.2006, P. Perz (lgsp2, P.P. 20061109-4, doc. vid.). – ibid., branch of *Salix*, on wood, 27.VIII.2007 (med2, P.P. 20070827-2, doc. vid.). – ibid., branch of *Pinus*, on bark, 21.VIII.2007 (lgsp2, P.P. 20070821-1 ø, doc. vid.). – 1.4 km SSW of Żelazno, Wapniarka Mt., on *Trametes* ?*hirsuta*, 21.III.2010, P. Perz (med2, P.P. 20100321-4, doc. vid.). – 11 km SW of Bystrzyca Kłodzka, ~1.5 km W of Gniewoszów, ~820 m, trunk of *Fagus sylvatica*, on bark, 1.VII.2007, P. Perz (med2, P.P. 20070701-2, doc. vid.). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, branch of *Tilia cordata*, on bark, 6.X.2007, P. Perz (lgsp2, P.P. 20071006-8, doc. vid.). – **Lesser Poland**, Vysoké Tatry, 2.5 km WSW of Tatranská Javorina, Bielovodská valley, 988 m, log of *Alnus incana*, on bark, 1.XI.2018, A. Polhorský (med1, doc. vid.). — **CZECHIA**: **Central Bohemia**, 27 km SE of Praha, W of Mnichovice, 'in nostro horto', 370 m, branch of *Lonicera tatarica*, on bark, VII.1926, J. Velenovský (lgsp1, PRM 152442, **holotype** of *O. fusispora* var. *microscopica*, H.B. 6131a ø). – 31 km SE of Praha, ~1 km S of Zvánovice, at foot of Pecny Mt., 500 m, branch of *Fagus sylvatica*, on bark, VII.1929, J. Velenovský (shsp, PRM 151740, **holotype** of *O. juliae*, H.B. 6191 ø). — **HUNGARY**: **Pest**, 4.5 km SE of Budapest, NIEH park, Albert Florian ut, 113 m, trunk of *Platanus* × *acerifolia*, on bark, 17.VIII.2010, D. Magyar (lgsp1, H.B. 9603). – ibid., 21.IX.2011 (lgsp1, H.B. 9600). – ibid., 6.V.2016 (med2, H.B. 10134 ø). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 8 km W of Korčula, Pupnat, 320 m, branch of *Hedera helix*, on wood, 11.VI.2000, H.O. Baral (lgsp1, H.B. 6697). — **SPAIN**: **Madrid**, 7.5 km S of Collado Villalba, 11 km ESE of San Lorenzo del Escorial, W of Colmenarejo, Arroyo Peraleda, 850 m, trunk of *Ulmus minor*, on bark, 24.I.2002, F. Prieto (lgsp1, AH 7420, H.B. 7095b ø). — **SERBIA**: **Vojvodina**, Fruška Gora, 14.5 km SSW of Novi Sad, 2.5 km NW of Vrdnik, 267 m, branch of *Carpinus betulus*, on bark, 28.XI.2019, D. Savić (doc. vid.). — **PORTUGAL**: **Santarém**, 10 km NNW of Santarém, 2.5 km SW of Achete, Val de Flores, SE of Trindade, 50 m, branch of *Ulex*, 29.XII.2004, J.P. Priou (med2, J.P.P. 24289, doc. vid.). — **AUSTRALIA**: **Western Australia**, Swan Coastal Plain, 59 km SW of Moora, 8 km NE of Cowalla, Moore River, Orange Springs Rd, 77 m, branch of *Eremaea pauciflora*, on bark, 5.IX.2006, G. Marson (med1, H.B. 8643j ø).

Not included. **POLAND**: **Lower Silesia**, 20 km WSW of Kłodzko, 1.6 km NW of Duszniki Zdrój, NE of Słoszów, 563 m, culms of *Phleum pratense*, 10.VIII.2009, P. Perz (shsp, P.P. 20090810-1, 20090819-1a, H.B. 9138b). — **COMOROS**: **Mayotte**, 11.5 km WSW of Mamoudzou, 2.2 km NE of Chiconi, Lycée Agricole, 125 m, log of *Albizia lebbeck*, on wood, 11.XII.2012, M. Pélissier, vid. J.P. Priou (lgsp2, J.P.P. 13004, H.B. 9748b ø, doc. vid.). — **CHINA**: **Beijing**, **Huairou**, Trumpet Gate Forest Park, on *Quercus* wood, 850 m, 10.VII.2002, B. Liu (shsp, HMAS 139525, doc. vid.; HMAS 139553, non vid.). – unlocalized (?lgsp, B.L. 6449, HMAS 139535, doc. vid.). – **Sichuan**, **Ngawa** (Aba), Jiuzhaigou, 2000–2500 m, on branch of indet. tree, 8.X.2006, J.W. Guo (shsp, J.W.G. zcw-j-4, doc. vid.). – ibid. (shsp, J.W.G. ys-j-8, Guo et al. 2014b as *H. juliae*). – **Zhejiang**, **Hangzhou**, Tianmushan, 600 m, substrate unknown, 21.IV.2005, B. Liu Bin, M.H. Sun & X.Z. Liu (?, HMAS 139529, non vid.).

Salix; **7a–b**. P.P. 20070701: ibid., on *Fagus*; **8a–c**. P.P. 20061109: ibid., on *Salix*; **9**. H.B. 7634: Luxembourg, Waldhaff, on *Aesculus*; **10**. P.P. 20070821: Poland, Kłodzko, on *Pinus*; **11a–b**. TAAM 161510: Estonia, Varbla, on *Inonotus*; **12**. H.B. 8017b: Germany, Tübingen, on *Acer*; **13**. 9.I.2005: ibid., on *Acer*; **14a–d**. H.B. 8447a: France, Niort, on *Ulmus*; **15**. P.P. 20100321: Poland, Żelazno, on *Trametes*; **16**. J.W.G. zcw-j-4: China, Sichuan, on indet. tree; **17**. H.B. 9494: Denmark, København, on *Tilia*.

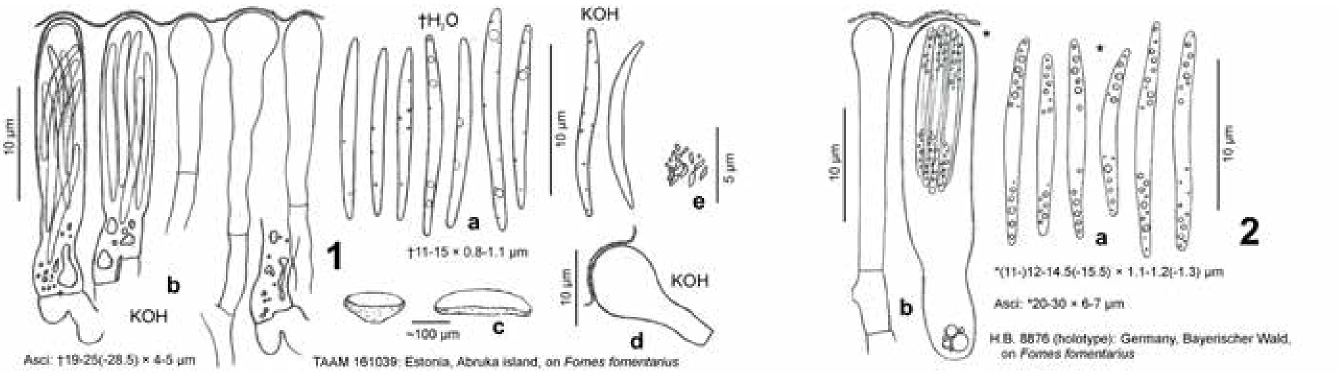


Plate 110. **1–2**: *Hyalorbilia fomentarii*. – **a**. ascospores; **b**. asci and paraphyses (ascus bases with croziers); **c**. rehydrated apothecia; **d**. marginal cortical cell; **e**. warted exudate on ectal excipulum.

Hyalorbilia fomentarii Baral, **sp. nov.**, MB 813464 — Pls 110–111

Etymology: named after the substrate, *Fomes fomentarius*.

Typification: Germany, Niederbayern, Zwiesel, on *Fomes fomentarius* on log of *Fraxinus excelsior*, 14.VI.2008, P. Welt (ex H.B. 8876, M-0276408, holotype).

Latin diagnosis: Hyalorbiliae juliae *similis sed ascosporae angustiores.*

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated 0.13–0.28 mm diam., 0.05–0.08 mm high (receptacle 0.04 → 0.03 mm), whitish-greyish to whitish-cream, translucent, ± round, medium gregarious; disc flat, margin thin, not protruding, very finely rough; sessile on an obconical base or with a distinct stipe 0.04 × 0.05–0.06 mm, superficial, dry pale cream. **Asci** *20–30 × 6–7 µm {1}, †19–25(–28.5) × 4–5.3 µm {2}, 8-spored, spores (*) in a parallel bundle, pars sporifera *15–16 µm long; **apex** (†) hemispherical (to very slightly truncate); **base** ± unstalked, arising from croziers {2} (rarely with a slit). **Ascospores** *(11–)12–14.5(–15.5) × 1.1–1.2(–1.3) µm {1}, †11–15 × (0.8–)0.9–1.1(–1.2) µm {2}, subcylindrical to narrowly fusoid, both ends rounded to obtuse, straight to ± inequilateral, exceptionally medium curved; **SBs** *0.3–0.5 µm diam. {1}, ~4–6 in each half, globose, intermingled with a few small LBs. **Paraphyses** apically uninflated to mostly slightly (rarely medium) clavate-capitate, terminal cells †14–20(–25) × (2–)2.5–4.5(–6) µm {2}, lower cells †5–6(–7) × 1.5–1.8 µm {1}; unbranched at upper septum. **Medullary excipulum** 15–30 µm thick in centre, of dense textura angularis(-intricata), non-gelatinized, indistinctly delimited. **Ectal excipulum** at base of 15–20 µm thick, ± vertically oriented t. prismatica-angularis, cells †12–18(–22) × (6–)8–12 µm {1}, thin-walled, at flanks of horizontal t. prismatica, 10 µm thick near margin, marginal cortical cells */†15–20 × 5–7.5 µm {2} (5–10 µm wide in surface view). **Anchoring hyphae** sparse at base, †(1.5–)2–3.5(–5) µm wide, walls 0.2 µm thick {2}. **VBs** unknown (no living paraphyses seen). **Exudate** over paraphyses, margin and flanks 0.2–0.5 µm thick, continuous, finely rough to small-cloddy, hyaline to pale yellow-ochraceous, lying over gel. **— ANAMORPH**: unknown.

Habitat: collected 0.1 m above the ground, on basidiocarps of *Fomes fomentarius* {2}, at border of pileus, mainly on pores, medium decayed, still-attached to strongly decayed logs of *Betula* sp. and *Fraxinus excelsior*, green filamentous algae sometimes abundant around apothecia. **Associated**: *Hypnum cupressiforme* {1}, *Lophocolea* sp. {1}, *Mnium* sp. {1}. **Desiccation tolerance**: after ~2 days dead in all parts. **Altitude**: 5 m a.s.l. (Estonia), 1015 m (Bayern). **Geology**: marine sand & clay over Ordovician rock; gneiss. **Phenology**: VI, IX.

Taxonomic remarks. *Hyalorbilia fomentarii* is characterized by extraordinarily long and narrow, ± straight, rarely distinctly curved ascospores. It is very closely related to H. *juliae* and *H. berberidis*. The former deviates in wider and sometimes also shorter spores, the latter in always distinctly curved spores. Due to infraspecific variation of these two related species, *H.*

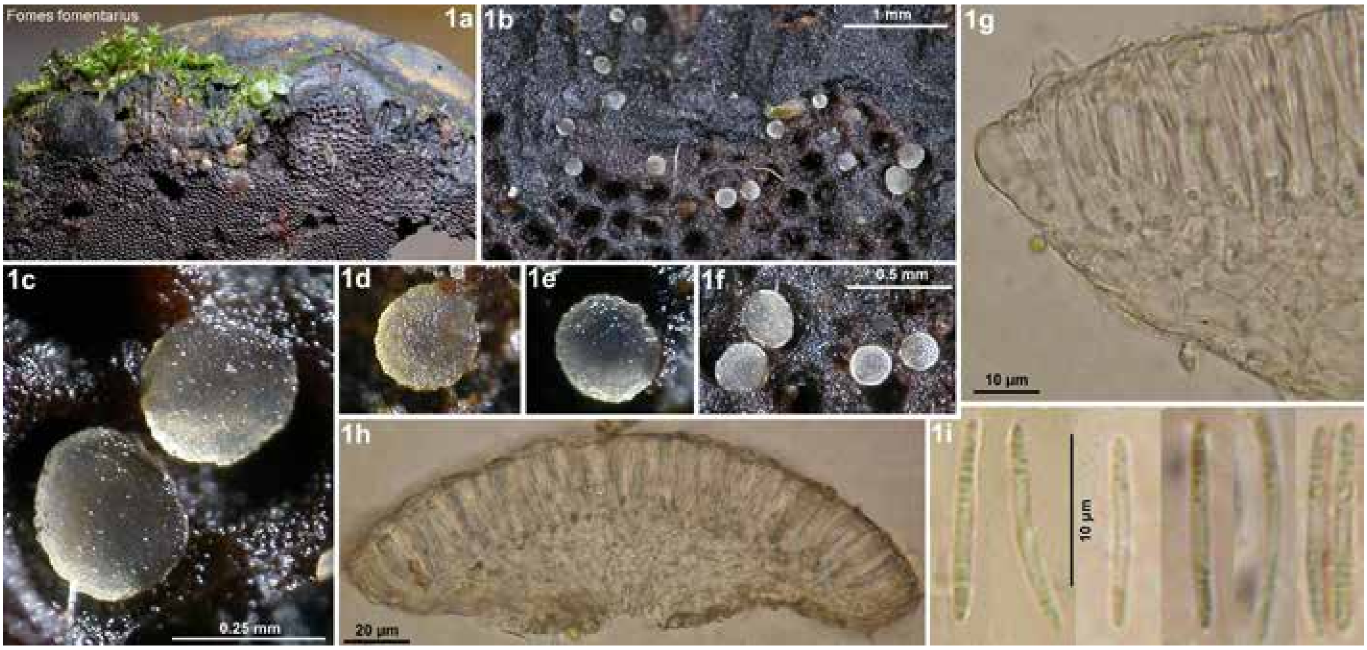


Plate 111. **1**: *Hyalorbilia fomentarii*. – **1a**. old fruitbody of *Fomes fomentarius*; **1b–f**. fresh apothecia; **1h**. apothecium in median section; **1g**. id., marginal region; **1i**. ascospores. – Living state. — **1a–i**. H.B. 8876 (holotype): Germany, Bayerischer Wald, on *Fomes*.

fomentarii is only tentatively separated from these. However, the close morphological resemblance of the two so far known collections, and the very similar ecology at the two rather distant sites support separation at the species level.

Four collections on basidiocarps (*Fomitiporia*, *Hymenochaetopsis*, *Trametes*, *Xanthoporia*) included in *H. juliae* differ from *H. fomentarii* in distinctly shorter and wider spores (*/†9–12(–13) × 1.1–1.5 µm). The description of *Orbilia polyporacea* Velen. (?= *H. berberidis*) on *Phylloporia ribis*, with rather long ('15 µm') and narrow spores, resembles *H. fomentarii*, but the spores are described as consistently slightly curved (the holotype is without apothecia, see under *H. berberidis*).

Not included collections. Two samples on *Hymenochaete* and *Phellinus* (IVV: J.P.P. 24240, 29205) with a spore size of *9–12 × 0.8–1.2 µm resemble *H. juliae* in spore shape. However, spore width excludes this species, whereas spore length is too short to include them in the description of *H. fomentarii*.

Ecology. Apothecia of the two known records of *Hyalorbilia fomentarii* grew on decayed basidiocarps of *Fomes fomentarius* in subcontinental humid forests of orotemperate central and hemiboreal northeastern Europe. The two not included samples on *Hymenochaete* and *Phellinus* are from atlantic and subatlantic western Europe on calcareous Lower Jurassic and Oligocene clay, marl- & limestone.

Specimens included. **ESTONIA**: **Saaremaa**, 12 km S of Kuressaare, island of Abruka, 5 m, on *Fomes fomentarius* on log of *Betula*, 14.IX.1993, K. Põldmaa (TAAM 161039, H.B. 5209 ø). — **GERMANY**: **Bayern**, **Niederbayern**, Bayerischer Wald, 9 km NE of Zwiesel, Höllbachspreng, 1015 m, on *F. fomentarius* on log of *Fraxinus excelsior*, 14.VI.2008, P. Welt (ex H.B. 8876, M-0276408, **holotype**).

Not included. **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 5.5 km ESE of Guer, NNW of Les Brulais, Rue des Buis, 60 m, on *Hymenochaete rubiginosa*, 19.XI.2004, J.P. Priou (J.P.P. 24240, doc. vid.). – **Bourgogne**, **Côte-d'Or**, 30 km NW of Dijon, 3 km ENE of Salmaise, Eremitage St-Jean-de-Bonnevaux, 432 m, on *Phellinus* (on *Acer*), 26.X.2009, A. Gardiennet, vid. J.P. Priou (J.P.P. 29205, doc. vid.).

Hyalorbilia berberidis (Velen.) Baral, in Baral & G. Marson, Micologia 2000: 44 (2001) — Pls 112–113, Map 16

≡ *Orbilia berberidis* Velen., Monogr. Discom. Bohem.: 99, pl. 11 fig. 27 (1934)

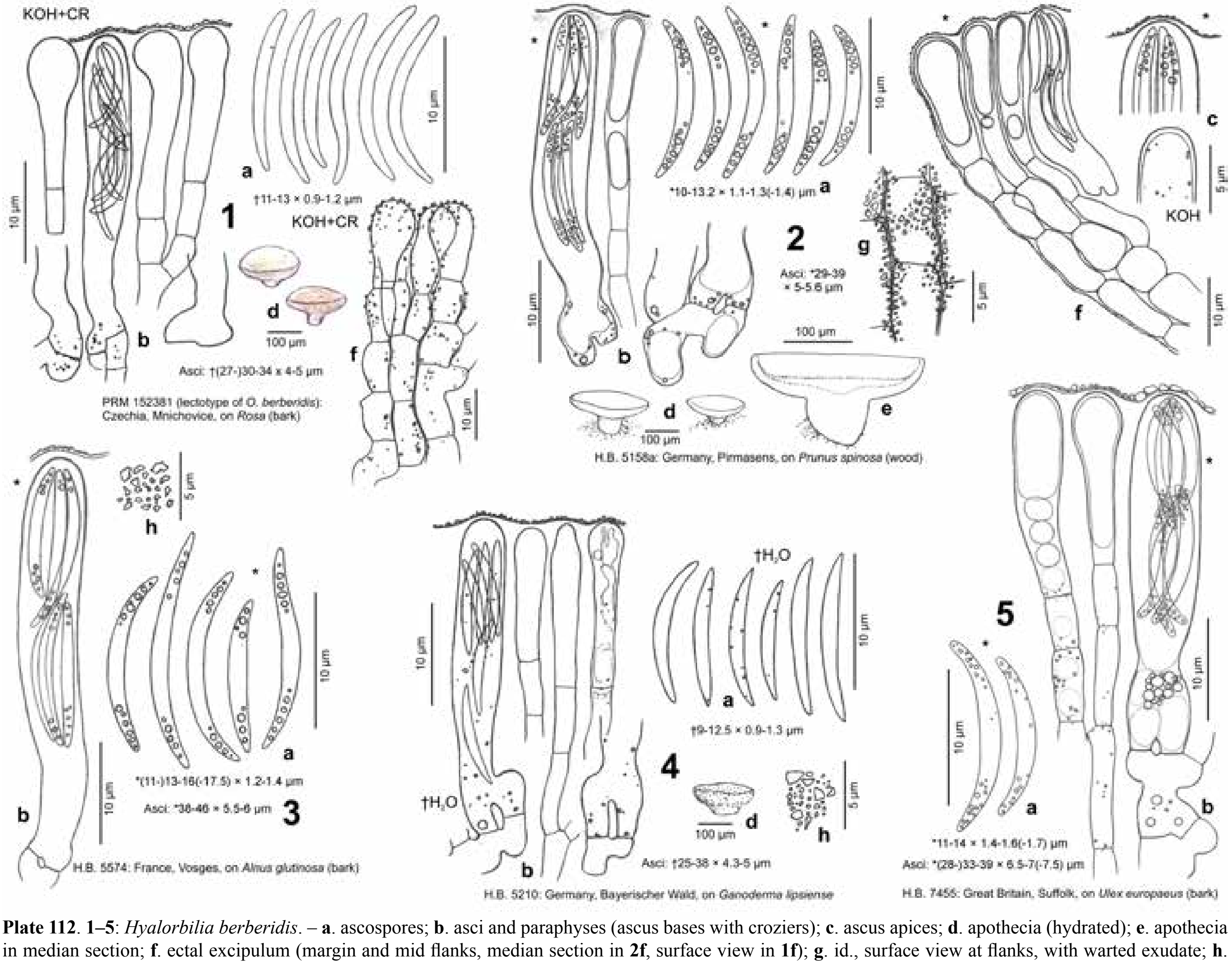
= *Orbilia exigua* Velen., Monogr. Discom. Bohem.: 100, pl. 11 fig. 2 (1934)

= *Orbilia polyporacea* Velen., Monogr. Discom. Bohem.: 100, pl. 11 fig. 1 (1934)

= *Orbilia emarginata* Velen., Monogr. Discom. Bohem.: 100 (1934)

Etymology: *berberidis*, *polyporacea*: referring to the substrate (*Berberis*, *Phylloporia ribis*); *emarginata*: named after the shape of the ascus base (with a deep notch); *exigua*: named after the minute apothecia.

Typification: Czechia, Mnichovice, branch of *Rosa*, VIII.1926, J. Velenovský (PRM 152381, lectotype of ***Orbilia berberidis***, designated by Svrček 1954: 11); Belgium, Dessel, Prinsenpark, branch of *Fagus sylvatica* and indet. resupinate polypore, 28.IX.2018, F. Bartholomeeusen (BR5020213021208V, epitype, designated here, MBT385109; sq.: MK473403). — ibid., *Phylloporia ribis*, VII.1929, *Quercus palustris*, VII.1930, J. Velenovský (PRM 152458,



PRM 152381 (lectotype of *O. berberidis*): Czechia, Mnichovice, on *Rosa* (bark)

H.B. 5158a: Germany, Pirmasens, on *Prunus spinosa* (wood)

H.B. 5574: France, Vosges, on *Alnus glutinosa* (bark)

H.B. 5210: Germany, Bayerischer Wald, on *Ganoderma lipsiense*

H.B. 7455: Great Britain, Suffolk, on *Ulex europaeus* (bark)

Plate 112. **1–5**: *Hyalorbilia berberidis*. – **a**. ascospores; **b**. asci and paraphyses (ascus bases with croziers); **c**. ascus apices; **d**. apothecia (hydrated); **e**. apothecia in median section; **f**. ectal excipulum (margin and mid flanks, median section in **2f**, surface view in **1f**); **g**. id., surface view at flanks, with warted exudate; **h**. warted-cloddy exudate on hymenium (**3h**) and ectal excipulum (**4h**).

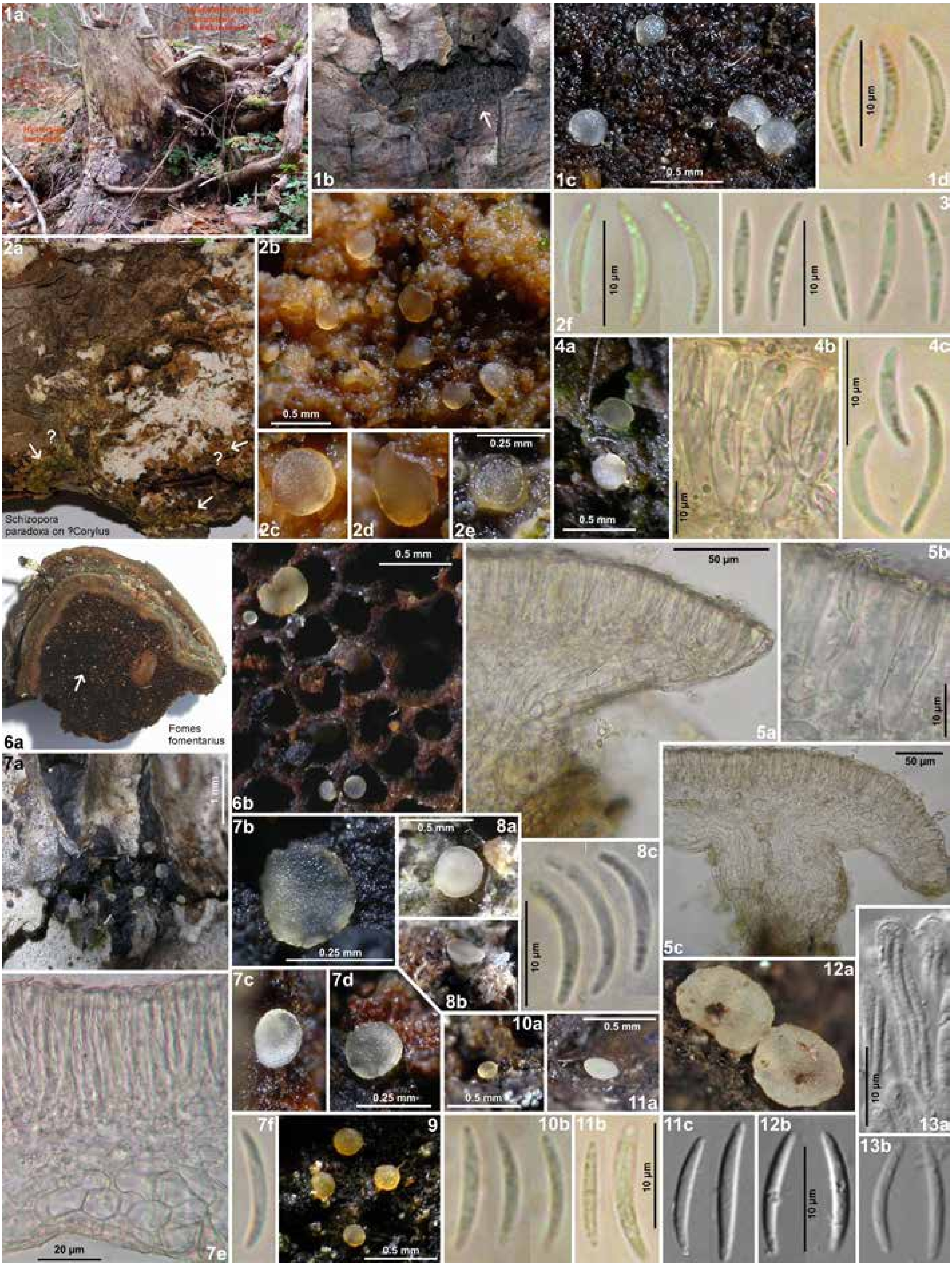


Plate 113. **1–13**: *Hyalorbilia berberidis*. – **1a**. mixed forest, cut *Pinus sylvestris* stump; **1b**. detail of bark; **2a**. *Schizopora paradoxa* on a dead ?*Corylus* branch lying on wet ground; **1c**, **2b–e**, **4a**, **8a–b**, **12a**. fresh apothecia; **6a–b**, **7a–d**, **9**, **10a**, **11a**. rehydrated apothecia (**6** & **9**: after 10–11 years); **5a**, **c**. apothecia in median section; **7e**. id., lower flanks; **4b**, **5b**, **13a**. asci (and paraphyses); **1d**, **2f**, **3**, **4c**, **7f**, **8c**, **10b**, **11b–c**, **12b**, **13b**. ascospores. – Living state, except for **10b**, **11b–c**, **12b**, **13a–b** (in H_2O). – **1a**, **2a–f**, **7e–f**: phot. P. Perz; **11c**, **12a–b**; **13a–b**: phot. J.W. Guo (DIC). — **1a–d**. H.B. 8605a: Poland, Kłodzko, on *Pinus*; **2a–f**. P.P. 20091226: ibid., on *Schizopora*; **3**. 4.X.2009: Netherlands, Boxmeer, on *Quercus*; **4a–c**. H.B. 7866: Great Britain, Suffolk, on *Ulex*; **5a–c**. H.B. 7648b: ibid., on *Ulex*; **6a–b**. TAAM 161661: Finland,

152384, syntypes of ***O. polyporacea***). — Czechia, Zvánovice, log of *Picea abies*, VIII.1933, J. Velenovský (PRM 151746, holotype of ***O. emarginata***). — Czechia, Stránčice, log of *Cornus sanguinea* (holotype of ***O. exigua***: illustration in Velenovský pl. 11 fig. 1).

Misapplied name: Saccardo (1878: 429), as *O. chrysocoma* (identity uncertain).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.08–)0.12–0.4(–0.6) mm diam., 0.09–0.2 mm high (receptacle 0.06–0.1 → 0.04–0.045 mm), whitish, finally pale to light yellowish-cream, translucent, round to slightly undulating, non-gelatinous, ± scattered or in small groups; disc flat, margin thin, indistinct, smooth; subsessile or often with a distinct, obconical or cylindrical stipe 0.03–0.11 × 0.06–0.15 mm, superficial or very slightly immersed; dry yellowish-ochraceous-amber(-reddish). **Asci** *(25–)30–40(–46) × 5–7.5(–8) µm {9}, †(21–)23–35(–40) × 3.8–5.2 µm {8}, 8-spored, spores *4-seriate in two superimposed bundles, also mixed in one bundle, pars sporifera *(16–)19–26(–31) µm long; **apex** (†) hemispherical to slightly truncate; **base** with very short, thick stalk, arising from croziers {12} without or often with small, round or slit-like perforation; often with a group of medium-sized LBs inside stalk near base {6}. **Ascospores** *(9.5–)11–14(–17.5) × (1.1–)1.2–1.6(–1.8) µm {14}, †(9–)10–13(–15) × (0.9–)1–1.2(–1.3) µm {9}, narrowly fusoid (± cylindrical in middle part), rarely one end less tapered than the other, both ends rounded to subacute (obtuse to acute when dead), consistently slightly to strongly curved (falcate, sometimes slightly helicoid), in dead state very slightly to medium curved; 3–6 **SBs** in each half towards the poles (18), globose (to broadly ellipsoid), 0.3–0.8 × 0.3–0.6 µm {5}; LBs sparse, minute. **Paraphyses** apically uninflated to medium (rarely strongly) clavate-capitate, terminal cells *16–21 × 3–5.5 µm {3}, †11.5–20 × (1.8–)2.6–5(–6) µm {3}, lower cells *5.5–10(–12) × 2–3.5(–4) µm {2}, †4–8 × 1.5–3 µm {3}. **Medullary excipulum** 10–35 µm thick, of dense textura globulosa-angularis or medium dense t. intricata, non-gelatinized, medium sharply delimited. **Ectal excipulum** slightly gelatinized, in stipe of vertical t. prismatica, 20–110 µm thick near base, cells */†(9–)12–30(–40) × 7–16(–19) µm {6}; at flanks of thin-walled, horizontally oriented t. (angularis-)prismatica(-porrecta), cells *7–23 × 5–13 µm {4}, 10–15 µm thick near margin, marginal cortical cells ± strongly clavate, *8–24 × (4–)5–9 µm {3}, †10–19 × 4–9.5 µm {2}. **Anchoring hyphae** sparse, only at base, *2.2–4 µm wide {1}, †1.7–3.7 µm {3}, up to 5 µm at insertion, walls 0.2–0.3(–0.4) µm thick {4}. **VBs** in paraphyses and marginal cortical cells rather low-refractive, either one large elongate or some smaller globose VBs. **Exudate** over paraphyses 0.1–1.2 µm thick, continuous, strongly warted; over margin and flanks finely granular, pale yellowish-amber. — **ANAMORPH**: unknown.

Habitat: usually lying on moist ground or on a pile 0.2–0.5 m above the ground, corticated, 9–40 mm thick branches, also on thick stumps or logs, of *Alnus glutinosa* {1}, *Berberis vulgaris* {2}, *Betula* sp. {2}, *Corylus avellana* {1}, *Cytisus scoparius* {1}, *Fagus sylvatica* {2}, *Ilex canariensis* {1}, *Picea abies* {1}, *Pinus sylvestris* {1}, *Prunus spinosa* {1}, *Pseudotsuga menziesii* {1}, *Quercus* sp. {1}, *Q. robur* {1}, *Rosa* sp. {1}, *Ulex europaeus* {7}, unidentified angiosperm {3}, on 0.5–2 mm deep strongly decayed bark {12} (on periderm or edges of bast), wood {10}, or boring dust {1}; herbaceous stems of *Hydrangea* sp. {1}; on or rarely in pores of *Fomes fomentarius* {1}, *Fomitiporia punctata* {2}, *Fomitopsis pinicola* {1}, *Ganoderma applanatum* {2}, *Phylloporia ribis* {1}, *Physarum* sp. {1}, *Schizopora paradoxa* {1}, *Stereum rugosum* {1}, indet. resupinate polypore {1}, basidiomata sometimes internally with abundant insect galleries, sometimes on old stromata of *Diatrypella favacea* {1}; substrate ungreyed or ± blackened, without or sometimes with abundant green algae. **Associated**: *Ascotremella faginea* {1}, *Bionectria ralfsii* {1}, *Cacumisporium capitulatum* {1}, *Hymenoscyphus phiala* {1}, *Hyalorbilia inflatula* {1}, *H. polypori* {1}, *H. ?subfusispora* {1}, *Hyaloscypha leucostigma* {1}, *Hypomyces albidus* {1}, *Lophocolea* sp. {1}, *L. heterophylla* {1}, *Mollisia* sp. {1}, *Orbilia eucalypti* {1}, *O. vinosa* {1}, *Polydesmia pruinosa* {1}, *Schizophyllum commune* {1}, *Torrubiella* sp. {1}, *Trichaptum biforme* {1}, *Venturiocistella ulicicola* {1}. **Desiccation tolerance**: after 1–6 days in the herbarium only the spores survived. **Altitude**: 12–1050 m a.s.l. (central Europe), ~1800–2730 m (southern China). **Geology**: Europe: Ordovician & Silurian marble, shale, silt- & sandstone, Devonian & Carboniferous sediments, Buntsandstein, Cretaceous flysch, Tertiary calcareous clay- & marlstone, molasse, Pleistocene sand, clay & till; granite, granodiorite, granitoid (syenitoid), basalt, biotite-amphibolite & quartz diorite, mica schist, gneiss, serpentinite; China: Paleozoic & Jurassic rock. **Phenology**: throughout the year.

Phenology of *H. berberidis*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
3	0	1	0	1	4	2	7	6	5	3	3

Taxonomic remarks. *Hyalorbilia berberidis* is characterized by comparatively long, very narrowly fusoid, more or less distinctly curved (falcate) ascospores. Populations with only slightly curved spores approach the straighter-spored *H. fomentarii* or *H. juliae* in which some slightly curved spores sometimes occurred. In contrast to *H. berberidis*, *H. juliae* prefers distinctly more xeric substrate. A somewhat intermediate taxon (*H. fomentarii*) differs from both in narrower spores. *H. arcuata* differs from *H. berberidis* in much shorter and more curved spores. *Orbilia auricolor* and related species may be confused with *H. berberidis* due to their arcuate, similarly sized though heteropolar spores. This superficial similarity was also stated by Svrček (1959: 214, as *O. curvatispora*).

Variation. The examined collections of *H. berberidis* somewhat vary among each other, mainly in spore length (from 9.5–13 to 13–16 µm in situ) and in the strength of spore curvature, also in ascus size. Seemingly straight spores (Pl. 113: 3) probably belong to slightly curved spores seen in dorsal view. Nine out of 33 collections of *H. berberidis* were on basidiomycetes, and they did not differ in their microscopic features from those on bark and wood. Three records from southern China (Pl. 113: 11–13) are obviously conspecific, although the spores are mostly only slightly curved and a few even straight in the dead state, approaching *H. juliae*. In a collection on wood of *Sorbus aucuparia* from central Boehmia, Svrček (1959: 214) measured rather narrow spores (9–12 × 0.5–1 µm), but this might be an error since he measured too narrow spores also in the lectotype (compare measurements here gained from the lectotype, see below). The Belgian specimen (BR5020213021208V, with sequence) had spores of the short range (*9.5–13.5 × 1.2–1.4 µm, medium curved, IVV: 28.IX.2018) and is herewith designated as **epitype** of *H. berberidis*.

Type studies. Velenovský mentioned five substrates in the protologue. The lectotype of ***H. berberidis*** (PRM 152381, on branch of *Rosa*) was reexamined. It contained ~16 mature apothecia (rehydrated 0.15–0.25 mm in diam.) on decayed bark. Svrček (1954: 11) reported them as 0.1–0.5 mm, and the ascospores (11–14 × 0.7–0.8 µm) and paraphysis apices (up to 3 µm) distinctly narrower compared to the present result [Pl. 112: 1b, paraphyses (2–)4–6 µm wide]. Svrček designated the specimen on *Rosa* as lectotype, because he could not find apothecia in three of the remaining four paralectotypes of *H. berberidis*: *Hedera helix* (PRM 147718), *Prunus avium* (PRM

Lieksa, on *Fomes*; **7a–f**. H.B. 8653: Poland, Kłodzko, on *Diatrypella*; **8a–c**. H.B. 7638: Great Britain, Suffolk, on *Ulex*; **9**. TAAM 161311: Finland, Tammela, on *Fomitopsis*; **10a–b** H.B. 7655b: Portugal, Serra da Estrela, on *Cytisus*; **11a–c**. H.B. 8933: China, Yunnan, Dali, on indet. angiosperm; **12a–b**. H.B. 8934: ibid.; **13a–b**. J.W.G. xs-j-23: China, Yunnan, Kunming, on indet. angiosperm.

152396), and *Quercus palustris* (PRM 152414). Also in the present study no apothecia could be found in them. Svrček did not mention the collection on *Berberis vulgaris* (PRM 614783), however, perhaps because it was unavailable to him.

The protologue of *O. berberidis* appears to be derived mainly from the description of the *Berberis* collection, which was the first of Velenovský's five collections recorded on his manuscript sheet, and the measurements in the protologue (asci 30–35 × 5 µm, spores 10–12 µm) are exactly those on the only drawing on this sheet, which obviously concerns the *Berberis* collection. On this drawing the spores are about 0.5–1 µm wide, while on the modified drawing on pl. XI fig. 27 of the protologue they are about 0.3–0.8 µm wide. No apothecia could be found in the present examination of the *Berberis* collection.

Similarly, no apothecia were found in the type convolutes of ***O. emarginata*** (PRM 151746, on wood of *Picea*) and ***O. polyporacea*** (PRM 152458, on *Phylloporia ribis*), neither by Svrček nor in the present study. According to Svrček (1954: 19), a syntype of *O. polyporacea* (PRM 152384, on wood of *Quercus*) contains immature apothecia reminiscent of *O. tremulae* (as *O. xanthostigma*). No type material exists for ***O. exigua*** (on rotten stump of *Cornus sanguinea*, Svrček 1954: 14).

Velenovský (1934) did not explain why he distinguished four different species with so similar arcuate spores. Manuscript sheets with drawings exist for all of them. Spore length in *O. polyporacea* was given as 15 µm, whereas the other three had spores of 10–12 µm (*O. berberidis*, *O. emarginata*) or 12 µm (*O. exigua*). Since Velenovský did not always indicate the spore length range and omitted spore width, the differences remain obscure. The *Berberis* collection is described with the longest asci (30–35 × 5 µm). This length well corresponds to the measurement of dead asci in the lectotype on *Rosa* by Svrček (28–35 × 3.5–4.5 µm) and in the present study (Pl. 112: 1). On his manuscript sheet Velenovský described only the *Berberis* collection, but since he referred different collections to *O. berberidis*, it remains unclear to which of them his drawing belongs. The illustration provided by Velenovský (1934) for *O. berberidis* deviates somewhat from that on his manuscript sheet. In the other three taxa the asci are stated to be shorter (20–25 µm). Nevertheless, Svrček (1954: 14, 18) considered all of them as synonyms of *O. berberidis*, with the consequence that *H. berberidis* attains priority over them (ICN Art. 11.5). We more or less share Svrček's synonymisation here, because ascus length in *H. berberidis* was found to vary to some degree among the material included here, therefore, dead mature asci of 20 µm length might indeed occur in this species.

O. exigua shows rather strongly curved spores in the protologue, and Velenovský's illustration leaves little doubt about the identity with *H. berberidis*. In *O. polyporacea* and *O. emarginata* the spores are described and figured less curved. The figure of *O. emarginata* in Velenovský's manuscript shows somewhat heteropolar spores and an angular excipulum, which recalls a member of *Orbilia* section *Arthrobotrys*. However, the ascus base is illustrated unstalked, with 2 short legs and a deep notch between, suggestive of a perforated crozier, which is typical of *H. berberidis*. Hence *O. emarginata* clearly belongs to *Hyalorbilia*. The 'parenchymatic' excipulum of *O. exigua* was described as 'small-celled' (no cell size stated), and that of *O. polyporacea* as 'large-celled', but the excipulum of the latter is not figured on Velenovský's manuscript sheet.

Velenovský placed these four taxa in his subgroup 'IIa *Spirospora*', characterized by 'filiform, arcuate-curved' spores and unstalked asci, together with a fifth taxon, *O. oreadum*, with much shorter, very strongly curved spores (yet, in the type of *O. oreadum* all five apothecia examined showed almost straight spores, see Pl. 72: 1a). The name *Spirospora* is misleading since the spores do not form clear spirals in either of the included taxa.

Misapplication. *O. chrysocoma* s. Saccardo (1878: 429, Italy, [Venice, Treviso,] Conegliano, on *Morus alba*) might represent *H. berberidis*, judging from the brief description (nearly sessile asci, slightly curved spores 14–15 × 0.75–1 µm). The interpretation of *O. chrysocoma* was, however, highly different among the authors (Rehm 1891: 458), and the taxon is today used for a *Dacrymyces* (see p. 1665).

Phylogeny. A sequence comprising SSU (lacking S1506 intron), ITS, and LSU was gained from apothecia of the Belgian specimen. When analysing ITS or LSU separately (not shown), *H. berberidis* clustered, like *H. tortuosa*, unresolved in the core clade of *Hyalorbilia*, despite its morphological resemblance with *H. juliae*. When analysing ITS+LSU (Phyl. 6), *H. berberidis* clustered weakly supported with *H. tortuosa*, from which it differs in the ITS by 15% (8.3% in LSU D1–D2), which seems to be the lowest distance in comparison to other species (e.g., *H. fusispora* 21.5%). An environmental strain from Minnesota (H7, ITS) that clusters with *H. tortuosa* differs from *H. berberidis* by 15.7%.

In the LSU D1–D2 the lowest distance was 6.2% to *H. juliae* (ITS ~25%), 6.5% to *H. inflatula* (H.B. 9080, ITS 19%), and 7% to *H. helicospora* (ITS 19%). In the SSU V7–V9 *H. berberidis* fully concurs with *H. tortuosa*, while other available *Hyalorbilia* sequences differ in the V8–V9 region by 1–5 nt, the closest being *H. inflatula* (H.B. 9080 & 9915).

H. berberidis is unique within *Hyalorbilia* in the Orb5.8s3F primer region, differing by at least 1 nt from other taxa (*inflatula-polypori* clade, *H. subfusispora*, *H. latispora*) (Tab. 18). In the first 4 nt of ITS2 (AGTG) it concurs with only a few *Hyalorbilia* species, including *H. subfusispora* (Tab. 20). *H. berberidis* is also unique in stem-loop 8 of 5.8S where it concurs only with environmental strains (H7–8), although it did not cluster with them.

Two environmental sequences from Sweden in GenBank (FMOTU 3018, 5464), comprising partial 5.8S and ITS2, are very close to the present sequence of *H. berberidis*. In the entire ITS2 they differ from *H. berberidis* by 0.9% (FMOTU 5464) and 1.7% (FMOTU 3018), although they differ from each other by 2.5%. In stem-loop 8 and Orb5.8s3F of 5.8S and in the first 4 nt of ITS2 they concur with our *H. berberidis* sequence. Together with a high ITS distance to other *Hyalorbilia* spp. this seems to indicate that the Swedish extracts are conspecific with *H. berberidis*.

Ecology. The wide ecological amplitude of *Hyalorbilia berberidis* includes rotten bark and wood of hygric or sometimes mesic branches and stumps of trees and shrubs of angio-, rarely gymnosperms, also perennial basidiocarps, and even herbaceous stems. The species was found in various parts of planar to altimontane, humid or sometimes sub- or semihumid, atlantic to subcontinental Europe, with a meso- to orotemperate but also hemi- to mesoboreal and sometimes supra- to thermomediterranean climate. The vegetation includes gardens and orchards, alder swamps, conifer forests, atlantic *Ulex* and xerothermic *Cytisus* scrubs. The environmental isolates from Sweden (FMOTU 3018) came from *Pinus sylvestris* monocultures of very different age on acidic grass- or later moss-covered soil (Umbric podzol) over sandy, loamy till with many boulders, with increasingly abundant *Picea abies* in understory (A. Rosling & P. Fransson pers. comm., see also Hagenbo et al. 2017). The origin of FMOTU 5464 could not be clarified (A. Rosling & P. Fransson pers. comm.). In Macaronesia it grew in the thermomediterranean subhumid laurel forest zone of Monte de las Mercedes in northeastern Tenerife. Collections from southern China are from subtropical humid (winter-dry) evergreen forests.

H. berberidis was collected on hygric or mesic substrate close to the ground, often on branches lying on a pile, also on the lower side of logs. In a few collections the apothecia grew on more xeric substrate: dry standing *Hydrangea* stem at a shady and moist place, dry *Picea* wood (type of *O. emarginata*), *Cytisus* branch with *O. vinosa*. This indicates a certain desiccation tolerance of the apothecia, though our tests did not reveal such a tolerance so far.

Specimens included. **SWEDEN**: **Uppsala**, 32 km NNE of Uppsala, 8 km SSW of Österbybruk, 71 m, soil isolate from 46 years old *Pinus sylvestris* forest, X.2014, P. Fransson (FMOTU 3018, mol. extr., sq.: KU062739). – ibid., 3 km SW of Österbybruk, 63 m, 12 years old *Pinus sylvestris* forest (FMOTU 3018, mol. extr.). – ibid., 2.8 km SSW of Österbybruk, 54 m, 160 years old *Pinus sylvestris* forest (FMOTU 3018, mol. extr.). – unlocalized (FMOTU 5464, mol. extr., sq.: KU062066). — **FINLAND**: **North Karelia**, 14 km WNW of Outokumpu, Rikkaranta, Pennala farm, ~125 m, on *Fomitiporia punctata* on log of *Salix*, 27.VI.2010, M. Pennanen (ex M.P. 100634, JOE, doc. vid.). – 26 km SSW of Lieksa, 1.5 km SE of Koli, ENE of Forest Research Institute, ~180 m, on *Fomes fomentarius*, 11.VIII.1995, K. Põldmaa (TAAM 161661, H.B. 5361 ø). – **Kanta-Häme**, 18 km SSE of Tammela, 0.4 km N of Korteniemi, Liesjärvi, Ahonnokka spruce forest, 110 m, on *Fomitopsis pinicola* on log of *Betula*, 11.IX.1994, K. Põldmaa (TAAM 161311, H.B. 7978 ø). — **ESTONIA**: **Harjumaa**, 6 km WSW of Aespa, 6 km NE of Kernu, Metsanurga, 55 m, on *Fomitiporia punctata* on log of *Corylus avellana*, 26.IX.1994, K. Põldmaa (TAAM 161475, H.B. 7979 ø). — **POLAND**: **West Pomerania**, 20 km SE of Szczecin, 1.7 km NE of Dobropole Gryfiński, Puszcza Bukowa, 88 m, on *Ganoderma applanatum*, 21.III.2009, P. Perz & G. Domian (H.B. 9160a). **Lower Silesia**, 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 420 m, on *Diatrypella favacea* and bark of branch of *Betula*, 27.VIII.2007, P. Perz (P.P. 20070827-1, H.B. 8653). – ibid., on stump of *Pinus sylvestris*, on bark, 21.XI.2006, P. Perz (P.P. 20070820-1, H.B. 8605a). – 12.5 km SE of Bystrzyca Kłodzka, 8.5 km NE of Miedzylesie, N of Nowa Wies, 525 m, on *Schizopora paradoxa* var. *paradoxa* on branch of ?*Corylus*, 26.XII.2009, P. Perz (P.P. 20091226-2, doc. vid.). — **GREAT BRITAIN**: **East England**, **Suffolk**, 4 km ESE of Halesworth, 0.4 km NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Ulex europaeus*, on bark, 14.I.2004, S. Francis & E. Batten (E.B. 4472, H.B. 7455). – ibid., NNE of Wenhaston, Blyford Lane, Garden Hill Cottage, 12 m, branch of *U. europaeus*, on bark, 8.XII.2004, E. Batten (E.B. 4573, H.B. 7638 ø). – ibid., branch of *Ulex europaeus*, on bark, 10.I.2005, E. Batten (H.B. 7648b ø). – branch of *U. europaeus*, on bark, 5.VIII.2005, E. Batten (E.B. 4619, H.B. 7866). – ibid., branch of *U. europaeus*, on bark, 19.IX.2005, S.M. Francis (H.B. 7905a). — **NETHERLANDS**: **Noord-Brabant**, 4 km NNW of Boxmeer, 1 km W of Helbroek, De Vilt, 12 m, branch of *Quercus*, on wood, 4.X.2009, S. Helleman (S.H. 641, doc. vid.). — **BELGIUM**: **Vlaanderen**, **Antwerpen**, 13 km SE of Turnhout, 5 km WSW of Dessel, Prinsenpark, 27 m, branch *Fagus sylvatica*, on wood and indet. resupinate polypore, 28.IX.2018, F. Bartholomeeusen (ex F.B. 20180928PP01, BR5020213021208V, doc. vid., **epitype** of *H. berberidis*; sq.: MK473403). — **FRANCE**: **Bretagne**, **Morbihan**, 2 km S of La Gacilly, S of Lestun, Pré Naval, 17 m, branch of *Ulex europaeus*, on wood, 5.XI.2013, J.P. Priou (J.P.P. 13222, doc. vid.). – **Nord-Pas-de-Calais**, **Pas-de-Calais**, 17 km WSW of Calais, 1.4 km SSW of Wissant, la Motte du Bourg, 10 m, branch of *Ulex europaeus*, on bark, 29.X.2016, J.P. Priou (J.P.P. 16279, doc. vid.). – **Champagne-Ardenne**, **Ardennes**, 3 km WSW of Charleville- Mézières, 1 km W of Prix-lès-Mézières, rue de Moulin, 150 m, stem of *Hydrangea*, 18.VIII.2001, R. Collot (ø, doc. vid.). – **Lorraine**, **Vosges**, 4 km SE of Gérardmer, La Ferme de Grouvelin, 1050 m, branch of *Alnus glutinosa*, on bark, 4.IX.1996, H.O. Baral (H.B. 5574). — **GERMANY**: **Sachsen**, 9.5 km SE of Chemnitz, 1.3 km NW of Dittmannsdorf, 375 m, branch of *Quercus robur*, on wood, 4.VIII.2014, B. Mühler (ø, doc. vid.). – **Rheinland-Pfalz**, Pfälzer Wald, 14 km SE of Pirmasens, 0.8 km SE of Dahn, below military cemetery, 250 m, branch of *Prunus spinosa*, on wood, 2.X.1994, H.O. Baral & G. Marson (H.B. 5158a). – **Bayern**, **Niederbayern**, Bayerischer Wald, ~12 km SE of Zwiesel, ~4.5 km NNE of Spiegelau, Lärchenberg (southern slope of Großer Rachel), 890 m, on *Ganoderma applanatum*, 25.V.1990, N. Luschka 1658 (M, H.B. 5210 ø). — **CZECHIA**: **Central Bohemia**, 27 km SE of Praha, Mnichovice, ~370 m, branch of *Rosa*, on bark, VIII.1926, J. Velenovský (PRM 152381, **lectotype** of *O. berberidis*, H.B. 6064 ø). – ibid., 'in our garden', *Phellinus ribis*, VII.1929, J. Velenovský (PRM 152458, **syntype** of *O. polyporacea*, doc. vid., no apothecia found). – ~29 km SE of Praha, Zvánovice, ~480 m, log of *Picea abies*, on wood, VIII.1933, J. Velenovský (PRM 151746, **holotype** of *O. emarginata*, doc. vid., no apothecia found). – 22 km SE of Praha, ~2.5 NW of Stránčice, ~420 m, log of *Cornus sanguinea*, VII.1926, J. Velenovský (**holotype** of *O. exigua* [illustration], doc. vid.). – ~10 km SW of Praha, Radotín, ~300 m, log of *Berberis vulgaris*, 6.VI.1926, J. Velenovský (PRM 614783, **paralectotype** of *O. berberidis*, doc. vid., no apothecia found). — **AUSTRIA**: **Wien**, 5.5 km SSE of Wien, 1.3 km E of Favoriten, Laaer Wald, 248 m, branch of *Berberis vulgaris*, on wood, 8.XI.2013, R. Moosbeckhofer, vid. B. Wergen (H.B. 9857 ø). — **SERBIA**: **Vojvodina**, Fruška Gora, 11.5 km S of Novi Sad, 5.8 km NNW of Irig, Iriški venac, SW of WWII memorial, 437 m, log of *Fagus*, on *Stereum rugosum*, 11.XII.2018, D. Savić (doc. vid.). – ibid., W of WWII memorial, 430 m, branch of *Pseudotsuga menziesii*, on wood, 20.IX.2019, D. Savić (doc. vid.). — **PORTUGAL**: **Guarda**, Serra da Estrela, 3.5 km NE of Sabugal, 1 km SW of Rendo, 820 m, branch of *Cytisus scoparius*, on wood, 1.I.2005, J.P. Priou (H.B. 7655b ø). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Tegueste, 5 km NNW of San Cristóbal de La Laguna, 1.5 km NE of Tegueste, La Hoya del Palomo, 665 m, branch of *Ilex canariensis*, on wood, 16.VI.2012, L. Quijada & E.V. Rodríguez (TFC Mic. 23530, doc. vid.). — **CHINA**: **Yunnan**, **Dali**, Yongping, 35 km ENE of Baoshan, Jinguangsi, 2730 m, branch of indet. angiosperm, on bark, 25.X.2008, H.Y. Su, X.M. Gao & Y.G. Yan (H.Y.S. jgs-22, CBCD, H.B. 8933 ø). – ibid. (H.Y.S. jgs-23, CBCD, H.B. 8934 ø, doc. vid.). – **Kunming**, 12 km SW of Kunming, SW of Bijizhen, Xishan, 2050 m, branch of indet. angiosperm, on wood, 16.VI.2006, J.W. Guo (J.W.G. xs-j-23, YMFT, doc. vid.).

Map 16. Known distribution of *H. berberidis* in Europe and Macaronesia.

Hyalorbilia fusispora (Velen.) Baral & G. Marson, Micologia 2000: 44 (2001) — Pls 114–115, Map 17

≡ *Orbilia fusispora* Velen., Monogr. Discom. Bohem.: 96, pl. 11 fig. 38 (1934)

Etymology: referring to the fusiform (rhomboid) shape of the ascospores.
Typification: Czechia, Central Bohemia, Mnichovice, branch of *Lonicera tatarica*, VII.1926, J. Velenovský (PRM 152442, holotype); France, Deux Sèvres, Niort, trunk of *Ulmus*, 2.III.2007, M. Hairaud (ex H.B. 8447b, M-0291770, epitype, designated here, MBT385108; sq.: KT222379).
Misinterpretation of *H. fusispora*: Liu (2006: 33, 2007b), (?)= *H. ulicicola*; Guo et al. (2014b), ?= *H. texensis* or *H. ulicicola.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–1.5(–2.2) mm diam., 0.14–0.25 mm high (receptacle 0.1–0.19 → 0.06–0.09 mm), pale chlorinaceous-olivaceous to mostly light yellowish-cream or ochraceous-orange-amber, bright red-brown with age, semitranslucent, round to slightly undulating, not or only slightly gelatinous, very scattered or subgregarious in small groups; disc slightly to strongly concave, eventually flat, margin thin or thick, 0–15 µm rising

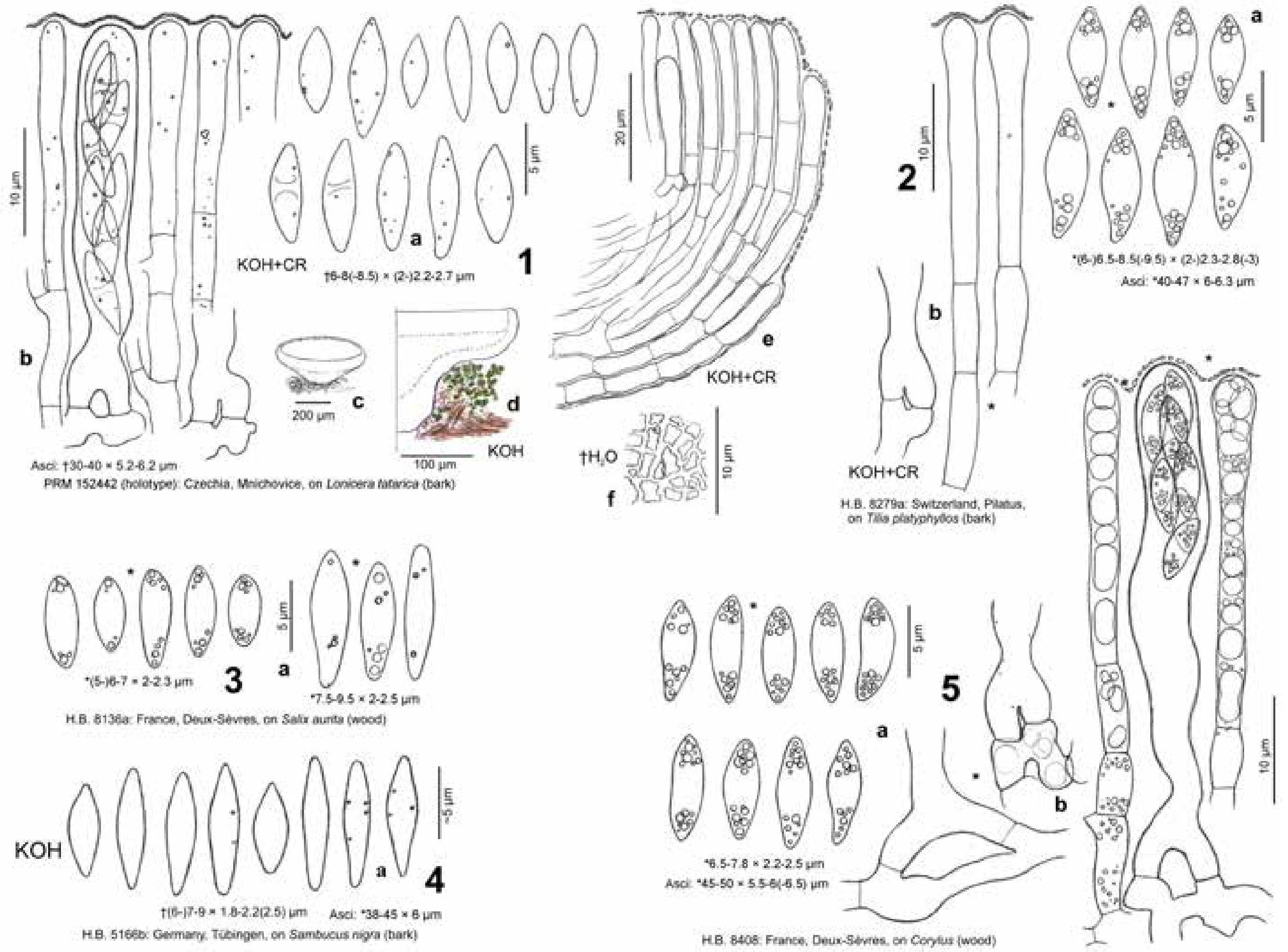


Plate 114: **1–5**: *Hyalorbilia fusispora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. apothecium (rehydrated); **d**. apothecium in median section; **e**. id., ectal excipulum at margin and mid flanks; **f**. cloddy exudate on ectal excipulum in surface view.

above disc, smooth; subsessile or with a distinct, obconical to cylindrical stipe 0.08–0.1 × 0.1–0.22 mm, superficial; dry light yellowish-ochre or bright orange-brown. **Asci** *(30–)35–47(–50) × (5.5–)5.7–6.5(–7) µm {6}, †(26.5–)30–47 × (4.5–)5–5.8(–6.2) µm {5}, 8-spored, spores 2–3-seriate, pars sporifera *15–28 µm long; **apex** (†) hemispherical; **base** with short to medium long, thick, ± flexuous stipe arising from croziers {8} with minute or often pore- to slit-like to very large perforation (base Y- to nearly T-shaped). **Ascospores** *((4.5–))(5–)6–9(–9.7)((–10.3)) × (2–)2.2–2.7(–3) µm {24}, †(4.5–)5.5–8(–9.5) × (1.7–)2–2.4(–2.7) µm {8}, fusoid to fusiform (rhomboid), rarely ellipsoid, ± homopolar, ends obtuse or mostly distinctly subacute to acute, straight to slightly, exceptionally distinctly inequilateral; (1–)2–5 globose **SBs** in each end, *0.3–0.8 µm diam. {6}; with a few minute LBs. **Paraphyses** apically uninflated or only slightly clavate, terminal cells *15.3–21 {1} or *23–33 {2} × 2.5–4.7 µm {3}, †12–19 × 2–3.8 µm {2} or †18–27 × (2–)2.5–3.5(–4) µm {T}, lower cells *6–11 × 2–3(–4) µm {2}, †5.5–11 × 1.7–3 µm {T}. **Medullary excipulum** 20 µm thick, of dense, non-gelatinized textura intricata-angularis, very indistinctly delimited. **Ectal excipulum** of thin-walled, rarely slightly gelatinized, horizontally oriented t. prismatica at base and flanks, at base ~40–120 µm thick, cells *(9–)15–35(–46) × 6–13(–26) µm {6}, †7–17 × 5–9 µm {T}, inner part of t. prismatica-porrecta (cells *20–60 × 8–12 µm), at flanks 10–30 µm thick, cells *7–20 × 4.5–7 µm {2}, †8–13 × 3–4.5 µm (T), at margin of t. porrecta, 10–20 µm thick, marginal cortical cells narrowly clavate, *8–22 × 3–5 µm {4}, †(8–)12–20(–25) {4} × 3–5 µm {7}, in surface view likewise 3–5(–6) µm wide. **Anchoring hyphae** sparse to very abundant, ± vertically radiating, */†2–4(–6), walls 0.2–0.4(–1) µm thick {7}. **VBs** in terminal cells of paraphyses and in marginal cortical cells low- to medium refractive, pale yellowish-chlorinaceous, multiguttulate to elongate; **LBs** in ectal excipular cells minute or absent. **Exudate** over paraphyses and complete ectal excipulum, 0.2–0.4(–1) µm thick, continuous to granular, mostly distinctly warted, light golden yellowish(-orange) mainly over excipulum. **— ANAMORPH**: unknown (but see below).

Habitat: collected 0.7–4 m above the ground, corticated to almost decorticated, 6–45 mm thick branches (and roots), also standing 20–30 cm thick living trunks of *Acer* sp. {1}, *A. pseudoplatanus* {1}, *Aesculus hippocastanum* {1}, *Artemisia thuscula* {1}, *Betula* sp. {1}, *Cornus sanguinea* {1}, *Corylus avellana* {2}, *Euonymus europaeus* {1}, *Ficus carica* {1}, *Frangula alnus* {1}, *Fraxinus excelsior* {3}, *Juniperus* sp. {1}, *Lonicera periclymenum* {1}, *L. tatarica* {1}, *Malus domestica* {1}, *Olea europaea* {1}, *Prunus avium* {1}, *P. ?serotina* {1}, *P. spinosa* {1}, *Quercus* sp. {1}, *Q. pubescens* {2}, *Robinia pseudoacacia* {1}, *Rubus fruticosus* {1}, *Salix* sp. {9}, *S. aurita* {1}, *Sambucus nigra* {2}, *Suaeda vera* {1}, *Tilia platyphyllos* {1}, *Ulmus* sp. {4}, indet. angiosperm {1}, on outer surface of (partially detaching) bark (periderm and bast) {28} or wood {19} (but often close to bark), up to 1 mm deep medium to very strongly decayed, sometimes on edges of bark or hidden in cracks and holes, slightly greyed (sometimes blackened), also on living leaves of *Frullania dilatata* {1}; green algae sparse to very abundant, often among lichens and small bryophytes. **Associated**: *Bryocentria brongniartii* {2}, *B. callicarpa* {1}, *Caloplaca* sp. {1}, *Dacrymyces* sp. {1}, *Decaisnella mesascium* {1}, *Diplolaeviopsis* sp. {1}, *Frullania dilatata* {1/1}, *Helicogermslita gaudefroyi* {1}, *Hyalorbilia inflatula* {1}, *H. juliae* {4}, *H. ulicicola* {1}, *Hysterium angustatum* {2}, *Karstenia idaei*

Plate 115. **1–11**: *Hyalorbilia fusispora*. – **1a**. Living *Acer* tree with dead attached branches; **4a**. dead corticated xeric branch of *Ulmus*, with *Xanthoria parietina*; **1b**, **2a–c**, **3a–b**, **4b**, **5a–c**, **7a–b**, **8a–d**, **10a–b**. rehydrated apothecia (**3a** with *Orthotrichum* & *Frullania dilatata*, **5a** with *Physcia*, **7a** with *Tortula ruralis*); **11a–b**. apothecia in median section; **3c**, **8e**, **10c**. id., marginal ectal excipulum; **8f**, **9a**. id., ectal excipulum at lower flanks; **5e**. exudate on hymenium; **5d**. mature ascus; **1c**, **6**, **7c**, **8g**, **9b**. ascospores; **10d**. conidium from substrate. – Living state, except for **9b**, **11a–b** (in KOH). — **1a–c**. 21.VII.2008: Luxembourg, Fentange, on *Acer*; **2a–c**. H.B. 8805c: France, Deux-Sèvres, on *Salix*; **3a–c**. H.B. 8485a: France, Aude, on *Juniperus*; **4a–b**. H.B. 8797b: France, Eure-et-Loire, on *Ulmus*; **5a–e**. H.B. 8408: France, Deux-Sèvres, on *Corylus*; **6**. 24.II.2007: ibid., on *Ulmus*; **7a–c**. H.B. 8447b (epitype): ibid., on *Ulmus*; **8a–g**. H.B. 8279a: Switzerland, Pilatus, on *Tilia*; **9a–b**. H.B. 8033: France, Deux-Sèvres, on *Salix*; **10a–d**. H.B. 8136a: ibid., on *Salix*; **11a–b**. PRM 152442 (holotype): Czechia, Mnichovice, on *Lonicera*.

{1}, *K. lonicerae* {1}, *K. rhopaloides* {5}, *Lecanora* sp. {1}, *Leptogium* sp. {1}, *Lophiostoma compressum* {1}, *L. myriocarpum* {1}, *Metzgeria* sp. {2}, *Nectria pseudopeziza* {1}, *Octospora affinis* {1}, *Octosporella erythrostigma* {1}, *Opegrapha atra* {1}, *Orbilia aprilis* {1}, *O. aurantiorubra* {1}, *O. eucalypti* {2}, *O. filiformis* {1}, *O. gambelii* {1}, *O. obtusispora* {1}, *O. pseudoaristata* {1}, *O. quaestiformis* {1}, *O. subclavuliformis* {1}, *O. ?trapeziformis* {1}, *O. vinosa* {1}, *Orthotrichum* sp. {2}, *O. affine* {1}, *Parmelia sulcata* {2}, *Patellaria atrata* {2}, *Physcia* sp. {5}, *Proliferodiscus tricolor* {1}, *Sclerococcum* sp. {1}, *Tortula ruralis* {1}, *Xanthoria parietina* {3}. **Desiccation tolerance**: excipular cells viable after 2 weeks, paraphyses and mature asci often already dead after 1 week. **Altitude**: 2–977 m a.s.l. **Geology**: Ordovician sand- & siltstone, Cambrian silt & wacke, Lower to Upper Jurassic sand-, lime- & marlstone, Cretaceous & Miocene mud-, silt- & sandstone, flysch, Tertiary molasse, Quaternary calcareous till, loess, sand, peat; granite, biotite-amphibolite & quartz diorite, basalt, volcanic tuff. **Phenology**: throughout the year.

Phenology of *H. fusispora*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
5	6	6	7	1	3	4	5	0	2	4	3

Map 17. Known distribution of *H. fusispora* in Europe and Macaronesia.

Taxonomic remarks. *Hyalorbilia fusispora* is characterized by broad, straight, fusoid to fusiform ascospores, a textura porrecta of rather narrow cells at the margin, and comparatively large, often distinctly ochraceous, desiccation-tolerant apothecia. For the similar *H. subfusispora* see under that species, p. 401. *H. texensis* and *H. polypori* differ in narrower spores eguttulate or with only a few minute drops at each end, the former also in shorter spores, the latter in more cylindrical spores and desiccation-sensitive apothecia with wider marginal cells. *H. ulicicola* deviates in much smaller spores and desiccation-sensitive apothecia. A collection from France (Niort, on *Ulmus*, ex H.B. 8447b, Pl. 115: 7), from which a sequence was gained and which well corresponds to the holotype, is designated here as **epitype** of *H. fusispora*.

Variation. The species shows some variability in ascus and spore size and in spore shape (between ellipsoid and fusiform), but this variation is often also observed within a collection. In the sample from Austria the spores were extraordinarily small (†5–6.5 × 1.7–2 µm).

Type studies. Svrček (1954) stated that the holotype convolute of *Orbilia fusispora* and *O. fusispora* var. *microscopica* (PRM 152442, a mixture in the same convolute) is empty. Yet, nine apothecia of *Hyalorbilia* (and some of *Karstenia rhopaloides*) were found on the three small fragments of bark. Three apothecia (each from a different bark fragment) were examined. Two were found to have broadly fusiform spores which fit very well Velenovský's protologue of *O. fusispora*. The third showed long and narrow, subcylindrical spores which closely match the protologue of *O. fusispora* var. *microscopica* (Pl. 108 Fig. 1), a taxon which is considered here to be a synonym of *H. juliae*. This was one of three distinctly smaller, more whitish apothecia, which all occur on the same chip of bark and which obviously represent the holotype of var. *microscopica*. The examined apothecia of *H. fusispora* are larger (rehydrated 0.2–0.5 mm) than indicated by Velenovský (0.1–0.3 mm) who seems to have included apothecial size of var. *microscopica* in the protologue of *O. fusispora*. Also the asci are larger (see Pl. 114: 1b) than stated by him (25–30 × 5 µm). The spores fit very well his drawing. Velenovský gave a length of 4–10 µm, although he wrote in his manuscript 4–6 µm. No data of further collections are mentioned. The large range of spore size probably includes var. *microscopica*, though spore length of that taxon in his manuscript is give as 12 µm. That Velenovský separated these two very different taxa only at the variety level is probably due to their mixed growth on the same branch. The extraordinary width of the spores observed in the holotype of *H. fusispora* (Pl. 114: 1a) appears to originate from artificial flattening.

Misapplication. Under the name *H. fusispora*, Liu (2006: 33) and Liu et al. (2007b) reported 13 collections from China which, because of their rather small ascospores, appear to fit better *H. ulicicola* (see p. 325). The same is true for eight Chinese collections reported by Guo et al. (2014b), except that spore shape is more similar to *H. texensis*. The spore bodies described by Guo et al. (one elongate terminal and 3–5 globose peripheral SBs 0.4–0.5 µm diam. in each spore half) recall *H. subfusispora*, but the spores of †4.3–6 × 1.3–1.5 µm are too small.

Anamorph. We observed in H.B. 8033 narrow, flexuous phragmoconidia (*28–30 × 1.5 µm, see IVV) and in H.B. 8136a one small dwayaangam yakuensis-like conidium (*35 × 20 µm, Pl. 115: 10d). Whether one of these conidial types represents the anamorph of *H. fusispora* is unclear.

Phylogeny. An ITS sequence of *H. fusispora* (H.B. 8447b) was gained from apothecia. It clustered unsupported and with a > 20 % distance sister to the *juliae-tenuifusaria* clade (Phyl. 5). When tentatively including it in the combined analysis (Phyl. 6, not shown), *H. fusispora* clustered unresolved, although the *juliae-tenuifusaria* clade received strong support. The morphologically similar *H. subfusispora* shows a 26 % distance and clustered sister to the *oviparasitica-multiguttulata* clade. In the 5.8S region, *H. fusispora* differs from the identical *H. tenuifusaria* and *H. juliae* by 1 nt, from *H. ulicicola* by 2 nt, and from *H. subfusispora* by 3 nt (all deviations in Orb5.8s3F, Tab. 18), whereas *H. lunata* differs by 6 nt (all deviations in Orb5.8s3F and stem-loop B8, Tab. S4).

Ecology. *Hyalorbilia fusispora* was found on ± rotten wood and bark of xeric branches and trunks of various angiosperm (rarely coniferous) trees and shrubs. From its consistent occurrence on exposed substrate, a drought tolerance higher than here observed can be expected. The species was collected in humid (rarely semihumid), atlantic to subcontinental Europe in a meso- to supratemperate but also suprasub- to mesosubmediterranean, rarely orotemperate to orosubmediterranean, or mesomediterranean climate. The vegetation comprises sun-exposed borders of mostly thermophilous forests, hedges, overgrown gardens, also marshland. A single record in Macaronesia (Tenerife) was in the inframediterranean semiarid cardonal xerophytic scrubland (*Periploco laevigatae-Euphorbietum canariensis*).

Specimens included. **GREAT BRITAIN**: **South East England**, **West Sussex**, 3.3 km NE of Crawley, Milton Mt. Lake, 72 m, branches of *Salix*, on bark, 1.I.2016, N. Aplin (N.P. 333, doc. vid.). — **NETHERLANDS**: **Gelderland**, 6 km SW of Nijmegen, W of Aldenhof, Staddijkpark, 12 m, branch of ?*Prunus serotina*, on wood, 17.II.2007, S. Helleman (S.H. 432, doc. vid.). – ibid., branch of *Salix*, on wood, 24.II.2007, S. Helleman (S.H. 434, doc. vid.). – **Noord-Brabant**, 5.5 km NW of Boxmeer, 3 km NW of Beugen, NW of Haart, 10 m, twig of *Prunus avium*, on bark, 22.III.2011, S. Helleman (ø, doc. vid.). – 4 km NNW of Boxmeer, 1 km NNW of Beugen, W of Helbroek, De Vilt, 12 m, branch of *Salix*, on wood & bark, 18.II.2007, S. Helleman (S.H. 433, doc. vid.). – 1 km NW of Boxmeer, Brestbos, 18 m, 9.VI.2015, twig of *Frangula alnus*, on wood, 9.VI.2015, S. Helleman (ø, doc. vid.). — **LUXEMBOURG**: **Gutland**: 6 km S of Luxembourg, 1.5 km WSW of Fentange, Mierchesfeld, 283 m, branches of *Acer pseudoplatanus*, on wood & bark, 21.VII.2008, G. Marson (ø). — **GERMANY**: **Baden-Württemberg**, 5.5 km NE of Tübingen, Pfrondorf, Blaihofstraße, 430 m, branch of *Sambucus nigra*, on bark, ~18.X.1994, H.O. Baral (H.B. 5166b). – **Bayern**, **Oberbayern**, 7.5 km SE of München, Klinikum Neuperlach, 542 m, trunk of *Acer*, on bark, 2.I.2013, B. Fellmann (MAMU 1936, doc. vid.). — **CZECHIA**: **Central Bohemia**, 27 km SE of Praha, W of Mnichovice, 'in nostro horto', 370 m, branch ('trunk') of *Lonicera tatarica*, on bark, VII.1926, J. Velenovský (PRM 152442, **holotype**, H.B. 6131b ø). — **AUSTRIA**: **Steiermark**, 36 km S of Graz, 3 km WNW of Großklein, 1 km S of Mantrach, 395 m, twig of *Malus domestica*, on bark, 9.II.2019, G. Friebes (G.F. 20190021, doc. vid.). — **RUSSIA (West)**: **Vologda**, **Kirovsk**, 130 km NW of Vologda, 2 km N of Kovarzino, 30 km E of Lake Beloje, Russky Sever, 170 m, on bark of *Salix*, 27.VIII.2002, E.S. Popov (LE 236684, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 12 km SW of Novi Sad, 1.3 km SW of Beočin, Erdelj, 270 m, branch of *Quercus pubescens*, on bark, 22.VII.2019, D. Savić (doc. vid.). — **MONTENEGRO**: 4.5 km NW of Herceg Novi, NW of Ratiševina, 170 m, branch of indet. angiosperm, on bark, N. Kulinović, vid. D. Savić (FG-1094, doc. vid.). — **LIECHTENSTEIN**: 7 km NNW of Vaduz, 1 km SW of Bendern, Bannriet, 460 m, branch of *Cornus sanguinea*, on bark, 5.VII.1997, H.O. Baral (ø). — **SWITZERLAND**: **Luzern**, 4 km NE of Küssnacht, 1.8 km NE of Immensee, 0.5 km ENE of Baumgarten, Zugersee, Chieme, 440 m, trunk of *Quercus*, on bark, 5.XI.2017, U. Graf (doc. vid.). – **Nidwalden**, 6 km S of Luzern, 1 km NW of Hergiswil, Bruustried, 600 m, branch of *Tilia platyphyllos*, on wood, 22.VIII.2006, U. Graf & H.O. Baral (H.B. 8279a). – ibid., branch of *Fraxinus excelsior*, on wood, 22.VIII.2006, H.O. Baral (ø). – **Solothurn**, 15 km NE of Solothurn, 1.2 km W of Oensingen, Leuental, 530 m, trunk of *Corylus avellana*, on bark, 29.XII.2019, U. Graf (doc. vid.). — **FRANCE**: **Bretagne**, **Morbihan**, Île de Groix, 14 km SSW of Lorient, SE of Locmaria, 13 m, branch of *Ficus carica*, on bark, 22.III.2012, J.P. Priou (J.P.P. 12073, doc. vid.). – 9 km NE of La Gacilly, 1.8 km E of Quelneuc, Bois Péchard, 15 m, trunk of *Fraxinus excelsior*, on leaves of *Frullania dilatata*, 27.III.2015, J.P. Priou (J.P.P. 15068 ø, doc. vid.). – 1.9 km NE of La Gacilly, SE of Le Lieuvy, 10 m, on twig of *Euonymus europaeus*, on wood, 30.III.2013, J.P. Priou (J.P.P. 13058, doc. vid.). – 1 km WNW of La Gacilly, Gazeau, 29 m, branch of *Betula*, on bark, 14.XI.2013, J.P. Priou (J.P.P. 13231, doc. vid.). – **Ille-et-Vilaine**, 15 km SW of Rennes, 1 km SW of Le Pont-Réan, NNE of Guichen, La Massaye, 68 m, branch of *Aesculus hippocastanum*, on wood, 15.II.2005, J.P. Priou (J.P.P. 25035, doc. vid.). – 14.5 km NE of Redon, 1.6 km WSW of St.-Just, (Ruisseau de) Cojoux, 37 m, branch of *Sambucus nigra*, on bark, 17.III.2006, J.P. Priou (H.B. 8115 ø, J.P.P. 26066 ø). – **Pays-de-la-Loire**, **Loire-Atlantique**, 13 km WSW of Nantes, NW of St.-Jean-de-Boiseau, Rue de la Rivière, 10 m, branch of *Fraxinus excelsior*, on wood & bark, 23.XII.2011, J.P. Priou (J.P.P. 11266, doc. vid.). – 2.3 km NE of Mesquer, l'Île de Rostu, 2 m, branch of *Suaeda vera*, 10.XI.2004, J.P. Priou (J.P.P. 24222, doc. vid.). – 3 km ESE of Piriac-sur-Mer, 0.5 km E of St.-Sébastien, 20 m, branch of *Lonicera periclymenum*, on bark, 12.XI.2004, C. Lechat (H.B. 7616 ø, J.P.P. 24220). – **Sarthe**, 9 km E of La Ferté-Bernard, 1.9 km WNW of Théligny, Aire de Montmirail, 190 m, branch of *Salix*, on wood, 25.I.2008, J.P. Priou (J.P.P. 28017, doc. vid.). – **Poitou-Charentes**, **Charente-Maritime**, Île de Ré, 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, stem of *Rubus fruticosus*, 16.IV.2008, H.O. Baral (ø). – **Deux-Sèvres**, 12.5 km WSW of Niort, 1 km ENE of Le Vanneau-Irleau, Marais Poitevin, 3 m, branches of *Salix*, on wood, 28.XII.2005, J.P. Priou (H.B. 8033, J.P.P. 25171). – ibid., branch of *Salix*, on bark, 15.IV.2008, J.A. Camy & H.O. Baral (H.B. 8805c). – 21 km W of Niort, 4 km NW of St.-Hilaire-La-Palud, Marais Poitevin, 4 m, branch of *S. aurita*, on bark, 25.IV.2006, H.O. Baral (H.B. 8136a). – 13.5 km N of Melle, 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 100 m, branch of *Prunus spinosa*, on wood, 17.IV.2008, S. Helleman (ø). – 9.5 km SSE of Niort, 1.7 km NNE of Fors, 37 m, trunk of *Ulmus*, on bark, 2.III.2007, M. Hairaud (ex H.B. 8447b, M-0291770, **epitype**; sq.: KT222379). – 14 km SSE of Niort, 0.7 km NE of Marigny, Le Tertre, 40 m, branch of *Ulmus*, on wood, 9.IV.2007, M. Hairaud (ø, non vid.). – 14 km SSE of Niort, Poivendre de Marigny, Impasse des Marronniers, 48 m, branch of *Corylus avellana*, on wood & bark, 14.I.2007, M. Hairaud (H.B. 8408). – 15 km ESE of Melle, 0.8 km E of Clussais-la-Pommeraie, 135 m, trunk of *Ulmus*, on bark, 24.II.2007, B. Coué (ø, doc. vid.). – **Centre**, **Eure-et-Loire**, 23 km NNW of Orleans, 1.3 km NE of Poupry, Le Aire Héron Cendré, 125 m, branch of *Ulmus*, on bark, 12.IV.2008, S. Helleman & H.O. Baral (H.B. 8797b ø). – **Auvergne**, **Cantal**, 14 km ENE of Aurillac, 3.5 km ESE of Polminhac, Les Huttes, 977 m, branch of *Salix*, on wood, 31.VIII.2011, J.P. Priou (J.P.P. 11085 ø, doc. vid.). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 15 km N of Digne-les-Bains, 3.7 km SSW of Barles, Clues de Barles, 910 m, trunk of *Quercus pubescens*, on bark, 14.VIII.2009, H.O. Baral (H.B. 9156c ø). – **Languedoc-Roussillon**, **Aude**, Pyrénées-Orientales, 20 km WSW of Quillan, 2.6 km NNW of Belcaire, Le Clôt de la Plaine, 970 m, twig of *Juniperus*, on bark, 30.IV.2007, C. Lecuru (H.B. 8485a). – **Midi-Pyrénées**, **Ariège**, 16.5 km ENE of St.-Girons, NE of Castelnau-Durban, les Mouns, 450 m, branch of *Robinia pseudoacacia*, on wood, 26.X.2011, J.P. Priou (J.P.P. 11170a, doc. vid.). — **SPAIN**: **País Vasco**, **Gipuzkoa**, 11 km ESE of Tolosa, 3.8 km SE of Berastegi, 423 m, branch of *Salix*, on bark, 5.I.2008, J.P. Priou (J.P.P. 28003, doc. vid.). — **PORTUGAL**: **Santarém**, 10 km NNW of Santarém, 2.5 km W of Achete, Val de Flores, 96 m, branch of *Olea europaea*, 16.VI.2017, J.P. Priou (J.P.P. 17151, doc. vid.). — **MACARONESIA**: **Canary Islands**, **Tenerife**, San Cristóbal de La Laguna, Anaga, 6 km NE of Tegueste, 2.3 km E of Punta Hidalgo, 1.2 km NW of Chinamada, 345 m, branch of *Artemisia thuscula*, on wood, 20.V.2013, L. Quijada (TFC Mic. 24236).

Hyalorbilia subfusispora Baral, G. Marson & P. Perz, **sp. nov.**, MB 813461 — Pls 116–118, Map 18

Etymology: named after the spores that resemble those of *H. fusispora*.
Typification: Germany, Baden-Württemberg, Tübingen, branches of *Salix caprea*, 26.III.1996, H.O. Baral (ex H.B. 5432a, M-0276418, holotype).
Misapplied name: Baral in Krieglsteiner (1999: 271), as *Orbilia vitalbae*.

Latin diagnosis: Hyalorbiliae fusisporae *similis sed apothecia minora*, *pallide colorata*, *cellulae marginales multo magis inflatae*, *ascosporae vivae prope polos plerumque duo corpuscula refringentia elongata continentes*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.08–)0.1–0.35(–0.5)((–0.65)) mm diam., (0.06–)0.08–0.15(–0.21) mm high (receptacle 0.05–0.11 mm), whitish-greyish, pale yellowish-cream to chlorinaceous, medium to strongly (glassy-)translucent, ± round, slightly or medium or strongly gelatinous, very scattered to gregarious in usually only small groups; disc slightly concave to flat, rarely slightly convex, margin thin, 0–5(–10) µm rising above disc, even; sessile on an obconical base or often with a ± distinct, obconical to cylindrical stipe 0.03–0.11(–0.18) × 0.04–0.14 mm, superficial; dry pale greyish-cream-chlorinaceous. **Asci** *(22–)25–35(–38) × (5.5–)6–7(–7.5) µm {8}, †19–25 {4} or 24–30(–35) {12} × (4.2–)4.8–6.2(–7) µm {16}, 8-spored, spores 2–4-seriate, rarely a single basal heteropolar spore inversely oriented, pars sporifera *15–20(–24) → 11.5–14 µm long; **apex** (†) hemispherical (to somewhat conico-truncate); **base** with short, thick stipe arising from croziers {9} with or without round to often slit-like perforation. **Ascospores** *(4.5–)5.5–8(–9.5) × (1.7–)1.9–2.3(–2.5) µm {32}, †(5–)6–8(–9.5) × (1.5–)1.7–2(–2.2) µm {7}, fusoid- to fusiform(-clavate), sometimes ellipsoid, ends subacute to acute, sometimes obtuse or acuminate, straight to slightly inequilateral, only a few slightly curved; 1 **SB** in each spore end, *(0.4–)0.6–1.4(–1.8) × (0.4–)0.5–0.8(–1) µm {15}, (sub)globose to ovoid or (elongate) tear-shaped, closely attached or sometimes with an inconspicuous, very short filum (mostly not seen), often 1–5 further, ± laterally arranged, ± globose SBs in each spore half, 0.3–0.6(–1) µm diam., sometimes all SBs globose; with a few minute LBs. **Paraphyses** apically uninflated or slightly (to medium) clavate-capitate, terminal cells *(10–)13–19(–25) × (2.5–)3–5(–5.5) µm {5}, †10–19(–21) × (2–)2.5–4.2(–5) µm {5}, lower cells *(3.5–)5–10 × 1.8–3 µm {2}, †6–10 × 1.3–2 µm {1}. **Medullary excipulum** 10–20(–50) µm thick, of non- or slightly gelatinized textura globulosa-intricata or t. prismatica-porrecta, indistinctly delimited. **Ectal excipulum** of very thin-walled or slightly gelatinized, indistinctly oriented t. globulosa-angularis or horizontal

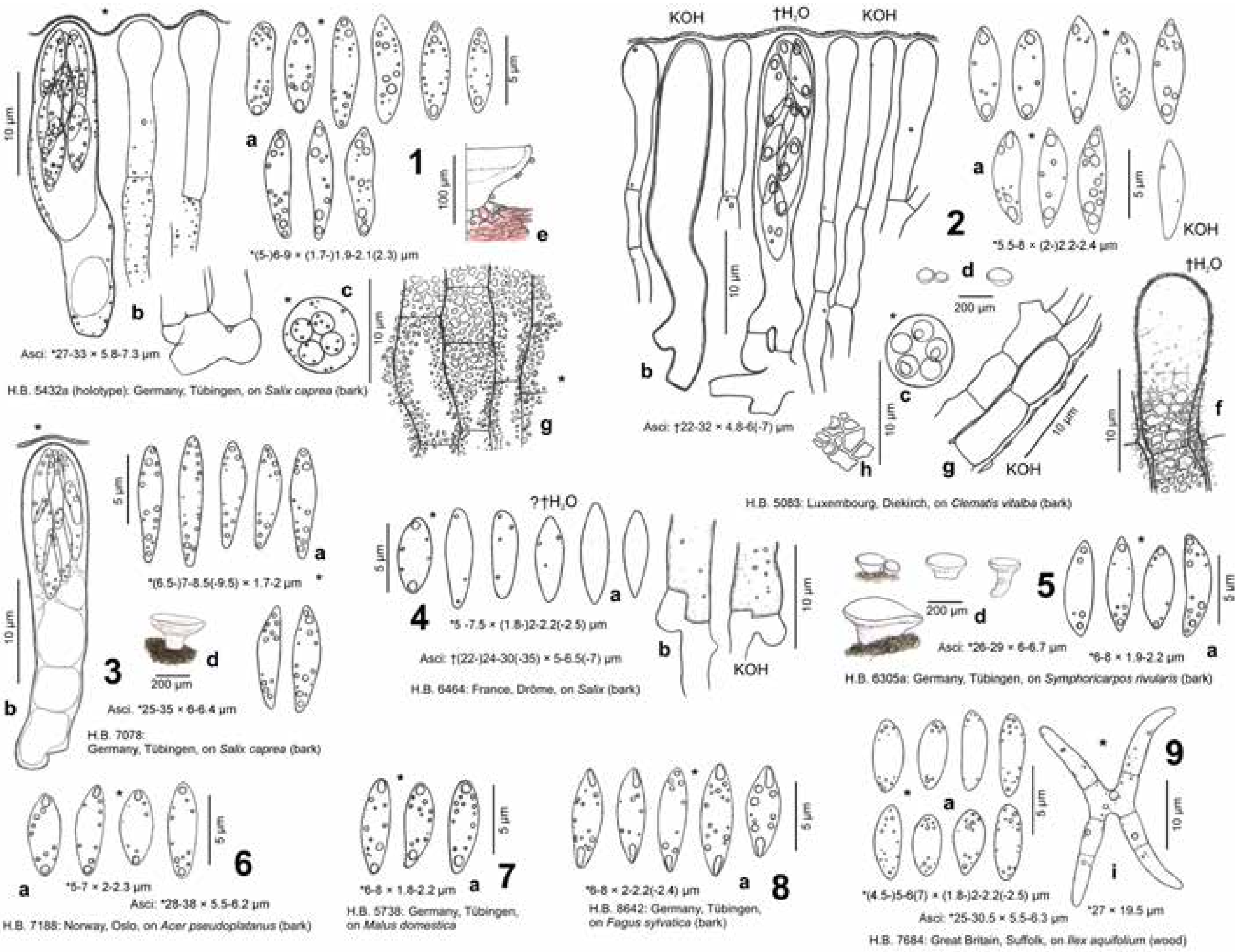


Plate 116. **1–9**: *Hyalorbilia subfusispora*. – **a**. ascospores; **b**. asci and paraphyses (ascus bases with croziers); **c**. asci with spores in optical cross section; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. marginal cortical cell (surface view); **g**. ectal excipulum at flanks (with warted exudate, surface view in **1g**, median section in **2g**); **h**. cloddy exudate on hymenium (top view); **i**. conidium from substrate.

t. angularis-prismatica from base to margin, at base ~40–50 µm thick, cells near stipe *10–27(–35) × 7–15(–23) µm {6}, at flanks 10–20 µm thick, cells */†(3–)5–12(–15)((–18)) × (2.5–)3–8(–11) × 8–11 µm {5}, marginal cortical cells broadly clavate, */†(8–)10–18(–20) × (3.5–)6–7.5 µm {16} [(5–)6–10(–12.5) µm wide in surface view]. **Anchoring hyphae** sparse to medium abundant, vertically radiating, */†(1.5–)2–4 µm wide, near insertion 4–5.5 µm, walls */†0.2(–0.3) µm thick {8}. **VBs** present in terminal cells of paraphyses, very low to medium refractive, very pale chlorinaceous, rarely yellowish, large but also multiguttulate; in marginal cortical cells absent or with 1 large VB; **LBs** in ectal excipulum near base: 1 or several large (1–2.8 µm) and some small ones in each cell {4}, but LBs absent or sparse and minute in a major part of collections. **Exudate** over paraphyses and excipulum 0.2–0.8 µm thick, continuous, nearly smooth or mostly distinctly rough to clod-shaped, pale chlorinaceous. — **ANAMORPH**: curucispora-like (presumed, from natural substrate {5}). **Conidiophores** not observed. **Conidia** mostly K-shaped (under cover slip, but forming a tetragonal structure when floating), with 3 arms and a stipe, rarely 2-armed or more than 4-armed, total size *27–45 × 11–22 µm {4} (K-conidia in side view in a plane), stipe *14–20 × 2.5–4.5 µm, 2–4-septate, arms *(10–)14–22 × 2–4(–4.5) µm, 2–4-septate; containing globose refractive SCBs.

Habitat: collected 0–4 m above the ground, corticated to partially, rarely entirely decorticated, 4–60 mm thick dead twigs and branches, also 10–20 cm thick living trunks of *Acer* sp. {2}, *A. campestre* {1}, *A. pseudoplatanus* {4}, *Aesculus hippocastanum* {1}, *Betula pendula* {1}, *Carpinus betulus* {1}, *Clematis vitalba* {8}, *Cornus* sp. {1}, *C. sanguinea* {5}, *Corylus avellana* {2}, *Cryptomeria japonica* {1}, *Cydonia oblonga* {1}, *Elaeagnus angustifolia* {1}, *Fagus sylvatica* {10}, *Fraxinus excelsior* {1}, *Ilex aquifolium* {3}, *Ligustrum vulgare* {1}, *Malus domestica* {3}, *Picea abies* {1}, *Pinus nigra* {1}, *Populus* sp. {1}, *Populus tremula* {1}, *Prunus avium* {1}, *P. domestica* {1}, *P. spinosa* {4}, *Quercus* sp. {4}, *Q. rubra* {1}, ?*Rhamnus cathartica* {1}, *Robinia pseudoacacia* {2}, *Rubus* (?)*bifrons* {1}, *R. fruticosus* {3}, *Salix* sp. {6/1}, *S.* ?*alba* {1}, *S. caprea* {13}, *S. cinerea* {2/1}, *Symphoricarpos albus* {2}, *Tilia* sp. {2}, *T. cordata* {1}, *Ulex europaeus* {2}, *U. parviflorus* {1}, *Ulmus laevis* {1}, *Vitis* sp. {1}; in gall of *Neonectria ditissima* {1}, on hymenophores or pilei of *Cerrena unicolor* {1}, *Hymenochaetopsis tabacina* {1}, *Trametes hirsuta* {1}; on (partially detaching) bark (periderm and bast) {72}, more rarely on wood {28}, (slightly to) medium or very strongly decayed (wood ~1 mm deep strongly rotten, core often also), in holes or on stub of broken twigs, old wounds, in small decorticated areas, in old beetle galleries, in lenticelles, on both sides of detached bark, often on edges of bark or hidden in cracks, sometimes slightly greyed, not or often medium to strongly covered by green, mainly coccoid algae, sometimes with lichens and small mosses, in black mould of *Sporidesmium* {1}, on stromata of *Diatrype stigma* {2}, *Eutypa spinosa* {1}, indet. pyrenomycetes {2}. **Further associated**: *Allophylaria macrospora* {1}, *Arachnopeziza aurata* {1}, *Bulbillomyces* sp. {1}, *Capronia* sp. {1}, *Crepidotus cesatii* {2}, *Cryptodiscus foveolaris* {2}, *Dacrymyces* sp. {2}, *Durella atrocyanea* {1}, *D. connivens* {2}, *Entoloma jahnii* {1}, *Eutypella* ?*prunastri* {1}, *Hamatocanthoscypha laricionis* {1}, *Hyalorbilia berberidis* {1}, *H. erythrostigma* {4}, *H. juliae* {4}, *H.*

latispora {2}, *H. rotifera* {2}, *Hyaloscypha intacta* {1}, *H. minuta* {3}, *Hyphodontia* sp. {1}, *Hypoxylon ?fuscum* {1}, *Hysterium pulicare* {1}, *?Hysterobrevium smilacis* {1}, *Hysteropatella elliptica* {1}, *H. prostii* {1}, *Karstenia idaei* {2}, *K. rhopaloides* {11/1}, *Lasiosphaeria* sp. {1}, *L. sorbina* {1}, *Lecophagus ellipsoideus* {2}, *Letendraea helminthicola* {1}, *Lophiostoma compressum* {2/1}, *Menispora glauca* {1}, *Merismodes* sp. {1}, *Micropeziza* sp. {1}, *Mollisia* sp. {1}, *M. ligni* {2}, *M. sublividula* {1}, *Octospora affinis* {1}, *Olla scrupulosa* {1}, *Orbilia aprilis* {4}, *O. aristata* {8}, *O. aurantiorubra* {3}, *O. breviaristata* {1}, *O. ?clavipisca* {1}, *O. clavuliformis* {3}, *O. corculispora* {1}, *O. eucalypti* {5}, *O. euonymi* {2}, *O. filiformis* {2}, *O. hesperidea* {1}, *O. ?liliputiana* {1}, *O. montigena* {1}, *O. obtusispora* {1}, *O. pleioeuonymi* {2}, *O. subclavuliformis* {1}, *O. trapeziformis* {2}, *O. ?tremulae* {2}, *O. vinosa* {11}, *O. vitalbae* {2}, *O. xanthoguttulata* {1}, *O. xanthostigma* {1}, *Orthotrichum* sp. {1}, *Parmelia ?saxatilis* {1}, *P. sulcata* {1}, *Patellaria atrata* {1}, *Pirottaea ?imbricata* {1}, *Physcia* sp. {2}, *Propolis farinosa* {1}, *Protounguicularia transiens* {1/1}, *Pseudohelotium sordidulum* {1}, *Pyrenopeziza caespiticia* {1}, *P. rubi* {1}, *Resupinatus applicatus* {2}, *Sclerococcum* sp. {1}, *Skyttea* sp. {2}, *Tubeufia cerea* {3}, '*Tympanis*' *xylophila* {1}, *Unguiculariopsis* sp. {3}, *U. ?rehmii* {1}, *Unguiculella eurotioides* {1/1}, *Vuilleminia comedens* {1}, *Xanthoria parietina* {2}. **Desiccation tolerance**: fully viable after 2 weeks up to 4 months. **Altitude**: 1–735 m a.s.l. (1035 m in Asturias). **Geology**: Cambrian, Ordovician & Devonian sandstone & shale, Buntsandstein, Muschelkalk, Keuper, Jurassic, Cretaceous & Tertiary sand- marl- & limestone, calcareous clay, molasse, Quaternary loess, till, silt & sand; mica schist, gneiss. **Phenology**: throughout the year (long-lived).

Phenology of *H. subfusispora*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
12	8	8	5	5	7	3	8	4	0	13	8

Taxonomic remarks. *Hyalorbilia subfusispora* is characterized by ± straight, fusoid to fusiform ascospores very similar to *H. fusispora*, from which it differs in smaller, less pigmented apothecia and much more inflated marginal cortical cells, also in the frequent presence of a large, often ± elongate SB at each spore end. Further tentative differences to *H. fusispora* are shorter asci, shorter terminal cells of paraphyses, and slightly narrower spores. However, the two species are morphologically not always easy to distinguish. *H. polypori* and *H. texensis* differ from *H. subfusispora* in almost eguttulate, distinctly narrower spores with rounded ends, the former also in more cylindrical spores. *H. polypori* and *H. ulicicola* differ in much larger, desiccation-sensitive apothecia, the latter species also in shorter spores. See also under the similar *H. rotifera* (with smaller spores), *H. lunata* (with curved spores), and *H. latispora* (with shorter spores without large SBs).

Variation. *H. subfusispora* shows rather strong variability, mainly in ascus and spore size, but also in spore shape and especially in spore content. Two very distinct subglobose to tear-shaped spore bodies, one at each spore end, were seen in many of the collections (e.g., Pl. 116: 1–2, 6–8). They are surrounded by a few often much smaller globose SBs, but sometimes there are several large SBs in each spore half (e.g., Pls 116: 2a; 117: 4d) and then the spore content resembles that of *O. fusispora*. However, SBs in *H. fusispora* were always globose whereas the large SBs of *H. subfusispora* tend to be ellipsoid to tear-shaped and narrowly attached to the spore ends. In some specimens (e.g., Pl. 116: 3, 5, 9) several rather small globose SBs in each spore half similar to *H. fusispora* were seen; these specimens are assigned here to *H. subfusispora* because of wide marginal cortical cells and rather small, pale-coloured apothecia. We have included in *H. subfusispora* also collections with rather short spores (e.g., Pls 116: 4, 6; 117: 10d) which appear to form a transition to *H. latispora*, but differ from that species in containing globose or tear-shaped polar SBs. This was also the case in a photo of H.B. 7684 (Pl. 117: 15), whereas the spores from another apothecium of the same sample (Pl. 116: 9a) were slightly shorter and did not show larger polar SBs. Perhaps this apothecium belonged to *H. latispora*, but the conidium observed nearby (Pl. 116: 9i) resembles those presumed as anamorph of typical *H. subfusispora*.

The spore ends are usually acute or subacute, but in some collections a strong tendency to obtuse was observed (Pl. 116: 9, see also the drawings by E. Batten, IVV). The ectal excipulum at the flanks varies between t. prismatica (Pls 116: 1g, 2g; 117: 8a), and t. globulosa-angularis (Pl. 117: 2f, 3f). The excipular cells at base and flanks contain large oil drops in some collections (e.g., Pl. 117: 2f) but such LBs were not observed in a major part of the specimens. A rich sample from Navarra collected on a branch on the moist ground deviates by extraordinarily large apothecia (0.38–0.65 mm).

Not included collections. A collection from southern France on branch of *Robinia* (IVV: H.B. 9621a, associated with *O. aprilis*) has slightly curved, lunate to helicoid spores which closely resemble those of *H. lunata*. It differs from *H. lunata* in small apothecia (0.15–0.35 mm) growing on xeric substrate. The Canadian record was only very briefly documented and is, therefore, doubtful.

Anamorph. Branched, K-shaped conidia (curucispora-like) with ± globose refractive bodies (SCBs) occurred on the natural substrate in five collections (see Pls 116: 9i; 118), but a proof for their connection to a teleomorph is wanting. In Gönczöl & Révay (2006: figs 7–8) and Révay & Gönczöl (2010: fig. 12) such conidia were figured as 'unknown sp. 1' from rainwater from Germany (Tübingen) on *Fagus* and *Carpinus* and from Hungary (Királyrét, Budapest, Börzsöny Mts.) on *Fagus*, *Taxus*, *Chamaecyparis*, and *Picea*. This anamorph remarkably resembles *Curucispora ponapensis* Matsush. described from Micronesia. In two collections of *H. subfusispora* (H.B. 7693 and H.B. 5387) we detected another type of conidia near the apothecia: slender, vermiform, slightly curved (†40–48 × 2 µm, 4–5-septate), similar to those observed near apothecia of *H. rotifera*. In the sample from Slovakia a vermispora-like, ~6-septate conidium of *48 × 3.7 µm occurred (A. Polhorský, IVV: A.P. 19/16).

Phylogeny. Sequences were gained from apothecia of five samples on *Cornus* and *Salix* from three sites in Luxembourg, comprising ITS, four also LSU D1 (two also D2–D3 or D2–D5). The S1506 intron is present in all of them. The five sequences vary in the ITS by 0–0.7% (0–3 nt) and in the intron by 0–0.6% (0–2 nt), while no variation occurs in the LSU D1–D3. One sample (G.M. 2019-01-28.4) comprised only one apothecium and was identified by its DNA. The other four were also too sparse to be preserved. They were tentatively identified by one of us (G.M.), but not microscopically documented.

In analyses of ITS, LSU, or ITS+LSU, *H. subfusispora* clustered unsupported (ITS) or with weak (LSU) or high support (ITS+LSU) sister to the *oviparasitica-multiguttulata* clade (Phyls 5–6, S5). In the LSU (D1–D2) the distance to most other members of the genus is 8–11% (including *H. juliae* with 9%), but 13% to *H. latispora*, 15–15.3% to *H. rotifera*, and 16–17% to *H. erythrostigma*. In the ITS *H. subfusispora* clustered with some uncultured clones (H13–H14), e.g., a clone from forest soil in Canada (FJ553822) with

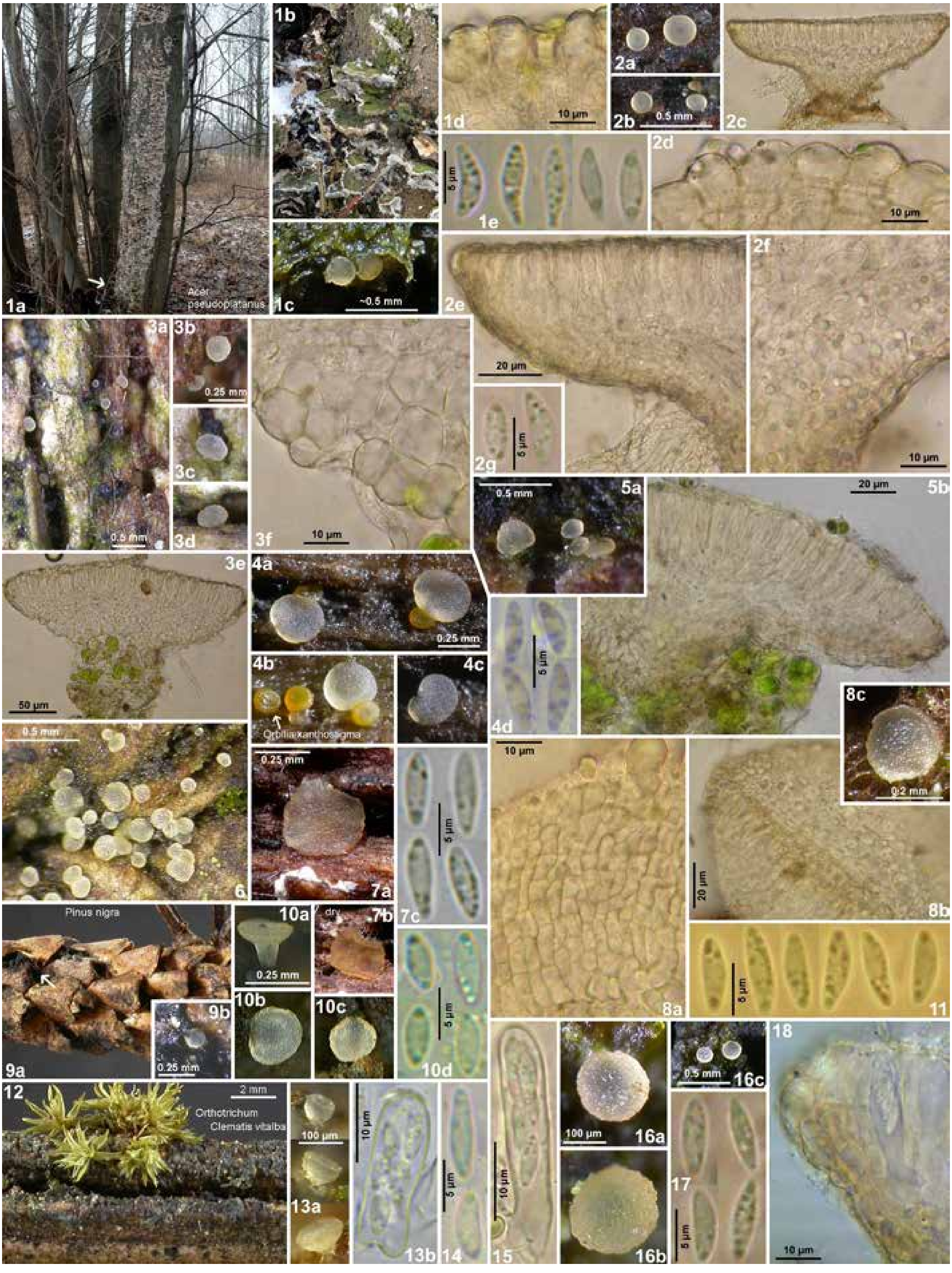


Plate 117. **1–18**: *Hyalorbilia subfusispora*. – **1a**. *Acer pseudoplatanus* overgrown by *Cerrena unicolor*; **1b**. closeup; **9a**, **12**. dead corticated xeric twigs of *Pinus nigra* and *Clematis vitalba*; **1c**, **2a–b**, **3a–d**, **4a–c**, **5a**, **6**, **7a**, **8c**, **9b**, **10a–c**, **13a**, **16a–c**. rehydrated apothecia; **7b**. dry apothecium; **2c**, **e**, **3e**, **5b**. apothecia in median section; **18**. id., marginal ectal excipulum; **2f**, **3f**. id., ectal excipulum at lower flanks; **8b**. apothecium in oblique top view; **8a**. mid flanks in surface view; **1d**, **2d**. marginal cortical cells in top view; **13b**, **15**. asci; **1e**, **2g**, **4d**, **7c**, **10d**, **11**, **14**, **17**. ascospores. – Living state, except for **1d**, **2d** (in KOH). – **1a–c**, **e**, **10a–d**, **14**, **18**: phot. P. Perz. — **1a–e**. H.B. 9019: Poland, Kłodzko, on *Cerrena* (on *Acer*); **2a–g**. H.B. 8401a: Germany, Amberg, on *Salix*; **3a–f**. H.B. 8642: Germany,

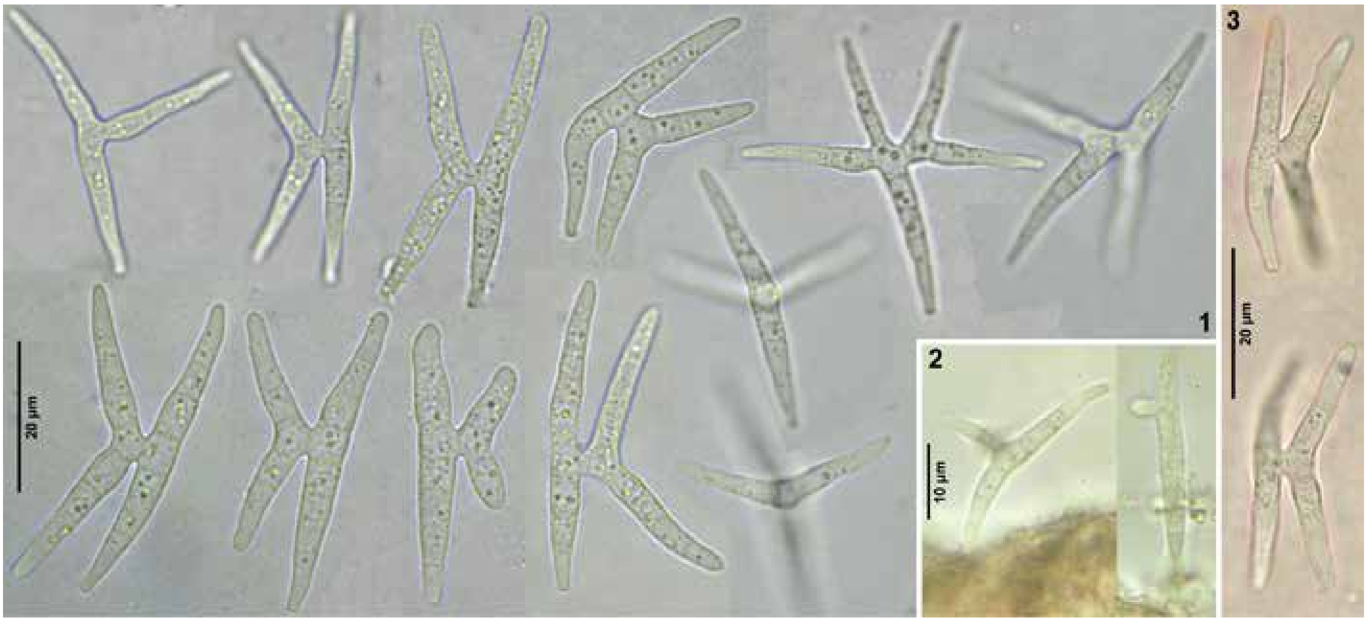


Plate 118. **1–3**: *Hyalorbilia subfusispora* (presumed anamorph). – Conidia from substrate (living state). – **2**: phot. P. Perz. — **1**. 8.XII.2009: Luxembourg, Graulinster, on *Fagus*; **2**. P.P. 20091007: Poland, Kłodzko, on *Salix*; **3**. H.B. 8429b: Germany, Tübingen, on *Prunus*.

a distance of 10 %, while the distance to the morphologically most similar species is much higher (20 % to *H. ulicicola*, 26 % to *H. fusispora*, 33–34 % to *H. rotifera*).

Ecology. *Hyalorbilia subfusispora* was collected on ± rotten bark (and wood) of xeric (rarely hygric) twigs and branches of various angiosperm (rarely coniferous) trees, shrubs, and climbers, also on stems of *Rubus*. It does not seem to differ ecologically from *H. juliae*, with which it was four times found in association. In both species the small and often very scattered, preferably corticolous apothecia are easily overlooked and do not differ by macroscopy.

H. subfusispora is a common species in cold-temperate humid, atlantic to subcontinental central Europe, where it also occurs in hemiboreal and orotemperate or mesotemperate humid, or suprasub- to mesosubmediterranean semihumid regions. The collection sites include sun-exposed borders of mostly thermophilous forests, hedges, old quarries, overgrown gardens, alluvial forests at rivers and lakes, and salt marshes, at planar to colline or montane altitude. The collection site in the southeast of Northern America was a warm-temperate subhumid *Quercus virginiana*/*Juniperus occidentalis* forest, that in the northeast a cold-temperate humid, mild continental conifer forest.

Specimens included. **GREAT BRITAIN**: **East England**, **Suffolk**, 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Ulex europaeus*, on bark, 7.IV.2004, S.M. Francis (E.B. 4509). – ibid., branch of *Acer pseudoplatanus*, on bark, 6.VI.2004, E. Batten (E.B. 4525, K(M) 227424, doc. vid.). – NNE of Wenhaston, Blyford Lane, Garden Hill Cottage, 12 m, twig of *Ulex europaeus*, on bark, 8.XII.2004, E. Batten (E.B. 4572, doc. vid.). – 6.3 km SW of Southwold, NW of Dunwich, Dunwich Forest, 15 m, branch of *Ilex aquifolium*, on bark, 29.VIII.2004, E. Batten (E.B. 4555, doc. vid.). – ibid., 20 m, twig of *I. aquifolium*, on wood, 11. & 19.II.2005, E. Batten (E.B. 4589, H.B. 7684, anam. substr.). — **NORWAY**: **Oslo**, Southern Coast, 3.5 km NW of Oslo, Marienlyst, Blindern University, 88 m, branch of *Acer pseudoplatanus*, on bark, 13.VIII.2002, G. Marson (H.B. 7188 ø). — **POLAND**: **Lower Silesia**, 20.5 km W of Kłodzko, 1.5 km NNW of Duszniki Zfrój, SW of Złotno, 605 m, of *Picea abies*, on bark, 1.IV.2009, P. Perz (ø, doc. vid.). – 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, branch of *Salix*, on bark, 3.X.2007, P. Perz (ø, doc. vid.). – ibid., 7.X.2009, P. Perz (P.P.20091007-1, doc. vid., anam. substr.). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, branch of *Tilia cordata*, on bark, 14.X.2007, P. Perz (ø, doc. vid.). – 12.5 km SE of Bystrzyca Kłodzka, 8.5 km NE of Miedzylesie, N of Nowa Wies, 525 m, trunk of *Acer pseudoplatanus*, on *Cerrena unicolor*, 7.III.2009, P. Perz (H.B. 9019, P.P. 20090307-1 & 2). – ibid., branch of ?*Salix*, on bark & old ?*Diatrypaceae*, 26.XII.2009, P. Perz (P.P. 20091226-1, doc. vid.). — **CZECHIA**: **Hradec Králové**, 2 km SW of Dobruška, 2 km ENE of Opočno, 300 m, branch of *Tilia*, on bark and pyrenomycete, 15.VIII.2010, P. Perz (P.P.20100815-2, doc. vid.). — **SLOVAKIA**: **Bratislava**, 10 km SE of Bratislava, 5 km S of Podunajské Biskupice, Topol'ové hony, 132 m, branch of *Clematis vitalba*, on bark & wood, 18.III.2019, A. Polhorský (A.P. 19/16, doc. vid.). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 25 km W of Ettelbruck, 2 km NE of Rombach-Martelange,

Map 18. Known distribution of *H. subfusispora* in Europe (yellow = not included collection).

Tübingen, on *Fagus*; **4a–d**. 28.VI.2007: Luxembourg, Remich, on *Quercus* (with *O. xanthostigma*); **5a–b**. H.B. 7989b: Germany, Tübingen, on *Cornus*; **6**. 25.XII.2006: Luxembourg, Graulinster, on *Rubus*; **7a–c**. 8.XII.2009: ibid., on *Fagus*; **8a–c**. H.B. 7693: Luxembourg, Echternach, on *Fagus*; **9a–b**. H.B. 5271b: Luxembourg, Bettendorf, on *Pinus*; **10a–d**. P.P. 20071003: Poland, Kłodzko, on *Salix*; **11**. 31.X.2004: Germany, Tübingen, on *Fagus*; **12**. H.B. 5380a: Germany, Würzburg, on *Clematis*; **13a–b**. 27.I.2007: Luxembourg, Echternach, on *Rubus*; **14**. P.P. 20071014: Poland, Kłodzko, on *Tilia*; **15**. H.B. 7684: Great Britain, on *Ilex*; **16a–c**. H.B. 8445d: Luxembourg, Remich, on *Rubus*; **17**. 27.XI.2004: Luxembourg, Waldhaff, on *Aesculus*; **18**. P.P. 20090401: Poland, Kłodzko, on *Picea*.

SE of Grumelange, Bruch, 365 m, branch of *Salix*, on *Hymenochaetopsis tabacina*, 3.V.2000, G. Marson (ø). – **Gutland**, **Diekirch**, 2 km S of Diekirch, 2.5 km N of Stegen, Këmpchen, 320 m, branch of *Clematis vitalba*, on bark, 23.V.1994, G. Marson (H.B. 5083, G.M. 5177). – 5.5 km ENE of Diekirch, 1.5 km NE of Bettendorf, Niderbierg, 390 m, branch of *Corylus avellana*, on wood, 27.IV.1995, H.O. Baral & G. Marson (ø). – ibid., branch of *Pinus nigra*, on bark, 27.IV.1995, H.O. Baral (H.B. 5271b). – **Echternach**, 10 km WNW of Echternach, 1.2 km SW of Beaufort, Längt, 340 m, trunk of *Fagus sylvatica*, on bark, 3. II.2007, G. Marson (ø). – 3.5 km SSW of Echternach, Haard, 355 m, branch of *F. sylvatica*, on bark, 20.II.2005, G. Marson (H.B. 7693). – 4 km SW of Echternach, 1.5 km E of Scheidgen, N of Michelshaff, 320 m, stems of *Rubus fruticosus*, 27.I.2007, G. Marson (ø). – NW of Graulinster, Marscherwald, Rippeger Deel, 375 m, stem of *Rubus fruticosus*, 25.XII.2006, G. Marson (ø). – **Capellen**, 4.5 km NW of Capellen, 1 km N of Koerich, southwest-end of Haereboesch, Carrière, 310 m, branch of *Salix caprea*, on bark, 8.V.1998, G. Marson (H.B. 6121c ø). – **Luxembourg**, 19.5 km NE of Luxembourg, 1.3 km NE of Graulinster, Marscherwald, 388 m, trunk of *Fagus sylvatica*, on bark, 8.XII.2009, G. Marson (ø, anam. substr.). – 10.5 km NE of Luxembourg, 1.2 km W of Ernster, Wuurzelwis, 350 m, trunk of *F. sylvatica*, on bark, 12.IX.2004, G. Marson (ø). – 6 km NE of Luxembourg, SE of Waldhaff, Gréngewald, Arboretum, 410 m, branches of *Aesculus hippocastanum*, on bark, 27.XI.2004, G. Marson (ø). – 5.3 km NE of Luxembourg, 3 km NE of Kirchberg, 347 m, trunk of *Fagus sylvatica*, on bark, 28.XI.2014, G. Marson (G.M. 2014-11-28.2, doc. vid.). – 2.6 km NE of Luxembourg, NE of Kirchberg, Märtesgrond, 336 m, stem of *Rubus fruticosus*, 23.XI.2006, G. Marson (ø). – 5 km S of Luxembourg, 1.5 km W of Hesperange, Biersak/Géisselbierg, 290 m, branch of ?*Rhamnus cathartica*, on bark, 6. VI.1994, G. Marson (ø). – ibid., branch of *Salix cinerea*, on bark, 21.X.2000, G. Marson (H.B. 6802). – 5 km SE of Luxembourg, 1.5 km E of Itzig, Reimeschbaach, 297 m, branch of *Salix*, on ?bark, 22.I.2019, G. Marson (G.M. 2019-01-22.3, sq.: MN978734). – ibid., branch of *Cornus*, on wood (G.M. 2019-01-22.5, sq.: MN151408). – ibid., branch of *Salix*, on wood, 28.I.2019, G. Marson (G.M. 2019-01-28.4, non vid., sq.: MN151407). – **Grevenmacher**, 3.8 km NE of Grevenmacher, 1 km NW of Mertert, Karel, 190 m, branch of *Malus domestica*, on bark, 2.II.1997, G. Marson (H.B. 5713d ø). – 3.8 km WSW of Grevenmacher, 1.5 km ESE of Potaschberg, Kiischteberg, 223 m, branch of *Cornus sanguinea*, on bark & wood, 12.IX.2014, G. Marson (G.M. 2014-09-12.2, sq.: KY419179). – **Remich**, 5.5 km NNW of Remich, 1.4 km WNW of Greiveldange, Néisbësch, 255 m, trunk of *Quercus*, on wood, 28.VI.2007, G. Marson (ø). – 8.5 km S of Remich, SW of Schengen, N of Stroumberg, 225 m, stem of *Rubus* (?)*bifrons*, on bark, 11.II.2007, G. Marson (H.B. 8445d ø). – **Esch-sur-Alzette**, 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, branch of *Salix cinerea*, 7.X.2015, G. Marson (G.M. 2015-10-07.4; sq.: MN151406). – 2 km SE of Dudelange, Bloklapp, 290 m, branch of *Salix caprea*, on bark, 13.III.2001, G. Marson (ø). – 4.2 km S of Bettembourg, 1.5 km E of Dudelange, railway, 290 m, twig of *Clematis vitalba*, 16.XI.2013, G. Marson (ø). — **GERMANY**: **Mecklenburg-Vorpommern**, 26 km N of Stralsund, Hiddensee, 2.8 km S of Vitte, 5 m, branch of *Salix* ?*cinerea*, on bark, 31.III.2018, T. Richter (ø). – **Sachsen**, 3 km WSW of Döbeln, Stockhausen, 220 m, branch of *Corylus avellana*, on wood, 14.II.2013, S. Pohlers (ø, doc. vid.). – **Rheinland-Pfalz**, 14 km SE of Pirmasens, SE of Dahn, military cemetery, 250 m, branches of *Salix caprea*, on wood & bark, 1.X.1994, H.O. Baral & G. Marson (H.B. 5155b). – **Baden-Württemberg**, 6 km N of **Stuttgart**, E of Weilimdorf, lake at Goslarer Straße, 325 m, branch of *Symphoricarpos albus*, on bark, 1.X.2000, H.O. Baral (ø). – ibid., branch of *Salix* (?)*alba*, on bark, 1.X.2000, H.O. Baral (ø). – 1.4 km SE of Weilimdorf, Rainweg, 350 m, branch of *Prunus spinosa*, on wood, 18.V.1997, H.O. Baral (H.B. 5800 ø). – 3.5 km NW of Stuttgart, 1.5 km SW of Feuerbach, Heimberg, 360 m, branch of *Quercus*, on bark, 13.III.2003, H.O. Baral (ø). – 0.5 km N of Horb, Kugler Hang, 470 m, branch of *Acer campestre*, on bark, 21.IX.2003, H.O. Baral (ø). – 4 km N of **Tübingen**, 1 km WSW of Bebenhausen, Goldersbach, 380 m, branch of *Prunus spinosa*, on bark, 27. II.1992, H.O. Baral & E. Weber (ø). – 2 km NNW of Tübingen, Morgenstelle, Botanical Garden, 440 m, trunk of *Elaeagnus angustifolia*, on bark, 7.VIII.2009, H.O. Baral (ø). – ibid., branch of *Cryptomeria japonica*, on bark, 18.VII.2005, H.O. Baral (H.B. 7844 ø). – 2 km NNW of Tübingen, Ursrainer Egert, 420 m, branches of *Clematis vitalba*, on bark, 25.I.1995, H.O. Baral (ø). – 2.5 km SW of Tübingen, Spitzberg, Sonnenhalde, 370 m, branch of *Clematis vitalba*, on bark, 28.VII.2002, V. Baral (ø). – 1.8 km WNW of Tübingen, S of Lustnau, 320 m, branch of *Cydonia oblonga*, on wood, 27.III.2000, H.O. Baral (ø). – 1.5 km N of Lustnau, Hägnach, 380 m, branch of *Carpinus betulus*, on bark, 4.VIII.2002, H.O. Baral (ø). – 8 km NE of Tübingen, 4 km N of Pfrondorf, Eisenbachhain, 485 m, branch of *Betula pendula*, on bark, 3.X.2006, H.O. Baral (ø). – 2 km N of Pfrondorf, Zeitungseiche, 470 m, branches of *Ligustrum vulgare*, on wood, 30.I.2000, H.O. Baral (H.B. 6559a). – 1.3 km SW of Pfrondorf, quarry near Bitzle, 420 m, branches of *Clematis vitalba*, on bark, 4.X.1994, H.O. Baral & K. Siepe (H.B. 5156a). – ibid., branches of *Salix caprea*, on bark, 26.III.1996, H.O. Baral (ex H.B. 5432a, M-0276418, **holotype**). – ibid., branch of *Prunus avium*, on bark, 17.I.2004, H.O. Baral (ø). – S of Pfrondorf, east-part of Bitzle, 350 m, branch of *Fagus sylvatica*, on wood, 31.X.2004, E. Weber (ø). – ibid., Pfrondorf, Obere Mähder, 390 m, branch of *Symphoricarpos albus*, on bark, 31.I.1999, H.O. Baral (H.B. 6305a). – ibid., branch of *Malus domestica*, on wood, 4.X.1994, H.O. Baral & K. Siepe (ø). – ibid., Höhe, 420 m, branch of *Malus domestica*, in gall of *Neonectria ditissima*, 23.III.1997, H.O. Baral (H.B. 5738 ø, anam. substr.). – 1 km SE of Pfrondorf, SE of Rauhalde, 345 m, branch of *Tilia*, on wood, 18. XI.2001, H.O. Baral (ø). – Pfrondorf, Blaihofstraße, 430 m, branch of *Robinia pseudoacacia*, on bark, 22.VII.2004, H.O. Baral (ø). – ibid., branch of *Cornus sanguinea*, on bark & wood, 4.VI.2009, H.O. Baral (H.B. 9067 ø). – 5.2 km NE of Tübingen, E of Pfrondorf, Einsiedlerweg, 415 m, branch of *Prunus domestica*, on bark, 26.II.2007, H.O. Baral (H.B. 8429b ø, anam. substr.). – NE of Pfrondorf, Gähklinge, 410 m, branch of *Prunus spinosa*, on bark, 30.XI.2011, H.O. Baral (ø). – NE of Pfrondorf, W of Tiefenbach, 415 m, *Salix caprea*, on pileus of *Trametes hirsuta*, 10.I.2008, H.O. Baral (ø). – ibid., branch of *Salix caprea*, on bark, 17.I.2008, H.O. Baral (ø). – ENE of Pfrondorf, Tiefenbach, 410 m, trunk of *Fagus sylvatica*, on bark, 7.X.2007, H.O. Baral (H.B. 8642). – ibid., 430 m, branch of *Salix caprea*, on bark, 14.X.2002, H.O. Baral (ø). – ibid., 22.X.2005 (ø). – ibid., branch of *Prunus spinosa*, on bark, 29.VI.2003 (ø). – 1.2 km E of Pfrondorf, Stangenhölzlesklinge, 430 m, branch of *Salix caprea*, on bark, 25. XI.2001, H.O. Baral (H.B. 7078 ø). – ibid., branch of *Quercus*, on bark & wood, 23.XI.2003, H.O. Baral (ø). – 2 km SE of Pfrondorf, Hinterpfand, 370 m, trunk of *Fagus sylvatica*, on bark, 29.I.2005, H.O. Baral (ø). – 1.6 km SE of Pfrondorf, Neckar river, 320 m, branch of *Cornus sanguinea*, on wood, 30.X.2005, H.O. Baral (H.B. 7989b ø). – 9 km SSW of Reutlingen, 2.3 km ESE of Gönningen, Gönninger Seen, 600 m, branch of *Salix caprea*, on bark, 5.X.2000, H.O. Baral (ø). – **Schwarzwald**, 7 km ESE of Schamberg, 0.7 km N of Eschbronn, Locherhof, 710 m, branch of *Fraxinus excelsior*, on bark, 28.X.2018, collector unknown, vid. B. Wergen (doc. vid.). – **Bayern**, **Unterfranken**, 29 km NW of Würzburg, 6 km NW of Karlstadt, Rammersberg, 320 m, branch of *Clematis vitalba*, 11.XI.1995, H.O. Baral (ø, as *O. vitalbae*). – 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz, 260 m, branches of *C. vitalba*, on bark, 11. XI.1995, H.O. Baral & L.G. Krieglsteiner (H.B. 5380a, as *O. vitalbae*). – ibid., branches of *Cornus sanguinea*, on wood & bark, 11.XI.1995, H.O. Baral & L.G. Krieglsteiner (H.B. 5387). – ibid., branch of *Salix caprea*, on bark & wood, 11.XI.1995, H.O. Baral (ø). – **Oberpfalz**, 12 km NNE of Amberg, 1.5 km W of Hirschau, Moosweiher, 420 m, branch of *Populus tremula*, on bark, 29.XII.2003, H.O. Baral (ø). – ibid., trunk of *Acer pseudoplatanus*, on bark, 28.XII.2004, H.O. Baral (H.B. 7639a ø). – 1.2 km NNW of Hirschau, Weinberg, 455 m, branch of *Salix caprea*, on bark, 27.XII.2003, H.O. Baral (H.B. 7450b ø). – ibid., branch of *S. caprea*, on wood, 27.XII.2005, H.O. Baral (ø). – 1.8 km NNW of Hirschau, Hintere Peneslohe, 460 m, branch of *S. caprea*, on bark, 26.XII.2006, H.O. Baral (H.B. 8401a). – 12.5 km NE of Tirschenreuth, 1.2 km S of Neualbenreuth, SE of Platzermühle, 550 m, branch of *Acer*, on bark, 3.VIII.1995, H.O. Baral (ø). – **Oberbayern**, 7.5 km SE of München, Neuperlach, 543 m, twig of *Acer*, on bark, 7.II.2019, B. Fellmann (ø, doc. vid.). – **Niederbayern**, 16 km NE of Regen, N of Zwieseler Waldhaus, 735 m, ?*Fagus*, on *Eutypa spinosa*, 14.VI.2008, B. Fellmann (ø, doc. vid.). — **AUSTRIA**: **Steiermark**, 8 km WNW of Bad Radkersburg, 4 km W of Halbenrain, Donnersdorfer Au, 218 m, branch of *Ulmus laevis*, on wood, 30.X.2011, G. Friebes (G.F. 20110195, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 12.5 km WSW of Novi Sad, 1.5 km S of Beočin, 270 m, branch of *Quercus*, on old pyrenomycete, 18.IV.2017, D. Savić (FG-531, doc. vid.). — **FRANCE**: **Bretagne**, **Morbihan**, 1 km WNW of La Gacilly, rue de Picardie, 38 m, branch of *Ilex aquifolium*, on wood and *Diatrype stigma*, 23.I.2004, J.P. Priou (J.P.P. 24033, doc. vid.). – **Pays-de-la-Loire**, **Île-de-France**, **Yvelines**, 20 km NW of Paris, 1.8 km NW of Maisons-Laffitte, Forêt St.-Germain-en-Laye, SE of Pavillon Muette, 47 m, branch of *Fagus sylvatica*, on bark and *Diatrype stigma*, 2.I.2004, J.P. Priou & J.L. Priou (ø). – **Rhône-Alpes**, **Ardèche**, 5 km E of Vallon-Pont-d'Arc, 4 km WNW of St.-Remèze, les Mouniers, 410 m, branch of *Ulex parviflorus*, on bark, 8.X.2002, G. Marson (ø). – **Drôme**, 7 km NNE of Pierrelatte, 2.3 km ESE of Donzère, 95 m, twig of *Salix*, on bark, 20.IX.1999, G. Marson (H.B. 6464). — **SPAIN**: **País Vasco**, **Gipuzkoa**, 15 km ENE of San Sebastián, Irun, N of train station, 7 m, branch of *Salix*, on wood, 8.V.1996, H.O. Baral (ø). – **Navarra**, 42 km WNW of Pamplona, 2 km ENE of Alsasua, 530 m, branch of *Quercus rubra*, on wood, 5.VIII.2015, J. Martin (ARAN-F 01600, doc. vid.). – **Asturias**, 18 km SSE of Pola de Lena, 2 km SSW of Pajares, Hayedo de Valgrande, 1035 m, wood of *Fagus sylvatica*, 22.VIII.2014, J.A. Sánchez (E.R.D. 6264, doc. vid.). — **USA**: **Texas**, Oaks and Prairies, 65 km W of Austin, ~2 km WSW of Johnson City, 380 m, branch of *Vitis*, on bark & wood, 18.VI.1996, G. Marson (H.B. 5554c ø).

Not included. **FRANCE**: **Midi-Pyrénées**, **Ariège**, 16.5 km ENE of St.-Girons, NE of Castelnau-Durban, les Mouns, 450 m, branch of *Robinia pseudoacacia*, on wood, 26.X.2011, J.P. Priou (J.P.P. 11179 ø, H.B. 9621a). — **CANADA**: **Nova Scotia**, 81 km ENE of Halifax, Taylor Head, Provincial Park, ~20 m, twig of ?*Abies*, on wood, X.1996, C. Peller (ø).

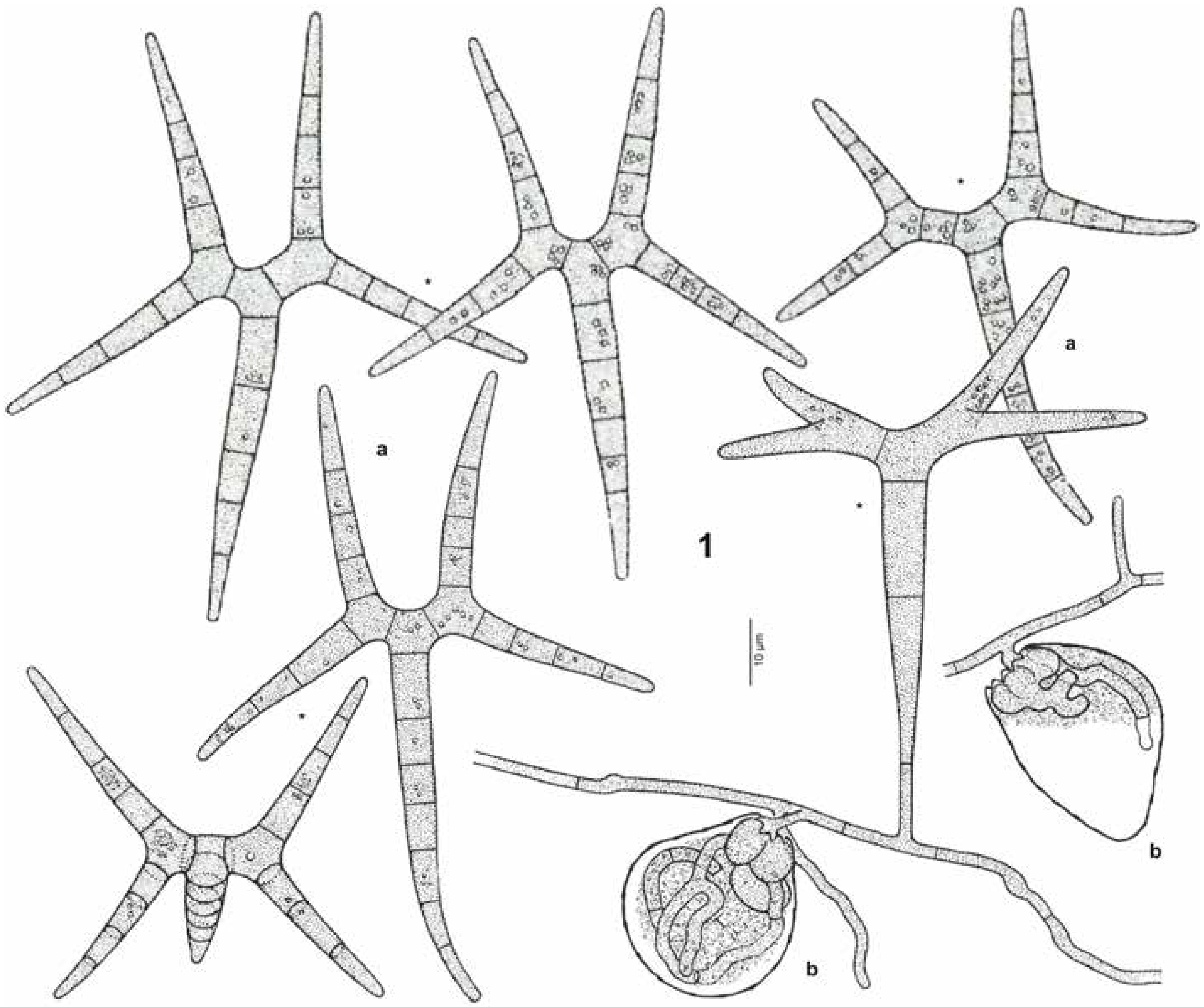


Plate 119. **1**: *Hyalorbilia quadridens* (holotype). – **a**. conidia (four in flattened condition under cover glass, lower right submature); **b**. testaceous rhizopods (*Euglypha laevis*) trapped by swollen protrusions. – From Drechsler (1962).

Hyalorbilia quadridens (Drechsler) Baral & E. Weber, in Baral et al., Mycol. Progr. 17 (1–2): 22 (2017) — Pl. 119

Basionym: *Triposporina quadridens* Drechsler, Sydowia 15(1–6): 19, pls 7–8 (1962) [1961]

≡ *Dwayaangam quadridens* (Drechsler) Subram., Kavaka 5: 96 (1978) [1977]

Etymology: according to the 4-armed (‘4-toothed’) conidia.

Typification: USA, Florida, Lakeland, herbaceous plant material, 12.IV.1959, C. Drechsler (holotype: illustration in Drechsler 1962: pls 7–8).

Description: — **TELEOMORPH**: unknown. – **ANAMORPH**: dwayaangam-like (isolated from herbaceous debris {T}). **Conidiophores** 10–12 × 1.8 µm, simple, non-septate, conidiogenesis terminal, singly. **Conidia** twice dichotomously branched in succession, *75–95 × 61–77 µm (when flattened), stipe 43–55 × 4.8–6.5 µm 5–6(–7)-septate, gradually tapered towards base, primary branches 6–11 × 4.5–6 µm, 0(–1)-septate, secondary branches *(20–)25–34 × 4–5.5 µm, (2–)3–4(–5)-septate, gradually tapered towards ends; containing one or several globose (?)SCBs 0.7–1.2 µm diam. in most of the cells. **Trapping organs**: capturing testaceous rhizopods (*Euglypha laevis*) by hyphal protrusions that form swollen lobes after capture within the aperture of the rhizopod.

Taxonomic remarks. In morphology of its staurosporous conidia the fungus unquestionably belongs to the *Orbiliomycetes*, and the detailed protologue leaves little doubt about its placement in *Hyalorbilia*. The capacity of capturing rhizopods by means of small, apparently adhesive protrusions seems to be unique in the genus *Dwayaangam* as currently circumscribed, which originally included only *D. quadridens*. Also Drechsler (1962) saw such a relationship when he wrote: ‘in its manner of taking prey the fungus displays close parallelism to *Dactylella passalopaga*’, a species here presumed to be the anamorph of *Hyalorbilia inflatula*. Drechsler’s drawing of living conidia shows groups of medium-sized drops which he illustrated also in *D. passalopaga*. These are very probably KOH-sensitve (SCBs), and are quite characteristic of *Hyalorbilia* (see, e. g., Pl. 59).

Ecology. Drechsler collected rotten herbaceous plant material from a grassy area near a lake in subtropical subhumid central Florida, predacious on testaceous rhizopods. The maize-meal-agar plate, in which the fungus finally developed, contained abundant mycelium of the plant pathogen *Pythium ultimum*, to which Drechsler added the collected plant material.

Specimens included. **USA**: **Florida**, ~23 km ENE of Lakeland, Lake Alfred, 40 m, from herbaceous plant material, predatory on *Euglypha laevis*, 12.IV.1959, C. Drechsler (**holotype**, doc. vid.).

Hyalorbilia tenuifusaria (Juan Chen, L.L. Xu, B. Liu & Xing Z. Liu) E. Weber & Baral, in Baral et al., Mycol. Progr. 17 (1–2): 15 (2017) — Pl. 3: f

≡ *Dactylella tenuifusaria* Xing Z. Liu, R.H. Gao, K.Q. Zhang & L. Cao, Mycol. Res. 100(2): 236 (1996), nom. inval., ICN Art. 40.7

≡ *Brachyphoris tenuifusaria* Xing Z. Liu, R.H. Gao, K.Q. Zhang & L. Cao ex Juan Chen, L.L. Xu, B. Liu & Xing Z. Liu, Fungal Diversity 26(1): 124 (2007)

Etymology: named after the shape of the slender, fusiform conidia.
Typification: China, Guizhou, Fanjingshan, forest soil, 25.VI.1994, X.Z. Liu (HMAS 70427, holotype; ex-type culture: CBS 617.95, sq.: DQ494371).

Description: — **TELEOMORPH**: unknown. – **ANAMORPH** (from Liu et al. 1996 & Chen et al. 2007c): brachyphoris-like (isolated from soil {T}). **Conidiophores** 8–67 × 1–4 µm, simple, densely septate, unbranched to strongly branched, conidiogenesis terminal, singly. **Conidia** unbranched, 88–120 × 4–6 µm, fusiform with tapered, filiform ends, straight, (9–)10–13(–14)-septate. **Trapping organs** forming short undifferentiated protrusions ~2–4 × 2–4 µm.

Taxonomic remarks. The capability of *H. tenuifusaria* to trap rhizopods by means of small, apparently adhesive protrusions (Liu et al. 1996, Chen et al. 2007c) supports a relationship with '*Dactylella*' *passalopaga* (?= *H. inflatula*). Since we have never seen such long conidia in any of the *Hyalorbilia* species studied, we assume that *H. tenuifusaria* represents a species of its own. Also Liu et al. (1996) compared it with '*Dactylella*' *passalopaga*, differing in distinctly longer conidia with more septa. The original drawing by Liu et al. shows conidia without contents, which leaves the question open whether they were studied in the living or dead state, while Liu et al.'s and Chen et al.'s photographs (at high magnification) clearly show dead conidial cells.

In the protologue of *Dactylella tenuifusaria* the holotype was given as 'HMAS 70427, CBS 617.95', for which reason the name was considered as invalid (P. Kirk pers. comm.). Chen et al. (2007c) unmistakably cited the single specimen HMAS 70427 as holotype by making the name valid.

Phylogeny. A sequence of the type strain gained by Chen et al. (2007a) comprises ITS (whether it possesses the S1506 intron is unclear) and an unofficial LSU sequence in the CBS database. In our analysis of the ITS region, the strain clustered unresolved in an unsupported clade containing *H. juliae*, together with various environmental isolates from soil and leaf litter from North America, Europe, Australasia, and Africa (Seychelles) (H17–H26), but with an over 20 % distance to any of them (Phyl. 5). In the combined ITS+LSU analysis (Phyl. 6), however, the support of this clade, which we call *juliae-tenuifusaria* clade, was strong (for *H. fusispora* see under that species, p. 400).

Ecology. *Hyalorbilia tenuifusaria* was isolated from soil in a evergreen mountain forest in subtropical humid (winter-dry) southern China.

Specimens included. **CHINA**: **Guizhou**, Fanjingshan, 1770 m, forest soil, predatory on rhizopods, 25.VI.1994, X.Z. Liu (HMAS 70427, holotype, doc. vid.; ex-type culture: CBS 617.95; sq.: DQ494371).

Hyalorbilia brevistipitata Bin Liu, Xing Z. Liu & W.Y. Zhuang, Nova Hedwigia 81: 147, fig. 1 (2005) — Pls 120–121

= *Brachyphoris brevistipitata* (Bin Liu, Xing Z. Liu & W.Y. Zhuang) Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu, Fungal Diversity 26: 120, 128 (2007), nom. inval., ICN Art. 41.5

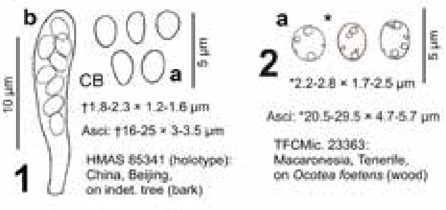


Plate 120. **1–2**: *Hyalorbilia brevistipitata*. – **a**. ascospores; **b**. ascus. – **2** redrawn from photo (see Pl. 121: 2c).

≡ *Dactylella brevistipitata* Bin Liu, Xing Z. Liu & W.Y. Zhuang, Nova Hedwigia 81: 148 (2005)

Etymology: refers to the very short conidiophores and the short apothecial stipes.
Typification: China, Beijing, indet. broad-leaved tree, 24.VI.2002, B. Liu (HMAS 85341, holotype of teleomorph; HMAS 86810 permanent slide culture, holotype of anamorph; ex-type culture: CBS 113946; sq.: AY514636, DQ656699, KT215221, HQ110702).
Misapplied name: Zhuang & Hyde (2001: 185), as *Pithyella* cf. *erythrostigma*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.7 mm diam., 0.08–0.14 mm thick, whitish to pale yellowish when fresh, pale yellowish-beige on drying, translucent, ± round, slightly to medium gelatinous, scattered to gregarious in small groups; disc flat, margin smooth or slightly uneven, not protruding; sessile or with a distinct obconical stipe 0.04–0.2 × 0.05–0.1 mm, superficial. **Asci** *20.5–29.5 × 4.7–5.7 µm {1}, †15.5–25 × 3–4.5 µm {3}, 8-spored, spores */†1–2-seriate, pars sporifera *12.5–15.5 µm long; **apex** (†) hemispherical to obtuse; **base** with short, thick stalk arising from croziers {1}. **Ascospores** *(2–)2.2–2.6(–2.8) × (1.7–)1.8–2.2(–2.5) µm {2}, †(1.5–)1.8–2(–2.3) × (1.1–)1.2–1.7(–1.8) µm {3}, subglobose to broadly ellipsoid(-ovoid); **SBs** 0.2–0.7 µm diam. {2}, globose, peripheral, ± bipolar, (2–)4–7(–10) per spore. **Paraphyses** apically uninflated to slightly clavate, terminal cell *9–20 × 2.6–3.2 µm {1}, †(1.5–)2–3 µm wide {3}, lower cells *6–8 × 2–2.7 µm {1}, sometimes branched at upper septum. **Medullary excipulum** 20–35 µm thick, of dense. slightly gelatinized textura intricata. **Ectal excipulum** at base 60–90 µm thick, at flanks 15–45 µm thick, of thin-walled, horizontally oriented t. angularis-prismatica, slightly gelatinized (common walls *0.5–1 µm thick), cells *13–19 × 5.5–9 µm {1}, †5–15 × 2.5–5 µm {2}, 6–14 µm thick at margin, marginal cells *7–17 × 3–6 µm {1}. **Anchoring hyphae** *2.5–3.5(–4) µm wide, wall 0.2–0.3 µm. **SCBs** in marginal excipulum globose; **VBs** in terminal and lower cell medium refractive, elongate. **Exudate** over paraphyses 0.3–0.8 µm thick, ± continuous to cloddy, hyaline. — **ANAMORPH**: brachyphoris-like (data from Liu et al. 2005b, from ascospore isolate {1}). **Conidiophores** reduced, simple, 1.5–5(–10) × 2–4 µm, 1.5–3 µm wide at apex, non-septate, monoblastic or sympodial (with 1–3 additional scars resembling nodules). **Conidia** unbranched, narrowly fusoid, tapering evenly towards the blunt apex and base, usually straight, occasionally slightly curved, especially at the distal end, †23–52 × 3–4 µm, 3–5-septate.

Habitat: lying on the moist ground, on decorticated or corticated, 20–250 mm thick branch and log of *Ocotea foetens* {1}, indet. angiosperm tree {T}, on bark {1} or wood {1}; on very rotten stems of bamboo on or close to old pyrenomycete {1}. **Further associated**: none observed. **Desiccation tolerance**: unknown (probably slightly desiccation-tolerant). **Altitude**: 120–775 m a.s.l. **Geology**: China: volcanic & felsic plutonic rock; Tenerife: volcanic sedimentary deposits, tephritic and phonolitic mafic flows. **Phenology**: II, VI–VII.

Taxonomic remarks. *Hyalorbilia brevistipitata* is characterized by very small, ovoid to subglobose or almost globose ascospores with about 2–10 small, peripheral, ± symmetrically arranged (bipolar) SBs, also by rather small asci, and by a brachyphoris-like anamorph with unbranched conidia. In contrast, the similar *H. erythrostigma* and *H. ulmi* contain a single, distinctly larger, eccentric SB in the living

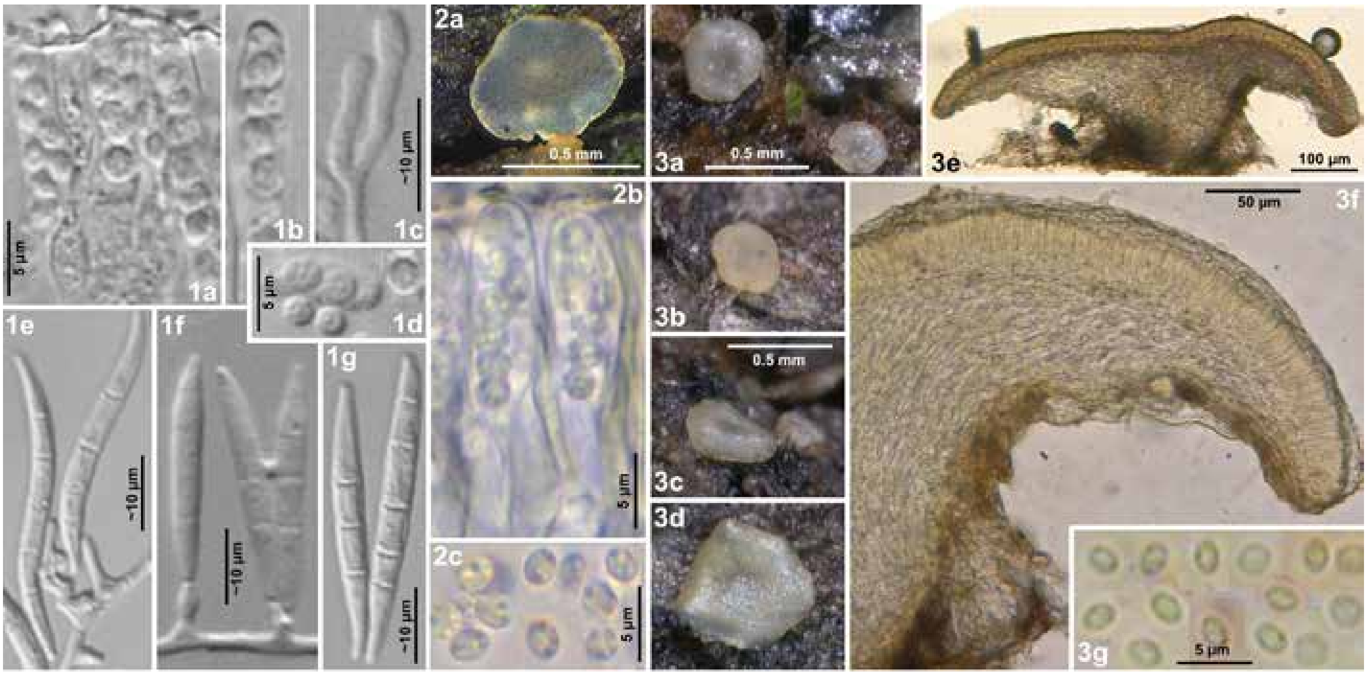


Plate 121. **1–2**: *Hyalorbilia brevistipitata*; **3**: *H.* cf. *brevistipitata*. – **2a**. fresh apothecium, **3a–d**. rehydrated apothecia; **3e–f**. apothecia in median section; **1a–b**, **2b**. asci; **1c**. paraphysis; **1d**, **2c**, **3g**. ascospores; **1e–g**. conidia and conidiophores (in culture). – Living state, except for **1c**, **e–g**, **3e** (in H_2O), asci in **1a–b**, **3f–g** (in KOH). – **1a–g**: from Liu et al. (2005b, DIC), **2a–c**: phot. L. Quijada (p.p. from Quijada et al. 2014a). — **1a–g**. HMAS 85341 (holotype): China, Beijing, on indet. tree; **2a–c**. TFC Mic. 23363: Macaronesia, Tenerife, on *Ocotea*; **3a–g**. H.B. 9276a: Ethiopia, on *Lobelia*.

spores, and the apothecia were mainly found on xeric instead of hygric substrates. *H. erythrostigma* further differs in larger asci and spores and in a trinacrium-like anamorph, and *H. ulmi* in slightly longer and narrower, more ellipsoid-ovoid spores, while its anamorph is unknown.

A collection from Australia mentioned under *H. erythrostigma* has spores very similar in size and shape, but here a single SB could be discerned as faint eccentric region in several spores (Pl. 126: 10).

Besides ascus and spore size, Liu et al. (2005b) separated *H. brevistipitata* from *H. erythrostigma* by flat instead of convex apothecia, and by short instead of long apothecial stipes. However, in the present concept of *H. erythrostigma* the apothecia varied strongly in shape of discs and length of stipes, and also the asci and spores vary to some extent in both size and shape. Therefore, the morphological differences between the two species are much less sharp than the authors believed.

The above description is based on the protologue of both morphs (Liu et al. 2005b), a copy of which can be found in Liu (2006: 27), and on our examination of a slide of the teleomorph from Beijing kindly supplied by B. Liu. The protologue of the teleomorph represents a mixture of the holotype from Beijing and a paratype from Hong Kong on bamboo, reported by Zhuang & Hyde (2001) as *Pithyella* cf. *erythrostigma*.

Liu et al. (2005b) described the spores as 'broadly ellipsoid to almost globose' (Latin diagnosis), while the given size in the English description suggests perfectly globose spores [*1.8–2 × 1.8–2 µm in water, †1.5–1.8 × 1.5–1.8 µm in CB_L]. The given spore size refers to the holotype, whereas spore measurement by Zhuang & Hyde (l.c.), who figured broadly ellipsoid-ovoid spores (though stating 'ovoid to subspherical'), were not included in the protologue. The present examination of a preparation of the holotype (Pl. 120: 1) revealed broadly ellipsoid to ovoid spores and suggests that Liu et al.'s illustration of ± globose living spores on their fig. 1D–E refers to spores seen more or less in top view. Only the upper left spore in fig. 1E (see Pl. 121: 1d) looks broadly ellipsoid and their size can be evaluated as *2.6 × 2.2 µm, while the remaining spores look globose or almost so and measure *2–2.3 × 1.8–2 µm according to the scale. B. Liu (pers. comm.) considered this ellipsoid spore as aberrant. Yet, also those spores inside asci in fig. 1 F–I (Pl. 121: 1a–b) tend to be broadly ellipsoid.

Liu et al. reported a single globose eccentric spore body 0.5 µm diam. in each spore, although on their fig. 1E–F (Pl. 121: 1a–d) the spores appear to contain several small peripheral SBs. Until further collections of *H. brevistipitata* are documented in the living state, we here characterize the living ascospores of this species as consistently multiguttulate due to several peripheral SBs of ~0.3–0.5 µm diam., in contrast to one eccentric SB 0.6–0.8 µm diam. in *H. ulmi*.

The asci in the protologue of *H. brevistipitata* are given as (†)18–25 × 3–3.5 µm, which again appears to refer solely to the holotype, although the few asci seen in the permanent slide were found to measure only †16 × 3–3.5 µm (Pl. 120: 1). In Liu et al.'s (2005b) fig. 1G–M, however, the scale is probably erroneous because the asci would measure †16–18 × 2.5 µm, which is in disagreement with both the description and the scale on their fig. 1F. In the specimen from Hong Kong the asci measured †15–17 × 3–3.8 µm, evaluated according to the scale in Zhuang & Hyde (2001: fig. 7) and the original sketch to this drawing made by a drawing tube (W.Y. Zhuang pers. comm.), although they are given as 19–21 × 3.3–4 µm in their description. Judging from the concordant spore width, the scale appears to be correct, and the ascus length of 19–21 µm could be erroneous, at least asci of that length were not figured.

The specimen from Hong Kong appears to fit the type, but it was only studied in the dead state, therefore, it is unknown whether the living spores contained several or only one spore body. A record from Macaronesia examined in the living state by L. Quijada (pers. comm.) concurs quite well with the holotype in ascus and spore size, though the asci tend to be wider. The living spores consistently contained 2–5(–7) peripheral SBs with a size of 0.2–0.7 µm, sometimes in a bipolar arrangement (Quijada et al. 2014a: fig. 2, Pls 120: 2; 121: 2).

Not included collection. A collection from Ethiopia (Pl. 121: 3) closely resembles *H. brevistipitata* in ascus [†(19–)23–24.5 × 3.2–3.5(–4.5) µm] and spore size [†2–2.2(–2.4) × 1.6–1.8(–2) µm, broadly ellipsoid to ovoid], but the size and number of SBs in the spores is unknown because it was only studied in the dead state.

Anamorph. In pure culture of an ascospore isolate of the holotype of *B. brevistipitata*, Liu et al. (2005b) obtained an anamorph which they named *Dactylella brevistipitata*. In the similar *H. erythrostigma* and *H. multiguttulata*, on the contrary, we presume a trinacrium-like anamorph. Chen et al. (2007c) combined *D. brevistipitata* in *Brachyphoris* and stated that it is similar in morphology to *B. oviparasitica* and *B. helminthodes*. Although the latter two species are parasites of nematodes or fungal spores, tests with nematode eggs and oospores were negative in *B. brevistipitata* (Liu et al. l.c., Chen et al. l.c.).

Some of the scale bars in Liu et al. (l.c.) might be inexact, for instance, the conidia in fig. 2G–H measure 31–44 × 4–4.5 µm according to the scale, while those in fig. 2B measure 29–33 × 3 µm. It appears questionable whether the ex-type strain still exists at CBS, since it does not appear in the database, and also queries for the ITS or LSU region do not show it.

Phylogeny. Sequences were available from the ex-type strain (ascospore isolate 1144 fide X.Z. Liu pers. comm.) of *B. brevistipitata* (SSU, ITS, LSU) and from the not included specimen from Ethiopia (SSU, 5.8S, ITS2, LSU, from apothecia). In the ex-type strain the S1506 intron is absent, while the Ethiopian sequence does not cover the 3-end of SSU and also lacks much of the 5'-end of ITS. The ex-type strain was sequenced by B. Liu (AY514636, DQ656699) and simultaneously by G. Hagedorn (KT215221). Both sequences include the ITS and LSU D1–D2 domain. The LSU was also sequenced by X.Z. Jiang et al. (HQ110702, D1–D3). These rDNA sequences fully concur in the overlapping parts, except that Liu's ITS2 shows many gaps and ambiguities downstream of the motif GGGCACAG, and his LSU 1 insert in the D1 domain, both obviously being sequencing errors.

In addition to the mentioned morphological differences in the teleomorph and anamorph, the available molecular data indicate that *H. brevistipitata* is not closely related to *H. erythrostigma*: in the ITS region the distance lies in the range of ~27–33 % and in the LSU at 11–15 %. Also B. Liu (pers. comm.) found that the two Chinese specimens referred by him to *H. erythrostigma* (one of them was examined in the present study: Pl. 126: 4) strongly differ in the ITS region from the type of *H. brevistipitata*. Even in the 5.8S region 7 nucleotides differ (pos. 64, 83–84, 98, 140, 148, 155), including the signature GAGCGTC at the 3'-end of 5.8S (GAGCGT**G** in *H. erythrostigma*, see Tab. 18). Three further positions in the 5.8S of *H. brevistipitata* (pos. 122, 133–134) differ only from European *H. erythrostigma*.

The specimen from Ethiopia clustered with *H. brevistipitata* in a strongly (ITS) or weakly (ITS+LSU) supported clade (Phyls 5–6) but with 8 % distance in the ITS2, 5 deviating nt and 1 gap in the LSU (D1–D2), and 1 nt in the SSU (V8). In the 5.8S it fully matches both the type strain and *H. oviparasitica*, but no other available sequence of *Hyalorbilia*. In Phyls 6 and S5 (ITS+LSU; LSU) *H. brevistipitata* s.l. clustered with strong support as a sister clade to *H. oviparasitica*. Also Liu et al. (2005b) and Chen et al. (2007c) found that *H. brevistipitata* and *H. oviparasitica* are genetically closely related but different enough to be separated at the species level. *H. brevistipitata* actually differs from *H. oviparasitica* by 12.5–16 % in the ITS region, and the Ethiopian sample even more when comparing the available ITS2 region (for details see under *H. oviparasitica*, p. 411).

In the 99 nt of the V8 region by which SSU sequences of *H. oviparasitica* s.l. overlap with most available orbiliaceous SSU sequences, *H. brevistipitata* (A**CT**ATCCTTGG) differs by 1 nt from *H.* cf. *brevistipitata* (A**CC**ATCCTTGG). Both deviate by 2 nt from *H. oviparasitica* s.l and a majority of *Hyalorbilia* spp. which have A**TA**ATCCTTGG (in *H. tortuosa* A**TA**ATCCTTG**A**), and by 4 nt from *H. erythrostigma* (A**CA**ATCCTT**AA**).

Ecology. *Hyalorbilia brevistipitata* was found on decaying, hygric twigs and branches of broad-leaved trees as well as on rotten bamboo. In all collections the substrate was lying on the moist ground in a wet environment. The apothecia in the holotype grew on bark without a clear connection to a pyrenomycete (B. Liu pers. comm.), whilst in the paratype from Hong Kong they grew on or close to an old pyrenomycete. The collections originate from warm-temperate and subtropical humid (winter-dry) forests in eastern and southeastern China, and from the thermomediterranean humid laurel forest (*Lauro novocanariensis-Perseetum indicae*) in Tenerife, Macaronesia. The sample from the Ethiopian highlands was on a herbaceous stem of *Lobelia* very close to old pyrenomycetes, in a warm-temperate humid, evergreen afromontane forest. Based on the genetic similarity to *H. oviparasitica*, *H. brevistipitata* might also be a parasite on nematode eggs. However, Liu et al. (2005b) did not note any parasitism when testing their culture with nematode eggs (the genus of the used nematode is not stated).

Specimens included. **CHINA**: **Beijing**, **Mentougou**, 23 km WNW of Beijing, Xian Shan (Fragrance Mt.), 450 m, branch of angiosperm tree, on bark, 24.VI.2002, B. Liu (B.L. 6167, HMAS 85341, **holotype** of *H. brevistipitata*, H.B. 7809 ø; X.Z.L. 1144, HMAS 86810 dried culture, **holotype** of *B. brevistipitata*, CBS 113946 ex-type culture, anam. cult.; sq.: AY514636, DQ656699, KT215221, HQ110702). – **Hong Kong**, 8 km SE of Fanling, Tai Po Kau Forest Stream, ~SE of Lai Chi Hang, ~120 m, on indet. pyrenomycete on indet. bamboo, 15.VII.1998, D.Q. Zhou (HMAS 74869 = W.Y.Z. 2447, doc. vid.). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Santa Cruz de Tenerife, Anaga, 3.3 km ESE of Taganana, El Pijaral, 775 m, log of *Ocotea foetens*, on wood, 14.II.2012, L. & C. Quijada (TFC Mic. 23363, doc. vid.).

Not included. **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, Menagesha Suba State Forest, southern part, 2500 m, on stem of *Lobelia giberroa*, 26.III.2010, U. Lindemann (U.L. 0310-17 ø, H.B. 9276a; sq.: KY463701, KT222440).

Hyalorbilia oviparasitica (G.R. Stirling & Mankau) E. Weber & Baral, in Baral et al., Mycol. Progr. 17 (1–2): 15 (2017)

Basionym: *Dactylella oviparasitica* G.R. Stirling & Mankau, Mycologia 70(4): 777 (1978)

≡ *Brachyphoris oviparasitica* (G.R. Stirling & Mankau) Juan Chen, L.L. Xu, B. Liu & Xing Z. Liu, Fungal Diversity 26(1): 79 (2007)

Etymology: named after the ability to parasitize nematode eggs.

Typification: USA, California, Parlier, Sorenson ranch, roots of *Prunus persica*, from eggs of *Meloidogyne* sp., X.1976, G.R. Stirling (BPI 418238 [formerly BPI 71878], holotype, dried culture ['isolate S']; ?ex-type culture in CBS 379.84).

Misinterpretation of *H. oviparasitica*: Smith & Jaffee (2009) = *H.* aff. *multiguttulata* (strain DoUCR50).

Description: — **TELEOMORPH**: unknown. — **ANAMORPH**: brachyphoris-like (data from Stirling & Mankau 1978 and Chen et al. 2007c, from nematodes). **Conidiophores** reduced, simple, 2–10(–

28) × 2.5–3 µm, tapering to 1–2 µm at apex, non-septate, monoblastic or sometimes sympodial (with one additional scar). **Conidia** unbranched, narrowly fusoid, medium tapered towards obtuse apex and truncate base, straight, *(31–)40–60(–65.5) × (2.7–)3.5–5 µm, (4–)6–7(–9)-septate.

Habitat: in soil and nematode cysts, parasitic in nematode eggs, fourth stage juveniles, and females. **Altitude**: -40–+900 m a.s.l.

Taxonomic remarks. *Hyalorbilia oviparasitica* is the type species of the genus *Brachyphoris* and is only known from its anamorph. Because we did not have the opportunity to study this species, we here refer to the descriptions of Stirling & Mankau (1978) and Chen et al. (2007c) (see also Seifert et al. 2011: pl. 195A and p. 217–219). The species differs from the anamorph of *H. brevistipitata* in slightly longer, consistently ± straight conidia.

H. oviparasitica was originally isolated from infected eggs of the nematode *Meloidogyne* from soil in different peach orchards of central California. The conidia in the holotype measured *31–60 × 2.7–5 µm, with (4–)6–7 septa, whereas in the paratypes Stirling & Mankau (l.c.) observed longer conidia up to *51–81 × 3.3–6 µm. Isolate S produced millions of conidia under optimum conditions, whereas isolates K and C showed only few conidia (Stirling ined., thesis, J.O. Becker pers. comm.). Since the conspecificity of these strains was not affirmed by molecular data, we refrained from including the larger measurements in the description. Two strains from Stirling & Mankau's laboratory, which are not exactly identical in the ITS rDNA, exist in official culture collections (ATCC 38908 and CBS 379.84). Whether the latter is an ex-type isolate is not fully certain.

Uncultured DNA isolates of this species were also obtained from juveniles and adult females of *Heterodera schachtii* in sugar beet soil in southern California: at Riverside (DoUCR60) and the Imperial Valley (various UCR numbers, Witte et al. 2014), and from manure treated soil in southern India (NBAII DOP1). Three culture isolates from nematode eggs of *Globodera rostochiensis* were obtained in a potato field in the Netherlands at a single site and day in 1985 deposited at CBS 347–349.85. From all isolates other than *Meloidogyne* no morphological data were available. In fact, all strains obtained from *Heterodera* 'did not produce conidia on any media or conditions we have tested', including the aberrant strain UCR50 mentioned below (J.O. Becker pers. comm.).

Chen et al. examined the authentic Californian isolate CBS 379.84 and the three Dutch CBS cultures, and described the conidia as *40–65.5 × 3.5–5 µm, with 5–9 septa. Contrary to the protologue which gives a conidiophore length of 'rarely more than 2 µm', Chen et al. observed 3–28 µm long conidiophores but figured them scarcely longer than 10 µm. From which culture their photos were taken was not stated and cannot now be clarified (J. Chen pers. comm.).

Type studies. The type strain was preserved as dried culture and slides at BPI (see BPI database). A living culture from '*Meloidogyne* sp. egg masses' was deposited by G.R. Stirling at ATCC 38908 with the remark 'type strain: no' (see ATCC website), and one from 'California, nematode egg' by R. Mankau at CBS 379.84 in 1984 with the remark 'authentic' in the CBS database but 'type' by Chen et al. (2007c) and in GenBank (NG_064136). The history of these two living strains could not be clarified, but it seems probable that also CBS 379.84 was from *Meloidogyne*. The strain from which the sequences AY185771 (ITS) and AY185772 (SSU) were obtained by Yin et al. (2003) was received by J.O. Becker (pers. comm.) from R. Mankau's culture collection but was later lost when an incubator malfunctioned. The perfect match in the ITS region between this lost culture and the ATCC strain, for which ITS and LSU sequences are included at the ATCC website, might suggest that both had the same origin. That ATCC 38908 represents an ex-type strain seems unlikely because of the negative statement at the ATCC website.

Chen et al. (2007c) appears to be in error when stating that the type strain, from which the type specimens at BPI derive, was obtained by R. Mankau in June 1984: in fact it was isolated by G.R. Stirling in X.1976. The database of the US National Fungus Collection at Beltsville (BPI) gives this information, together with the new numbers of the type isolates, which were mentioned by Chen et al., and the corresponding old numbers used in the protologue. Chen et al. considered CBS 379.84 as ex-type culture of *Dactylella oviparasitica*. This strain was actually deposited at CBS by R. Mankau in 1984, according to the CBS database. However, in the BPI database no mention is made of this CBS strain, nor of the ATCC culture.

Phylogeny. Eight ± complete ITS sequences of *Hyalorbilia oviparasitica* were available, which appear to refer to seven different strains (three from a locality in Netherlands on *Globodera rostochiensis*, four from two different regions in California on *Meloidogyne* sp. and *Heterodera schachtii*, and one from India). SSU (V4–V8) exists for one Californian strain (ATCC 38908, on *Meloidogyne*), LSU (D1–D3) for two Californian strains (ATCC 38908, on *Meloidogyne*; CBS 379.84, on ?*Meloidogyne*) and three from the Netherlands (CBS 347–349.85, on *Globodera*). 15 further sequences, obtained from *Heterodera* in the Californian Imperial Valley by Witte et al. (2014), comprise only a large part of 5.8S and a short part of ITS2 (KM250092–KM250106).

The distance among the complete ITS sequences lies at 0–2.5 %, irrespective of whether strains of one or different continents are compared. For instance, the lowest distance of 0–0.5 % is observed between ATCC 38908 from California, CBS 349.85 from the Netherlands, and NBAII DOP1 from India. The highest distance of 2.5 % is noted between the Californian CBS 379.84 and DoUCR60. Between CBS 379.84 and ATCC 38908 the distance is 1.5 %. Variation occurs mainly in the ITS2, whereas in the ITS1 only 1–2 nt differ as a maximum among the seven strains. The 15 incomplete sequences likewise vary somewhat in the short part of ITS2. In the LSU the five sequences were identical.

H. oviparasitica formed with some other taxa the strongly supported *oviparasitica-multiguttulata* clade in all of our analyses (Phyls 5–6, S6). Also the phylogenetic analyses of the ITS region by Liu et al. (2005b) and Yang et al. (2012b) showed that isolates from California and the Netherlands (erroneously 'China' in Yang et al.) are conspecific and clustered as a supported clade sister to *Hyalorbilia brevistipitata*. A distance of 12.5–16 % is observed between *H. oviparasitica* and *H. brevistipitata* in the ITS region. This high distance comes from a strongly deviating ITS1 region (23–26 %; 0.4 % variation within *H. oviparasitica*), whereas the ITS2 differs only by 8–12 % (1–5 % variation within *H. oviparasitica*). The distance between *H. oviparasitica* and *H.* cf. *brevistipitata* from Ethiopia, for which only 5.8S+ITS2 was available, ranges at 15.5–18.5 % in the ITS2. For the distance to *H. multiguttulata* see p. 416.

A separate clade is formed by another Californian culture isolate from *Heterodera schachtii* (DoUCR50, also called

'UCR-50' or 'strain 50'), uploaded under the name *Dactylella oviparasitica* and originating from the same sugar beet field as DoUCR60 (J.O. Becker pers. comm.). This was named '*Dactylella oviparasitica*-like' by Yin et al. (2003) and is referred to as *Hyalorbilia* aff. *multiguttulata* here (see also under *H. multiguttulata*, p. 416). From the same field various further ITS DNA isolates from *Heterodera schachtii* are found in GenBank (DACITS2–DACITS6, Yin et al. 2003), which are identical with DoUCR50 (max. 2 nt or 2 gaps difference; Phyl. 5). The homogeneity of this clade and its distance to *Hyalorbilia oviparasitica* (10.5–14 %) strongly suggests a species of its own.

SSU (V4–V8) was available for 12 strains of *H.* aff. *multiguttulata* (AY123746–57, AY123763). Differences are absent among these sequences and in comparison with the one SSU sequence of *H. oviparasitica*, except that *H. oviparasitica* possesses the S943 intron with 400 nt, but not *H.* aff. *multiguttulata*. Two nucleotides in the overlapping V8 region permit distinction from *H. brevistipitata* (see p. 410).

LSU (D1–D3) was available for one strain of *H.* aff. *multiguttulata* (DoUCR50, EF446019, JQ638669), which differs from both *H. oviparasitica* and *H. brevistipitata* by 2.5–3 % in the D1–D2 domain. The distance between the latter two species is with 0.4 % unexpectedly low (1 nt in D1, 1 nt in D2). Despite the 2.5–3 % distance, *H. oviparasitica* and *H.* aff. *multiguttulata* concur at the two mentioned deviating positions. In the D3 domain *H. oviparasitica* and *H. brevistipitata* differ by 3 nt, and here *H.* aff. *multiguttulata* and *H. brevistipitata* surprisingly fully concur.

Ecology. *Hyalorbilia oviparasitica* was isolated from eggs as well as fourth-stage juveniles and adult females of different nematodes on which it parasitizes. The fungus was able to act as a biocontrol agent by reducing the population density of its prey and establish thereby a nematode-specific disease-suppressive soil (Yin et al. 2003, Yang et al. 2012b). It is so far known from irrigated peach orchards in warm-temperate semiarid central California and from sugar beet fields in subtropical semiarid (hot-summer mediterranean) southern California, from a potato field in oceanic temperate humid Netherlands, and from farm yard manure treated soil in the savannah climate of tropical monsoon-dominated southern India. In the peach orchards it preys on the root-knot nematode *Meloidogyne* sp., in the sugar beet field on the beet cyst nematode *Heterodera schachtii*, and in the potato field on the potato cyst nematode *Globodera rostochiensis*.

Based on the molecular finding that *H. multiguttulata* may occur in soil, it can be speculated that also *H. oviparasitica* is able to produce apothecia on dead plant substrate.

Sequenced specimens. **USA**: **California**, central California, San Joaquin Valley, ~25 km SE of Fresno, Parlier, Sorenson ranch, 100 m, roots of *Prunus persica*, on eggs of *Meloidogyne*, X.1976, G.R. Stirling (isolate S, BPI 418238 [old number BPI 71878], **holotype**, dried culture; BPI 418236, 418237 [old number BPI 71879 for both], **isotypes**, dried culture or slide; conid. isol., doc. vid.); – (?)ibid., on nematode eggs, undated (CBS 379.84, ?ex-type strain, X.Z. Liu 1420, conid. isol.; sq.: AY776168, HQ110703, NG_064136). – 2 km SE of Parlier, Kearney Agricultural Research Station, 105 m, on eggs of *Meloidogyne*, undated (isolate K, conid. isol., doc. vid.). – ?SE of Fresno, Chandler ranch, 95 m, on eggs of *Meloidogyne*, undated (isolate C, conid. isol., doc. vid.). – ibid., unlocalized, on eggs of *Meloidogyne*, undated (ATCC 38908, conid. isol.; sq.: ATCC, AY185771, AY185772). – southern California, Riverside, 4.7 km ENE of Riverside, 2 km WSW of UCR, Agricultural Operations, 300 m, sugar beet field 9E, roots of *Beta vulgaris*, from parasitized females of *Heterodera schachtii*, ~2009, J.I. Yang (DoUCR60, mol. extr.; sq.: JQ638670). – ibid., as uncultured soil fungus (mol. extr., KM250092–KM250105). – Imperial Valley, Brawley, -30–+40 m, various sugar beet fields, from parasitized females of *Heterodera schachtii* (mol. extr.; sq.: KM250092–KM250106). — **NETHERLANDS**: **Gelderland**, Wageningen, Mierenbos, 45 m, on eggs of *Globodera rostochiensis*, 9.VI.1985, D. Hugo (CBS H-3748, H-3749, myc. only; CBS 347.85; sq.: AY514637; CBS 348.85, X.Z. Liu 1536; sq.: DQ494372, HQ110704; CBS 349.85; sq.: DQ494373, MH873576). — **INDIA**: **Karnataka**, Bangalore, 900 m, soil with farmyard manure, V. 2010 (NBAII DOP1, mol. extr.; sq.: JF923815, JX403725).

Hyalorbilia biguttulata Baral, M.L. Wu & Y.C. Su, in Wu et al., Fungal Diversity 25: 239, figs 16–26 (2007) — Pls 122–123

Etymology: named after the two large spore bodies in the ascospores.

Typification: Taiwan, Liouguei, branch of indet. angiosperm, 27.VIII.2005, Y.C. Su (TNM F20071, holotype).

Description: — **TELEOMORPH**: **Apothecia** fresh (0.25–)0.3–0.5(–0.6) mm diam., 0.12–0.15 mm high (receptacle 0.08–0.1 → 0.05 mm), pale yellow-chlorinaceous to cream-ochraceous, translucent, ± round, hardly to distinctly gelatinous, (sub)gregarious; disc flat to slightly convex, margin indistinct, not protruding, smooth; with a very short, broad obconical base, superficial; dry light ochraceous-buff. **Asci** *26–31 × 5–5.8 µm {1}, †21–27(–32) × (3.5–)4–5(–5.7) or (5–)6–7(–7.5) µm {2}, 8-spored, spores (*/†) biseriate, at lower end almost uniseriate, pars sporifera *16–19 µm long; **apex** (†) hemispherical (subconical to slightly truncate); **base** with or without a short and thick stalk, arising from croziers (mostly no perforation seen) {2}. **Ascospores** *(3.3–)3.6–5(–5.7) × (2.2–)2.4–2.7(–2.9) µm {2}, †3.3–5.2 × (2–)2.2–2.7 µm {2}, broadly ellipsoid to very slightly fusoid († also slightly limoniform), homopolar, both ends rounded to obtuse; **SBs** *0.8–1.2(–1.5) µm diam. {2}, globose, 1 at each end, closely attached to wall or at a short distance, with 1(–2) further smaller SBs and 0–3 minute LBs in each half. **Paraphyses** apically slightly (to medium) clavate-capitate, terminal cells *3.5–4.5 µm wide {1}, †19–25 × 2.5–4.5(–5.3) µm {2}, lower cells †5–7 × 1.5–3 µm {2}. **Medullary excipulum**, ~20–50 µm thick, of dense, ± non-gelatinized textura prismatica(-angularis), indistinctly to medium sharply delimited. **Ectal excipulum** of (†) thin-walled to slightly gelatinized, horizontally oriented t. prismatica from base to margin, ~50–70 µm thick near base, cells †10–27 × 8–15 µm

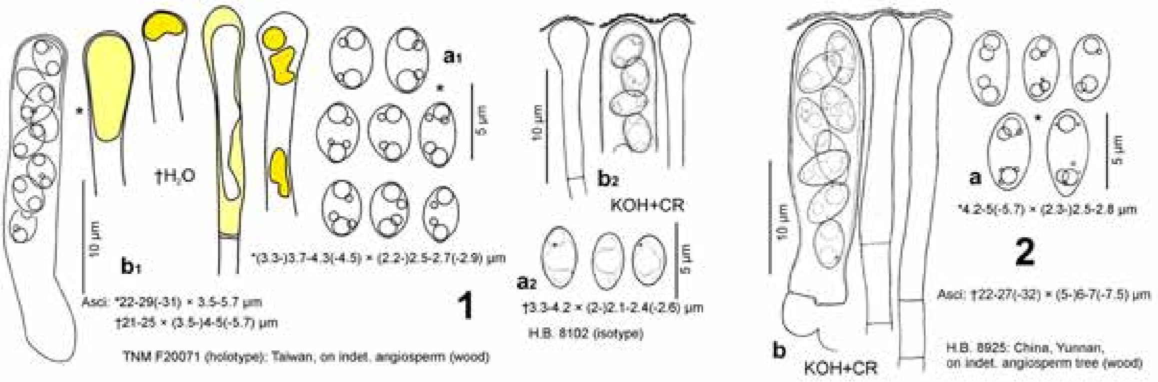


Plate 122. **1–3**: *Hyalorbilia biguttulata*. – **a**. ascospores; **b**. asci and paraphyses. – **1a**$_1$, **b**$_1$: from Wu et al. (2007).

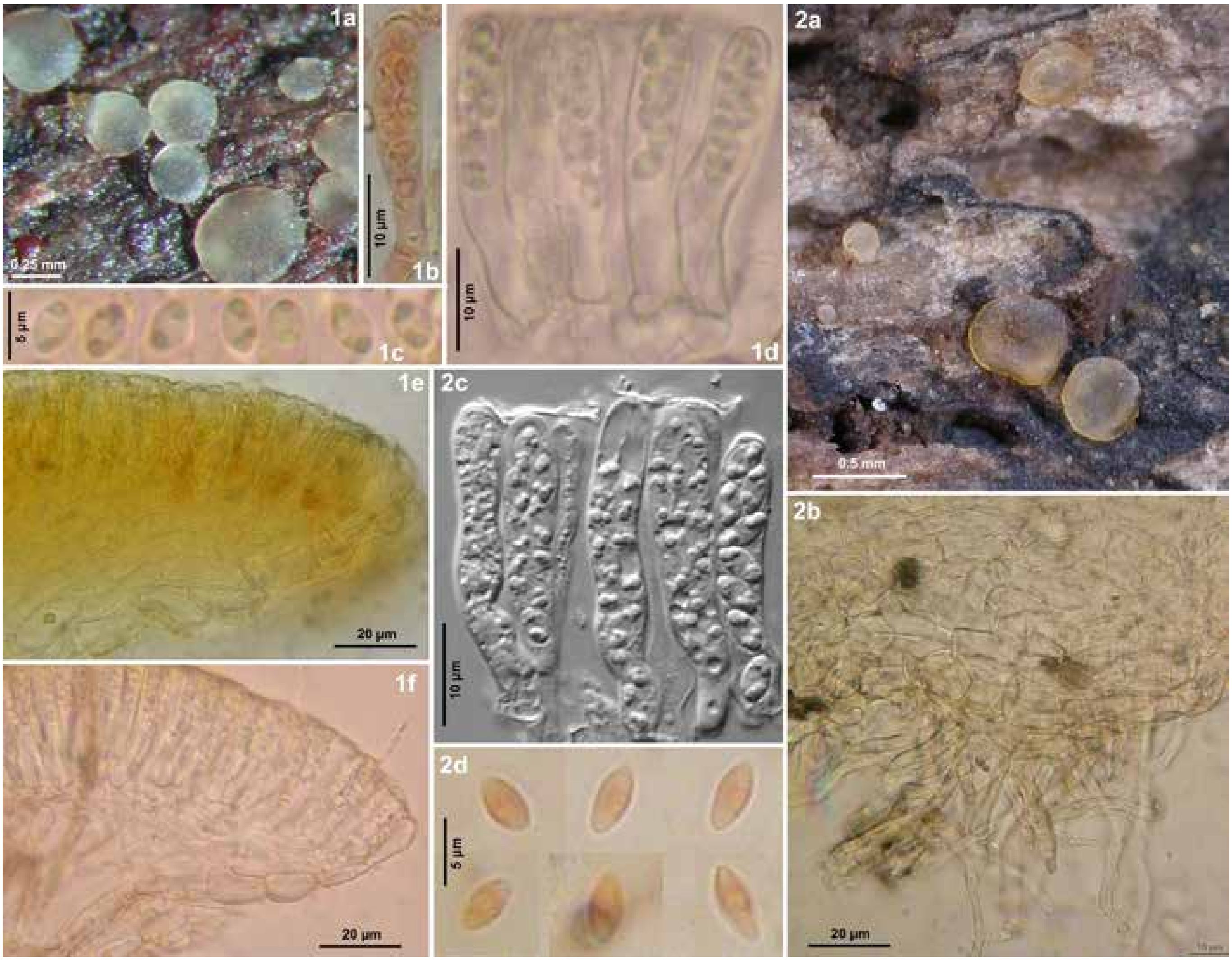


Plate 123. **1–2**: *Hyalorbilia biguttulata*. – **1a**. fresh apothecia; **2a**. rehydrated apothecia; **1e–f**. marginal ectal excipulum in median section; **2b**. ectal excipulum near base, with anchoring hyphae (median section); **1b**, **d**, **2c**. asci and paraphyses; **1c**, **2d**. ascospores. – Living state, except for **1b**, **e**, **2b**, **d**, asci in **2c** (**1e** in KOH+IKI, **2b** in H_2O, **1b** and **2d** in KOH+CR). – **1a**, **c–d**, **f**: from Wu et al. (2007, holotype). – **2c**: phot. H.Y. Su. — **1a–f**. TNM F20071/H.B. 8102 (holo-/isotype): Taiwan, on indet. angiosperm; **2a–d**. H.Y.S. glgs-1/H.B. 8925: China, Yunnan, Baoshan, on indet. angiosperm.

{2}; 10 µm thick near margin, marginal cortical cells †13–18 × (3–)4–7.5 µm {2}, clavate, thin-walled. **Anchoring hyphae** abundant at base, radiating, †2–4.5(–5.7) µm wide, walls 0.2–0.5(–0.7) µm thick {2}. **VBs** in living terminal cells of paraphyses slightly refractive, pale yellow to orange (deeper in dead state), globose to elongate. **Exudate** over paraphyses and marginal excipulum 0.2 µm thick, continuous, finely granular-warted, at margin as distinct small angular warts. — **ANAMORPH**: unknown.

Habitat: collected on the very wet ground, corticated, ~5–20 mm thick branches of indet. broad-leaved trees {2}, on 0.2 mm deep medium to very decayed wood {2}, sometimes on blackened areas, no algae. **Associated**: ?*Capronia* sp. {1}. **Desiccation tolerance**: intolerant, after 5–6 weeks some spores still alive. **Altitude**: 800–1845 m a.s.l. **Geology**: Proterozoic metamorphic rock, Paleogene sedimentary rock. **Phenology**: VIII.

Taxonomic remarks. Among the species with globose to broadly ellipsoid spores, *H. biguttulata* is readily recognized in the living state by ascospores with two large polar SBs, besides 2–3 smaller SBs near to them. In the dead state, however, the characteristic spore contents are only very difficult to discern. The closest relative appears to be *H. multiguttulata*: here the SBs also occur at both spore ends, but they are all of the small size and occur in higher number. Contrary to *H. biguttulata*, the spores of *H. multiguttulata* are almost globose. In an intermediate Chinese specimen included in *H. multiguttulata* (Pls 124: 3; 125: 5) the SBs are less in number and have about the same size as in *H. biguttulata*, but also here the spores are almost globose. *H. erythrostigma* and *H. anonyma* sharply differ in having a single eccentric SB.

Variation. A collection from Yunnan (Pl. 123: 2) is considered here to be conspecific with the type of *H. biguttulata*, although it differs in longer spores and the SBs being less closely associated with the spore ends, also in distinctly wider asci.

Not included collections: A sample from eastern England on *Cytisus* was studied by E. Batten. The spores are only slightly smaller (*2.6–4.2 × 1.8–2.4 µm), but their 1–3 medium-sized guttules were not tested for whether they disappear in dead spores.

Ecology. *Hyalorbilia biguttulata* was found on ± decayed wood and bark of hygric branches of unidentified angiosperm trees. The holotype is from a tropical humid monsoon-influenced climate in southern Taiwan. The collection from Yunnan was in a montane subtropical humid (winter-dry) evergreen broad-leaved forest at the southern end of Hengduan Shan, the southeastern extension of Himalaya. In the type some apothecia grew in close association with a ?*Capronia* and in the Yunnan collection over blackened areas.

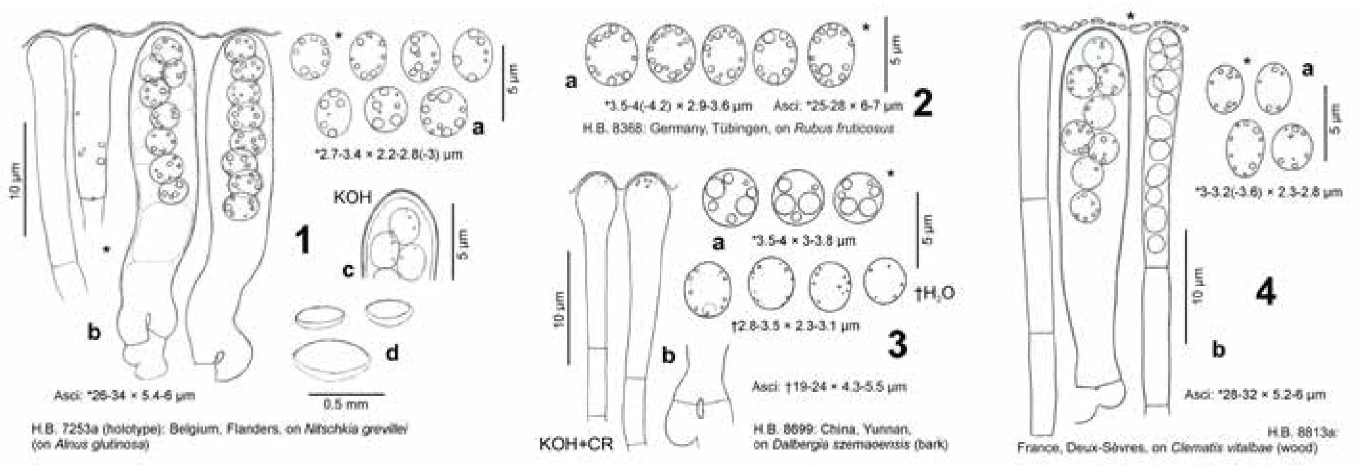


Plate 124. **1–4**: *Hyalorbilia multiguttulata*. – **a**. ascospores; **b**. asci and paraphyses, ascus bases with croziers; **c**. ascus apex; **d**. apothecia (fresh).

Specimens included. **CHINA**: **Taiwan**, **Kaohsiung**, 54 km NE of Kaohsiung, 4.5 km SE of Liouguei, Shanping Natural Education Center, 800 m, branch of indet. angiosperm, on wood, 27.VIII.2005, Y.C. Su (TMUE S050827T2, TNM F20071 **holotype**, doc. vid.; H.B. 8102 **isotype**). – **Yunnan**, **Baoshan**, Tengchong, 52 km SW of Baoshan, 31 km SE of Tengchong, Gaoligongshan, 1845 m, branch of indet. angiosperm, on wood, 4.VIII.2008, X.J. Su, H.Y. Su & X.N. Zhao (H.Y.S. glgs-1, CBCD, H.B. 8925).

Not included. **GREAT BRITAIN**: **East England**, **Suffolk**, 3.7 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 10 m, branch of *Cytisus scoparius*, on wood, 16.IV.2006, S. Francis, vid. E. Batten (E.B. '4667' ø, doc. vid.).

Hyalorbilia multiguttulata Baral & B. Declercq, **sp. nov.**, MB 813457 — Pls 124–125

Etymology: referring to the fact that a number of small spore bodies occur in the ascospores.

Typification: Belgium, Vlaanderen, Wachtebeke, branch of *Alnus glutinosa* (on *Nitschkia grevilli* and on bark), 23.XI.2002, B. Declercq (ex H.B. 7253a, M-0276415, holotype).

Latin diagnosis: *Differt ab* Hyalorbilia erythrostigmate *ascosporis vivis pluria corpuscula refringentia continentibus.*

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated 0.1–0.9 mm diam., 0.08–0.13 up to 0.19–0.26 mm high (receptacle 0.05–0.11 → 0.03–0.07 mm), whitish to pale (yellowish-)chlorinaceous-amber or greyish-cream, ± translucent, round to slightly undulating, slightly gelatinous, scattered to subgregarious in small groups; disc flat (to slightly convex), margin thin or thick, 0–15 µm protruding, smooth; sessile or with a distinct cylindrical stipe 0.035–0.07 × 0.05–0.09 up to 0.2 × 0.3 mm, superficial. **Asci** *(22–)24–34(–37.5) × (4.7–)5–6.5(–7) µm {5}, †(18.5–)20–25(–30) × (4–)4.3–5.3(–5.6) µm {5}, 8-spored, spores *1–2-seriate, pars sporifera *20–23 → 14–18 µm long; **apex** (†) hemispherical to subconical; **base** unstalked, with croziers {8} with or without small perforation. **Ascospores** *(2.5–)3–3.7(–4.2) × (2.2–)2.3–3.5(–3.8) µm {8}, †2.5–3.3(–3.6) × 2–3.1 µm {4}, subglobose to nearly globose, also broadly ellipsoid; **SBs** *0.3–0.4 µm {5} or 0.3–0.8 µm {3} or 0.7–1.5 µm {1} diam., ~2–6 in each spore half, ± globose, often closely attached to wall (here often ± flattened); with a few minute LBs. **Paraphyses** apically uninflated to slightly or medium clavate-capitate, terminal cells *11–22 × 2.2–3.5 µm {2}, †14.5–18 {1} × (2.5–)3–4.5(–5.5) µm {2}, lower cells *9–12.5 × 2–2.5 µm {1}, †6–8 × 1.3–1.5(–2) µm {1}; unbranched at upper septum. **Medullary excipulum** only present in centre, 15–30 µm thick, of dense textura intricata-prismatica-globulosa, non-gelatinized, very indistinctly delimited. **Ectal excipulum** at base of thin-walled to sometimes slightly to medium gelatinized, oriented t. globulosa-angularis, inner parts of ± obliquely upwards oriented t. prismatica, 50–200 µm thick, cells *5–15 {3} or (8–)15–30(–37) {2} × 4–12 µm {4}, at flanks 10–15 up to 35–60 µm thick, of horizontal t. prismatica(-globulosa), cells */†7–22 × 4–10 µm {3}, thin-walled; 10–15 µm thick near margin, marginal cortical cells cylindrical, *6–12 × 3.5–5 µm {1}, †8–10 × 2.5–4 µm {2} or †4.5–12 × 4.5–6.5 µm {1}, or clavate-pyriform, */†10–18 × 5–8 µm {3} (6–10 µm wide in surface view), thin- or firm-walled. **Anchoring hyphae** sparse to abundant, */†2–4(–5) µm wide (at insertion up to 5–7 µm), walls 0.2(–0.3) µm thick {6}. **VBs** globose to angular, low- to medium refractive {1}, also absent. **Exudate** over paraphyses 0.2(–0.3) µm thick, continuous (smooth to slightly rough), or 0.3–0.7(–1.2) µm thick, cloddy, very pale chlorinaceous; over margin and flanks finely punctate to cloddy, hyaline to pale yellow. **— ANAMORPH**: unknown (but see below).

Habitat: lying on shady, moist ground {2} or collected 1–1.8 m above the ground {2}, on corticated or decorticated, 1–5 cm thick branches of *Alnus glutinosa* {1}, *Carpinus betulus* {1}, *Clematis vitalba* {1}, *Dalbergia szemaoensis* {1}, *Populus* sp. {1}, *Ulmus* sp. {1}, indet. angiosperm {1}, stem of *Rubus fruticosus* agg. {1}, on bark {3} (periderm & bast, also on inner surface) and wood {3}; on rotten *Fomes fomentarius* {1}, living mature perithecia of *Nitschkia grevillii* {1}, old stroma of *Diatrype* sp. {1}; wood up to 5 mm deep very decayed and furrowed, with beetle galleries, sometimes on dark brown detritus, also on scar area or broad clefts of periderm, strongly greyed, ± algae-covered. **Further associated**: *Calycina* sp. {1}, *Eutypella quaternata* {1}, *E. scoparia* {1}, *Hyalorbilia japonica* {1}, *Hypnum cupressiforme* {1}, *Karstenia rhopaloides* {1}, *Lophiostoma compressum* {1}, *Orbilia binchuanensis* {1}, *O. breviaristata* {1}, *O. clavuliformis* {1}, *Physcia* sp. {1}, *Porella platyphylla* {1}, *Pyrenopeziza rubi* {1}, *Tremella* sp. {1}. **Desiccation tolerance**: some mature asci still viable after 2 weeks, basal excipular cells and spores after 5 months. **Altitude**: 8–452 m a.s.l. (Europe), 1850–2700 m (southern China). **Geology**: Cambrian wacke, Devonian-Carboniferous rock, Middle Jurassic calcareous clay, Keuper (Knollenmergel), Cretaceous flysch, Tertiary molasse; mica schist, serpentinite, mafic volcanic rock. **Phenology**: IV–VI, X–XI.

Taxonomic remarks. *Hyalorbilia multiguttulata* closely resembles *H. erythrostigma* in size and shape of the ascospores. The species sharply differs in the presence of several rather small, scattered SBs, all being closely attached to the spore wall. In *H. erythrostigma*, only one large eccentric SB is found in each living spore which is not visibly attached to the spore wall (exceptionally by a fine filum). The close attachment of all SBs in the spores of *H. multiguttulata* was only visible when observing living free spores floating in the medium. Further distinguishing characters between the two species are quite wanting, even in the presumed anamorph. For the differences to the closely related *H. biguttulata* see p. 413. *H. brevistipitata* possesses smaller spores which contain a very similar pattern of minute SBs (Pl. 121: 1a, d, 2b–c).

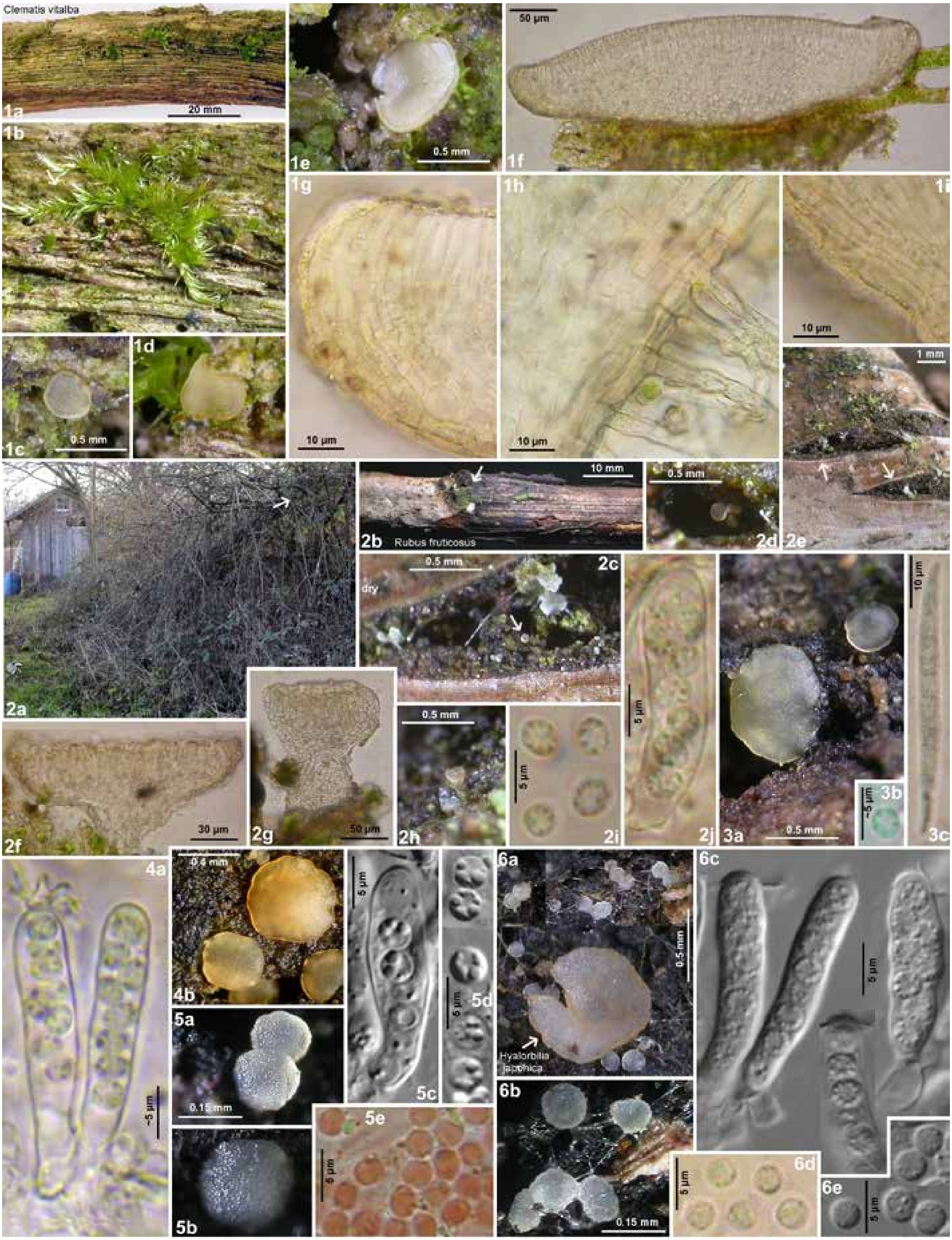


Plate 125. **1–6**: *Hyalorbilia multiguttulata*. – **2a**. old *Rubus fruticosus* growing over *Salix purpurea*; **1a–b**. decorticated xeric branch of *Clematis vitalba*, with *Hypnum cupressiforme* and *Porella platyphylla*; **2b**, **e**. dead corticated xeric stems of *Rubus fruticosus*; **4b**. fresh apothecia; **1c–e**, **2d**, **h**, **3a**, **5a–b**, **6a–b**. rehydrated apothecia; **2c**. dry apothecium; **2g**. lateral view of apothecium (squash mount); **1f**, **2f**. apothecia in median section; **1g**. id., marginal ectal excipulum; **1h–i**. id., ectal excipulum at lower flanks (**1h** with anchoring hyphae); **2i–j**, **3b**, **4a**, **5c–e**, **6c–e**. asci and ascospores; **3c**. conidium from substrate. – Living state, except for **6d–e** (in H_2O); **5e** (KOH+CR); asci in **5c**, **6c**. – **5c–d**: phot. Z.F. Yu (DIC); **6c**, **e**: phot. H.Y. Su (DIC). — **1a–i**. H.B. 8813a: France, Deux-Sèvres, on *Clematis*; **2a–j**. H.B. 8368a: Germany, Tübingen, on *Rubus*; **3a–c**. H.B. 9850: France, Bretagne, on *Ulmus*; **4a–b**. H.B. 9865: Austria, Meidling, on *Populus*; **5a–e**. H.B. 8699: China, Yuxi, on *Dalbergia*; **6a–e**. H.B. 8979b: China, Dali, on indet. angiosperm.

Variation. The seven collections here referred to *H. multiguttulata* differ in apothecial size, ranging from 0.1–0.3 up to 0.4–0.9 mm. Similarly, the thickness of the apothecia strongly varies because of a very different height of the ectal excipulum. The holotype is intermediate concerning apothecial size, but has a rather thin, small-celled ectal excipulum. The collections on *Clematis* and *Ulmus* differ from the others in narrower, more cylindrical marginal cortical cells, the former also in smaller SBs, the latter in rather small spores (*2.5–3 × 2.5–3 µm). Also in the sample on *Fomes* (IVV: 22.XI.2018) the spores were rather small (*2.8–3 × 2.4–2.7 µm) and contained only a few SBs, while the marginal cortical cells were intermediate.

A Chinese specimen on bark of *Dalbergia* (Pls 124: 3; 125: 4) closely resembles European *H. multiguttulata* in its almost globose spores, but differs in fewer, distinctly larger SBs (0.7–1.5 µm diam), also rather large, especially wide spores. Three further specimens from the same locality (7.VI. and 17.VII.2007, on bark of unidentified broad-leaved trees) were not documented in the living state (H. Su pers. comm.). The collection on *Dalbergia* is somewhat intermediate to *H. biguttulata*, from which it differs in much wider, globose spores and not regularly bipolarly arranged SBs. Another Chinese specimen (Pl. 125: 6) has smaller SBs and herein fits well European *H. multiguttulata*. We have included it in the description, although some paraphyses were medium capitate and, therefore, distinctly wider (up to †4–5.5 µm) than found in European material.

Anamorph. A pure culture of *Hyalorbilia multiguttulata* was not obtained in the present study, because the ascospores did not easily germinate on our agar media, and the germinated spores early stopped growing. In two collections we found conidia on the natural substrate near apothecia. In the sample on *Ulmus* (Pl. 125: 3c) a single phragmoconidium was seen (*51 × 3 µm, 6-septate) that resembles conidia of the closely related *H. brevistipitata* or *H. oviparasitica*, whereas in the sample on *Rubus* (Pl. 124: 2) trinacrium-like conidia occurred, some of which are thought to belong to *H. erythrostigma* (Pl. 127: 6). Cultures belonging to the environmental DNA isolate from soil in California (dm2s_a1) have not been obtained, therefore, morphological data of the anamorph is lacking.

Not included collections. Two records from Riverside (California), one cultured, the other only as DNA isolate, were reported by Smith & Jaffee (2009) under the name *Dactylella oviparasitica*. Their molecular data place them closer to *H. multiguttulata*, but the high distance prevents to include them in this species. They are referred to as *H.* aff. *multiguttulata*, because any morphological data has not been obtained.

Phylogeny. An ITS sequence was gained from apothecia of the sample on *Ulmus* (Bretagne, H.B. 9850, Pl. 125: 3, see also IVV). It lacks the S1506 intron and clustered in the strongly supported *oviparasitica-multiguttulata* clade (Phyl. 5), though with 15–17% distance to *H. oviparasitica* and 10.5% to *H.* aff. *multiguttulata*. Two uncultured DNA extracts from Californian soil (dm2s_a1, dm4w_a8) and an unlocalized strain (1070) comprise partial 5.8S and ITS2, the former two also LSU. Two of them deviate from *H. multiguttulata* and from each other merely by 1 nt in the ITS2, which suggests that *H. multiguttulata* occurs also in North America, whereas isolate dm4w-a8 (H15) shows a much higher distance to either of these taxa.

When comparing the 5.8S region, *H. multiguttulata* and *H.* aff. *multiguttulata* concur but deviate from *H. oviparasitica* and *H. brevistipitata* s.l. and any other *Hyalorbilia* at pos. 134 (Tab. 18), and from *H. erythrostigma* at 6 positions. In the LSU (434 nt), *H. multiguttulata* (EF446003) differs from *H. brevistipitata* by ~3% and from *H. erythrostigma* by ~11%. The very high molecular distance to *H. erythrostigma* confirms the high taxonomic importance that spore body characters in living ascospores provide.

Ecology. *Hyalorbilia multiguttulata* was found on rotten bark and wood of hygric branches or logs of *Alnus*, *Populus*, and *Ulmus*, and of a xeric branch of *Clematis* and stem of *Rubus*, in supra- to mesotemperate and mesosubmediterranean humid, atlantic western, and subcontinental central Europe. The holotype was collected on the ground of a wet but drained *Populus-Acer-Alnus* forest plantation with *Urtica*. The two paratypes on *Rubus* and *Clematis* were found 1–1.8 m above the ground, suggesting that *H. multiguttulata* is desiccation-tolerant and has a wide host range. In the holotype, some apothecia grew on perithecia of *Nitschkia grevillii* which, however, did not show any sign of damage to their hymenia. The Serbian samples were on rotten, ± xeric *Fomes* and *Diatrype* on fallen *Carpinus* and *Fagus* branches and logs. The two south Chinese collections were on bark lying on the moist ground, in subtropical humid (winter-dry) evergreen broad-leaf forest. The Californian soil isolate was from a mild-maritime humid coastal area.

H. aff. *multiguttulata* was isolated from *Heterodera schachtii* in a sugar beet field in subtropical semiarid (hot-summer mediterranean) southern California. An improved isolation technique of the fungus was developed, in which soil samples from sugar beet fields are infested by greenhouse-reared juveniles of the nematode, and females are later picked from the roots for DNA extraction (J.O. Becker pers. comm.).

Specimens included. **BELGIUM**: **Vlaanderen**, **Oost-Vlaanderen**, 15 km NE of Gent, 2.5 km SSE of Wachtebeke, Puyenbroeck, 8 m, on *Nitschkia grevillii* and bark of branch of *Alnus glutinosa*, 23.XI.2002, B. Declercq (ex H.B. 7253a M-0276415, **holotype**; B.D. 02083 **isotype**). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 7 km E of Rennes, 2.2 km SE of Cesson-Sévigné, Forgé, 47 m, branch of *Ulmus*, on wood, 24.V.2013, J.P. Priou (J.P.P. 13120 ø, H.B. 9850, anam. substr.; sq.: KT222345). – **Poitou-Charentes**, **Deux-Sèvres**, 13.5 km N of Melle, 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 100 m, branch of *Clematis vitalba*, on wood, 17.IV.2008, S. Helleman (H.B. 8813). — **GERMANY**: **Baden-Württemberg**, Tübingen, 5 km NE of Tübingen, 0.6 km S of Pfrondorf, Obere Mähder, 395 m, stem of *Rubus fruticosus*, 20.XI.2006, H.O. Baral (H.B. 8368a ø). — **AUSTRIA**: **Wien**, 5 km SSW of Wien, SE of Meidling, Wienerberg, 225 m, log of *Populus*, on wood, 29.XI.2013, R. Moosbeckhofer, vid. B. Wergen (H.B. 9865). — **SERBIA**: **Vojvodina**, Fruška Gora, 13 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, W of WWII memorial, 440 m, on *Fomes fomentarius* (on *Fagus sylvatica* log), 22.XI.2018, D. Savić (FG-944, doc. vid.). – 11.5 km S of Novi Sad, 5.7 km NNW of Irig, 452 m, branch of *Carpinus betulus*, on *Diatrype*, 26.IX.2019, D. Savić (doc. vid.). — **CHINA**: **Yunnan**, **Dali**, 42 km NNE of Dali, Jizushan Nature Reserve, 2700 m, branch of indet. angiosperm, on bark, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (H.Y.S. jz-3, CBCD, H.B. 8979b, mixture in M0276443 [type of *O. binchuanensis*]). – **Yuxi**, Tonghai, 35 km SE of Yuxi, ~2 km S of Tonghai, Xiushan Forest Park, ~1850 m, branch of *Dalbergia szemaoensis*, on bark, 7.VI.2007, J.W. Guo & S.F. Li (J.W.G th2-12(2), YMFT, H.B. 8699). — **USA**: **California**, central California, ~30 km WSW of Santa Rosa, Bodega Bay, from soil (dm2s_a1, as *Brachyphoris* sp. 1, mol. extr., non vid.; sq.: EF446003). — **Unlocalized**: from soil (1070, as uncultured *Orbiliales*, mol. extr., sq.: MF482281)

Not included (**O**. **aff**. ***multiguttulata***). **USA**: **California**, southern California, 4.7 km ENE of Riverside, 2 km WSW of University of California, Agricultural Operations, sugar beet field 9E, 300 m, roots of *Beta vulgaris*, isolated from parasitized females of *Heterodera schachtii*, ca. 2003, R. Olatinwo (DoUCR50, myc. only, as *D. oviparasitica*; sq.: AY970525, EF446019, JQ638668, JQ638669). – ibid. (soil from field 9E placed in cups in greenhouse), on females of *H. schachtii* (UCR, DACITS2–6, as uncultured soil fungus, mol. extr.; sq.: AY123746–57, AY123763, AY185766–AY185770).

Hyalorbilia erythrostigma (W. Phillips) Baral & G. Marson [as '(Berk. & Br.) Baral & G. Marson'], Micologia 2000: 44 (2001) — Pls 126–128, Maps 19, 20

≡ *Peziza erythrostigma* Berk. & Broome, Ann. Mag. Nat. Hist., ser. 3, 18: 126, pl. 4 fig. 31 (1866), nom. illegit., ICN Art. 53.1 [non *Peziza erythrostigma* Mont. 1842, ≡ *Octosporella erythrostigma* (Mont.) Döbbeler 2004]

≡ *Lachnella erythrostigma* W. Phillips, Man. Brit. Discomyc.: 254 (1887)

≡ *Dasyscyphus erythrostigma* (W. Phillips) Sacc. [as '*Dasyscypha*'], Syll. Fung. 8: 453 (1889)

≡ *Atractobolus erythrostigma* (W. Phillips) Kuntze, Revis. Gen. Pl. 3: 445 (1898)

≡ *Pithyella erythrostigma* (W. Phillips) Boud., Hist. Class. Discom. Eur: 125 (1907)

≡ *Orbilia erythrostigma* (W. Phillips) Matočec et al. [as '(Berk. & Broome) Boud.'], Öst. Z. Pilzk. 14: 324 (2005), nom. inval., ICN Art. 41.5; nom. illegit., ICN Art. 53.1 [non *Orbilia erythrostigma* (Mont.) Quél. 1886, ≡ *Octosporella erythrostigma* (Mont.) Döbbeler]

?= *Trinacrium angamosense* Matsush., Matsush. Mycol. Mem. 8: 40, pl. 20 figs 839–840 (1995)

Etymology: *erythrostigma*: derived from the pale red colour of the apothecia looking like reddish spots; *angamosense*: named after the type locality, Colonia Angamos (Peru).

Typification: Great Britain, Somerset, Batheaston, *Chaetosphaerella phaeostroma*, on ?*Rosaceae*, 15.I.1859, [no collector,] (K, herb. Broome, holotype of ***Peziza erythrostigma***); Luxembourg, Kockelscheier, branch of *Salix*, on *Diatrype bullata*, 17.VI.2009, G. Marson (ex H.B. 9077a, M-0291773, epitype, designated here, MBT385106; sq.: KY463699, KT222441). — Peru, Colonia Angamos, petioles of indet. *Arecales*, VII.1994, T. Matsushima (MFC 4P479, dried culture, holotype of ***Trinacrium angamosense***).

Misapplied name: Hawksworth & Sivanesan (1975: 109) and Ellis & Ellis (1985: 12), as *Orbilia euonymi*.

Misinterpretation of *H. erythrostigma*: Zhuang & Hyde (2001: 185, as *Pithyella*), = *H. brevistipitata*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.3(–0.4) mm diam., in total 0.05–0.18(–0.25) mm high (receptacle 0.05–0.1 mm), whitish-subhyaline or pale to light cream or chlorinaceous-ochraceous to yellowish-amber throughout, translucent (especially stipe), round (young globose), slightly to moderately gelatinous, very scattered to gregarious; disc slightly concave to mostly flat, finally somewhat convex, margin even, protruding for 0–4 µm, exterior glabrous, stipe lacking {4} or distinct {9}, cylindrical to obconical, 0.03–0.1 mm {8} or 0.1–0.2 mm {T} high, 0.06–0.12(–0.15) mm wide {9}, superficial, rarely ± immersed; dry pale to light yellow-chlorinaceous to golden-amber(-orange), slightly contracted. **Asci** *(21–)24–35(–40) × (3.7–)4–5.3(–5.8) µm {19}, †(18–)21–33(–38) × (3.2–)3.5–4.7(–5) µm {6}, 8-spored (some asci only 6–7-spored {2}, then 1–2 spores larger), spores */†1(–2)-seriate, orientation in all directions, pars sporifera *(11–)13–20 → 10–15 µm long, †16–20 µm {T}; **apex** (†) ± hemispherical, also subconical or subtruncate (only slightly depending on the viewing direction); **base** ± unstalked or with a short, thick stalk, arising from croziers {12} with vertical slits {7} 2–4 µm long, rarely with 3 basal septa (Pl. 126: 6). **Ascospores** *(2.2–)2.5–3.2(–3.5) × (1.7–)1.9–2.5(–2.7) µm {22}, †(2–)2.2–2.8(–3.3) × (1.4–)1.7–2.4 µm {4}, in 6–7-spored asci a few spores *3.5–4 × 2.7–3 µm {1, Pl. 126: 1a right}, subglobose (to broadly ellipsoid), rarely obovoid or almost globose, with a single globose, strongly eccentric **SB** (0.8–)1–1.3(–1.5) µm diam. {13}, very close to one end but not visibly attached; with (0–)1(–2–5) minute **LBs**. **Paraphyses** apically cylindrical or often slightly, rarely ± strongly clavate, terminal cells *8.5–20 × (2.5–)3–4.5(–5.2) µm {4}, †9–16 × 2–5.5 µm {2}, lower cells */†(3.7–)4–8(–11.5) × (1.2–)1.7–2.7(–3) µm {3}, sometimes branched near base or very rarely at upper septum. **Medullary excipulum** 10–50(–80) µm thick, of medium dense, thin-walled textura intricata with a few to many inflated angular-prismatic cells, ± upwards oriented in centre, indistinctly delimited. **Ectal excipulum** at stipe and lower of thin-walled, t. globulosa-angularis to t. prismatica oriented parallel to outside, at flanks and margin of horizontally oriented t. prismatica(-porrecta), rarely t. globulosa(-prismatica), ~30–100 µm thick in stipe, ~15–30 µm thick at lower flanks, cells in stipe and lower flanks *(6–)9–18(–26) × 6–13(–16) µm {4}, †5–8 {2} or 7–19 {2} × (3–)4–8 µm {4}; towards margin 8–13 µm thick, marginal cortical cells *8–15(–22) × (3–)3.5–6.5 µm {3}, †(6–)8–12 × (2.7–)4–6(–7) µm {3}, clavate, thin-walled. **Anchoring hyphae** sparse to ± abundant, */†(1.3–)2–3(–4.5) µm wide {5}, walls 0.2(–0.3) µm thick {4}. Refractive globose **SCBs** in ectal and medullary excipulum at flanks, 2.5–4 µm diam., medium refractive, 1 per cell {H.B. 5641a}, absent near base, not observed in other collections. **VBs** in apex of terminal cells of paraphyses large, globose to ellipsoid or elongate, sometimes divided, ± strongly refractive {8}, 3–10 × 2–3.8(–4.5) µm, in marginal cortical cells, (2–)6–13 × (2–)3–5.5 µm; **LBs** ± sparsely present in some or many paraphyses (in both terminal and lower cells), 0.3–1 µm diam. {4}, in ectal excipulum near base 0.3–1.8 µm diam. {1}; comtaining pale to light golden yellow carotenoids. **Exudate** 0.3–1.2 µm thick, hyaline to pale yellowish, over paraphyses continuous, externally minutely warted {4} or as ± rough tubercules or clods {4}, rarely smooth {1} (especially in KOH), warts KOH-resistant but less distinct; at margin and flanks almost smooth or (towards margin) finely warted, warts small and low {3} or forming large clods {1}. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {4}). **Conidiophores** */†10–20 × 2.3–2.8 µm {2}, 1.4–1.6 µm wide above, ± flexuous-geniculate, unbranched, conidiogenous cells apparently monoblastic. **Conidia** branched (T- to Y-shaped, 2-armed), arms of ± similar length, exceptionally asymmetrical, moderately curved downwards, ends pointing slightly upwards to downwards; Peru: †33 × 24 µm, stipe 28 × 2.2 µm, 4-septate, arms 12 × 2.4 µm, 2-septate{1}, Europe: */†19.5–29 × 15–24.5 µm, stipe */†14.5–27 × 2–3 µm, 1–4-septate, arms */†7.5–12 × 1.8–2.3 µm, 0–2-septate {3}.

Habitat: collected either on moist or dry ground or mostly 0.1–2 m above the ground, on ± corticated, rarely decorticated, slightly to strongly decayed, 2–40 mm thick twigs and branches (rarely thick trunks) of *Clematis vitalba* {3}, *Cornus* sp. {1}, *Corylus avellana* {1/1}, *Crataegus monogyna* {1}, *Cytisus scoparius* {3}, *Fagus sylvatica* {1}, *Ficus carica* {1}, *Geijera parviflora* {1}, *Hydrangea macrophylla* {1}, *Ilex aquifolium* {1}, *Koelreuteria paniculata* {1}, *Pistacia lentiscus* {1}, *Prunus lusitanica* subsp. *hixa* {1}, *P. spinosa* {2}, *Quercus* sp. {5}, *Q. rotundifolia* {1}, *Q. rubra* {1}, indet. ?*Rosaceae* {1}, *Robinia pseudoacacia* {1/2}, *Rubus ulmifolius* {1}, *Salix* sp. {1/1}, *S. caprea* × *cinerea* {1}, *S. cinerea* {1}, *Sambucus nigra* {1}, *Sophora microphylla* {1}, *Tilia* sp. {1}, *Ulex europaeus* {1}, *Ulmus* (?)*minor* {1}, indet. angiosperm {3}, on medium to strongly detached bark {15} (periderm and bast) and wood {7}; petiole of *Arecales* {1}, stem of *Sambucus ebulus* {1}, frequently fungicolous: on slightly to strongly decayed fruitbodies of *Annulohypoxylon* sp. {1}, *Bionectria ralfsii* {1}, *Chaetosphaerella phaeostroma* {T}, *Cosmospora* sp. {2}, *Diaporthe* sp. {1}, *Diatrypaceae* {2}, *Diatrype* sp. {2}, *D. bullata* {3}, *D.* ?*stigma* {1}, *Diatrypella* sp. {1}, *D.* ?*favacea* {1}, *D. quercina* {2}, ?*Tremellales* {2}, *Eutypa* sp. {1}, *Eutypella tetragona* {2}, *E. caricae* {1}, *E. leprosa* {1}, *Exidia recisa* {1}, *Jackrogersella minutella* {1}, *Peroneutypa scoparia* {2}; green algae absent to abundant on periderm. **Further associated**: *Capronia nigerrima* {1}, *Cosmospora* spp. {2}, *C. episphaeria* {1}, *Diatrype bullata* {1}, *Diatrypella quercina* {1}, *Eutypa* ?*lata* {1}, *Hyalorbilia orbiliicola* {2}, *H. rotifera* {2}, *H. subfusispora* {2}, *H. ulicicola* {1}, *Hyaloscypha intacta* {1}, *Mollisia cinerea* {1}, *M. prunicola* {1}, *Nectria magnusiana* {1}, *Olla scrupulosa* {1}, *Orbilia* ?*cejpii* {1}, *O. comma* {1}, *O. quaestiformis* {1}, *O. subclavuliformis* {1}, *O. subtrapeziformis* {1}, *Polydesmia pruinosa* {1}, *Proliferodiscus pulveraceus* {1}, *Unguiculariopsis* ?*rehmii* {1}, *Xerombrophila crystallifera* {1}, foliose and fruticose lichens (*Physcia* etc.), acro- (*Orthotrichum*) and pleurocarpous mosses and foliose liverworts. **Desiccation tolerance**: fully viable for up to 1 month, after 4 months some conidia and basal cells of paraphyses still alive. **Altitude**: 2–1410 m a.s.l. (Europe), 150–4350 m (Peru), 450–800 m (SE Asia). **Geology**: Cambrian silt & wacke, Ordovician, Devonian & Carboniferous schist, silt & sandstone, Keuper (marl & sandstone), Lower & Upper Jurassic and Cretaceous marl-, sand- & limestone,

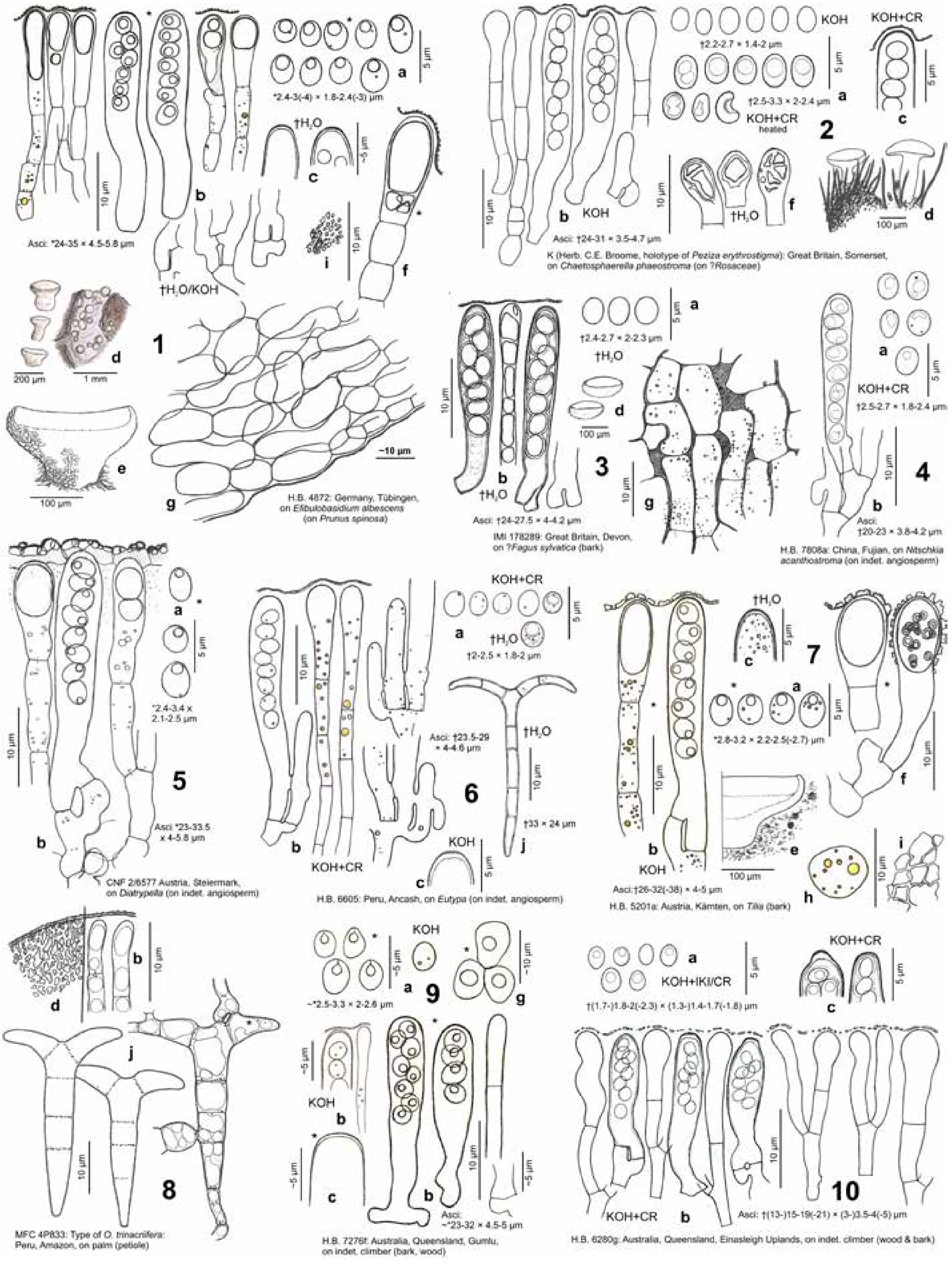


Plate 126. **1–3**, **5–7**: *Hyalorbilia erythrostigma*; **9**: *H.* cf. *erythrostigma*; **4**, **8**, **10**: *H.* aff. *erythrostigma*. – **a**. ascospores (in **2a** lower right spore collapsed); **b**. asci and paraphyses, ascus bases with croziers; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. marginal cells of ectal excipulum (right cell in **7f** with damaged VB that formed strongly refractive drops or rings); **g**. ectal excipulum at flanks in median section (**1**) or external view (**3**, here with scattered warts on wall surface); **h**. ectal excipular cell near base with yellow LBs; **i**. warted (**1**) to cloddy (**7**) exudate on ectal excipulum; **j**. conidia from substrate (**6**) or pure culture (**8**, right conidium germinating; conidia could instead be a contamination by an *Orbilia* with trinacrium incurvum-like anamorph). – **5**: del. N. Matočec, **8j** two left conidia: del. Matsushima (1995).

Tertiary molasse, Quaternary marl, clay, silt & sand, travertine; ortho-plagioclase, granite, basalt. **Phenolgy**: throughout the year (long-lived).

Phenology of *H. erythrostigma* within Europe											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
7	6	4	7	2	3	4	2	4	5	3	3

Taxonomic remarks. *Hyalorbilia erythrostigma* is characterized by small, subglobose ascospores with a single, eccentric, globose, comparatively large SB, and by minute, subhyaline to pale cream or yellowish, often stipitate apothecia growing on ± decayed pyrenomycetes, jelly basidiomycetes, or plant substrate. The morphologically very similar but ecologically different *H. orbiliicola* grows parasitically on the margin of *Orbilia* apothecia and mainly differs in much shorter, ± globose to subglobose VBs in paraphyses and marginal cells. However, molecular data indicate that *H. erythrostigma* is still heterogeneous.

H. erythrostigma may also be confused with *H. anonyma*, *H. brevistipitata*, *H. biguttulata*, and *H. multiguttulata*. *H. anonyma* merely deviates in a few gradual characters and is, therefore, here only tentatively separated at the species level. *H. brevistipitata* differs in smaller spores that contain several small peripheral SBs per spore, and in unbranched conidia. Also *H. biguttulata* and *H. multiguttulata* differ in the contents of the living spores, with either two large or several small SBs, respectively. From dead material the latter three species can hardly be distinguished, although the difference in spore contents is highly consistent and striking in well-developed living specimens. Therefore, the distinction at the species level is justified. Since the protologue of *Peziza erythrostigma* is devoid of vital characters, the identity of the holotype could only be resolved from the presence of remnants of SBs in the dead spores, which were discerned as very faint, eccentric, transparent regions (Pl. 126: 2a lower row).

In order to fix the name, a specimen from Luxembourg on *Diatrype bullata* on a *Salix* branch (ex H.B. 9077a, Pl. 127: 5), from which a sequence was gained, is herewith designated as **epitype** of *H. erythrostigma*.

Variation. Among the collections here referred to *H. erythrostigma*, some variation especially in size and length/width ratio of ascospores and asci, size of SBs, and length of apothecial stipes was noted. Yet, no reliable correlation was discovered between apothecial micromorphology and the inhabited substrate (pyrenomycetes, basidiomycetes, angiosperm substrate). Exceptionally narrow asci (*3.9–4.1 µm, †3.2–3.8 µm) were measured in the samples from Vizcaya and Tenerife (on pyrenomycetes), and in that from Tenerife spore size was with *2.2–2.5 × (1.5–)1.7–2.1 µm at the lower range (IVV: 14.IX.2014). In the holotype on *Chaetosphaerella phaeostroma*, variation in spore size was noted; however, this might originate from different preparation methods (unheated KOH vs. heated KOH+CR, Pl.126: 2a).

Based on the few DNA data from Europe, samples on bark and wood possibly belong to a species different from those on pyrenomycetes. Between two samples from Luxembourg (on *Diatrype* on *Salix*, epitype, IVV: H.B. 9077a; on *Clematis* bark, IVV: G.M. 2017-11-19.4) a rather high ITS distance is observed (see below), correlated with a different SB size (1–1.5 µm vs. 0.8–1 µm diam.), although the spores are of equal size (*2.5–3 × 2–2.4 vs. *2.7–3 × 2–2.2 µm, respectively). However, similarly small SBs (0.8–1.1 µm) have been observed in two Austrian samples on *Tilia* bark and *Diatrypella* (Pl. 126: 5, 7).

In the holotype the apothecia showed the longest and narrowest stipes (Pl. 126: 2d), unlike most of the other specimens studied in which the stipes were either shorter and wider, or ± absent. Yet, the presence and length of stipes might depend on the structure of the substrate: no distinct stipes are formed when growing on naked wood and bark, while the long stipes in the holotype appear to be due to growth among the dark setae of *Chaetosphaerella*. Distinct stipes of about the same height and width have mainly been seen in collections on stromatic pyrenomycetes, but sometimes also on naked wood.

The epithet '*erythrostigma*' and the remark 'pale red' in the protologue misleads to imagine a red discomycete. However, all recently collected apothecia were rehydrated nearly hyaline to light chlorinaceous-cream, and dry yellowish(-orange). Also in the examined holotype the apothecia were pale yellow when rehydrated and golden yellow-amber when dry.

Not included collections. Two Australian specimens are not included in the description. One was on an unidentified climber (Pl. 126: 9) and had comparatively large spores (*2.5–3.3 × 2–2.6 µm) with SBs visibly attached by a short filum, and the croziers were without perforation (here no associated conidia were seen). A more abundant sample which differs in smaller spores was only studied in the dead state; the associated conidia were small and ± symmetrical (Pls 126: 10; 128: 3). In a few spores a single SB could be discerned as a faint eccentric region. From *H. ulmi* this sample differs in shorter, more subglobose spores and in larger apothecia, and from *H. brevistipitata* in spore guttulation, although this feature is very difficult to assess in dead spores. Vital studies on further collections from Australia are necessary in order to clarify spore contents and species limits in this group, and to find out whether conidia with asymmetric arms growing on *Orbilia* spp. belong to a species different from European *H. orbiliicola*.

Records of *H. erythrostigma* from eastern Asia were reported by Liu (2006, Fujian, Pls 126: 4; 128: 1), Guo et al. (2014b, Yunnan and Zhejiang), and Ekanayaka et al. (2018, Thailand). Liu's two samples on *Nitschkia acanthostroma* have short-stalked apothecia of 0.1–0.2 mm diam., rather short asci (†16–22 × 3.6–3.8 and 20–23 × 3.8–4.2 µm), and spores of †2.2–2.6 × 1.8–2.4 and 2.5–2.7 × 1.8–2.4 µm (Liu 2006 and present study). Guo et al.'s three samples (on *Dalbergia* bark, sometimes on black fungi) have sessile to short-stipitate apothecia 0.1–0.3 mm and spores *2.5–3.3 × 2–2.3 µm with large eccentric SB. Ekanayaka et al.'s sample (on *Annulohypoxylon*) was described with apothecia 0.38–0.43 mm diam. with a prominent stipe and rather small spores (†1.7–2.3 × 1.6–2.2 µm), whereas ascus size (†30–33 × 3–3.5 µm) fits *H. erythrostigma*. Because of strong deviations in the DNA data, we refrained from including southeastern Asian collections in the description.

For two collections from South America (Peru), Matsushima's *Orbilia trinacriifera* and *Trinacrium angamosense*, see under Type studies and Anamorph, respectively.

Anamorph. Only a few detached conidia of the presumed trinacrium-like anamorph could be observed on the natural substrate (pyrenomycetes) in three samples (Peru: Pl. 126: 6; Luxembourg: Pl. 127: 5d; Spain: IVV: 27.VII.2017). This anamorph can hardly be distinguished from that of *H. orbiliicola*. In a German sample on *Rubus* (Pl. 127: 6) very similar conidia were observed near apothecia of *H. multiguttulata*, and we assume here that these conidia belong to *H. erythrostigma*, because *H. multiguttulata* more probably

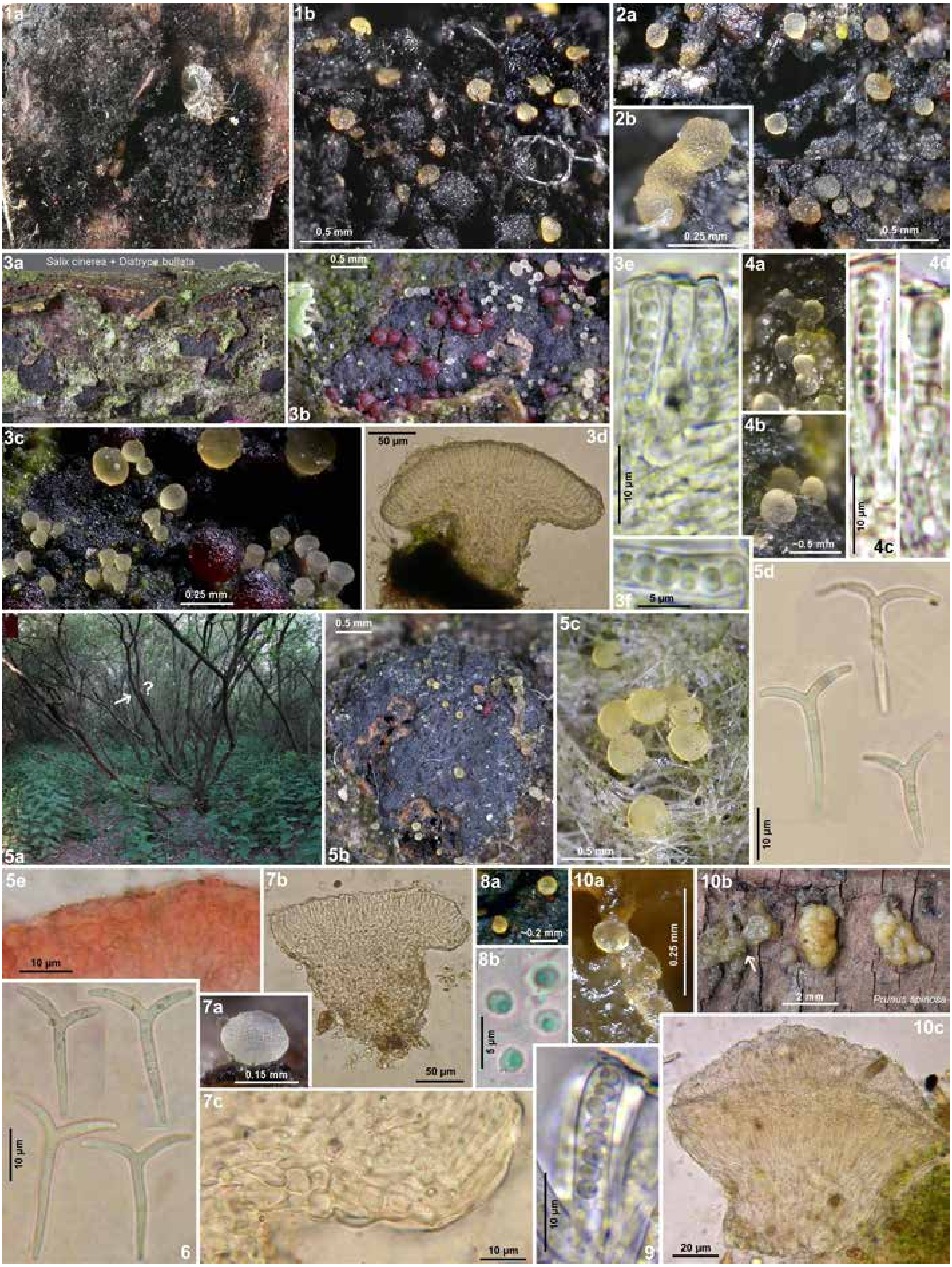


Plate 127. 1–10: *Hyalorbilia erythrostigma*. – **5a**. *Salicetum* with *Urtica* (same site as Pl. 130: 1); **1a**. bark with *Chaetosphaerella phaeostroma* (dry); **1b**, **2a–b**, **3a–c**, **4a–b**, **5b–c**, **7a**, **8a**, **10a–b**. rehydrated apothecia growing on *Sordariomycetes* or *Sebacinales*; **10c**. apothecium in lateral view (squash mount); **3d**, **7b**. apothecia in median section; **7c**. id., ectal excipulum at margin and flanks; **5e**. margin in top view; **3e**, **4c**, **9**. asci; **4d**. marginal paraphysis; **3f**, **8b**. ascospores; **5d**, **6**. conidia from substrate. – Living state, except for **5e** (in CR); **7b–c**, **10c** (in KOH), lower left conidium in **5d**. – **4a–c**: phot. E. Rubio; **8a–b**: phot. J.P. Priou. — **1a–b**. K (herb. Broome, holotype): Great Britain, Bath, on *Chaetosphaerella phaeostroma* (on ?*Rosaceae*); **2a–b**. H.B. 6605: Peru, Cordillera Blanca, on *Eutypa* (on

possesses phragmoconidia and *H. orbiliicola* so far never occurred parasitic on *Hyalorbilia* apothecia. No conidiophores could be seen in any of these samples. In those from Peru and Spain the sparse conidia had 4-septate stipes, a feature so far not observed in *H. orbiliicola*, whereas in those from Luxembourg and Germany they had 2–3-septate stipes as in *H. orbiliicola*. In the sample from Luxembourg on *Diatrype*, *H. orbiliicola* on *O. eucalypti* occurred at a distance of ~10 cm on the same *Salix* branch, nevertheless, the figured conidia (Pl. 127: 5d) were found near apothecia on *Diatrype*.

Trinacrium angamosense Matsush., described from Peru on palm petioles (Pl. 22: b), very probably belongs in the *H. erythrostigma* aggregate, but its synonymy with *H. erythrostigma* or *H. orbiliicola* is uncertain. Also *Trinacrium parvisporum* (see Pl. 22: c), described by Matsushima (1987) from basidiocarps of *Tremella* in Taiwan, could be a synonym of *H. erythrostigma*, although the two arms often show some asymmetry.

In the not included small-spored Australian collection on indet. climber (Pl. 126: 10) a few rather small conidia (†14–18 × 11–22 µm) were observed on the substrate close to the presumed teleomorph (Pl. 128: 3j). In one conidium the arms are downwards curved, whereas in others they are straight or curved upwards (not shown); however, this depends on which branch is considered to be the stipe. A mixture of different *Orbilia* spp. was observed in this sample (*O. mammifera*, *O. neocomma*, *O. paracaudata*, *O. scandens*, *O. subfabacearum*), and the connection between them and the different observed anamorphs was difficult to assess.

Nomenclature and type studies. ***Peziza erythrostigma*** Berk. & Broome is a later homonym of *P. erythrostigma* Mont. and thus illegitimate. Phillips (1887) was the first to transfer Berkeley & Broome's epithet to another genus in which there is no earlier competing homonym. Therefore, Phillips' combination must be taken as a nomen novum based on the same type as Berkeley & Broome's illegitimate name (Art. 58.1, Turland 2018).

The holotype from Batheaston (Somerset) was described and figured with convex apothecia and rather long, mostly curved stipes composed of large prismatic cells (Berkeley & Broome 1866). Clearly, the illustrated individual cells are macroscopically only visible when using the strong magnification of a compound microscope. Cooke (1871) and Phillips (l.c.) merely copied the protologue. Cooke's statement (in Phillips) that the fungus is hairy must be an error.

In the holotype in K, Korf & Zhuang (1987) found the asci slightly larger [†27–33(–40) × 3.7–5 µm] than in the present study of the same specimen, whereas the given spore size (†2–3.5 × 1.8–2.5 µm) concurs very well. Spore shape in *H. erythrostigma* was always described and figured as subglobose or broadly ellipsoid (Berkeley & Broome l.c., Phillips l.c., Dennis 1972: 473, Korf & Zhuang l.c., present study). The spores were always completely smooth (Pl. 126: 2a) in concordance with Korf & Zhuang (1987) who stated that they are not distinctly marked, unlike the type species of *Pithyella* which has globose warted spores.

When Matsushima (1995: pl. 20 fig. F-841, pl. 21 figs F-842–844, pl. 34 figs P-335–337, pl. 35 figs P-338–340) described ***Orbilia trinacriifera*** from palm leaves in Peru, he obviously overlooked the strong similarity with *H. erythrostigma*. The type collection was reexamined from a living culture kindly sent by T. Matsushima in 1996. This contained many overmature *Trinacrium* conidia (Pl. 126: 8j) and densely gregarious, living, immature apothecia of 0.1–0.15 mm diam. with excipulum and paraphyses covered by a warted exudate (Pl. 126: 8b, d). During further incubation the apothecia did not produce asci and ascospores. The microfeatures (strongly gelatinized apothecia, small angular warts of the exudate, excipulum of horizontal t. prismatica) clearly refer the species to the genus *Hyalorbilia*. The protologue describes the ectal excipulum of t. globulosa (Pl. 128: 2a), a feature which was also seen once in a European specimen of *H. erythrostigma* (Pl. 127: 7c).

A micrograph of the hymenial elements provided by Matsushima (l.c., pl. 35 fig. 338; see Pl. 128: 2b) shows living mature asci which contain living subglobose spores with large globose eccentric SBs. Ascus size evaluated from this plate is about *24–26 × 4 µm and spore size *2.5–2.8 × 1.7–2 µm, with SBs 0.9–1.2 µm diam. Another photo (l.c., pl. 34 fig. 337) shows free, dead spores without SBs. Different photos in his electronic publication (Matsushima 2005) show living spores inside dead asci. SB size can here be evaluated as 1–1.3 µm diam. when taking the scale bar as 10 µm instead of the erroneous 20 µm. In the protologue the asci are given as 23–30 × 2.5–4 µm, and the spores as uniguttulate, 2–3 µm, with a length/width ratio of 1:0.7–1:0.8, which means a spore width of 1.5–2.3 µm. Obviously, ascus dimensions in the protologue include also dead asci. In ascus and spore width this specimen lies at the lower end of the range of *H. erythrostigma* and *H. orbiliicola* though fitting well these species.

The anamorph obtained by Matsushima (1995) in culture differs from that of European *H. erythrostigma* and *H. orbiliicola* in distinctly larger conidia with markedly wider arms and much wider stipes (Pl. 126: 8j left), which suggests that the conidia studied here from the living type culture were not secondarily inflated due to an overmature stage (Pl. 126: 8j right). Matsushima isolated his strain from leaves, perhaps from conidia growing on them but this was not stated, while the described apothecia and conidia developed in his agar culture. Since *H. orbiliicola* grows parasitic on apothecia of *Orbilia* spp., it cannot be excluded that the trinacrium-like conidia reported by him belong to a species of *Orbilia* that served as the host of *H. orbiliicola* or closely related species. The studied isolate would then be a mixture of two orbiliaceous species and would require lectotypification, while the true anamorph of *O. trinacriifera* (?= *H. orbiliicola*) could be *Trinacrium angamosense*, which was described from the same region and substrate (Peru, Colonia Angamos, palm petioles). On the other hand, the shape of the conidia described for *O. trinacriifera* fits well the *H. erythrostigma* aggregate, except that much wider conidial stipes [27–40 × 4.5–6 µm, (2–)3–4(–5)-septate] and arms (7–13 × 3–5 µm, 1-septate) suggest a species of its own.

When Matsushima (1995) described *O. trinacriifera*, he cited a '*Trinacrium* sp. MFC-6700' previously reported by him from Taiwan (Matsushima 1980). This *Trinacrium* he apparently considered as conspecific with that obtained in the *O. trinacriifera* culture, although it has longer, more downwards curved arms. Later, Matsushima (1993) described the new

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indet. angiosperm); **3a–f**. H.B. 8960a: Luxembourg, Kockelscheier, on *Diatrype bullata* (on *Salix*); **4a–d**. E.R.D. 4771: Spain, Asturias, on indet. pyrenomycete (on *Hydrangea*); **5a–e**. H.B. 9077a (epitype): Luxembourg, Kockelscheier, on *Diatrype bullata* (on *Salix*); **6**. H.B. 8368b: Germany, Tübingen, on *Rubus*; **7a–c**. H.B. 6908a: Belgium, Arlon, on *Sambucus* (wood); **8a–b**. J.P.P. 26042: France, Bretagne, on *Diatrypella quercina* (on *Quercus*); **9**. 19.XI.2017: Luxembourg, Hesperange, on *Clematis* (bark); **10a–c**. H.B. 4663: Germany, Tübingen, on *?Tremellales* sp. (on *Prunus*).

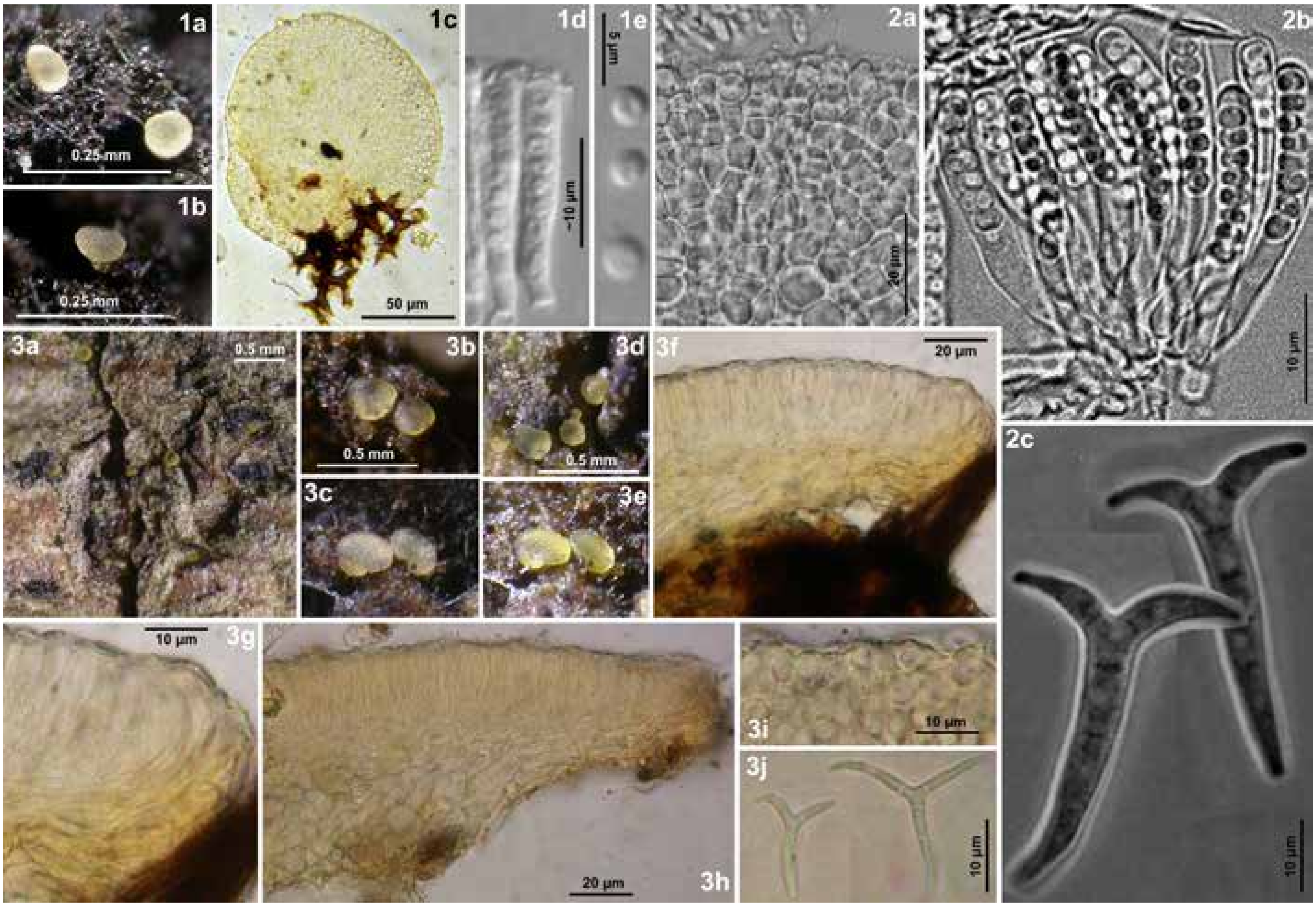


Plate 128. **1–3**: *Hyalorbilia* aff. *erythrostigma*. – **1a–b**, **3a–e**. rehydrated apothecia; **1c**. apothecium from below, with spiny hyphae of ?*Nitschkia acanthostroma*; **3f**, **h**. apothecia in median section; **3g**. id., marginal region; **2a**. ectal excipulum in external view; **3i**. margin in top view; **1d**, **2b**. asci; **1e**. ascospores; **2c**, **3j**. conidia (**2c** from pure culture, **3j** from substrate). – Dead state (**1d–e**, **3j** in H_2O; **1c**, **3f–i** in KOH), except for **2a–c**. – **1d–e**: from Liu et al. (2007b, fig. 5); **2**: from Matsushima (1995, 2005). — **1a–e**. B.L. 6427 (= H.B. 7808a): China, Fujian, on indet. angiosperm; **2a–c**. MFC-4P833 (holotype of *Orbilia trinacriifera*): Peru, Amazon basin, on indet. *Arecales* (petiole); **3a–j**. H.B. 6280g: Australia, Queensland, on indet. climber.

species *T. incurvum* based on an isolate from Peru, which he stated to be conspecific with that from Taiwan based on a very similar conidial morphology. It remains a mystery why Matsushima (1995) did not refer to *T. incurvum* as anamorph of *O. trinacriifera*, although citing the Taiwanese isolate as reference. The connection of *T. incurvum* to a teleomorph remains unsettled since very similar conidia with downwards curved arms were repeatedly observed by us as anamorph in several species from different sections of *Orbilia* (*O. ocellata* and related species, *O. corculispora*, *O. pilifera* and related species).

Misapplications. A British collection reported by Hawksworth & Sivanesan (1975), followed by Ellis & Ellis (1985), under the name *Orbilia euonymi* was described with 'globose' spores, which were found to be subglobose in the present reexamination (Pl. 126: 3). The specimen appears to fit *H. erythrostigma*. However, no trace of SBs was detected in the dead spores, therefore, it could well also be *H. multiguttulata*. Hawksworth & Sivanesan reported apothecia of 0.2–0.5 mm diam., but now only some with 0.12–0.17 mm diam. were found (rehydrated).

Phylogeny. Available rDNA data suggests that *H. erythrostigma* is an aggregate of several taxa. For the time being, we here present a concept which excludes the very similar *H. orbiliicola* but includes samples on pyrenomycetes and gelatinous basidiomycetes. Sequences were gained in the present study from five samples from Luxembourg on different substrates (*Diatrype*: ITS+LSU D1, Pl. 127: 5; *Exidia*: LSU D1–D3, IVV: 4.VII.2013; bark of *Clematis*: SSU+ITS+LSU D1–D4, IVV: 19.XI.2017, 23.XI.2017; wood of *Cornus*: ITS, 22.I.2019). Further sequences are those of Liu et al. (2006a) from two samples from Fujian, China (both on *Nitschkia*: ITS, one also LSU D1–D2, Pls 126: 4; 128: 1), all from apothecia. The S1506 intron is absent in four of them (that on *Exidia* does not cover the SSU region).

Rather high similarity is observed between some of these samples while others strongly differ. Those on bark/wood are completely identical; also the two on *Nitschkia* are identical in the ITS (some gaps and deviations at the 5'-end might be erroneous). The one on *Diatrype* shows an ITS distance of 5.7–6.2 % to those on bark/wood, whereas the *Nitschkia* samples differ by 9.7 % from that on *Diatrype* and by 11 % from those on bark/wood. In the LSU D1 domain only 1 nt differs between the *Diatrype* and *Exidia* sample, and 2–3 nt in comparison to those on *Clematis*. In the D2, however, 10 nt differ between *Exidia* and *Clematis* which is 0.7 % in the D1–D2, and the *Nitschkia* sample differs hereof by 3.2–3.5 % in this region. *H. orbiliicola* differs in the D1–D2 from *H. erythrostigma* s.l. by 5–5.2 % and from *H. latispora* by 13 %.

Also 1 nt in the V8 region of SSU (pos. 52, number according to Tab. 60) differs between samples on *Diatrype* (CGAGTA**C**) and *Clematis* bark or *Cornus* wood (CGAGTA**T**). **T** is typical of most orbiliaceous sequences whereas **C** was otherwise only observed in *H. brevistipitata* s.l., clones U1–3 and U5, *O. polyspora*, and series *Orbilia* p.p.maj.

Two environmental North American soil isolates from Illinois (2321, 3674) clustered with *H. erythrostigma*, but comprise only partial 5.8S and ITS2 (Phyl. 5). In the ITS2 region, the latter differs by 21–23 % from the former and all remaining strains of the *erythrostigma-orbiliicola* clade. KX194742 differs from European *H. erythrostigma* by 3.5 % (*Diatrype*) and 5.5 % (bark/wood), from Chinese *H. erythrostigma* by 10.5 %, and from *H. orbiliicola* by 12.5 % (between European and Chinese *H. erythrostigma* the distance is 9–12.5 %).All this appears to indicate that at least six different species of the *H. erythrostigma* aggregate are involved, three in Europe (including *H. orbiliicola*), one in China, and two in North America. This surprising result raises the question whether *H. anonyma* from Ecuador or the here in *H. erythrostigma* incorporated Peruvian samples (including the type of *O. trinacriifera*) might be conspecific with one of these North American strains.

Specific nucleotides. All ITS sequences of the *erythrostigma-orbiliicola* clade show three remarkable deviations from the current situation in ascomycetes: (1) the 3'-end of 5.8S (pos. 155) is GAGCGT**G** instead of GAGCGT**C** (Tab. 61); (2) the 5'-end of LSU is T**C**ACCT instead of T**G**ACCT; (3) 2 adjacent nucleotides in the 5.8S (pos. 83–84) have AAT**CT**AGT instead of AAT**TC**AGT or rarely AAT**CC**AGT (Tab. 61), with the exception that **CT** also occurs in five North American (California, Canada) and two Chinese (Changbaishan) soil isolates (clades H29–32) which clustered unresolved near the *erythrostigma-orbiliicola* and *Vermispora* clade (Phyl. 5). Another position in the 5.8S (pos. 64) is AG**G**TA, which also occurs in *H. latispora*, the uncultured H30–32, the *Vermispora* clade of *Hyalorbilia*, and the *Lecophagus* clade, whereas the core of *Hyalorbilia* concurs with *Orbilia* in having AG**T**TA (Tab. 61).

Phylogenetically, the *erythrostigma-orbiliicola* clade falls quite distant from the core of *Hyalorbilia*. When analysing the ITS region, it clustered unsupported sister to all the remaining taxa of *Hyalorbilia* (Phyl. 5). Even when restricting the analysis to 5.8S, the distance to other species of the genus, including *H. multiguttulata* (6 nt), is obvious. Also when analysing ITS+LSU or LSU, the *erythrostigma-orbiliicola* clade clustered, like *H. latispora*, unresolved between *Hyalorbilia* s.str. and the *Vermispora* clade (Phyls 6, S5).

Ecology. *Hyalorbilia erythrostigma* in the here circumscribed sense has a wider ecological amplitude than hitherto known. Previously the species was repeatedly recorded on senescent pyrenomycetes (including the type). In various of the here studied collections the apothecia grew on pyrenomycetes, particularly *Diatrypaceae*. For instance, Matočec et al. (2005), who unintentionally placed the species in *Orbilia*, listed a total of four Austrian samples on *Diatrypella* spp. In other samples the apothecia occurred on wood or bark without a visible association with other fungi, and in two samples they grew on basidiomata of *Exidia recisa* and ?*Tremellales* sp. *H. erythrostigma* was considered by Berkeley & Broome (1866) as a parasite.

The species aggregate was collected on ± xeric branches of various angio-, rarely gymnosperm trees and shrubs. The type of *O. trinacriifera* was isolated from rotten petioles of a palm. Collections are from atlantic to subcontinental, humid to rarely semihumid Europe, with a supra- to mesotemperate, more rarely oro- or thermotemperate and orosub- or mesomediterranean climate (see Map 19), where the species occurred, e. g., at sun-exposed borders of forests, thermophilous old shrubs or hedges in quarries, also more shady forests with *Alnus*, *Fraxinus*, *Frangula alnus*, and *Salix* (Luxembourg). Collections from South America are from an orotemperate (subalpine) subhumid *Polylepis* woodland in the Peruvian Andes and a tropical humid rainforest in the Amazon basin, and two environmental isolates of *H. erythrostigma* s.l. (2321, 3674) indicate occurrence in warm continental humid North America.

Map 19. Known distribution of *H. erythrostigma* in Europe and Macaronesia.

The not included collection from Macaronesia was in a lower mesomediterranean subhumid laurel forest (*Lauro novocanariensis-Perseetum indicae*, L. Quijada pers. comm.), and those from Australia occurred on bark and wood of decaying xeric branches of an unidentified climber in the tropical wet and dry (subhumid savannah) northeast, east of the Great Dividing Range (see Map 20). One Australian sample (H.B. 7276f) showed a strong drought tolerance, the medullary excipular cells being still viable after 4.25 years. Samples from Asia include the monsoon-dominated subtropical east of China and tropical north of Thailand.

Specimens included. **GREAT BRITAIN**: **South West England**, **Somerset**, ~5 km NE of Bath, Batheaston, ?100 m, indet. angiosperm (?*Rosaceae*), on *Chaetosphaerella phaeostroma*, 15.I.1859, [no collector,] (K, herb. Broome, holotype of *Peziza erythrostigma*, H.B. 5346 ø). – **Devon**, 35 km ESE of Plymouth, 0.9 km SSE of Slapton, Slapton Ley, north side of Lower Ley, 10 m, log of indet. angiosperm, on bark, 16.VIII.1973, D.L. Hawksworth (IMI 178289, as *O. euonymi*, 'decorticated', H.B. 5013 ø). — **NETHERLANDS**: **Noord-Brabant**, 4 km NNW of Boxmeer, 1.3 km NW of Beugen, W of Helbroek, De Vilt, 12 m, branch of *Quercus rubra*, on indet. pyrenomycete, 29.XI.2008, S. Helleman (S.H. 600, doc. vid.). — **BELGIUM**: **Wallonie**, **Luxembourg**, 8 km SE of Arlon, 0.7 km SE of Sterpenich, 325 m, branch of *Sambucus nigra*, on wood, 23.IV.2001, H.O. Baral (H.B. 6908a). — **LUXEMBOURG**: **Gutland**, **Luxembourg**, 5 km SSW of Luxembourg, N of Kockelscheier, Weier, 300 m, branch of *S. cinerea*, on *Diatrype bullata* and bark, 2.IX.2008, G. Marson (H.B. 8960a). – ibid., branch of *Salix caprea* × *cinerea*, on *Exidia recisa*, 4.VII.2013 (G.M. 2013-07-04.1, sq.: KT380064). – 5 km SE of Luxembourg, 1.5 km E of Itzig, Reimeschbaach, branch of *Cornus*, on wood, 22.I.2019, G. Marson (G.M. 2019-01-22.4, non vid., sq.: MN151402). – ibid., branch of *Salix*, on wood & bark, 28.I.2019, G. Marson (G.M. 2019-01-28.3, non vid.). – **Esch-sur-Alzette**, 5.7 km S of Luxembourg, 1 km SE of Kockelscheier, N of Uecht, 305 m, branch of *Salix*, on *Diatrype bullata*, 17.VI.2009, G. Marson (ex H.B. 9077a, M-0291773, anam. substr., epitype; sq.: KY463699, KT222441). – 1.2 km SSW of Hesperange, SW of Fentange, Wéineguecht, 277 m, branch of *Clematis vitalba*, on bark, 19.XI.2017, G. Marson (G.M. 2017-11-19.4; sq.: MH221046). – SE of Fentange, Wénkel, 265 m, branch of *C. vitalba*, on wood, 20.III.1994, G. Marson (ø). – **Echternach**, Petite Suisse, 7 km W of Echternach, 4 km SW of Berdorf, Schnellert, 230 m, branch of *Crataegus monogyna*, on

Diatrype stigma, 20.X.1996, G. Marson (H.B. 5641a). – 10 km WNW of Echternach, 1.2 km SW of Beaufort, Längt, 340 m, trunk of *Fagus sylvatica*, on bark, 3.II.2007, G. Marson (ø). – **Esch-sur-Alzette**, 4.2 km S of Bettembourg, 1.6 km E of Dudelange, 2.7 km NW of Zoufftgen, 298 m, branch of *Clematis vitalba*, on bark, 23.XI.2017, G. Marson (G.M. 2017-11-23.1; sq.: MH221047). — **GERMANY**: **Mecklenburg-Vorpommern**, 6 km NNW of Rehna, 1 km E of Roduchelstorf, 45 m, branch of *Corylus avellana*, on *Diatrypella ?favacea*, 21.I.2017, T. Richter (H.B. 10045). – **Nordrhein-Westfalen**, 4 km E of Duisburg, 1 km NW of Raffelberg, 35 m, on stem of *Sambucus ebulus*, 11.IV.2012, K. Müller (H.B. 9673). – 14 km NW of Brilon, 3 km NE of Warstein, 308 m, branch of ?*Corylus avellana*, on ?*Diatrype stigma* and bark, 28.IX.2012, S. Helleman (S.H. 724, doc. vid.). – **Baden-Württemberg**, Schönbuch, 4 km N of Tübingen, 0.7 km W of Bebenhausen, Mühlbach, 365 m, branch of *Prunus spinosa*, on ?*Tremellales* sp. and bark, 1.V.1992, H.O. Baral (H.B. 4663a). – ibid., 20.IV.1993 (H.B. 4872). – 5 km NE of Tübingen, S of Pfrondorf, Obere Mähder, 395 m, stem of *Rubus fruticosus*, 20.XI.2006, H.O. Baral (H.B. 8368b ø, anam. only). — **AUSTRIA**: **Kärnten**, 12 km SE of Klagenfurt, 0.5 km NNE of St. Margareten, Stariwald, 582 m, branch of *Tilia*, on bark, 11.XII.1994, W. Jaklitsch (H.B. 5201a). – **Steiermark**, 4.5 km N of Graz-Andritz, ~1 km NE of Stattegg, southwest-slope of Schöckl, ravine Falschgraben, ~630 m, branch of indet. angiosperm, on *Diatrypella*, 3.VIII.2003, N. Matočec (CNF 2/6577, doc. vid.). – 3 km NNW of Graz, Reinerkogel, 470 m, branch of *Robinia pseudoacacia*, on *Diatrype* and *Cosmospora*, 16.XII.2013, I. Wendelin, vid. G. Friebes (ø, doc. vid.). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 15 km SSW of Rennes, 4 km NE of Guichen, Le Boël, 45 m, branch of *Quercus*, on *Diatrypella quercina*, 17.II.2006, J.P. Priou (J.P.P. 26042, doc. vid.). – 17 km SW of Rennes, 2.6 km S of Bréal-sous-Montfort, 70 m, branch of *Cytisus scoparius*, on *Eutypella tetragona*, 6.II.2009, J.P. Priou (J.P.P. 29010, doc. vid.). – **Morbihan**, 8.5 km WNW of Redon, 1.9 km E of St.-Jacut-les-Pins, Moulin de Calléon, 13 m, branch of *Quercus*, on *Diatrype bullata*, 4. & 13.II.2006, J.P. Priou (J.P.P. 26029, 26040, doc. vid.). – 12.5 km NNW of La Gacilly, N of La Grée Basse, Le Pouilo, 115 m, branch of *Cytisus scoparius*, on *Eutypella tetragona*, 19.II.2009, J.P. Priou (J.P.P. 29024, doc. vid.). – 1.3 km W of La Gacilly, NW of La Glouzie, Buhan, 50 m, branch of *Ulex europaeus*, on *Eutypella leprosa*, 1.IV.2010, J.P. Priou (J.P.P. 10012, doc. vid.). – 2.8 km SW of La Gacilly, 3 km NW of Glénac, La Forêt Neuve, 90 m, branch of *Quercus*, on *Jackrogersella minutella*, 27.X.2010, J.P. Priou (J.P.P. 10182 ø, doc. vid.). – 1 km WNW of La Gacilly, rue de Picardie, 38 m, branch of *Ilex aquifolium*, on *Diatrype*, 9.II.2011, J.P. Priou (J.P.P. 11009 ø, doc. vid.). – 3 km WSW of Malestroit, St.-Marcel, 58 m, twig of *Sophora*, on *Diaporthe microphylla* and bark, 20.XII.2011, J.P. Priou (J.P.P. 11265, doc. vid.). – 5.5 km SE of Vannes, 1.5 km E of Séné, Falguérec, 2 m, branch of *Quercus*, on *Cosmospora* (on *Diatrypella quercina*), 31.I.2014, J.P. Priou (J.P.P. 14026 ø). – **Midi-Pyrénées**, **Ariège**, 12 km E of St.-Girons, 1.5 km SE of Rimont, Le Baup, 560 m, branch of *Robinia pseudoacacia*, on *Peroneutypa scoparia*, 30.X.2011, A. Gardiennet, vid. J.P. Priou (J.P.P. 11169, doc. vid.). – 12 km ENE of St.-Girons, 2 km NNE of Rimont, Las Muros, 475 m, branch of *Ficus carica*, on *Eutypella caricae*, 25.IV.2010, J. Fournier (J.F. 10019). – **Champagne-Ardenne**, **Ardennes**, 31 km W of Charleville-Mézières, SW od Aouste, bois Sainte Marselle, 240 m, branch of *Quercus*, on *Diatrypella quercina*, 11.I.2001, R. Collot (ø). – **Poitou-Charentes**, **Deux-Sèvres**, 14 km SSE of Niort, Poivendre de Marigny, 50 m, twig of *Koelreuteria paniculata*, on *Diatrype*, 23.V.2012, M. Hairaud (MH 190512, doc. vid.). — **SPAIN**: **Asturias**, 2 km SSW of Piedras Blancas, Las Bárzanas, eucalypt plantation in Las Bárzanas, 80 m, stem of *Hydrangea macrophylla*, on indet. pyrenomycete, 25.IV.2009, E. Rubio (E.R.D. 4771, doc. vid.). – 6 km SW of Pola de Somiedo, 5 km SSE of Vilar de Vildas, Braña Los Cuartos, 1410 m, branch of *Cytisus scoparius*, on bark, 8.VI.2017, H.O. Baral (H.B. 10099b ø). – **País Vasco**, **Gipuzkoa**, 11 km SSE of Zarautz, 2.8 km WSW of Asteasu, 265 m, branch of *Ulmus* (?)*minor*, on perithecia of *Bionectria ralfsii*, 8.III.2014, J. Martin (ARAN-F A3042115). – **Vizcaya**, 11 km SE of Bilbao, 3.5 km SSW of Usansolo, SW of Lekubaso Embalse, 130 m, branch of *Robinia pseudoacacia*, on ostioles of *Peroneutypa scoparia*, 27.VII.2017, R. Ibarretxe (ø, anam. substr., doc. vid.). – **Aragón**, **Zaragoza**, 29 km N of Zaragoza, 12 km WNW of Zuera, cuatro camino, 539 m, branch of *Quercus rotundifolia*, on indet. pyrenomycete, 10.III.2018, R. Blasco (doc. vid.). – **Andalucía**, **Jaén**, 20 km S of Jaén, SW of Valdepeñas de Jaén, 913 m, stem of *Rubus ulmifolius*, on black (?)apothecia, 4.I.2014, S. Tello (JA-CUSSTA 7800, doc. vid.). – 14 km SSE of Jaén, 2.7 km SE of Otiñar, 650 m, twig of *Pistacia lentiscus*, on *Diatrypaceae*, 20.VII.2014, S. Tello (JA-CUSSTA 8263, doc. vid.). — **MACARONESIA**: **Canary Islands**, **Tenerife**, San Cristóbal de La Laguna, Anaga, 1.5 km NNE of Las Mercedes, W of Cruz del Carmen, Carretera Las Mercedes, 895 m, branch of *Prunus lusitanica* ssp. *hixa*, on *Diatrypaceae*, 14.IX.2014, R. Negrín (ø, doc. vid.). — **PERU**: **Ancash**, Cordillera Blanca, 21 km NE of Carhuaz, Quebrada Ulta, E of Huascarán Mt., 2 km W of pass Punta Olimpica, ~4350 m, branch of indet. angiosperm, on *Eutypa*, 1.VI.1998, L. Beenken & C. Hahn (L.B. 1277, H.B. 6605, anam. substr.).

Not included. **AUSTRALIA**: **Queensland**, Brigalow Belt North, 49 km SE of Ayr, 4 km ESE of Gumlu, Bruce Hwy, 12 m, branch of indet. climber, on wood & bark, 19.X.1998, G. Marson (H.B. 7276f ø). – Einasleigh Uplands, 75 km SSW of Townsville, 2 km WSW of Mingela, 286 m, branches of indet. climber, on wood & bark, 17.X.1998, G. Marson (H.B. 6280g, anam. substr.). — **USA**: **Illinois**, Champaign County, rhizosphere of *Alnus* and *Betula*, IV.2012, J.O. Dawson (clone 2321, mol. extr.; sq.: KX194742). – ibid. (clone 3674, KX196095). — **PERU**: **Loreto**, Amazon basin, 135 km SSW of Iquitos, Colonia Angamos, ~150 m, indet. *Arecales*, on petiole, of VII.1994, T. Matsushima (MFC-4P833, **holotype** of *Orbilia trinacriifera*; H.B. 5524). – ibid. (MFC-4P479, holotype of *Trinacrium angamosense*). — **CHINA**: **Fujian**, **Longyan**, 45 km ENE of Shanghang, 25 km NW of Longyan, Gutian, 700 m (erron. as 1180 m in Liu et al. 2007b), branch of indet. angiosperm, on *Nitschkia acanthostroma*, 17.IV.2003, B. Liu & L.M. Zhang (B.L. 6427, HMAS 139527, H.B. 7808a; sq.: DQ656653, DQ656698). – **Jiangxi**, 100 km NW of Ganzhou, Jinggangshan, ~15 km S of Longtan, 800 m, on *N. acanthostroma*, 2.X.2005, B. Liu & J. Chen (B.L. 779, HMAS 139528; sq.: DQ656652, doc. vid.). – **Yunnan**, **Honghe**, Pingbian, Daweishan, branch of indet. angiosperm, 7.VI.2013, J.W.Guo (pb-j-1). – **Yuxi**, Tonghai, Xiushan, branch of indet. angiosperm, 16.VII.2007, J.W. Guo & S.F. Li (th2-1). – **Zhejiang**, **Kaihua** Gutianshan, branch of indet. angiosperm, 5.IX.2009, J.W. Guo (gts-38). (Not specified by Guo et al. 2014b: fig. 6 which collection was illustrated.). — **THAILAND**: **Northern Thailand**, **Chiang Rai**, 16 km NNE of Chiang Rai, Mae Fah Luang University, ~460 m, on *Annulohypoxylon*, 20.IV.2015, A.H. Ekanayaka (hd028, MFLU 16-0589, doc. vid.).

Hyalorbilia orbiliicola Baral, G. Marson, Polhorský & E. Weber, **sp. nov.**, MB 829493 — Pls 129–130, Map 20

Etymology: according to the parasitism on apothecia of *Orbilia* spp.

Typification: Slovakia, Žilina, Tvrdošín, Brezovica, on apothecia of *O. aurantiorubra* on branch of *Salix*, 31.XII.2017, A. Polhorský (ex A.P. 18/50, BRA-CR29844; sq.: MK028717).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.06–)0.1–0.15(–0.22)((–0.25)) mm diam. (immature 0.035–0.08 mm), in total 0.05–0.14 mm high (receptacle 0.05–0.065 mm), whitish-subhyaline to pale cream or yellowish, ± translucent, round (young globose), gregarious; disc flat, margin even, not protruding, exterior glabrous, sessile or often with a short stipe of 0.01–0.07 × 0.03–0.09 mm, superficial; dry whitish to light cream, slightly contracted. **Asci** *(26–)29–43 × (4–)4.5–5.5 µm {5}, †22–33(–38) × 3.5–5(–6) µm {3}, 8-spored, spores */†1(–2)-seriate, orientation in all directions, pars sporifera *15–22 µm long; **apex** (†) hemispherical to subconical or subtruncate; **base** ± unstalked or with a short, thick stalk, arising from croziers {2} with vertical slits 2–3 µm long. **Ascospores** *(2.5–)2.7–3.2(–3.5) × (2.2–)2.4–2.7(–2.8) µm {5}, †2–2.8 × 1.5–2 µm {2}, subglobose (to broadly ellipsoid), with a single globose, strongly eccentric **SB** (1–)1.2–1.4(–1.5) µm diam. {4}, very close to one end but not visibly attached; with 1–2 minute **LBs**. **Paraphyses** apically cylindrical to slightly or sometimes strongly clavate-capitate, terminal cells *7–10.5 × 2.2–3(–4) {2} µm, †1.7–3.2 µm wide {2}, lower cells *6–8 × 2–2.4 µm {2}, †4–5 × 1.5–2.2 µm, branched or unbranched near base. **Medullary excipulum** ~10–30 µm thick, of dense, thin-walled textura globulosa-angularis, indistinctly delimited. **Ectal excipulum** at stipe and flanks of thin-walled to slightly gelatinized t. globulosa-angularis or t. prismatica oriented parallel to outside or irregular, ~30 µm thick in stipe, ~10–15 µm thick at lower flanks, cells in stipe and lower flanks *6–12 × 3–8 µm {2}, †5–8 {2} or 7–19 {2} × (3–)4–8 µm {4}; towards margin 6–8 µm thick, marginal cortical cells *6.5–8 × 2.4–2.8 {1} or 10–13 × 3–4 µm {1}, cylindric-clavate, thin-walled. **Anchoring hyphae** not observed. **VBs** in apex of terminal cells of paraphyses ± globose, strongly refractive, 1.5–5 × 1.5–3.7 µm {2}, in marginal cortical cells 1.5–5 × 1.5–5 µm {2}; **LBs** sparsely present in paraphyses and ectal excipulum, minute, hyaline to pale yellowish. **Exudate** over paraphyses and ectal excipulum 0.3–0.8 µm thick, hyaline, continuous, externally smooth to finely rough. — **ANAMORPH**: trinacrium-like (both morphs from natural substrate {14}, molecular data from conidial isolate {1}, only anamorph observed {10}). **Conidiophores** projecting in abundance from margin or hymenium of host apothecia, */†10–30 × 1.5–2.8 µm {2}, ± flexuous-geniculate, unbranched, conidiogenous cells apparently monoblastic. **Conidia** branched (T-

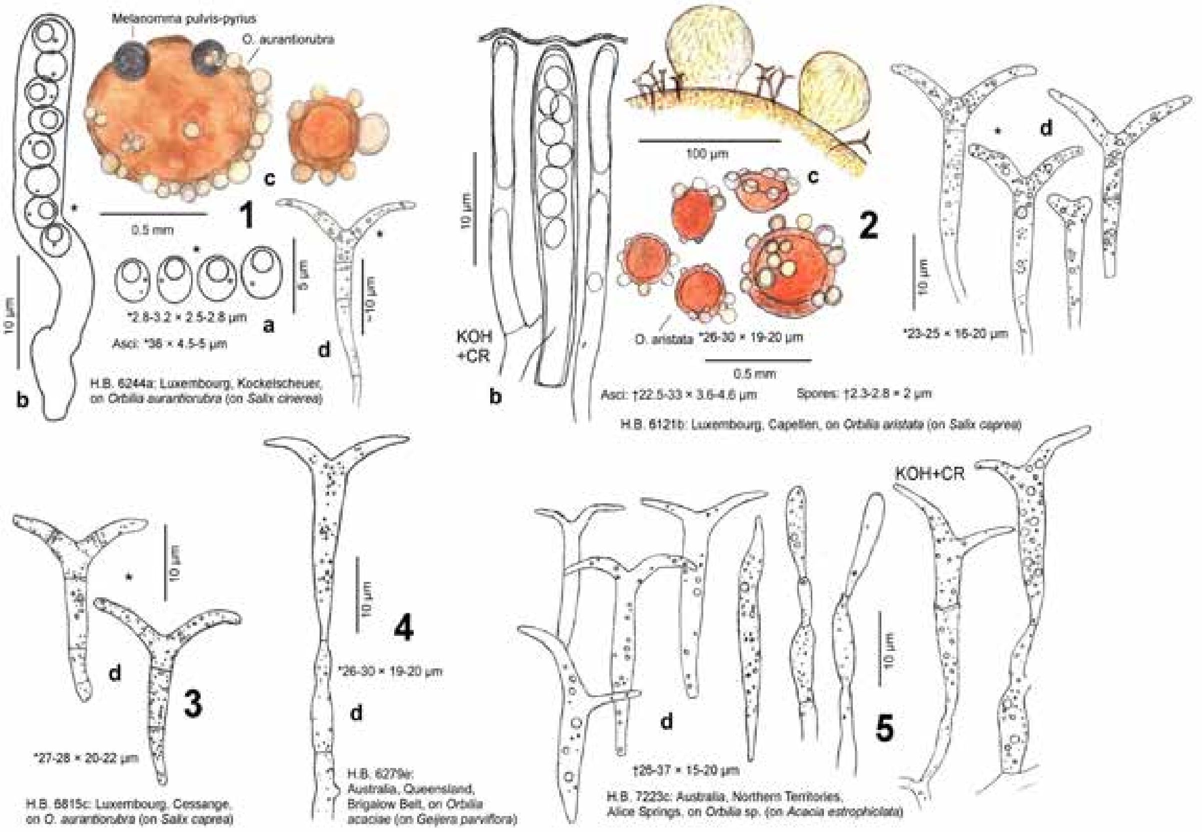


Plate 129. **1–3**: *Hyalorbilia orbiliicola*; **4–5**: *H.* aff. *orbiliicola*. – **a**. ascospores; **b**. asci and paraphyses; **c**. rehydrated apothecia growing on *Orbilia* spp.; **d**. conidia and conidiophores from substrate (*Orbilia* spp.)

to Y-shaped), 2-armed, branches gradually tapering towards ends, */†(14–)19–29(–35) × (13–)16–25 µm {7}, stipe *15–20(–25) × 2.2–3(–3.3) µm (†2–2.5 µm wide), 1–3-septate, arms *(5–)8–12 × 2–2.7 µm, 0–1(–2)-septate, of ± similar length (exceptionally asymmetrical), slightly to medium curved downwards but still pointing ± upwards or laterally.

Habitat: undisturbed, shady and moist but also thermophilous, deciduous or mixed forests, often with ruderal plants (*Rosa*, *Rubus*, *Urtica*), 1–2 m above the ground or rarely on the ground, xeric, decayed, corticated to partially decorticated, 10–50 mm thick branches of living or often dead trees and shrubs of *Cedrus atlantica* {1}, *Cercis siliquastrum* {1}, *Cornus* sp. {1}, *C. sanguinea* {1}, *Eucalyptus camaldulensis* {1}, *Larix decidua* {1}, *Picea ?glauca* {1}, *Punica granatum* {1}, *Salix* sp. {8}, *S. alba* {1}, *S. aurita* × *caprea* {1}, *S. caprea* {4/1}, *S. cinerea* {5/1}, *S. ?viminalis* {1}, *Spartium junceum* {1}; growing almost exclusively on living apothecia of *Orbilia aristata* {3/1}, *O. aurantiorubra* {13/1}, *O. eucalypti* {8}, *O. flagellispora* {1}, *O. ?gambelii* (or *O. albidorosea*?) {1}, *O. mali* {1}, *O. subaristata* {1}, *O. vinosa* {2}; host apothecia in holes of periderm or mostly on inner surface of bark (bast) being slightly to strongly detached (projecting or often ± large pieces hanging from branch), exceptionally on wood {1, on *Spartium* in beetle galleries}, green algae sparse to abundant. **Further associated**: *Allophylaria macrospora* {1}, *Caloplaca holocarpa* {1}, *Cistella ?chlorosticta* {1}, *Cryptocoryneum condensatum* {1}, *Cryptodiscus foveolaris* {1}, *Durella connivens* {1}, *Glyphium elatum* {1}, *Hyalorbilia erythrostigma* {2}, *H. subfusispora* {2}, *Hysteropatella elliptica* {3}, *Karstenia idaei* {1}, *K. rhopaloides* {1}, *Lecophagus ellipsoideus* {1}, *Melanomma ?pulvis-pyrius* {1}, *Mollisia ligni* {1}, *Orbilia aristata* {1}, *O. carpoboloides* {3}, *O. ?cejpii* {1}, *O. clavuliformis* {1}, *O. gambelii* {2}, *O. pleiogambelii* {1}, *O. spermoides* {1}, *O. subaristata* {2}, *O. subclavuliformis* {1}, *O. ?tremulae* {1}, *O. xanthoguttulata* {1}, *Rutstroemia punicae* {1}, *Sclerococcum* sp. {1}, *Trichopeziza perrotioides* {1}, *Unguiculariopsis* sp. {1}, *Xerombrophila crystallifera* {1}. **Desiccation tolerance**: after 15 months many cells of ectal excipulum still alive, conidia after 3.5 months. **Altitude**: 8–1447 m a.s.l. **Geology**: Buntsandstein, Keuper (gypsum), Lower Jurassic sandstone and shale (sometimes covered by Pleistocene loess), Cretaceous & Oligocene limestone & calcareous marl, flysch, Tertiary molasse, Quaternary sand; migmatite & gneiss. **Phenology**: throughout the year (long-lived).

Phenology of *H. orbiliicola* (teleomorph and/or anamorph)											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2	2	5	1	3	3	3	3	3	3	3	1

Taxonomic remarks. *Hyalorbilia orbiliicola* is very similar to *H. erythrostigma* and mainly differs in its unusual habitat, apothecia of *Orbilia* spp., also in consistently short apothecial stipes and in much shorter, ± globose to subglobose VBs in paraphyses and marginal excipular cells (strongly elongated in *H. erythrostigma*). The two species even concur in their conidia which were frequently observed on the natural substrate in *H. orbiliicola* but rarely in *H. erythrostigma*. Due to its special habit of growing on the apothecial margin of *Orbilia*, the minute apothecia of *H. orbiliicola* may at first glance be mistaken for marginal teeth of the host.

Anamorph. Trinacrium-like conidia have been observed by us in close association with the apothecia in about half of the collections (Pls 129: 1–5; 130: 5, 6b; 131: 1–5). Like the apothecia of the *Hyalorbilia*, the short conidiophores emerge from the margin of the host apothecia. That the trinacrium-like anamorph belongs to the host fungus (mainly *Orbilia aurantiorubra* and *O. eucalypti*) rather than to the parasite can be excluded since these two host taxa produce very different conidia in pure culture (vermispora- and dicranidion-like, respectively). The connection between apothecia and anamorph was eventually proved by molecular data (see

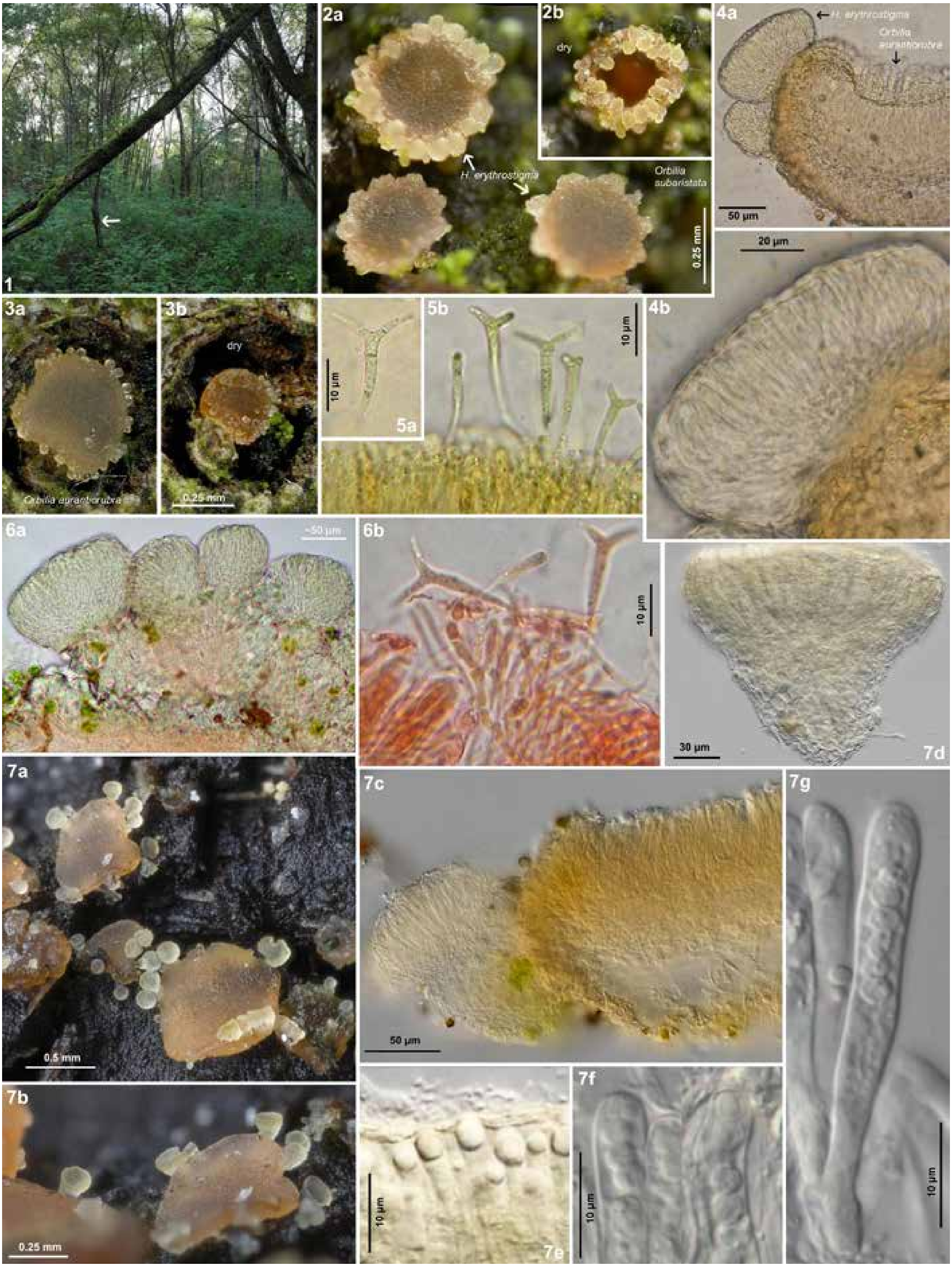


Plate 130. **1–7**: *Hyalorbilia orbiliicola*. – **1**. Shady forest with *Salix cinerea* × *caprea*, large piece of detached bark hanging from broken trunk; **2a–b**, **3a–b**. whitish immature apothecia of *Hyalorbilia* on margin of orange apothecia of *Orbilia* spp. (rehydrated and dry); **7a–b**. id., mature (rehydrated); **4a–b**, **7c**. apothecia in median section (with host apothecium); **6a**. id., squash mount; **7d**. apothecium in median section; **7e**. subglobose VBs in cells of marginal ectal excipulum; **7f–g**. asci with ascospores; **5a–b**, **6b**. conidia and conidiophores arising from host apothecia. – Living state: **7c–g**, dead state: **4a–b**, **5a** (in KOH), **5b** (in KOH+IKI), **6b** (in KOH+CR). – **7a–g**: phot. A. Polhorský. — **1**. 13.X.2010: Luxembourg, Kockelscheier, on *Orbilia aurantiorubra* (on *Salix*); **2a–b**. 28.III.2007: ibid., Mersch, on *O. subaristata* (on *Cornus*); **3a–b**. 7.VII.2011: ibid., Bridel, on *O. aurantiorubra* (on *Salix*); **4a–b**. H.B. 6244a: ibid., Kockelscheier, on *O. aurantiorubra* (on *Salix*); **5a–b**. H.B. 6209a: ibid., Alzingen, on *O. eucalypti* (on *Salix*); **6a–b**. H.B. 7604c: France, Sisteron, on *O. flagellispora* (on *Cedrus*); **7a–g**. A.P. 18/50: Slovakia, Brezovica, on *O. aurantiorubra* (on *Salix*).

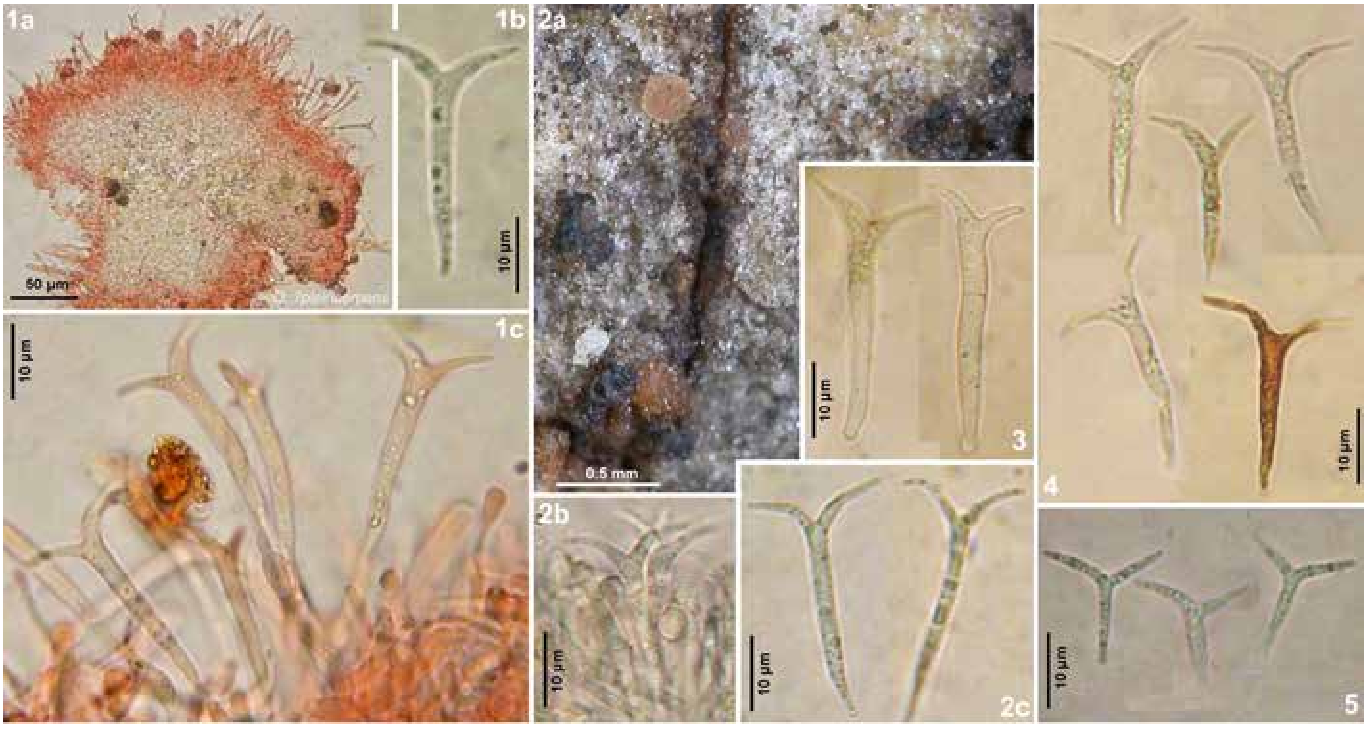


Plate 131. **1–4**: *Hyalorbilia* aff. *orbiliicola*; **5**: *H.* cf. *orbiliicola*. – **2a**. *Orbilia coronohesperidea* (above) and *O. pleioserpens* (with macroscopically invisible *H.* aff. *orbiliicola*). **1a**. host apothecium infected by trinacrium-like anamorph (squash mount); **1b**, **2b–c**, **3**, **4**, **5**. conidia and conidiophores. – Dead state (**2b–c**, **4** in H_2O or IKI, **1a–b** in KOH or KOH+CR), except for **3**. — **1a–c**. H.B. 7215e: Western Australia, Carnarvon, on *O. ?pleioserpens* (on *Acacia*); **2a–c**. H.B. 8976i: Western Australia, Pilbara, on *O. pleioserpens* (on *Acacia*); **3**. H.B. 8727j: ibid., Carnarvon, on *Orbilia* sp. (on *Acacia*); **4**. H.B. 6279e: Queensland, Banana, on *O. acaciae* (on *Geijera*); **5**. H.B. 8608b: ibid., Cairns, on *O. neocomma* (on indet. climber).

below). This anamorph closely resembles that observed in *H. erythrostigma* which merely differs in a slight tendency to form longer stipes and more septa in stipes and arms. For the questionable *Orbilia trinacriifera* see discussion under *H. erythrostigma* (p. 421).

H*. cf. *orbiliicola (conidia symmetrical, Pl. 131: 5). In an Australian sample a single apothecium of 0.06 mm diam. was found growing on *Orbilia neocomma* (H.B. 8608a). It closely concurs with European *H. orbiliicola* in size of asci (†19–22 × 4–5 µm) and spores (†2–2.8 × 1.7–1.8 µm) (both unillustrated). Yet, the associated conidia differ in their smaller size (†14–17 × 13.5–15.5 µm) due to shorter stipes and more straight arms, therefore, this collection is doubtfully conspecific.

H*. aff. *orbiliicola (conidia ± asymmetrical, Pls 129: 4–5; 131: 1–4). In seven Australian populations of different *Orbilia* spp. (*O. acaciae*, *O. bicknellensis*, *O.* aff. *myriella*, *O. pleioserpens*, immature *Orbilia* spp.), trinacrium-like conidia abundantly emerged from the host apothecia. Contrary to the above sample, the 2 conidial arms are predominantly curved and of distinctly different size, thus showing a more or less strong asymmetry. Furthermore, the rather thick stipes are non- or only 1-septate and the 2 strongly attenuated arms always non-septate. Compared to European *H. orbiliicola*, the conidia tend to be longer and their arms shorter (total size */†22–40 × 10–20 µm, stipe */†15–29 × 2.5–4 µm, arms */†5–10 × 1.2–2.2 µm).

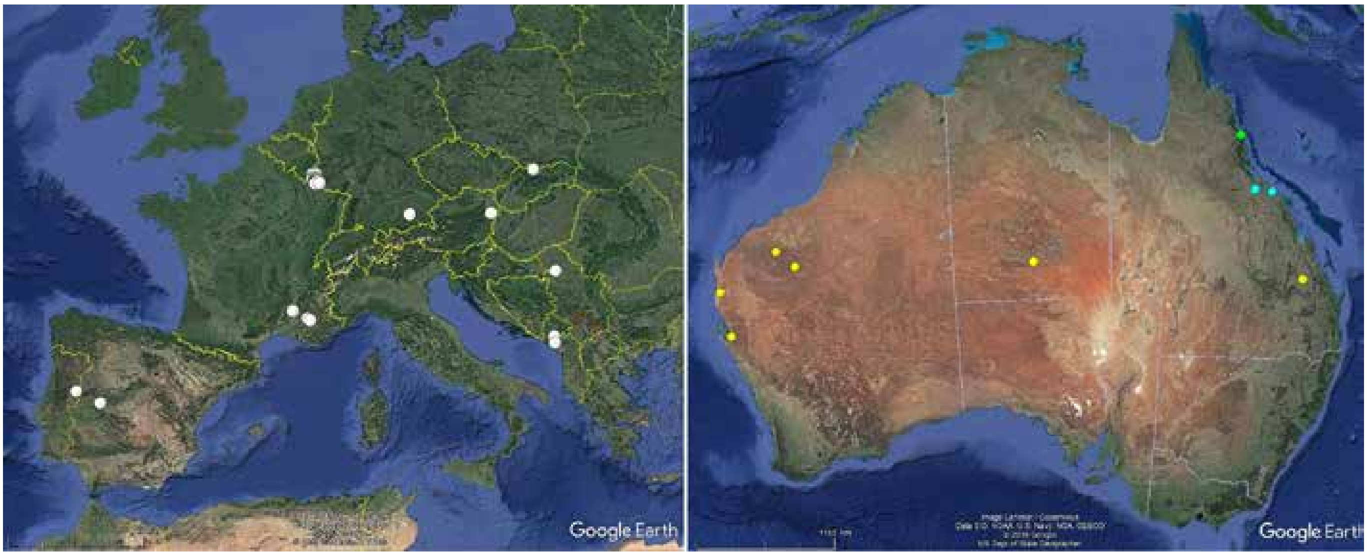
Only in one of these samples (on *Orbilia acaciae*, IVV: H.B. 6279e) a few apothecia occurred in association with the conidia. These differ from *H.* cf. *orbiliicola* in larger asci (†29–35 × 5–5.8 µm) and spores (globose, *3–3.5 µm diam.). The spores did not contain SBs, perhaps because of immaturity.

Both the paucity of septa and the asymmetry of conidial arms are quite unusual features when comparing typical *H. orbiliicola* or the form genus *Trinacrium* as a whole. Together with the presumed slightly deviating teleomorph in H.B. 6279e, Australian populations with asymmetrical conidia might belong to a different, closely related species in which apothecia are rarely formed. However, a slight conidial asymmetry was also sometimes observed in European samples, e.g., from Montenegro (20.II.2016) or Austria (27.I.2013) (IVV).

In *Trinacrium parvisporum* (see Pl. 22: c) the two arms also frequently differ in length but the conidia are mostly multiseptate.

Very similar asymmetrical conidia as in *H.* aff. *orbiliicola* were reported by Hudson & Ingold (1960) for an unidentified aquatic hyphomycete on rotten leaves in Jamaica [as '*Heliscus* (?)']. Comparable conidia were described in the coelomycetous genus *Cornutispora* Piroz. (Pirozynski 1973, Punithalingam 2003). However, the conidia of *H.* aff. *orbiliicola* are freely formed, not within yellowish- to dark brown pycnidia as in *Cornutispora*. In the eight known species of *Cornutispora* the pycnidia occur on ascomata of the rhytismatalean genus *Therrya* (type species) or on lichens. Moreover, the conidia always possess a basal arm-like downward extension.

Phylogeny. Sequences from apothecia were gained of a sample from Luxembourg (Howald, on *O. eucalypti* on *Cornus*, ITS+LSU D1–D3) and one from Slovakia (ITS, on *O. aurantiorubra* on *Salix*). Another sequence derives from abundant conidia in another sample from Luxembourg (Dudelange, on *Salix*, ITS+LSU D1–D6), but here also apothecia of *H. orbiliicola* were present, therefore, it cannot fully be excluded that only DNA from conidia came into the extract. All sequences lack the S1506 intron and fully concur in the ITS region, also the two LSU sequences are identical in the overlapping D1–D3 domain. The ITS/LSU D1–D2 distances to the different strains of *H. erythrostigma* are 6.3/4.9 % (China), -/4.2 % (*Exidia*), 8/4.4 % (bark & wood and Illinois clone), and 10/4.4 % (*Diatrype*).



Map 20. Known distribution of *H. orbiliicola* s.str. in Europe (left) and of *H. orbiliicola* s.l. and *H.* cf. *erythrostigma* in Australia (right): white = *H. orbiliicola*, green = *H.* cf. *orbiliicola*, yellow = *H.* aff. *orbiliicola*, cyan = *H.* cf. *erythrostigma*.

H. orbiliicola clustered with *H. erythrostigma* in a strongly supported clade when analysing ITS, LSU, or both in combination (Phyls 5, 6). A very rare exception is observed in the 5.8S of *H. orbiliicola*: at pos. 145 it has A whereas any other *Orbiliomycetes* (including *H. erythrostigma*) has G. A comparable proportion in the occurrence of A and G at pos. 145 is observed within the *Helotiales*.

Ecology. According to the numerous records it can be concluded that *Hyalorbilia orbiliicola* is an obligate parasite growing on the margin of living, desiccation-tolerant apothecia of different species of *Orbilia*. The minute apothecia grew abundantly together with the conidiophores on the margin, rarely the hymenium, of living, often rather intact apothecia of *Orbilia* spp. Often a majority of the *Orbilia* population were infected, but sometimes only 20–30 %. The asci of the host apothecia were often not fully developed or sometimes even absent. We were unable, however, to detect hyphae of the *Hyalorbilia* in the host tissue, or haustoria in the marginal excipular cells of the host apothecia on which the *Hyalorbilia* apothecia superficially insert.

Collections included in *H. orbiliicola* comprise supra- to orotemperate humid central Europe and northeastern North America, and orosub- to mesomediterranean, humid to semihumid southern Europe. The not included Australian records occurred on apothecia of different *Orbilia* spp. on decaying xeric branches, but usually only the anamorph was present. The population with ± symmetrical conidia was from the tropical humid (wet and dry) northeast, while those with ± asymmetrical conidia are from subtropical arid to semiarid western and central Australia (e.g., in eucalypt open woodlands) and one from subtropical subhumid (winter-dry savannah to monsoon climate) eastern Australia east of the Great Dividing Range (see Map 20).

Specimens included. **LUXEMBOURG**: **L'Oesling**, **Redange**, 10 km W of Ettelbruck, 1.5 km NW of Grosbous, near Bruch (an der Wark), 400 m, on *Orbilia eucalypti* on bark of *Salix cinerea*, 26.III.2001, G. Marson (H.B. 6990c, anam. substr.). – ibid., on *O. aurantiorubra* on bark of *Salix*, 24.IV.2001, G. Marson & H.O. Baral (ø, anam. only). – ibid., on *O. aurantiorubra* on bark of *S. cinerea*, ?26.III.2001, G. Marson (H.B. 6991b ø, anam. substr.). – **Gutland**, **Diekirch**, 3.5 km ESE of Ettelbruck, 1.7 km SE of Ingeldorf, Jongeboesch, Béibert, 353 m, on *O. aurantiorubra* on bark of *Salix*, 18.VI.2001, G. Marson (ø, anam. only). – **Mersch**, 5.3 km SE of Mersch, 3 km NNE of Lorentzweiler, Lëtzert, 395 m, on *O. subaristata* on bark of *Cornus sanguinea*, 28.III.2007, G. Marson (ø). – **Capellen**, 1.7 km SSE of Eischen, 1.5 km ENE of Clairefontaine (Belgium), Aechels, at river Eisch, 310 m, on *O. eucalypti* on bark of *Salix ~caprea*, 15.VII.2000, G. Marson (H.B. 6726a, anam. only). – 5 km NW of Capellen, 1 km NNW of Koerich, Haereboesch, Carrière, 300 m, on *O. aristata* on bark of *S. caprea*, 8.V.1998, G. Marson (H.B. 6121b, anam. substr.). – 5 km NNW of Luxembourg, 1.2 km E of Bridel, Gipsweieren, 260 m, on *O. aurantiorubra* on *S. cinerea*, 15.V.2004, G. Marson (ø). – ibid., ~7.VII.2011, G. Marson (ø). – **Luxembourg**, 3.5 km S of Luxembourg, 1 km SW of Howald, 295 m, on *O. eucalypti* on bark of *Cornus*, 30.X.2014, G. Marson (G.M. 2014-10-30.1, anam. substr.; sq.: MK473404 [from apothecia]). – 4.5 km SW of Luxembourg, SW of Cessange, Bois de Cessange, on *O. aurantiorubra* on bark of *Salix caprea*, 5.XI.2000, G. Marson (H.B. 6815c, anam. substr.). – 5 km SSW of Luxembourg, N of Kockelscheier, Weier, 300 m, on *O. aurantiorubra* on bark of *S. cinerea*, 15.IX.1998, G. Marson (H.B. 6244a, anam. substr.). – ibid., on *O. aurantiorubra* on bark of *S. aurita* × *caprea*, 13.X.2010, G. Marson (ø). – 5 km SE of Luxembourg, 1.5 km E of Itzig, Reimeschbaach, branch of *Salix*, on *O.* ?*aristata*, 28.I.2019, G. Marson (G.M. 2019-01-28.2). – 6.5 km SE of Luxembourg, 2 km ESE of Alzingen, Héid, 290 m, on *O.* ?*tremulae* on bark of *S. caprea*, 13.VIII.1998, G. Marson (H.B. 6209a, anam. substr.). – **Esch-sur-Alzette**, 5.7 km S of Luxembourg, 1 km SE of Kockelscheier, N of Uecht, 305 m, on *O. eucalypti* on bark of *Salix*, 17.VI.2009, G. Marson (H.B. 9077b, anam. substr.). – 9.5 km ESE of Esch-sur-Alzette, 2 km SE of Dudelange, Bloklapp, 288 m, on *O. aurantiorubra* on bark of *S. caprea*, 13.III.2001, G. Marson (H.B. 6882e, anam. substr.). – 2.3 km SE of Dudelange, Därebësch, 255 m, on *O. eucalypti* on bark of *S. cinerea*, 30.X.2014, G. Marson (G.M. 2014-10-30.3, anam. substr.; sq.: MK473405 [from conidia]) – **Remich**, Valée de Moselle, 6 km S of Remich, 1 km E of Remerschen, 145 m, on *O. eucalypti* on *S.* ?*viminalis*, 16.VII.2001, G. Marson (ø). — **GERMANY**: **Bayern**, **Oberbayern**, 8.5 km SE of München, 1 km ESE of Neuperlach, 543 m, on *O. eucalypti* on bark of *Salix*, 12.III.2015, B. Fellmann (anam. only, doc. vid.). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 13 km SE of Montélimar, 0.4 km SW of Abbaye d'Aiguebelle, 215 m, on *O. aurantiorubra* on bark of *Cercis siliquastrum*, 22.IX.2009, G. Marson (H.B. 9238b, anam. only). – Préalpes du Dauphiné, 10 km ESE of Sederon, W of Curel, 765 m, on *O. vinosa* on wood of *Spartium junceum*, 17.VIII.2001, G. Marson (H.B. 7024a, anam. substr.). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 16 km SW of Sisteron, 6.5 N of St.-Étienne-les-Orgues, 2.7 km SW of Sommet de Lure, 1447 m, on *O. flagellispora* on bark of *Cedrus atlantica*, 8.VIII.2003, G. Marson (H.B. 7604c, anam. substr.). — **SPAIN**: **Extremadura**, **Cáceres**, 9.3 km SE of Jarandilla de la Vera, 8.5 km NNE of Talayuela, Cuestas de Torresca, 363 m, associated with *O. albidorosea* & *O. gambelii* on bark of *Eucalyptus camaldulensis*, 28.II.2016, E. Rubio (E.R.D. 6658, doc. vid., anam. only). — **PORTUGAL**: **Guarda**, 4 km ENE of Sabugal, 2.3 km S of Rendo, Quinta dos Prados, 843 m, branch of *Salix*, on apothecia of ?*O. aurantiorubra*, 23.XI.2019, M.A. Ribes (anam. only, doc. vid.). — **AUSTRIA**: **Burgenland**, 2.5 km SSE of Eisenstadt, 2 km NW of Trausdorf, motorway junction, 150 m, branch of *Salix* (?)*cinerea*, on *O. aurantiorubra*, 27.I.2013, Z. Jorgovanovic, vid. I. Wagner (I.W. 130127, anam. substr., doc. vid.). — **SLOVAKIA**: **Žilina**, 7.7 km W of Tvrdošín, 1.2 km SE of Brezovica, 750 m, branch of *Salix*, on *O. aurantiorubra*, 31.XII.2017, A. Polhorský (ex A.P. 18/50, BRA-CR29844, **holotype**, doc. vid.; sq.: MK028717). — **SERBIA**: **Vojvodina**, Fruška Gora, 12 km SSE of Novi Sad, 6.5 km NNW of Irig, N of TV tower, 511 m, branch of *Salix alba*, on apothecia of *O. aristata*, 26.VI.2019, D. Savić (FG-1096, anam. substr., doc. vid.). – 6 km NNW of Irig, W of WWII memorial, 430 m, branch of *Larix decidua*, on apothecia of *O. aristata*, 18.IX.2019, D. Savić (doc. vid.). — **MONTENEGRO**: 15 km NNW of Podgorica, 1.9 km NE of Donje Selo, Glizica, 210 m, twig of *Punica granatum*, on *O. mali*, 8. & 15.V.2016, B. Perić (B.P. Dgf/C7D-15-05-16, anam. only, doc. vid.). – 17 km SSW of Podgorica, 1 km W of Bistrice, 8 m, branch of *Salix*, on *O. aurantiorubra*, 20.II.2016, B. Perić (B.P. Dgf/C7D-20-02-16, anam. only, doc. vid.). — **CANADA**: **Prince Edward Island**, 16 km WSW of Charlottetown, 1.4 km ENE of Bonshaw, 4 m, twigs of *Picea ?glauca*, on *O. vinosa*, 26.XI.2018, A. Carter (anam. only, doc. vid.).

Not included. ***H*. cf. *orbiliicola*** (with rather small, ± symmetrical conidia): **AUSTRALIA**: **Queensland**, Wet Tropics, 3 km NW of Cairns, E of Edge Hill, Cairns Botanical Garden, 5 m, on *O. neocomma*, on branch of indet. climber, 26.VIII.2006, G. Marson (H.B. 8608b ø, anam. substr.).

H*. aff. *orbiliicola (with ± asymmetrical conidia): **AUSTRALIA**: **Western Australia**, **Carnarvon**, 117 km NNE of Carnarvon, 7 km SSE of Minilya Roadhouse, NW Coastal Hwy, Barrabiddy Creek, 13 m, on *O. ?myriella* (H.B. 8997c) on branch of *Vachellia farnesiana*, 6.XI.2007, G. Marson (H.B. 8997d ø, anam. only). – 183 km SSE of Carnarvon, 10 km W of Overlander Roadhouse, 12 km NE of Hamelin Pool, Denham-Hamelin Rd, 67 m, on *O. ?pleioserpens* (H.B. 7215f) on branch of *Acacia*, 7.XII.2001, G. Marson (H.B. 7215e, anam. only). – ibid., on *Orbilia* sp. on twig of *Acacia*, 6.XI.2007, G. Marson (ex H.B. 8727j, mixture in MEL 2389251 [type *O. myrioauris*], anam. only). – **Pilbara**, 1.5 km SW of Wittenoom, Wittenoom Gorge, 467 m, on *O. pleioserpens* on branch of *Acacia*, 29.X.2007, G. Marson (H.B. 8976i, anam. only). – 30 km NW of Newman, Great Northern Hwy, northern border of Ophthalmia Range, 706 m, on *O. octoserpentina*, on bark of *Psydrax latifolia*, 27.XI.2001, G. Marson (H.B. 7416d ø, anam. only). – **Northern Territories**, MacDonnell Ranges, 50 km SW of Alice Springs, SE of Waterhouse Range, Stuart Hwy, 613 m, on *Orbilia* sp. on branch of *Acacia estrophiolata*, 10.X.1998, G. Marson (H.B. 7223c ø, anam. only). – **Queensland**, Brigalow Belt South, 138 km SSW of Rockhampton, 11 km SW of Banana, Dawson Hwy, 136 m, on *O. acaciae* on twig of *Geijera parviflora*, 22.X.1998, G. Marson (H.B. 6279e, anam. substr.).

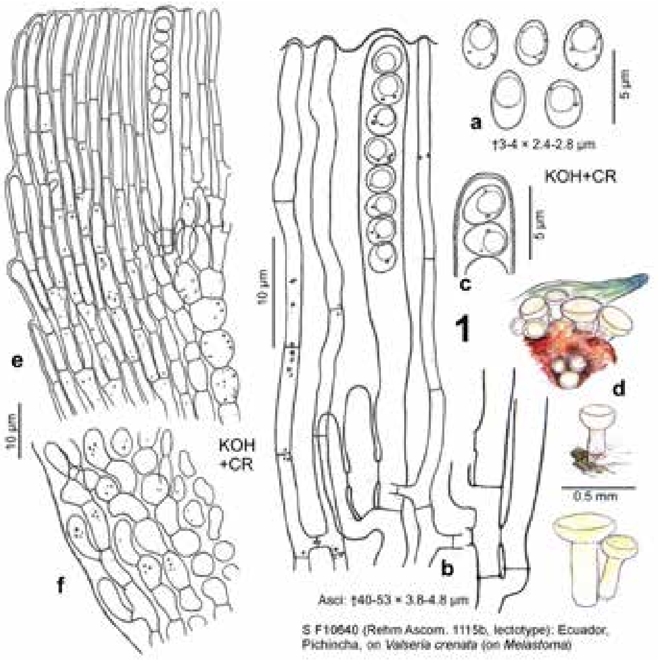


Plate 132. **1**: *Hyalorbilia anonyma*. – **a**. ascospores; **b**. ascus and paraphyses, ascus bases with croziers; **c**. ascus apex; **d**. rehydrated apothecia; **e**. median section of ectal excipulum (margin and mid flanks); **f**. id., at lower flanks.

Hyalorbilia anonyma (Rehm) Baral, **comb**. **nov**., MB 813453 — Pl. 132

Basionym: *Pezizella anonyma* Rehm, Hedwigia 34, Beibl.: (165) (1895)
≡ *Mollisiella anonyma* (Rehm) Rehm, Hedwigia 44: 9 (1905)
≡ *Helotiopsis anonyma* (Rehm) Höhnel, Österr. Bot. Z. 63: 301 (1913) (superfluous combination by Sherwood & Korf, Mycotaxon 3: 323, 1976)
≡ *Pithyella anonyma* (Rehm) Korf & W.Y. Zhuang, Mycotaxon 29: 4 (1987)

Etymology: not explained by the author.

Typification: Ecuador, Quito, branch of *Melastoma*, VII.1892, G. v. Lagerheim (Rehm Ascomyc. 1115b, S-F10640, lectotype, designated by Sherwood & Korf 1976).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.3 mm diam., pale yellowish-chlorinaceous to bright honey-yellow, ± gregarious; disc ± flat, margin even; stipe very distinct, 0.1–0.5 × 0.1–0.2 mm. **Asci** †40–53 × 3.8–4.8 µm, 8-spored, spores (†) uniseriate; **apex** (†) hemispherical, firm-walled (0.4 µm thick); **base** with medium long, ± thick stalk, apparently simple-septate but with crozier-like connection (anastomosis) between the asci (no typical crozier observed). **Ascospores** †3–4 × 2.4–2.8 µm, subglobose to broadly ellipsoid, rarely ovoid; **SBs** (†) visible as a very inconspicuous, ± globose, eccentric region 1.5–2 µm diam.; with 2–6 minute **LBs**. **Paraphyses** apically uninflated, terminal cells †13–28 × 1.2–2.3 µm, lower cells †8–14 × 1–1.7 µm, unbranched. **Medullary excipulum** forming vertical chains of globose-prismatic cells †5–9 × 5–7 µm giving rise to paraphyses. **Ectal excipulum** in stipe of non-gelatinized textura prismatica-porrecta, cells †17–30 × 6–10 µm, at lower flanks of strongly gelatinized horizontal t. angularis-prismatica, cells †~4–10 × 3–5 µm, common walls 1–3 µm thick; near margin of less gelatinized t. porrecta, marginal cortical cells in median section †~10–15 × 1.5–3 µm. **Anchoring hyphae** abundant at base, long, radiating, †(1.5–)2.5–3.5(–4) µm wide, walls 0.2–0.3 µm thick, often moniliform, densely septate. **Exudate** over paraphyses, margin and flanks 0.2–0.3 µm thick, continuous, smooth. **— ANAMORPH**: unknown.

Habitat: on gall- or canker-like, light ochre-brown, warted, 2–3 mm thick stromata of (?immature) '*Valsaria crenata* Rehm' [in sched., = *V. baccharidis* (Pat.) Rehm 1895: 164], on a corticated, 7 mm thick undecayed branch of *Melastoma* sp. **Associated**: thallose liverwort. **Desiccation tolerance**: unknown. **Altitude**: ~2830 m a.s.l. **Phenology**: VII (tropical belt).

Taxonomic remarks. In concordance with Korf & Zhuang (1987), we here accept *H. anonyma* as a species distinct from *H. erythrostigma*, although we are not sure about whether it is more than only a marginal population of that species. Korf & Zhuang did not mention the differential characters between the two taxa. Judging from their illustration of *Pithyella erythrostigma* and the description of *Helotiopsis anonyma* in Sherwood & Korf (1976), the differences were apparently seen in the marginal excipulum being hyphoid and gelatinized in *H. anonyma* but wide-celled and thin-walled in *H. erythrostigma*, perhaps also in a longer apothecial stalk and shorter asci in *H. erythrostigma* (the difference in spore shape is due to an error, see below).

Examination of the fully mature, abundant lectotype material in S revealed that *H. anonyma* differs in exceptionally long asci, narrower marginal cortical cells of the ectal excipulum, rather narrow, uninflated apices of paraphyses with longer individual cells, and slightly longer ascospores. Another specimen from South America (Peru, Pl. 126: 6) was assigned by us to *H. erythrostigma* because of much shorter asci, smaller spores, wider paraphyses (2–4 µm), and wider marginal cortical cells (†10–12 × 3–5 µm).

A further distinguishing character could lie in the ascogenous hyphae, which appear to arise from croziers with a slit-like perforation as in *H. erythrostigma*, but the downward protuberance at the beginning of crozier formation (see Pl. 126: 2, 6) was not seen here. Rather, the ascus formation appears to be of the simple-septate type, except that an anastomosis is formed between the asci near their base. Further research is necessary on this peculiarity, which might well have been overlooked in other species of *Hyalorbilia*.

An indistinct bluish IKI-reaction which turned negative at higher concentration was observed in the region of the medullary excipulum. This reaction is probably due to the presence of carotenoids. Korf & Zhuang (1987) were unsure whether the spores are smooth or finely warted. Yet, as in *H. erythrostigma* it was impossible in the present study to see any trace of spore markings under oil immersion. A large globose eccentric SB could be discerned as a very faint region in the dead spores.

Rehm (1895) gave the asci as 45 × 5 µm and thought they were immature, but later (1905) he gave a size of 45–50 × 5 µm and found globose spores 3 µm diam., uniseriate. The apothecia are described as 0.1–0.5 mm diam., with a short and thin stipe, yellowish-hyaline, dry turning amber. Sherwood & Korf (1976) designated the here examined duplicate in S as lectotype, but studied also an isolectotype in NY. Their description in part relies on Rehm's, and also includes globose spores 2–3 µm diam., in disagreement with the present result of broadly ellipsoid spores.

Rehm (1905) compared *Mollisiella anonyma* with *Pseudohelotium apicale* (Berkeley & Broome) Sacc. Korf & Zhuang (1987) transferred both species to *Pithyella* Boud., and accepted Boudier's placement of *Pithyella erythrostigma* in that genus. They considered *Pithyella apicalis* as 'at best critically distinct' from the type species of *Pithyella*, *P. hypnina* (Quél.) Boud., and thought the genus to belong to the *Helotiales* (see p. 209).

Not included collection. O. Ceska (pers. comm.) studied a collection on an *Alnus* branch from Newfoundland (eastern Canada) with apothecia growing mainly on old stromata (IVV: 23.VIII.2017). This deviates in longer spores of *(4–)4.5–5(–5.5) × (2–)2.5–3 µm with a rather small SB at one end. A trinacrium-like conidium with very narrow stipe and arms was observed, which resembles those of *H. erythrostigma*.

Ecology. *Hyalorbilia anonyma* grew abundantly on deformations of the bark caused by *Valsaria baccharidis* on branches of *Melastoma* sp. The collection derives from a subtropical humid highland climate in the northwest of South America. Both the host fungus and the inhabited branch are very slightly decayed, indicating that *H. anonyma* could be a hyperparasite.

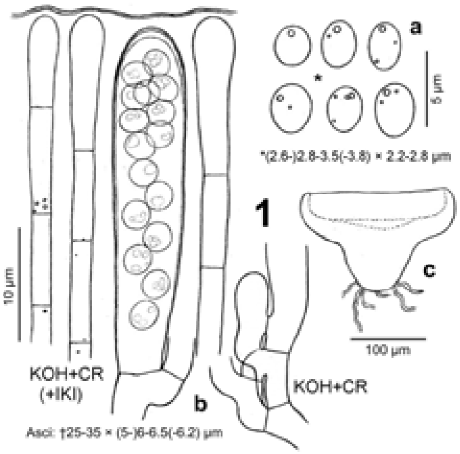


Plate 133. **1**: *Hyalorbilia pleioerythrostigma*. – **a**. ascospores; **b**. ascus and paraphyses, ascus base with croziers; **c**. apothecium in median section.

Specimens included. **ECUADOR**: **Pichincha**, La Sierra, ~4.5 km SSW of Quito, San Jorge, ~2830 m, branch of *Melastoma*, on deformations of bark, VII.1892, G. v. Lagerheim (S-F10640, Rehm Ascomyc. 1115b, **lectotype**, H.B. 6435 ø).

Not included. **CANADA**: **Newfoundland**, 8 km NW of Stephenville, Table Mt., 312 m, branch of *Alnus alnobetula*, on bark and old pyrenomycete, 23.VIII.2017, O. & A. Ceska (anam. substr., doc. vid.).

Hyalorbilia pleioerythrostigma Baral, **sp**. **nov**.,

MB 813454 — Pls 133–134

Etymology: named after the 16-spored asci and the resemblance to *H. erythrostigma*.

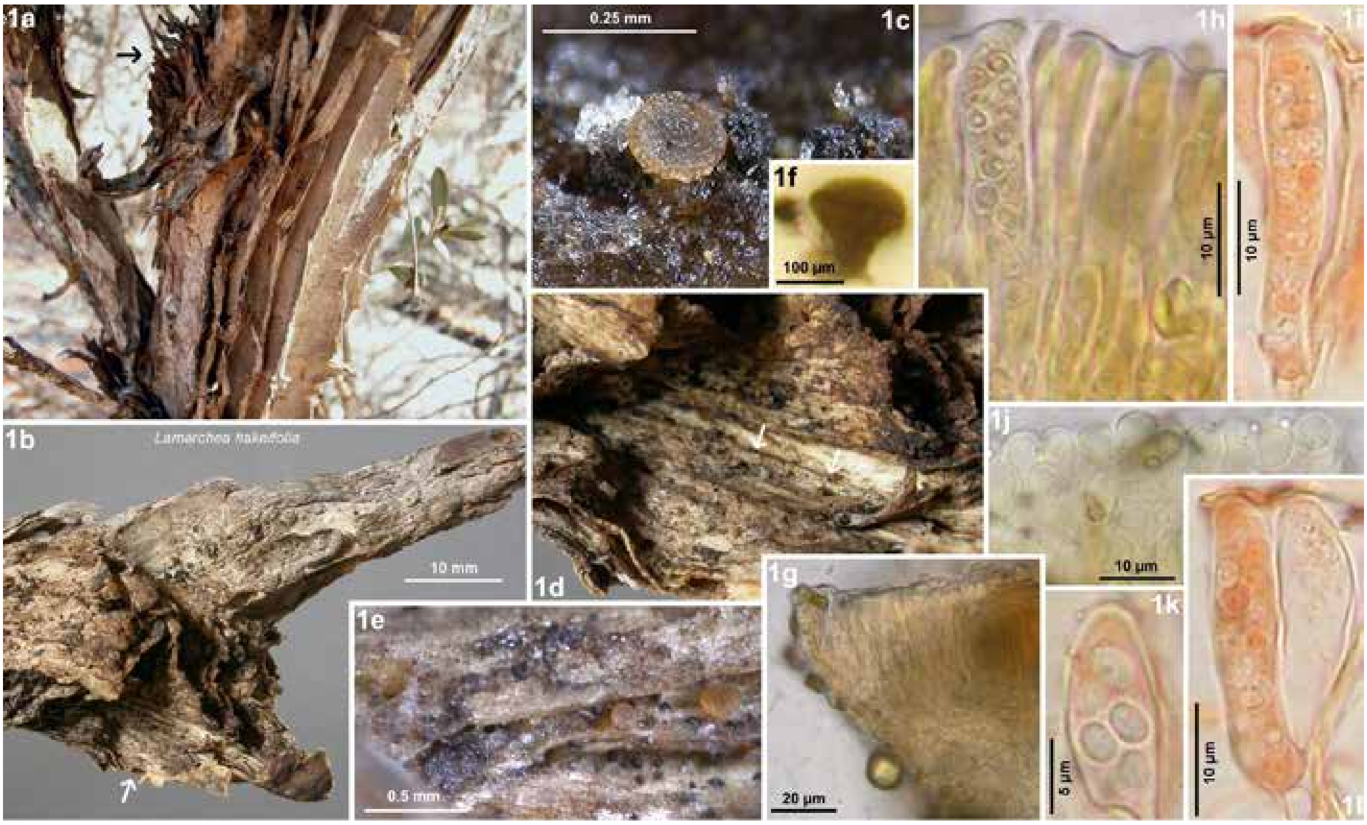


Plate 134. **1**: *Hyalorbilia pleioerythrostigma*. – **1a**. living trunk of *Lamarchea hakeifolia* in semiarid acacia shrubland; **1b**. detached xeric bark; **1c–e**. rehydrated apothecia; **1f**. apothecium in lateral view; **1g**. apothecium in median section; **1j**. margin in top view; **1h–i**, **l**. asci and paraphyses; **1k**. ascospores. – Dead state (**1j** in KOH; **1h** in KOH+IKI; **i**, **k–l** in CR) except for **1g** (with some living cells). — **1a–l**. H.B. 9020 (holotype): Western Australia, Geraldton, on *Lamarchea*.

Typification: Western Australia, Yalgoo, Toolonga, trunk of *Lamarchea hakeifolia*, 8.XI.2007, G. Marson (ex H.B. 9020b, MEL 2389274, holotype).

Latin diagnosis: *Apothecia in statu rehydratata 0.15–0.25 mm diam., pallide ochraceo-aurantiaca, margine subglabro. Asci 16-spori. Ascosporae *2.6–3.8 × 2.2–2.8 µm, subglobosae, guttulis paucis minutis continentes. Habitat ad corticem siccum valde putridum trunci vivi erecti* Lamarcheae hakeifoliae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.25 mm diam., 0.13 mm high (receptacle 0.06 → 0.05 mm), pale cream-rose-orange, slightly translucent, round, non-gelatinous, singly or very scattered; disc flat, margin distinct, 5 µm protruding, ± rough; with a ± cylindrical stipe 0.07 × 0.09 mm, superficial but also in small clefts. **Asci** †25–35 × (5–)6–6.5(–7.2) µm, 16-spored, spores †2–4-seriate; **apex** (†) hemispherical to slightly conical, thin-walled (wall 0.4 µm thick); **base** unstalked, arising from croziers with or without a slit-like perforation. **Ascospores** *(2.6–)2.8–3.5(–3.8) × 2.2–2.8 µm, †2.5–3 × 2–2.5 µm, subglobose to broadly ellipsoid; **SBs** absent (?), with a few **LBs** 0.1–0.5 µm diam. **Paraphyses** apically slightly to medium clavate, terminal cells †8–15 × 2.5–3.7 µm, lower cells †8–9 × 1.6–2.2 µm; unbranched at upper septum, firmly agglutinated in gel. **Medullary excipulum** 10 µm thick, of non-gelatinized textura angularis, indistinctly delimited. **Ectal excipulum** in stipe of (†) thin-walled t. globulosa, 80 µm thick, cells *10–15(–18) × 7–11 µm; at flanks of indistinctly horizontally oriented t. globulosa-angularis-prismatica, cells *6–13 × 5–9 µm, in surface view of t. prismatica, cells †5–10 × 3–6 µm, marginal cortical cells */†9–17 × 4–7.5 µm, thin-walled. **Anchoring hyphae** sparse, †2–5 µm wide, walls 0.2–0.3 µm thick, radiating. **SCBs** and **VBs** unknown. **Exudate** over paraphyses and marginal excipulum 0.2–0.6 µm thick, continuous, smooth, hyaline, lying over gel. — **ANAMORPH**: unknown.

Habitat: collected 0.5–1.5 m above the ground, corticated, 10–18 cm thick living trunk of *Lamarchea hakeifolia* sp., on very decayed, ± detached bark, strongly greyed, no algae. **Associated**: *Capronia* spp. {2}, *Claussenomyces* sp., *Orbilia austroobtusispora*, *O. gemma*, *O. kingsiana*, *O. lamarcheae*, *O. myriolilacina*, *O. pseudoflagellispora*, *O. ?pubescens*, *Ostropales*, *Symbiotaphrina desertorum*, *Xerotrema* sp. **Desiccation tolerance**: excipular cells and some ascospores still viable after 16.5 months. **Altitude**: 190 m a.s.l. **Geology**: Cretaceous sedimentary rock (red-brown sand). **Phenology**: XI (southern hemisphere).

Taxonomic remarks. *Hyalorbilia pleioerythrostigma* closely resembles *H. erythrostigma* except for the 16-spored asci and the fact that no SBs were seen in the living ascospores. Since only a few living spores could be found, it is possible that they were not fully mature. However, some dead asci with apparently mature dead spores were seen in the examined apothecia, therefore, the population seems to be well developed.

Ecology. The very sparse, minute apothecia of *H. pleioerythrostigma* were detected on detaching xeric bark of a vital trunk of *Lamarchea hakeifolia* in a semiarid subtropical acacia open shrubland of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, NW Coastal Hwy, 190 m, trunk of *Lamarchea hakeifolia*, on bark, 8.XI.2007, G. Marson (ex H.B. 9020b, MEL 2389274, **holotype**).

Hyalorbilia latispora Baral, G. Marson & P. Perz, **sp. nov.**, MB 813460 — Pls 135–136

Etymology: referring to the short ascospores.

Typification: Netherlands, Noord-Brabant, Tilburg, stem of *Senecio*, 11.X.2004, L. Rommelaars (ex H.B. 7592b, M-0276413, holotype).

Latin diagnosis: Hyalorbiliae rotiferae *similis*, *sed ascosporae distincte latiores.*

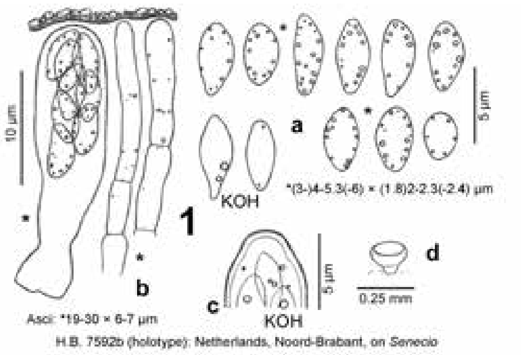


Plate 135. **1**: *Hyalorbilia latispora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium (fresh).

Description: — **TELEOMORPH**: rehydrated 0.12–0.22 mm diam., 0.07 mm high (receptacle 0.035 mm), whitish, translucent, round, scattered; disc flat, margin thin, not protruding, smooth; subsessile or with distinct stipe, superficial. **Asci** *18–25(–30) × 5.5–6.5(–7) µm {5}, †18–27(–31) × 4.5–5.9 µm {2}, 8-spored, spores *3–4-seriate, pars sporifera *11–14 µm long; **apex** (†) hemispherical to distinctly conical; **base** with short, thick stalk, with croziers {3}, with or without perforation. **Ascospores** *(3–)4–5.5(–6) × (1.8–)2–2.3(–2.5) µm {6}, †(3–)3.7–5(–5.5) × 1.6–2.2 µm {1}, broadly (cylindric-) ellipsoid to fusoid or fusiform, ends obtuse (to subacute), base rarely shortly attenuated, sometimes ± inequilateral; **SBs** 0.15–0.25 µm diam., globose, ~3–5 in each half, oriented at the periphery {5}; with a few minute, rarely medium-sized LBs. **Paraphyses** apically uninflated or slightly clavate, terminal cells *11–14 × 2–3 µm {1}, lower cells *5–8.5 × 1.7–2 µm {1}; unbranched at upper septum. **Medullary excipulum** not examined. **Ectal excipulum** at base and flanks of non-gelatinized t. angularis-prismatica, cells *8–11 × 4–7 µm {1}, horizontally oriented at flanks; 5 µm thick near margin, of t. prismatica, cortical cells *3–3.5 {T} or †4.5–6.5 µm {1} wide, in some populations ± protruding and hair-like, *~12–15 × 5–8.5 µm, ± conical, firm-walled (0.3–0.5 µm thick) {2}. **Anchoring hyphae** sparse, *1.3–2.3 µm wide, walls 0.2 µm thick {1}. **Exudate** over paraphyses and margin 1–2 µm thick, continuous, with coarse adhering granules. — **ANAMORPH**: curucispora-like (from ascospore isolate {1}). **Culture**: ascospores shot on agar tardily germinating, hyphae very slow-growing, *1.5–3 µm wide. **Conidiophores** short, not clearly seen. **Conidia** *11–12(–13.7) × 9.5–12 µm, with two ‘arms’ and two ‘legs’ (rarely one arm branched), legs lying in a plane vertical to the arms; upper arms curved downwards, actual length *5–8 × 2.5–3.3 µm, legs straight, bent downwards at their insertion, *6.5–9 × 2.5–2.8 µm, arms and legs 0–1-septate, with a few 0.5–1.2 µm large LBs and some smaller ones; one of the two arms has a truncate end and is in fact the conidial stipe by which the conidium was attached to the conidiophore.

Habitat: 0–1 m above the ground, on ~15 mm thick branches of *Clematis vitalba* {2}, on bark {2}; cupule (pericarp) of *Fagus sylvatica* {1}, stems of *Rubus fruticosus* {2}, stems of *Senecio* sp. {1}. **Associated**: *Hyalorbilia subfusispora* {2}, *Karstenia rhopaloides* {1}, *Lecophagus ellipsoideus* {2}, *Orbilia aristata* {1}, *O. breviaristata* {1}, *O. clavuliformis* {1}, *O. eucalypti* {1}, *O. filiformis* {1}, *O. obtusispora* {1}, *O. pleioeuonymi* {1}, *O. quaestiformis* {1}, *O. ungulata* {1}, *O. vinosa* {1}, *O. vitalbae* {2/1}, *Pyrenopeziza* sp. {1}, old pyrenomycete {1}; little greyed, algae absent or medium abundant. **Desiccation tolerance**: fully tolerant for at least 1 day. **Altitude**: 12–837 m a.s.l. **Geology**: Keuper (Knollenmergel), Lower Jurassic sandstone and shale; granite/granodiorite & gneiss. **Phenology**: I, VII–VIII, X–XI.

Taxonomic remarks. *Hyalorbilia latispora* is tentatively separated from *H. rotifera* by its wider, rarely distinctly heteropolar ascospores. The presence of spore bodies might be a further distinctive feature, but these were not consistently absent in *H. rotifera*, and not clearly seen in the specimen on *Fagus* cupule. *H. latispora* is also similar to *H. subfusispora*, but differs in shorter spores which never contain SBs larger

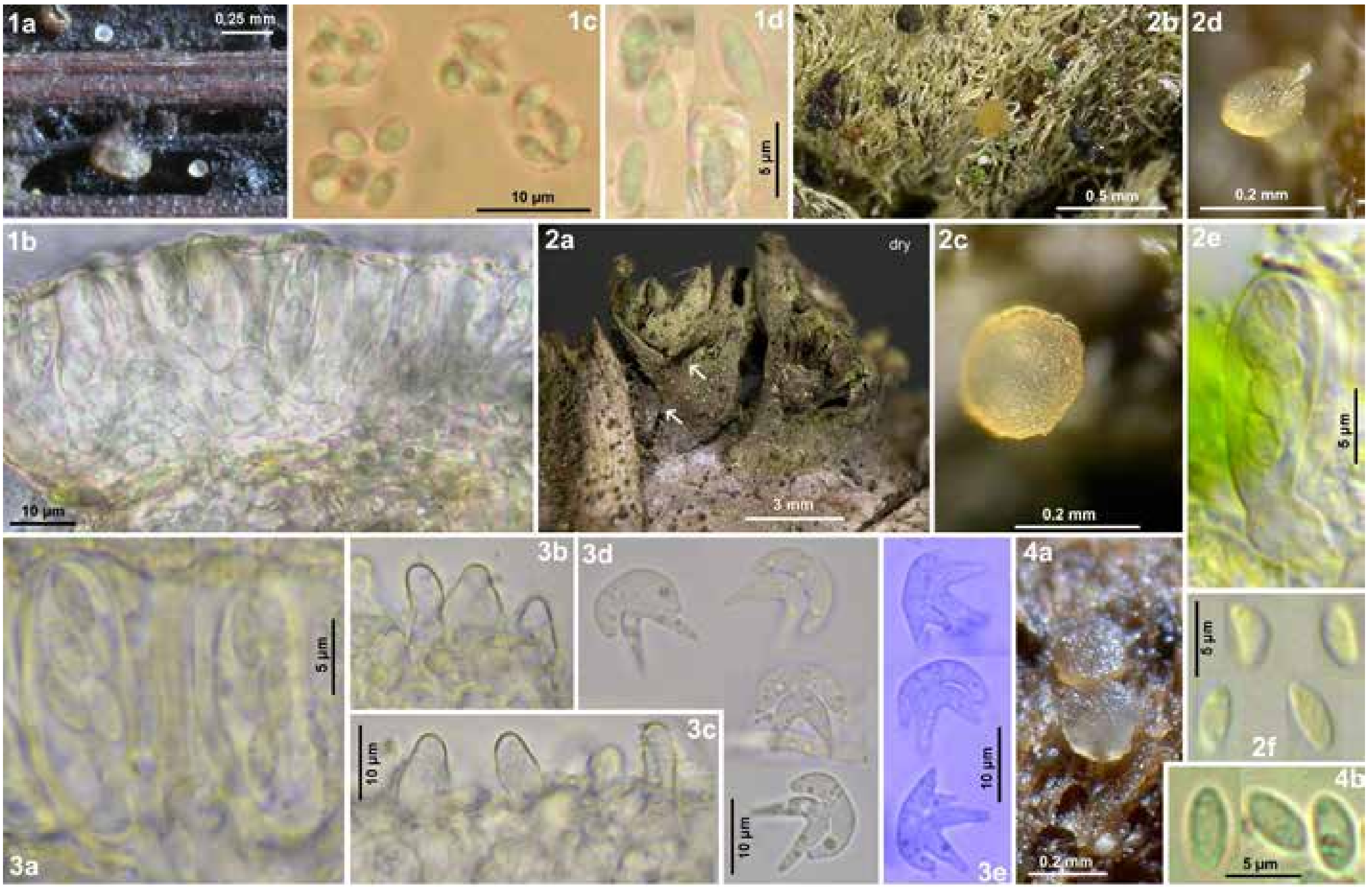


Plate 136. **1–4**: *Hyalorbilia latispora*. – **1a**, **2c–d**, **4a**. fresh apothecia; **2a–b**. dry apothecia 1b. apothecium in median section; **3b–c**. hair-like protuberances at the margin; **2e**, **3a**. asci; **1c–d**, **2f**, **3a**, **4b**. ascospores (**1c**: recently ejected and still in groups); **3d–e**. conidia from pure culture (**3e** in CRB). – Living state. – **4a–b**: phot. P. Perz. — **1a–c**. H.B. 7592b (holotype): Netherlands, on *Senecio*; **2a–f**. 27.I.2007: Luxembourg, Echternach, on *Rubus*; **3a–e**. G.M. 2013-11-16.3: Luxembourg, Dudelange, on *Clematis*; **4a–b**. P.P. 20100817-1: Poland, on *Fagus* cupule.

than 0.3 µm. For a very sparse similar collection on bark of *Ilex* see under *H. subfusispora* (Pls 116: 9; 117: 15).

Variation. The marginal cells seen in the holotype were distinctly narrower than in the specimen on *Fagus* cupule. Distinctly protruding, conical, firm- to thick-walled (0.2–0.5 µm) marginal cells were observed in the collections on *Rubus* (Germany) and *Clematis*. The ascospores vary somewhat in shape between (cylindric-)ellipsoid to fusoid-fusiform, but only slightly in size: *4.2–5.2 × 1.8–2.4 µm (*Clematis*), *(3.3–)3.8–5.5 × 2–2.5 µm (*Fagus*), *4–5.2 × 2–2.4 µm (*Rubus*, Luxembourg), *5–6 × 2–2.3 µm (*Rubus*, Germany).

Anamorph. Conidia were formed in the very slow-growing ascospore isolate from *Clematis* (Pl. 136: 3d–e; fig. 3x in Baral et al. 2017b erroneously as H.B. 9902c [= G.M. 2014-07-25.1]). They resemble *Curucispora flabelliformis* as described by Ando (1993). The apothecium from which the isolate originates was at first thought to be *Lecophagus ellipsoideus* which grew in association, but the narrow hyphae in the culture contradict this identity, and a sequence from apothecia sampled the next year from the same area and substrate confirmed identity of the culture with *H. latispora.*

Similar curucispora-like but slightly larger conidia were observed on *Ulmus* bark in association with *O.* cf. *frangulae* (Luxembourg, Holtz, IVV: 7.V.1999). Gönczöl & Révay (2006: figs 9–12) and Révay & Gönczöl (2010: fig. 13) figured very similar conidia as ‘unknown sp. 2’, collected from rainwater from Germany (Tübingen) on *Fagus* and *Prunus*, and from Hungary (Királyrét, Budapest) on *Quercus*, *Fagus*, *Chamaecyparis*, *Cupressus*, *Picea*, and *Taxus*, but with ~1.5–2× larger size. Gönczöl & Révay’s figures suggest to believe that all extremities lie in one plane. The conidia of the present culture, however, are clearly 3-dimensional, with the 2 ‘legs’ lying in a plane vertical to that of the ‘arms’. When viewed under the light-microscope, pressure by the cover slip forces such conidia in a 2-dimensional form.

Phylogeny. Sequences were taken from the ascospore isolate of the *Clematis* sample from 2013 and from apothecia sampled on *Clematis* in 2014, comprising ITS and LSU. The S1506 intron is absent in both. In the ITS they differ by 1.2% (5 nt in ITS1 and 3 nt in ITS2), while in the overlapping D1 domain of LSU they concur.

H. latispora clustered unresolved among *Hyalorbilia* s.str., the *Vermispora* clade, and the *erythrostigma-orbiliicola* clade (Phyls 5–6, S5), though with a very high distance in the ITS region (~27–31%). Even in the LSU the distance to any other species of *Hyalorbilia* lies in the range of ~10–14% (614 nt). Also in Baral et al. (2017b) *H. latispora* clustered unresolved within the *Hyalorbilia-Vermispora* clade.

Specific nucleotides. In the 5.8S *H. latispora* concurs at three characteristic positions with the *Vermispora* clade (pos. 30, pos. 64 [3’-end of Orb5.8s1F], pos. 98), which would support a relationship with this group (Tabs 18, 56). At pos. 64 and 98 it concurs also with *H. erythrostigma*/*orbiliicola*, and at pos. 140 only *H. erythrostigma*/*orbiliicola* concur with the *Vermispora* clade. In contrast to this, *H. latispora* and *H. erythrostigma*/*orbiliicola* concur at pos. 11 and 85 with *Hyalorbilia* p.p.maj., where the *Vermispora* clade differs (Tab. 61).

Ecology. The mostly very sparse apothecia of *Hyalorbilia latispora* appear to be plurivorous. The known hosts include herbaceous stems and woody branches as well as cupules. The collections were mainly on xeric substrate, except for the *Fagus* cupule that was lying on the moist ground. The collection sites comprise subatlantic to subcontinental, cold- to orotemperate humid areas. The two samples on stems of *Rubus fruticosus* each comprised only a single apothecium. The others were on herbaceous stems of *Senecio*, on *Fagus* cupule, and on a *Clematis* branch. In the collections on *Rubus* and *Clematis* from Luxembourg the similar *H. subfusispora* was present. The locations of the two *Clematis* samples were 160 m away from each other along a railway track bordered by a thermophilous forest stripe.

Specimens included. **LUXEMBOURG**: **Gutland**, **Echternach**, 4 km SW of Echternach, 1.5 km E of Scheidgen, N of Michelshaff, S of Seidemuer, 320 m, stem of *Rubus fruticosus*, 27.I.2007, G. Marson (ø). – **Esch-sur-Alzette**, 4.2 km S of Bettembourg, 1.7 km E of Dudelange, along railway, 290 m, branch of *Clematis vitalba*, on bark, 16.XI.2013, G. Marson (G.M. 2013-11-16.3, anam. cult.; sq.: MK493158). – ibid., branch of *C. vitalba*, on bark, 25.VII.2014, G. Marson (G.M. 2014-07-25.1, H.B. 9902c ø; sq.: KT222386). — **NETHERLANDS**: **Noord-Brabant**, 6 km SW of Tilburg, 5 km E of Gilze, Kaaistoep, 12 m, on stem of *Senecio*, 11.X.2004, L. Rommelaars (ex H.B. 7592b, M-0276413, **holotype**). — **POLAND**: **Lower Silesia**, 17 km SE of Bystrzyca Kłodzka, 1.7 km NE of Jodłów, 837 m, on cupule of *Fagus sylvatica*, 17.VIII.2010, P. Perz (P.P. 20100817-1, doc. vid.). — **GERMANY**: **Baden-Württemberg**, 5 km NE of Tübingen, S of Pfrondorf, Obere Mähder, 395 m, stem of *Rubus fruticosus*, 24.VII.2002, H.O. Baral (H.B. 7171d ø).

Hyalorbilia hergiswiliana Baral, Polhorský, D. Savić & E. Weber, **sp. nov.**, MB 813959 — Pls 137–138

Etymology: named after the village close to the type locality, Hergiswil (Luzern).
Typification: Switzerland, Hergiswil, branch of *Acer pseudoplatanus*, 15.VIII.2006, H.O. Baral (ex H.B. 8235b, M-0276492, holotype)

Latin diagnosis: Hyalorbiliae rotiferae *similis sed ascosporae leniter breviores et latiores, asci longiores, excipulum ectale textura globulosa, cellulae marginales angustiores, apothecia majores;* Hyalorbiliae latisporae *similis sed ascosporae leniter minores, absque corpusculis refringentibus KOH-sensitivis, asci angustiores, apice subtruncato. Habitat ad lignum putridum rami sicci* Aceri, Corni, Koelreuteriae *in zona oro- ad mesotemperata humida Europae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.3(–0.55) mm diam., 0.11–0.18 mm high (receptacle 0.045–0.09 mm), pale greyish(-rosaceous) to cream or light reddish-brownish, medium translucent, round or sometimes elongated, scattered; disc slightly concave to slightly convex, margin indistinct or distinct, not protruding, smooth; sessile on an obconical base or with a stipe of up to 0.085 × 0.1 mm, superficial but ± immersed in algal layer or in clefts in outer wood layer. **Asci** *(25.5–)27–35(–38) × 4.3–5.5 µm {3}, †21–26 or 28–37 × 3.6–4.7(–5.3) µm {T}, 8-spored, spores *2–4-seriate, pars sporifera *10–15 µm long; **apex** (†) slightly to medium truncate (never indented or laterally inflated), hemispherical in side view, thin-walled {2}; **base** sessile or with short to medium long, thick, ± flexuous stalk, often h-shaped, often forming croziers {2} with or without small to large slit-like perforation. **Ascospores** *(3.2–)3.5–4.2(–4.4) × (1.6–)1.8–2(–2.1) µm {3}, ellipsoid to fusoid, sometimes fusoid-clavate, apex obtuse, base sometimes attenuated, straight to slightly inequilateral; **SBs** apparently absent, some spores with 1–4 minute **LBs** {2}. **Paraphyses** apically uninflated to slightly or sometimes medium capitate, terminal cells *(13–)16–24 {2} × (2–)2.5–3.5(–4.5) µm {3}, †11–24 × 2–2.7 µm {T}, lower cells *5–9 × 1.8–2.7 µm {2}, †3–6 × 1.5–2 µm {T}; branched or unbranched at upper septum. **Medullary excipulum** hyaline, 35–50 µm thick, of dense, small-celled, non-gelatinized textura intricata, medium sharply delimited from ectal excipulum. **Ectal excipulum** hyaline {T} or with light reddish-ochre cortex, of (†) thin-walled t. globulosa(-prismatica) at base and lower flanks, 30-60 µm thick near base, cells *7–15(–18) × 5–11 µm {T} or *5–8 × 4–6 µm {2}; 30–50 µm thick at lower flanks, irregularly vertically oriented; 15–20 µm thick at mid flanks, indistinctly oriented at ~20–50°; 10–15 µm thick at margin, of t. porrecta oriented at 0–10°, marginal cortical cells *5–10 × 2.5–3(–4) {2} or †9–11 × 2–3 µm {T}; flanks covered by a 3–6 µm thick layer of *2–3(–3.5) µm wide hyphae. **Anchoring hyphae** very sparse, †1.3–2.5 µm wide, walls 0.2–0.3 µm thick {2}. **SCBs** in paraphyses {1} and upper part of medullary excipulum {T} globose, 1–1.5 µm diam., slightly to strongly refractive, disappearing in KOH; **VBs** absent {2} or medium refractive, roundish to elongate {1}. **Exudate** over paraphyses 0.1–0.4 µm thick, smooth or rough-granular, continuous, hyaline, loosely attached, over margin and flanks pale yellowish-chlorinaceous, 0.1–0.3 µm thick, smooth to warted. **— ANAMORPH**: dicranidion-like (presumed, observed on natural substrate {T}). **Conidiophores** unbranched, ~*10–20 × 1.8–2 µm {T}; **conidia** *32–58 × 11–20 µm, 2(–3)-armed, Y-shaped, when 3-armed then sometimes 1 reflexed (K-shaped), stipe *11–20 × 2–3 µm, 1–4-septate, arms *18–36 × 2.8–4 µm, 2–7-septate, containing some small peripheral LBs {T}.

Habitat: collected 0.1–1.8 m above the ground, decorticated, 2–5 cm thick branches of *Acer pseudoplatanus* {1}, *Cornus mas* {1}, *Koelreuteria paniculata* {1}, exposed, ± deeply strongly decayed wood {3}, sometimes in old beetle galleries, in abundant biofilm of

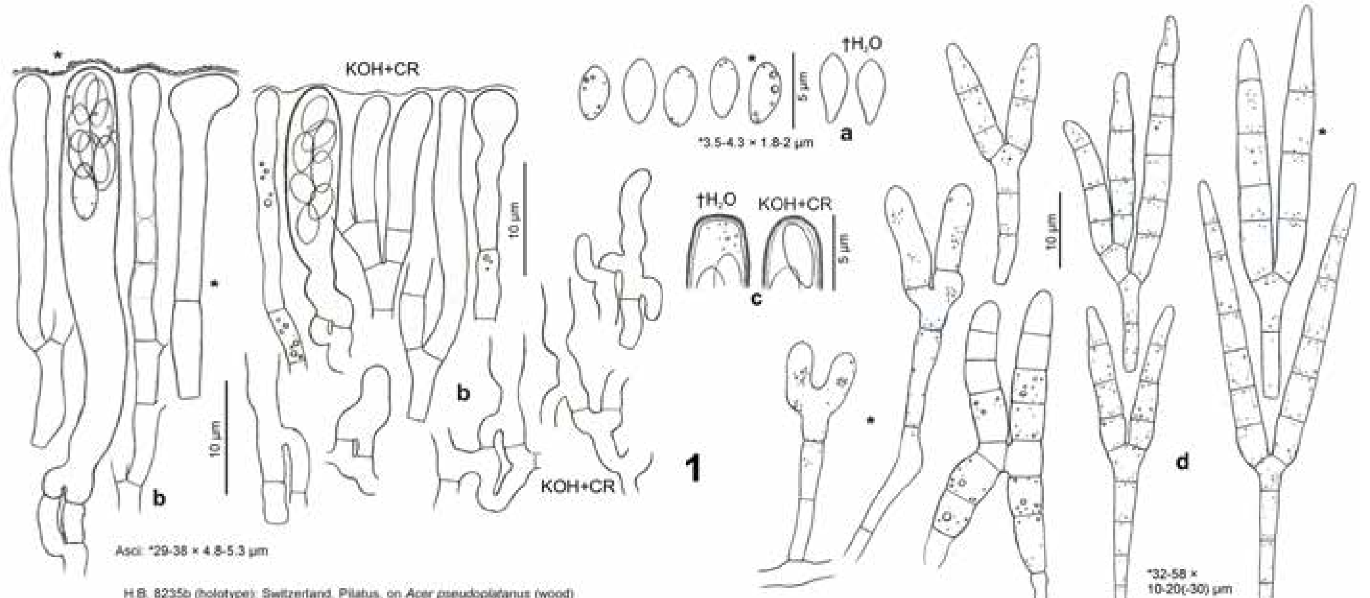


Plate 137. **1**: *Hyalorbilia hergiswiliana*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. conidia (found on associated apothecia of *O. vinosa*).

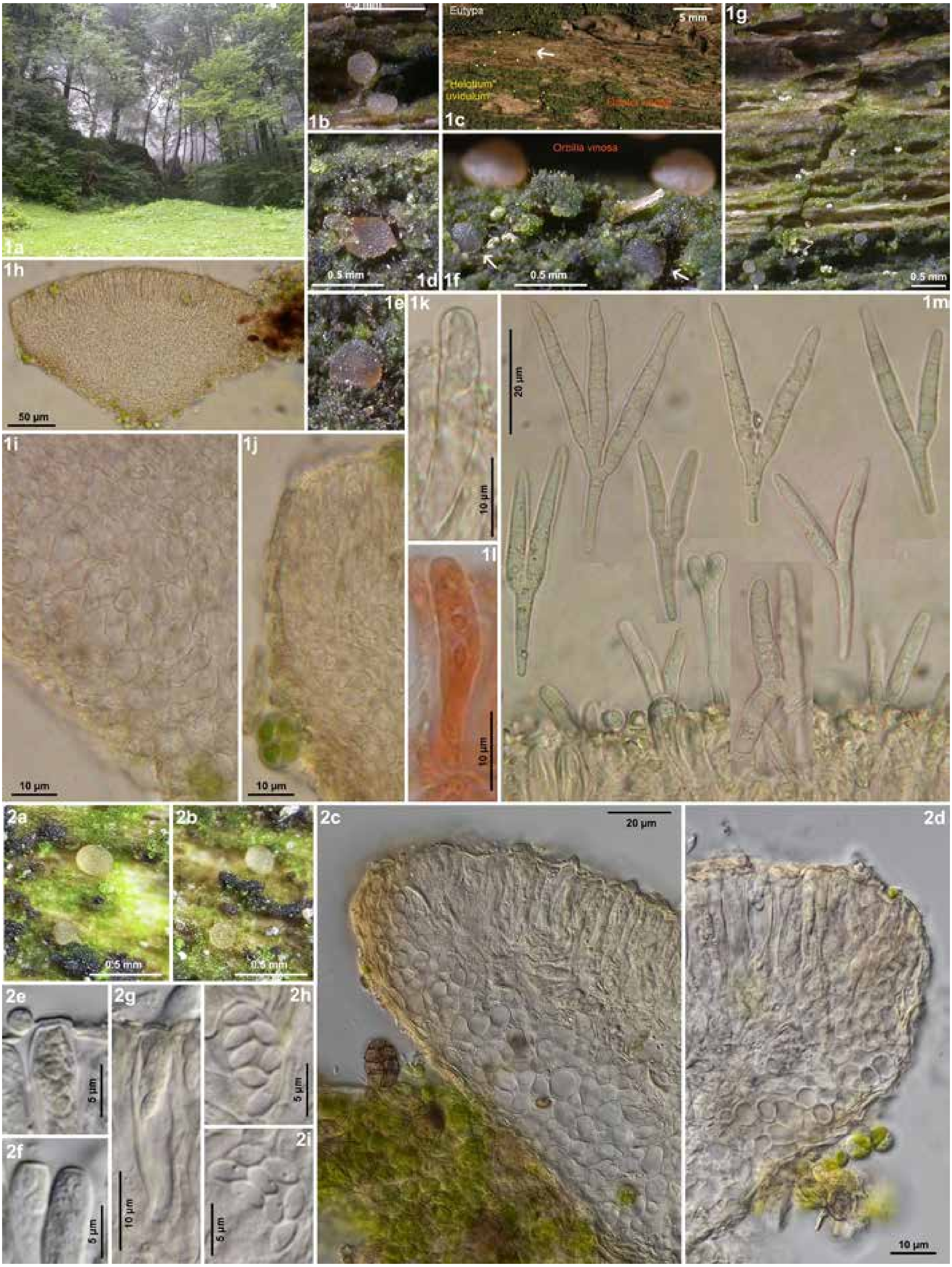


Plate 138. **1–2**: *Hyalorbilia hergiswiliana*. – **1a**. montane *Aceri-Fraxinetum* with *Asplenium scolopendrium*; **1c**. detail of decorticated rotten mesic branch of *Acer pseudoplatanus*, associated with *O. vinosa* and '*Helotium*' *uvidulum* (apothecia marked by dots, white = *H. hergiswiliana*); **1b**, **d–g**, **2a–b**. rehydrated apothecia (in **1f** associated with two apothecia of *O. vinosa*); **1h**. apothecium in median section; **1i**. id., ectal excipulum at lower flanks; **1j**, **2c–d**. id., ectal excipulum at flanks and margin; **1k–l**, **2g**. asci (and paraphyses); **2e–f**. ascus apices; **2h–i**. ascospores within dead asci; **1m**. conidia growing on hymenium of *O. vinosa*. – Living state, except for **1l** (in KOH+CR), **2e**, **f** (in H_2O), asci in **2h–i**. — **1a–m**. H.B. 8235b: Switzerland, Pilatus, on *Acer* (holotype); **2a–i**. A.P. 19/22a: Slovakia, Bratislava, on *Cornus*.

green algae (*Pleurococcus*) and brown hyphae. **Associated**: '*Helotium*' *uvidulum* {2}, *Orbilia aprilis* {1}, *O. montigena* {2}, *O. vinosa* {1}. **Desiccation tolerance**: fully viable for almost 3 weeks. **Altitude**: 132–890 m a.s.l. **Geology**: Cretaceous micrite (Schrattenkalk) & flysch, fluviatile sediment (sandy gravel). **Phenology**: V, VIII–IX.

Taxonomic remarks. *Hyalorbilia hergiswiliana* is only known from the holotype from Switzerland and the paratype from Slovakia. It particularly resembles *H. latispora* and *H. rotifera*, the former differing in slightly larger ascospores containing several minute peripheral SBs and in wider asci, the latter in shorter asci, slightly longer and narrower ascospores, a more prismatic, horizontally oriented ectal excipulum at the flanks, and wider marginal cortical cells. Both species differ from *H. hergiswiliana* in some of their asci having a somewhat conical apex (dead state), in shorter terminal cells of paraphyses, and smaller, more whitish apothecia.

Because of the partially bifurcate ascus base and occasional absence of croziers, and the ectal excipulum being composed at the lower flanks of textura globulosa(-prismatica) with an irregular vertical orientation, the species was also compared with series *Orbilia*, particularly *O. frangulae*. However, the finely warted exudate over the paraphyses, the occurrence of croziers, and the consistent absence of shoulders and indentations at the ascus apex point to a *Hyalorbilia*. Apart from this, *O. frangulae* differs in smaller spores, narrower asci, and in larger apothecia. Also in the presumed anamorph the two species are similar. *O. cejpii* differs in shorter spores with a small spore body and in much narrower asci.

Anamorph. In the holotype dicranidion-like conidia formed on very short conidiophores (Pls 137: 1d; 138: 1m) were observed emerging from the hymenium of *Orbilia vinosa*, which grew in close association with apothecia of *H. hergiswiliana*, sometimes only 0.3 mm away. The apothecia of *H. hergiswiliana* are smaller and less pigmented than those of the associated *O. vinosa* (Pl. 138: 1f). In the Slovakian sample *O. montigena* grew at ~5 mm distance from *H. hergiswiliana*, but here only trinacrium tothii-like conidia of unclear relationship were found on the natural substrate (A. Polhorský pers. comm., IVV: 18.V.2019).

Not included collections. In 11 further records of *O. vinosa* s.l. from various regions of Europe, very similar dicranidion-like conidia were observed, either on the apothecia or nearby on the plant substrate, but no apothecia of *H. hergiswiliana* were observed (see specimen list below). In spite of their close morphological match they are not included in the description of *H. hergiswiliana*. Gönczöl & Révay (2003: figs 1–4, as *Dwayaangam* sp.) illustrated the same type of conidia from a treehole in a trunk of *Fagus sylvatica* in the Börzsöny mountains in Hungary.

The occurrence of such dicranidion-like conidia with *O. vinosa* apothecia suggests at first glance that they belong to *O. vinosa* rather than *H. hergiswiliana*. However, in some of these collections, very differently shaped conidia occurred in addition: trinacrium tothii-like conidia in five samples of *O. vinosa* (e.g., Pl. 261: 1, type sample of *H. hergiswiliana*), and dwayaangam-like conidia in two samples of *O. arachnovinosa* (e.g., Pl. 269: 6) and one of *O. angiosubvinosa* (Pl. 267: 2). Trinacrium tothii- and dwayaangam-like conidia were assured in pure culture as anamorph of *O. vinosa* and *O. subvinosa*, respectively, which supports our hypothesis that the above dicranidion-like conidia do not represent the anamorph of those apothecia on which they grew. Instead, they seem to belong to a parasitic orbiliaceous fungus, possibly *H. hergiswiliana*. In a similar way, apothecia and conidia of *Hyalorbilia orbiliicola* specifically grow as a parasite on apothecia of *Orbilia* spp.

Phylogeny. A sequence was gained by A. Polhorský (pers. comm.) from apothecia of the Slovakian paratype of *H. hergiswiliana*, which comprises ITS (S1506 intron absent) and LSU D1–D4. In ML analyses (not shown) it clustered unresolved in *Hyalorbilia*, and also BLAST search for ITS yields solely that genus, though with only 37% query cover as a maximum, except for one sequence with 52%. Distances to other species of *Hyalorbilia* lie in the range of ~29–32% for ITS (p-distances evaluated with MEGA7) and 12% for LSU. An insert occurs in the ITS1 similar as in the genotype of *H. inflatula* with broad marginal cells, though being difficult to align. In its aberrant conservative motifs GAGC**A**TC (3'-end of 5.8S) and TGA**T**CT (5'-end of LSU) *H. hergiswiliana* resembles *H. erythrostigma* and *H. orbiliicola*, which likewise differ from almost any other orbiliaceous species in a further variant of these motifs (see p. 122 and Tab. 18).

The sequence that appeared on top with a 52% query cover was an environmental clone isolated from a *Picea* log in Sweden (GenBank HQ611287; ITS, S1506 intron absent). It shows the very same two aberrant motifs and clustered medium supported with *H. hergiswiliana*, though differing by a 21% and numerous gaps; therefore, it is named *H.* aff. *hergiswiliana* here. In the Orb5.8s3F primer this sequence concurs with *H. hergiswiliana*, whereas in the Orb5.8s1F primer it shows the predominant orbiliaceous variant, and in the 4 first nucleotides of ITS2 it concurs, unlike *H. hergiswiliana*, with *H. latispora* and others (Tabs 18, 20). In the LSU *H. hergiswiliana* shows the Orb28s2R motif of the core clade of *Hyalorbilia*, which does not occur in any other clades of *Hyalorbilia* or other orbiliaceous genera (Tabs 19).

The ITS distance between *H. hergiswiliana* and *H. latispora* or *H. rotifera* lies around 30%. Also clone from Amazonas (U2, KY687852/3; SSU+ITS+LSU), which shares with *H. hergiswiliana* s.l. the motif GAGC**A**TC, clustered unsupported herewith by showing a 29% ITS distance. In our combined analysis of *Orbiliomycetes* (Phyl. 2) this clone clustered weakly supported within the *Hyalorbilia* clade, whereas in our 5.8S+LSU analysis (Phyl. 1) it nested unsupported sister to *Hyalorbilia*.

Ecology. In the three known samples, *Hyalorbilia hergiswiliana* occurred on xeric, decorticated, very rotten wood of angiosperm branches, always in association with members of *Orbilia* series *Hesperideae* (*O. aprilis*, *O. montigena*, *O. vinosa*), in two samples also with the macroscopically similar '*Helotium*' *uvidulum*. The sparse apothecia in the holotype, which were almost used up during examination, grew on the upper side of an eroded branch of *Acer* lying with little soil contact on the forest floor of a montane, shady, calcareous *Aceri-Fraxinetum* with *Asplenium scolopendrium* in the orotemperate humid calcarean northern Alps. In the Slovakian sample on *Cornus*, the apothecia grew on an attached branch in a thermophilous (xerophilous) pannonian oak grove with *Acer campestris* and many *Cornus* shrubs in the temperate humid Danubian lowlands near an oxbow but outside the floodplain. In the Serbian sample on *Koelreuteria*, the branch was recently fallen to the ground in a supratemperate humid *Quercus*/*Tilia*/*Acer* forest with planted gymno- and angiosperms, next to a road near the top of Fruška Gora mountain in the south of the Pannonian Plain.

The not included conidial records comprise thermoboreal to cold- or orotemperate humid but also orosub- to suprasubmediterranean (semi)humid regions. The uncultured clone from a *Picea* log is from hemiboreal humid lowlands of eastern Sweden.

Specimens included. **SWITZERLAND**: **Nidwalden**, 8.5 km SSW of Luzern, 2 km SW of Hergiswil, Renggpass, 890 m, branch of *Acer pseudoplatanus*, on wood (presumed anamorph on associated apothecia of *O. vinosa*), 15.VIII.2006, H.O. Baral (ex H.B. 8235b, M-0276492, **holotype**, anam. substr.). — **SLOVAKIA**: **Bratislava**, 10 km SE of Bratislava, 5 km S of Podunajské Biskupice, Topol'ové hony, 132 m, branch of *Cornus mas*, on wood (no anamorph seen on associated apothecia of *O. montigena*), 18.V.2019, A. Polhorský (A.P. 19/22a, BRA-CR31730, doc. vid.; sq.: MN611701, MN607582). — **SERBIA**: **Vojvodina**, Fruška Gora, 13 km S of Novi Sad, 5.8 km NNW of Irig, Iriški venac, SW of WWII memorial, 493 m, branch of *Koelreuteria paniculata*, on wood, 25.IX.2019, D. Savić (doc. vid.).

Not included (anamorph only, for images see IVV). **SWEDEN**: **Gävleborg**, 12 km SSW of Hudiksvall, 3.5 km SSW of Iggesund, NE of Njutånger, 18 m, branch of *Populus tremula*, in apothecia of *O. vinosa*, 23.VII.2010, H.O. Baral & P. Perz (H.B. 9366c ø). — **FINLAND**: **North Karelia**, 42 km WNW of Joensuu, WNW of Outokumpu, Raivionmäki, 140 m, branch of *Prunus padus*, near *O. vinosa* on wood, 30.I.2011, M. Pennanen (ø, doc. vid.). — **GERMANY**: **Bayern**, **Oberpfalz**, 15 km NE of Cham, 3.5 NW of Furth im Wald, NW of Roberthütte, 750 m, branch of *Fagus sylvatica*, near *O. vinosa* on wood, 5.VIII.2005, E. Weber & H.O. Baral (H.B. 7861c ø). – **Oberbayern**, Kocheler Berge, 6.5 km WSW of Lenggries, NW of Latschenkopfhütte, S of Vorderer Kirchstein, 1600 m, branch of *Salix caprea*, near *O. arachnovinosa*, on wood, 21.VI.2005, P. Karasch & B. Fellmann (H.B. 7830c ø). — **SWITZERLAND**: **Nidwalden**, 8.2 km SSW of Luzern, 3.2 km W of Hergiswil, N of Bergstation Gschwänd, 1200 m, branches of *Salix appendiculata*, near *O. arachnovinosa*, on wood, 18.VIII.2006, H.O. Baral (H.B. 8248g). — **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 10 km ESE of Sederon, W of Curel, 765 m, branches of *Spartium junceum*, near *O. vinosa* on wood, 17.VIII.2001, G. Marson (H.B. 7024c). – **Rhône-Alpes**, **Drôme**, 2 km SSE of Nyons, 550 m, on wood & bark of (?)*Rosmarinus officinalis*, near *O. vinosa* on wood & bark, 7.VIII.1999, G. Marson (ø). — **SPAIN**: **Asturias**, 4.1 km ESE of Pola de Somiedo, 1.2 km NE of Valle de Lago, 1165 m, branch of *Corylus avellana*, in apothecia of *O.* cf. *subvinosa*, 4.VI.2013, T. Læssøe (H.B. 9813d). – **Aragón**, **Teruel**, 4.3 km N of Noguera de Albarracín, 1.8 km SW of Bronchales, 1695 m, branch of *Cistus laurifolius*, near *O. vinosa* on wood, 19.V.2011, R. Tena (R.T.L. 11051903, doc. vid.). – ibid., in apothecia of *O. vinosa*, 3.IV.2013 (ø). – **Zaragoza**, 9 km SE of Ágreda, 3.8 km SW of San Martín de la Virgen de Moncayo, SW Agramonte visitor center, 1140 m, branch of *Salix caprea*, in apothecia of *O. vinosa*, 3.VII.2011, R. Tena (ø, doc. vid.).
H. **aff.** ***hergiswiliana***: **SWEDEN**: **Uppsala**, 35 km WNW of Uppsala, around Knutby, ~30 m, log of *Picea abies*, before 2011, M.T. Banik (xan, 0618Banik_03D_20, uncultured clone; sq.: HQ611287).

Hyalorbilia ulmi Baral & E. Batten, **sp. nov.**, MB 813455 — Figs 139–140

Etymology: named after the substrate, *Ulmus minor*.
Typification: Great Britain, Suffolk, Halesworth, trunk of *Ulmus minor* (on pyrenomycete and on bark), 6.II.2005, E. Batten (ex E.B. 4586 & ex H.B. 7674, M-0276422, holotype).

Latin diagnosis: Hyalorbiliae erythrostigmati *similis sed asci breviores, ascosporae angustiores, corpusculo refringente minore.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.07–0.16 mm diam., (greyish-) whitish(-chlorinaceous), semitranslucent, round, scattered to subgregarious; disc slightly ± flat, margin not protruding, finely rough; subsessile or with distinct short stipe ~15 × 40 µm, superficial; dry yellowish-cream. **Asci** *14–17 × 4.2–5 µm, †(12–)14–16(–17) × (3–)3.5–3.7(–4) µm, 8-spored, spores (*/†) ± biseriate, some spores inverted (irregularly mixed), pars sporifera †9.5–11 µm long; **apex** (†) hemispherical; **base** with ± absent stalk, arising from croziers with small perforation. **Ascospores** *2.4–3.2 × 1.4–1.8 µm, †(1.8–)2.1–2.6(–3) × (1.2–)1.3–1.6(–1.8) µm, ellipsoid-ovoid, rarely (cylindric-)ellipsoid or fusoid, both ends obtuse (rarely subacute), straight; **SBs** *0.6–0.8 µm diam., globose, 0.4–0.5 µm away from apex (attachment invisible), with 1-2 minute LBs. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cells †11–14 × 1.8–2.5 µm, sometimes strongly inflated to a width of 5–8 µm, lower cells †3.8–4.7 × 1.3–2(–4) µm; branching not seen. **Medullary excipulum** not studied. **Ectal excipulum** of (†) ± thin-walled, horizontal textura angularis(-prismatica) at lower flanks, cells †8–15 × 4–12 µm, cubical; marginal cortical cells †13–18 × 4–7.5(–9) µm (3–6 µm wide in section). **Anchoring hyphae** not studied. **VBs** unknown. **Exudate** over paraphyses 0.1–0.2(–0.3) µm thick, finely granular, continuous, loosely attached, over margin smooth to granular. — **ANAMORPH**: unknown.

Habitat: 20 cm above the ground, on loose bark at base of a trunk of *Ulmus minor*, on remnants of stromatic pyrenomycete. **Associated**: abundant conidia of ?*Diplodia* below apothecia. **Desiccation tolerance**: after 1 week only some cells of ectal and medullary excipulum were viable. **Altitude**: 13 m a.s.l. **Geology**: Pleistocene till (sand & gravel). **Phenology**: II.

Taxonomic remarks. *Hyalorbilia ulmi* resembles *H. erythrostigma* in many respects, but differs in shorter asci, narrower spores, smaller SBs, also in some of the paraphyses being extraordinarily wide. Because the spores with their eccentric SBs have an elongate shape, they tend to be oriented with their SBs either up- or downwards rather than in all directions as in *H. erythrostigma*, which is an exceptional feature

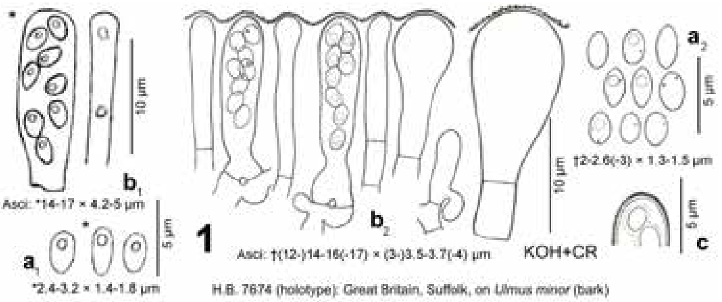


Plate 139. **1**: *Hyalorbilia ulmi*. – **a**. ascospores; **b**. asci and paraphyses, ascus bases with croziers; **c**. ascus apices. – **1a$_1$**, **b$_1$**: del. E. Batten.

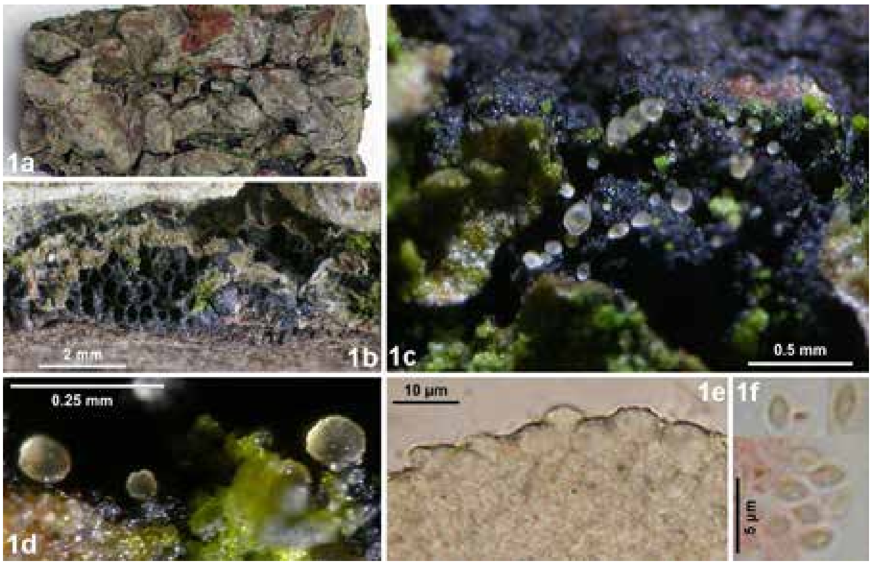


Plate 140. **1**: *Hyalorbilia ulmi*. – **1a–b**. exterior of xeric bark of *Ulmus minor*; **1c–d**. rehydrated apothecia; **1e**. margin in top view; **1f**. ascospores. – Dead state: **4e** in KOH; **4f** in KOH+CR. — **1a–f**. H.B. 7674 (holotype): Great Britain, Suffolk, on *Ulmus*.

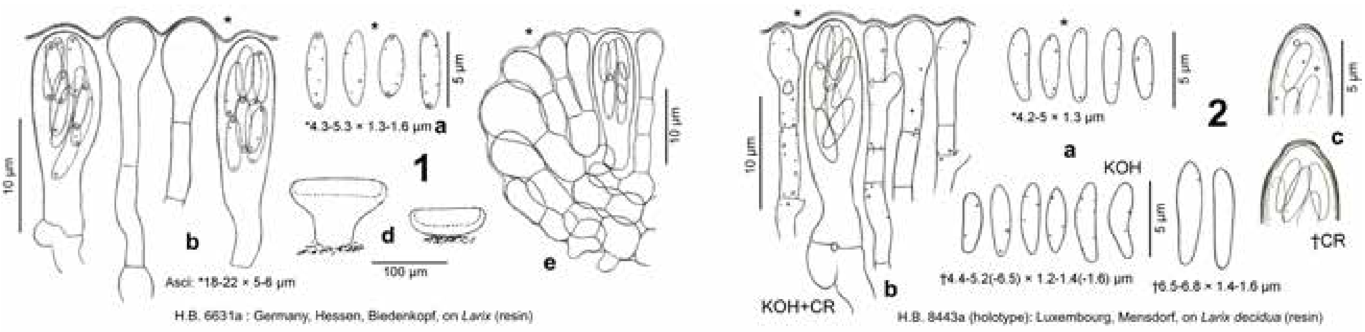


Plate 141. **1–2**: *Hyalorbilia resinae*. – **a**. ascospores; **b**. asci (with croziers) and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. ectal excipulum (margin and mid flanks, median section).

within *Hyalorbilia*. *H. brevistipitata* differs in multiguttulate, partially subglobose spores and a hygric habitat. Two somewhat intermediate collections from Australia and Africa are treated as *H.* cf. *erythrostigma* (Pls 126: 10; 128: 3) and *H.* cf. *brevistipitata* (Pl. 121: 3).

Ecology. *H. ulmi* grew on an old stromatic pyrenomycete which occurred on bark at the base of a standing tree of *Ulmus minor*, in oceanic, cold-temperate humid eastern England.

Specimens included. **GREAT BRITAIN**: **East England**, **Suffolk**, 4 km ESE of Halesworth, km NE of Wenhaston, path to Bicker's Heath, 10 m, on pyrenomycete and bark of trunk of *Ulmus minor*, 6.II.2005, E. Batten (ex H.B. 7674, M-0276422, **holotype**; E.B. 4586, K(M) 147142, **isotype**, doc. vid.).

Hyalorbilia resinae Baral, **sp. nov.**, MB 813465 — Pls 141–142

Etymology: named after the habitat, old resin of conifers.

Typification: Luxembourg, Mensdorf, branch of *Larix*, on resin, 5.III.2007, G. Marson (ex H.B. 8443a, M-0276416, holotype).

Latin diagnosis: Hyalorbiliae rotiferae *similis sed ascosporae angustiores, in statu vivo cum duobus corpusculis refringentibus minutis, paraphyses ad apicem partialiter valde inflatae. Habitat ad resinam nigram ramorum vulneratorum siccorum coniferarum in zona hemiboreale et temperata humida Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.08–0.18 mm diam., (0.03–)0.05–0.09 mm high [receptacle (0.03–)0.04–0.05 → 0.03–0.04 mm], whitish to very pale chlorinaceous, translucent, round, scattered to gregarious in small groups; disc flat, margin thin, 0–10 µm protruding, very finely to distinctly rough; sessile or with distinct stipe 0.02–0.05 × 0.05–0.06 mm, superficial, partially semiimmersed in black hyphomycete or biofilm, dry very pale yellowish or whitish-cream. **Asci** *16–22 {1} × 5–6.5(–7) µm {3}, †(13–)15–23(–26) × (4–)4.3–5.5(–6) µm {4}, 8-spored, spores *(2–)4-seriate, pars sporifera *9–13.5 µm long; **apex** (†) hemispherical to medium conical; **base** sessile or with short, thick, partially constricted stalk, with croziers {4}, partially with small, round to elongate perforation. **Ascospores** *(3.5–)4–5.3(–6) × 1.3–1.6(–1.8) µm {3}, †4.2–5.2 × (1.2–)1.3–1.4 µm {1}, subcylindrical to ellipsoid, sometimes fusoid-clavate, ends (rounded to) obtuse, straight to slightly inequilateral, rarely medium curved; **SBs** *0.2–0.25 µm {1}, globose, 1 at each end, also absent {2}. **Paraphyses** apically very slightly to medium or sometimes strongly clavate-capitate, terminal cells *9–13 × 3.5–5 µm {1}, †(5–)7–11(–13) × 1.8–3.3(–4.5) µm {3}, lower cells *7–9 × 1.8–2.3 µm {1}, †(2.5–)4–7 × 1.5–2(–2.5) µm {3}, sometimes branched at upper septum. **Medullary excipulum** 5–10 µm thick, non-gelatinized, partially distinctly delimited. **Ectal excipulum** of not or very slightly gelatinized, indistinctly (at mid flanks also horizontally) oriented textura (globulosa-)angularis from base to margin, 10–50 µm thick near base, cells */†(5–)6–10(–12.5) × (4–)5–7(–9.5) µm {3}; cells at flanks *~6–8 × 6–8 µm; 7–15 µm thick at margin, marginal cortical cells */†(7–)9–12(–15) × 5–8(–9) µm {4}, clavate-vesiculous, partially ± protruding, sometimes with angular outline or forming nipple-like protuberances 1–3 × 1.7–2.5 µm. **Anchoring hyphae** sparse to rather abundant at base, †1.5–3(–4) µm wide (at insertion 4–5 µm), walls 0.2((–0.3)) µm thick {4}. **SCBs** in paraphyses and ectal excipulum absent; **LBs** in excipular cells sometimes present. **Exudate** over paraphyses and excipulum 0.1–0.3 µm thick, continuous, ± smooth, on marginal cells also finely rough, very pale chlorinaceous. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate {2}). **Conidiophores** unknown. **Conidia** *(38–)47–62(–73.5) × (4.2–)4.5–6.5(–6.8) µm, fusiform, (4–)5–6(–8)-septate.

Habitat: fallen (lying ± close to ground) {3} or still-attached at 1–3 m above the ground {1}, corticated, 3–30 mm thick, partially living twigs and branches of *Larix* sp. {3}, *Picea abies* {1}, in large wounds (swollen to 25–50 mm) or on small thin patches of resin {2}, also on slightly decayed bark without resin close to apothecia {2}, resin blackened by a thick layer of a hyphomycete, green algae present or absent. **Associated**: *Ciliolarina* sp. {1}, *Cosmospora rishbethii* {1}, *Lachnum virgineum* {1}, *Lophium mytilinum* {2}, *Microthyrium abietis* {1}, *Mytilinidion gemmigenum* {1}. **Desiccation tolerance**: fully tolerant for at least a few days. **Altitude**: 50–370 m a.s.l. **Geology**: Lower Carboniferous sediment, Lower Jurassic sandstone; quartzite. **Phenology**: III, V.

Taxonomic remarks. *Hyalorbilia resinae* resembles *H. rotifera*, a species which differs in consistently uninflated or only scarcely inflated paraphyses, partially wider, fusoid ascospores, and in growing on angiosperm substrate. In spore shape *H. resinae* resembles *H. oreadum*, which differs in less inflated paraphyses, narrower marginal cortical cells, narrower spores and asci, and larger apothecia.

Variation. The paraphyses show a remarkable variability in their apical inflation, even within an apothecium. In the samples from Germany and Poland they are partially very strongly capitate, whereas this is much less so in the holotype (from Luxembourg) and the find from Norway. Also the cortical cells near the margin vary among the collections: they may project distinctly, and some of them tend to become angular and may form short protrusions (Pl. 142: 2e–g, 3e) similar as observed in a specimen of *H. juliae* (Pls 106: 7h; 107: 2d–f). In the other features the four included collections concur very well. In some asci of the holotype the spores were ellipsoid and measured *3.2–3.8 × 1.6–2 µm, but these seem to represent atypical spores; also a few oversized free spores (†6.5–6.8 × 1.4–1.6 µm, Pl. 141: 2a right) were observed which possibly arose from asci with a reduced spore number.

Anamorph. Brachyphoris-like conidia were abundantly seen on the natural substrate in the specimen from Norway (K. Homble pers. comm., Pl. 142: 3f). A similar conidium was found on the substrate in the German sample.

Ecology. *Hyalorbilia resinae* grew on old blackened resin of wounds, also on bark, of ± undecayed, dead or still-living twigs and branches of *Larix* and *Picea* in supratemperate humid,

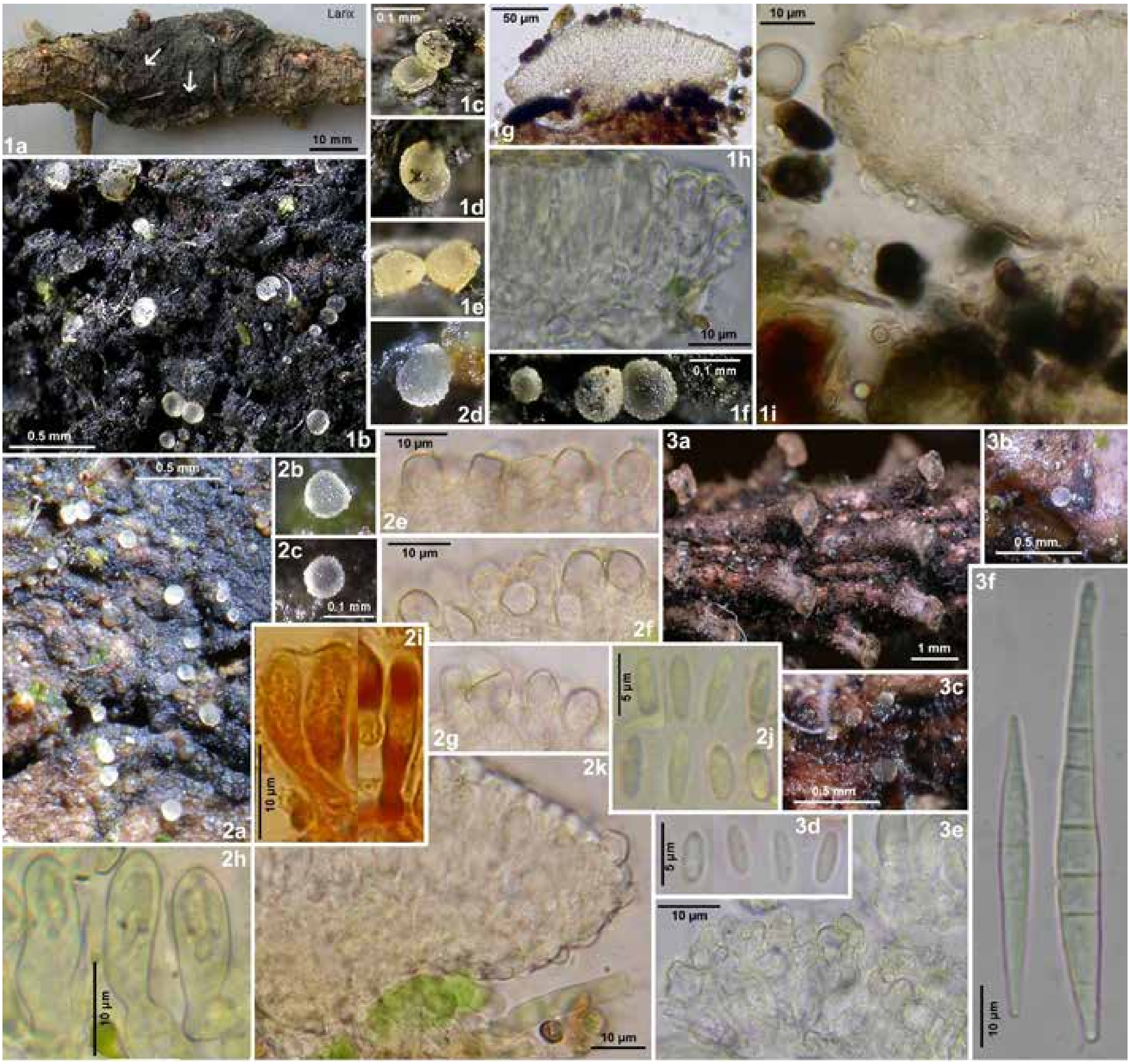


Plate 142. **1–3**: *Hyalorbilia resinae*. – **1a**. living *Larix* branch with blackened resinous wound; **3a**. fallen twig of *Picea abies;* **1b–f**, **2a–d**, **3b–c**. rehydrated apothecia; **1g**. apothecium in median section; **1h–i**, **2k**. id., marginal (and basal) part; **2e–g**, **3e**. marginal cortical cells (**2e–g** in top view); **2h–i**. asci (**2i** right immature); **2j**, **3d**. ascospores; **3f**. conidia (from substrate). – Living state, except for **1g**, **2e–g** (in H_2O); **1i**, **2k** (in KOH); **2i** (in KOH+IKI). – **2a**, **h**, **j**: phot. P. Perz; **3f**: phot. K. Homble. — **1a–i**. H.B. 8443a (holotype): Luxembourg, Mensdorf, on *Larix*; **2a–k**. H.B. 9169: Poland, Szczecin, on *Larix*; **3a–f**. H.B. 9687: Norway, Arendal, on *Picea*.

subcontinental central and in hemiboreal northern Europe. The vegetation includes shady mixed conifer forests. The sample from Luxembourg was on a still-attached xeric branch, whereas the others were on the ground, that from Poland even from a hygric habitat. Yet, also in the xeric collection the apothecia did not well withstand repeated rehydration.

Specimens included. **NORWAY**: **Aust-Agder**, 4.5 km WSW of Arendal, 1.5 km NW of Vrengen, Sagmyr, 50 m, twig of *Picea abies*, on bark, 9.V.2012, T.H. Dahl (H.B. 9687, anam. substr.). — **POLAND**: **West Pomerania**, 20 km SE of Szczecin, 1.7 km NE of Dobropole Gryfińskie, Puszcza Bukowa, 88 m, branch of *Larix*, on bark, 21.III.2009, P. Perz & G. Domian (H.B. 9169). — **GERMANY**: **Hessen**, Oberes Lahntal, ~5 km NW of Biedenkopf, ?1.5 km N of Wallau, Hainbachtal, 370 m, branch of *Larix*, on resin, 1.V.2000, L.G. Krieglsteiner & H.O. Baral (H.B. 6631a, anam. substr.). — **LUXEMBOURG**: **Gutland**, **Grevenmacher**, 14 km ENE of Luxembourg, 1.5 km E of Mensdorf, Widdebierg, 349 m, branch of *Larix*, on resin, 5.III.2007, G. Marson (ex H.B. 8443a, M-0276416, **holotype**).

Hyalorbilia herbicola Baral, Priou & Perz, **sp**. **nov**., MB 813458 — Pls 143–144

Etymology: named after the growth on herbaceous stems and culms.
Typification: France, Morbihan, La Gacilly, stem of *Reynoutria sachalinensis*, 12.VI.2008, J.P. Priou (ex H.B. 8880, M-0276410, holotype).

Latin diagnosis: Hyalorbiliae rotiferae *similis*, *sed asci et ascosporae angustiores*, *ascosporae subcylindricae. Habitat in caules uvidos herbarum in zona temperata humida Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.16 mm diam., 0.05–0.07 mm high (receptacle 0.03–0.04 mm), whitish, ± translucent, round, slightly non-gelatinous, scattered to gregarious; disc flat to slightly convex, margin indistinct, smooth; sessile or with a stipe 0.01–0.02 × 0.04–0.045 mm, superficial. **Asci** *(13.5–)15–28(–31) × 4.5–5.2 µm {2}, †18–24 × 3.8–4.2 µm {1}, 8-spored, spores *4-seriate, pars sporifera *10–14 µm long; **apex** (†) hemispherical to subconical; **base** unstalked or with short, thick stalk, with croziers {2}, with perforation. **Ascospores** *(3.2–)3.5–5(–5.5) × (1.1–)1.2–1.3(–1.4)

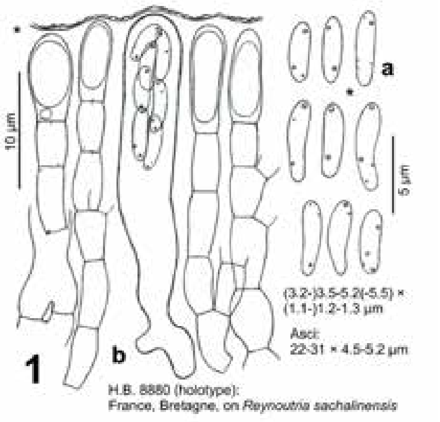


Plate 143. **1**: *Hyalorbilia herbicola*. – **a**. ascospores; **b**. asci and paraphyses.

µm {2}, subcylindrical to slightly ellipsoid-clavate, both ends rounded to obtuse, straight to slightly (rarely medium) curved; **SBs** *0.2–0.4 µm, globose, 1 at each end, also absent (perhaps always LBs?). **Paraphyses** apically uninflated, sometimes slightly clavate to ellipsoid or lageniform, terminal cells */†(4–)7–9(–10) × 2.5–3(–3.8) {1}, lower cells *(2–)3–6(–7.5) × 2–3 µm {1}, †1–5 × 2–3 µm {1}. **Medullary excipulum** ~15 µm thick, of thin-walled, non-gelatinized textura globulosa, very indistinctly delimited. **Ectal excipulum** at base of 25 µm thick, (†) thin-walled t. globulosa-angularis, cells *6–11 × 5–8.5 µm {1}, †5–9 × 4–7 µm {1}, at flanks of horizontal t. prismatica-angularis, cells †(3–)5–8 × 5–6 µm, 8–10 µm thick at margin, marginal cortical cells (*)/†(5–)8–10(–12) × 4–5.3(–6) µm {2}. **Anchoring hyphae** sparse, †1.5–3 µm wide, walls 0.2 µm thick {1}. **VBs** in paraphyses (very) slightly refractive, hyaline. **Exudate** over paraphyses 0.2–0.5 µm thick, very pale yellowish, continuous, finely rough, over excipulum smooth, pale yellow. **— ANAMORPH**: unknown (but see below).

Habitat: lying on the moist ground, on 1 cm thick stem of *Reynoutria sachalinensis* {1}, culm of *Phleum pratense* {1}, ungreyed but with some blackish patches, without algae. **Associated**: *Hyalorbilia ?juliae* {1}, *Lophiostoma* sp. {1}. **Desiccation tolerance**: only the spores survived for 1 day in the herbarium. **Altitude**: 4–570 m a.s.l. **Geology**: Upper Cretaceous calcareous clay-, marl- & limestone, flysch; quartzite & granite. **Phenology**: VI, VIII.

Taxonomic remarks. *Hyalorbilia herbicola* closely concurs with *H. rotifera*, from which it merely differs in distinctly narrower asci and ascospores, with the spore width not overlapping, also in growing on hygric herbaceous substrate. The spores of the lignicolous *H. oreadum* are also very similar though even slightly narrower. *H. oreadum* further differs from both taxa in distinctly larger and thicker apothecia, much larger, more elongate excipular cells at lower flanks, and distinctly longer terminal cells of paraphyses, also in the arrangement of the spores in the living asci (in *H. oreadum* strictly 4-seriate in two superimposed bundles). The latter feature is unknown for the type of *H. oreadum* because the spore arrangement is not stable in the dead state.

Variation. The collection on *Phleum* differs from that on *Reynoutria* merely in slightly shorter spores (*3–4.3 × 1.1–1.3 µm, Pl. 144: 1d).

Not included collections. More fusoid were ascospores in a British sample by N. Aplin (pers. comm.) on a dead standing stem of *Digitalis* (*4.3–5.8 × 1.2–1.5 µm, apothecia up to 0.3 mm diam., IVV: 18.VI.2016) and two Serbian samples by D. Savić (pers. comm.) on stems of *Centaurea* and indet. *Apiaceae* (*3.8–4.9 × 1.1–1.3 µm, apothecia 0.08–0.22 mm, partially with a finely crenulate margin due to broad protruding marginal cells, IVV: 11.VI.2019, I.VII.2019). A single apothecium (0.16 mm diam) on angiosperm bark from Ethiopia (IVV: H.B. 9246b) resembles *H. herbicola*, but differs in slightly wider asci (†17–18 × 4–4.5 µm) and spores [*3.5–4.5(–5) × 1.3–1.5 µm, without SBs] and appears intermediate to *H. rotifera*.

Anamorph. A single brachyphoris-like conidium was found on *Phleum*: ± straight, narrowly fusoid, *63 × 2.3 µm, with ?7 septa. Very similar conidia were observed four times near apothecia of *H. rotifera*.

Ecology. *Hyalorbilia herbicola* was detected on hygric herbaceous mono- and dicot stems lying on the moist ground, in mesotemperate atlantic to cold-temperate subcontinental humid Europe. The type locality is a moist *Reynoutria* stand, while the paratype derives from a wet meadow close to a spring. On *Phleum* the apothecia grew very close to perithecia of a *Lophiostoma*. The not included collection from mesotemperate atlantic humid England was on a standing stem of *Digitalis* 10 cm above the ground, in close association with a *Pyrenopeziza*, in a tall herb vegetation on the bank of a pond. That from Ethiopia grew in association with *Orbilia aethiopica* on angiosperm bark in a warm-temperate humid, evergreen afromontane forest in the central plateau of the Ethiopian highlands.

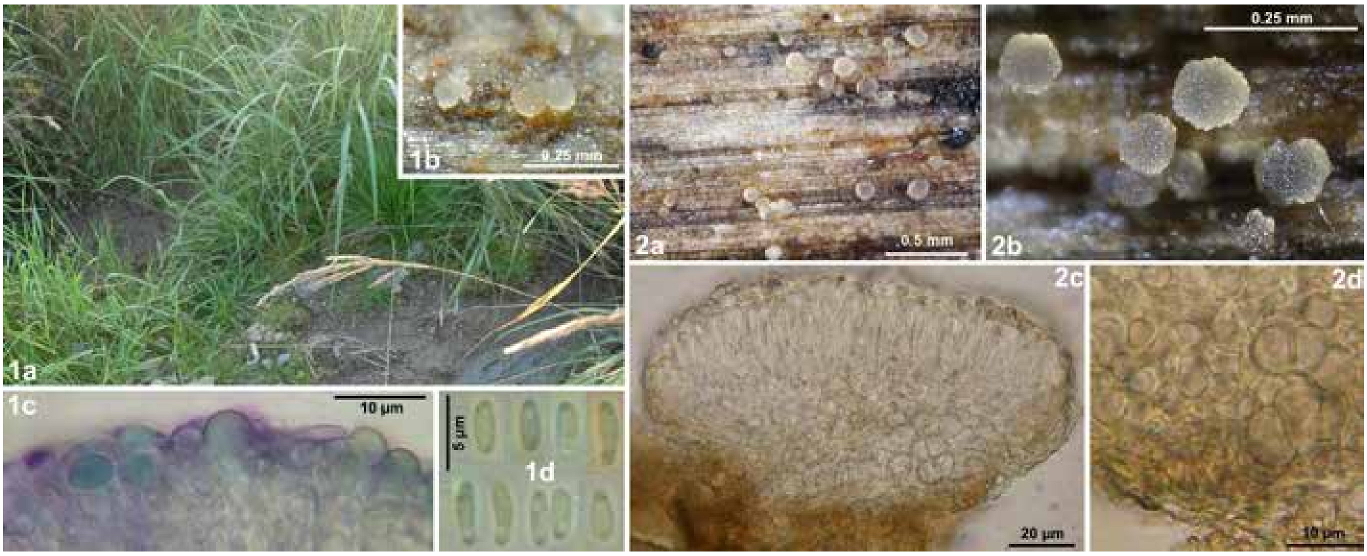


Plate 144. **1–2**: *Hyalorbilia herbicola*. – **1a**. wet meadow with *Phleum pratense*; **1b**, **2a–b**. fresh apothecia; **2c**. apothecium in median section; **2d**. id., central part in median section; **1c**. margin in top view; **1d**. ascospores. – Living state (**1c** in CRB). – **1a–d**: phot. P. Perz. — **1a–d**. H.B. 9138a: Poland, Kłodzko, on *Phleum*; **2a–d**. H.B. 8880 (holotype): France, Bretagne, on *Reynoutria*.

Specimens included. **FRANCE**: **Bretagne**, **Morbihan**, 5.3 km S of La Gacilly, 2 km N of St.-Vincent-sur-Oust, La Provostaie, 4 m, stem of *Reynoutria sachalinensis*, 12.VI.2008, J.P. Priou (ex J.P.P. 28131, ex H.B. 8880, M-0276410, **holotype**). — **POLAND**: **Lower Silesia**, 20 km WSW of Kłodzko, 1.6 km NW of Duszniki Zdrój, 1 km NE of Słoszów, Agroturistik 'Herbergerówka', 570 m, culms of *Phleum pratense*, 10.VIII.2009, P. Perz (P.P. 20090810-1, 20090819-1, H.B. 9138a).

Not included. **GREAT BRITAIN**: **South East England**, **West Sussex**, 4.5 km NNE of Crawley, SE of Gatwick Airport, 62 m, stem of *Digitalis purpurea*, 18.VI.2016, N. Aplin (N.A. 347, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 13 km SSW of Novi Sad, 1 km E of Brankovac, 430 m, stem of *Centaurea jacobaea*, 11.VI.2019, D. Savić (doc. vid.). – 12 km SSE of Novi Sad, 6.5 km NNW of Irig, N of TV tower, 511 m, stem of *Apiaceae*, I.VII.2019, D. Savić (FG-1098, doc. vid.). — **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, Menagesha Suba State Forest, 2500 m, branch of indet. angiosperm, on bark, 22.XII.2009, U. Lindemann (H.B. 9246b ø).

Hyalorbilia rotifera Baral & E. Batten, **sp. nov.**, MB 813459 — Pls 145–146

Etymology: *rotifera*: referring to the presence of an infected rotifer close to the apothecia in the holotype.

Typification: Great Britain, Suffolk, Halesworth, branches of *Ulex europaeus*, 27.III.2004, S.M. Francis & E. Batten (ex E.B. 4504 & ex H.B. 7507a, M-0276417, holotype).

Latin diagnosis: Hyalorbiliae subfusisporae *similis*, *sed apothecia minora*, *plerumque alba*, *ascosporae minores*, *partim basaliter curvatae*, *in statu vivo corpuscula refringentia plerumque carentes.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.05–)0.08–0.16(–0.19) mm diam., 0.05–0.06 mm high (receptacle 0.035 mm), whitish, sometimes very pale amber-yellowish, translucent, round, slightly gelatinous, scattered to gregarious; disc flat, margin thin, not protruding, smooth; sessile or often with indistinct obconical stipe, superficial; dry pale yellowish-cream or rosaceous. **Asci** *19–30 {5} × (4.8–)5.2–5.8(–6.2) µm {5}, †15–24(–32) × (4.2–)4.5–5.5(–6) µm {6}, 8-spored, spores *3–4-seriate, pars sporifera *15 → 11–12 µm long; **apex** (†) hemispherical or obtuse-subconical; **base** with or without medium long, thick, flexuous stalk, with croziers {4} (some with perforation). **Ascospores** *(4–)4.5–5.5(–6) × (1.4–)1.6–1.8(–2) µm {4}, †(3.5–)4.5–5.5(–6) × 1.3–1.7 µm {5}, (fusiform- to) (ellipsoid-)fusoid(-clavate), apex obtuse to subacute, base slightly to sometimes strongly attenuated, partially inequilateral or slightly curved towards base; **SBs** consistently absent {4}, rarely present {1}, minute, globose; with a few minute, rarely medium-sized LBs towards each end. **Paraphyses** apically uninflated, sometimes slightly to medium clavate-capitate, terminal cells †5.5–14 × (1.8–)2–2.5(–2.8) µm {2}, lower cells †3.5–7 × 1.8–2 µm {2}; not or rarely branched at upper septum. **Medullary excipulum** 10 µm thick, non-gelatinized, of medium loose, horizontally oriented textura prismatica-porrecta, medium sharply delimited. **Ectal excipulum** near base of (†) not or slightly gelatinized, indistinctly vertically oriented t. angularis, 30 µm thick, cells †8–11 × 5–8 µm {1}; at flanks of horizontal t. prismatica-globulosa, cells *6–11 × 4–10 µm, 10 µm thick near margin, marginal cortical cells */†(6–)7–12(–14) × (3–)4–8(–9) µm {6}, clavate to vesiculous, thin-walled. **Anchoring hyphae** sparse to medium abundant, */†1.8–3 µm wide, walls 0.2 µm thick {1}. **Exudate** over paraphyses 0.1–0.3 µm thick, continuous, smooth to finely rough, sometimes with scattered, loosely adhering granules; over margin and flanks 0.1 µm, smooth. — **ANAMORPH**: brachyphoris-like (presumed, from natural substrate {4}). **Conidiophores** not observed. **Conidia** unbranched, narrowly fusoid, slightly to medium curved (falcate to helicoid), especially towards ends, *44–60 {1} or 62–77.5 {1} × 2.1–2.5(–3) µm {2}, †44–56 × 1.6–2 µm {3}, ~3–6-septate, with several minute LBs in each cell, sometimes also with larger guttules.

Habitat: collected 0.5–2 m above the ground, corticated or partially decorticated, 7–38 mm thick branches or 5–30 cm thick standing trunks of *Cornus* ?*sanguinea* {1}, *Corylus* ?*colurna* {1}, *Fagus sylvatica* {5}, *Salix* sp. {2}, *S. caprea* {1}, *S.* ?*cinerea* {1}, *Sambucus nigra* {1}, *Ulex europaeus* {1}, on slightly to strongly decayed bark {12} (periderm {1} and bast {4}), rarely on wood {1}, often on inner surface or on edges of detaching bark, also in old scars of side twigs, slightly greyed to strongly blackened, with or without a few to many green algae. **Associated**: *Cryptodiscus* sp. {1}, *Glyphium elatum* {1}, *Hyalorbilia erythrostigma* {2}, *H. juliae* {2}, *H. subfusispora* {2}, *Hysteropatella elliptica* {1}, *Karstenia idaei* {1}, *Lachnum* sp. {1}, *Melanomma pulvis-pyrius* {1}, *Mollisia* sp. {2}, *Orbilia aristata* {2}, *O. auricolor* {1}, *Pyrenopeziza* sp. {1}, *Unguiculariopsis* ?*rehmii* {1}. **Desiccation tolerance**: mature asci still viable for at least 6 days. **Altitude**: 15–417 m a.s.l. **Geology**: Buntsandstein, Keuper (Stubensandstein), Lower Jurassic sandstone & marl, Pleistocene sand & gravel. **Phenology**: I–V, IX, XI.

Taxonomic remarks. *Hyalorbilia rotifera* is characterized by very small, usually whitish apothecia and small, (ellipsoid-) fusoid(-clavate) ascospores. From the similar *H. subfusispora* with partially larger and more chlorinaceous apothecia, *H. rotifera* differs in shorter and narrower spores which are sometimes slightly curved near the base. *H. latispora* differs in wider, broadly fusoid spores, and *H. resinae* in partially narrower spores besides a tendency to strongly inflated paraphyses and in growing on coniferous substrate. *H. oreadum* has larger apothecia and narrower spores. For the similar *H. herbicola* and *H. hergiswiliana* see there.

Variation. In the typical collections of *H. rotifera* (on bark of *Ulex* and *Fagus*) spore bodies could not be found in the living spores (all drops were KOH-resistant). In the sample on

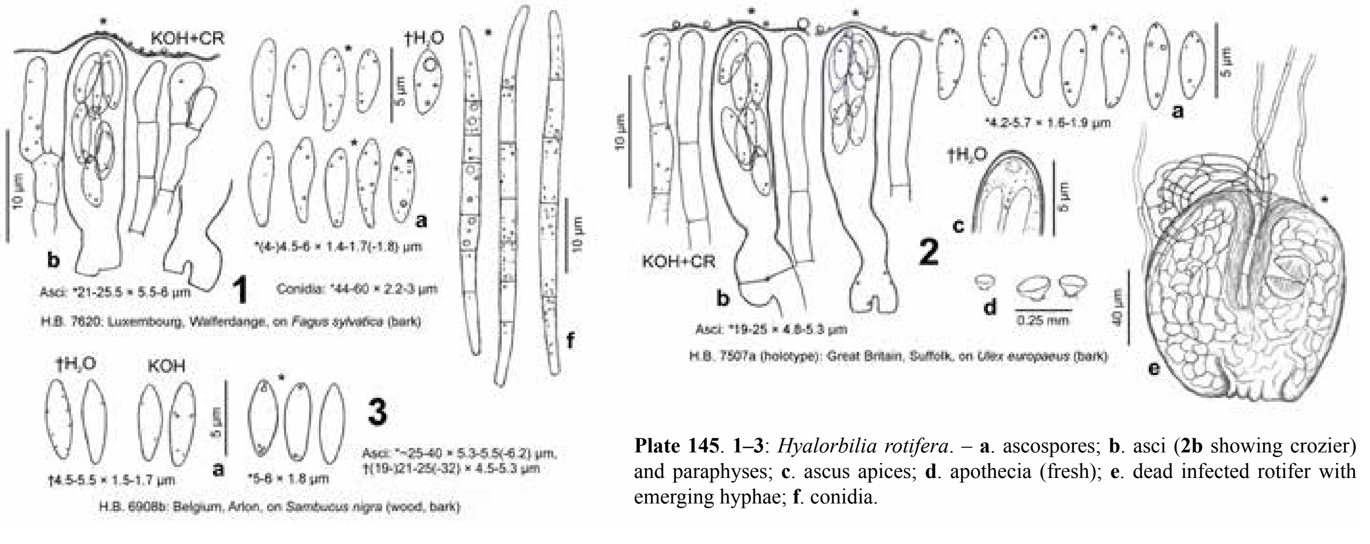


Plate 145. **1–3**: *Hyalorbilia rotifera*. – **a**. ascospores; **b**. asci (**2b** showing crozier) and paraphyses; **c**. ascus apices; **d**. apothecia (fresh); **e**. dead infected rotifer with emerging hyphae; **f**. conidia.

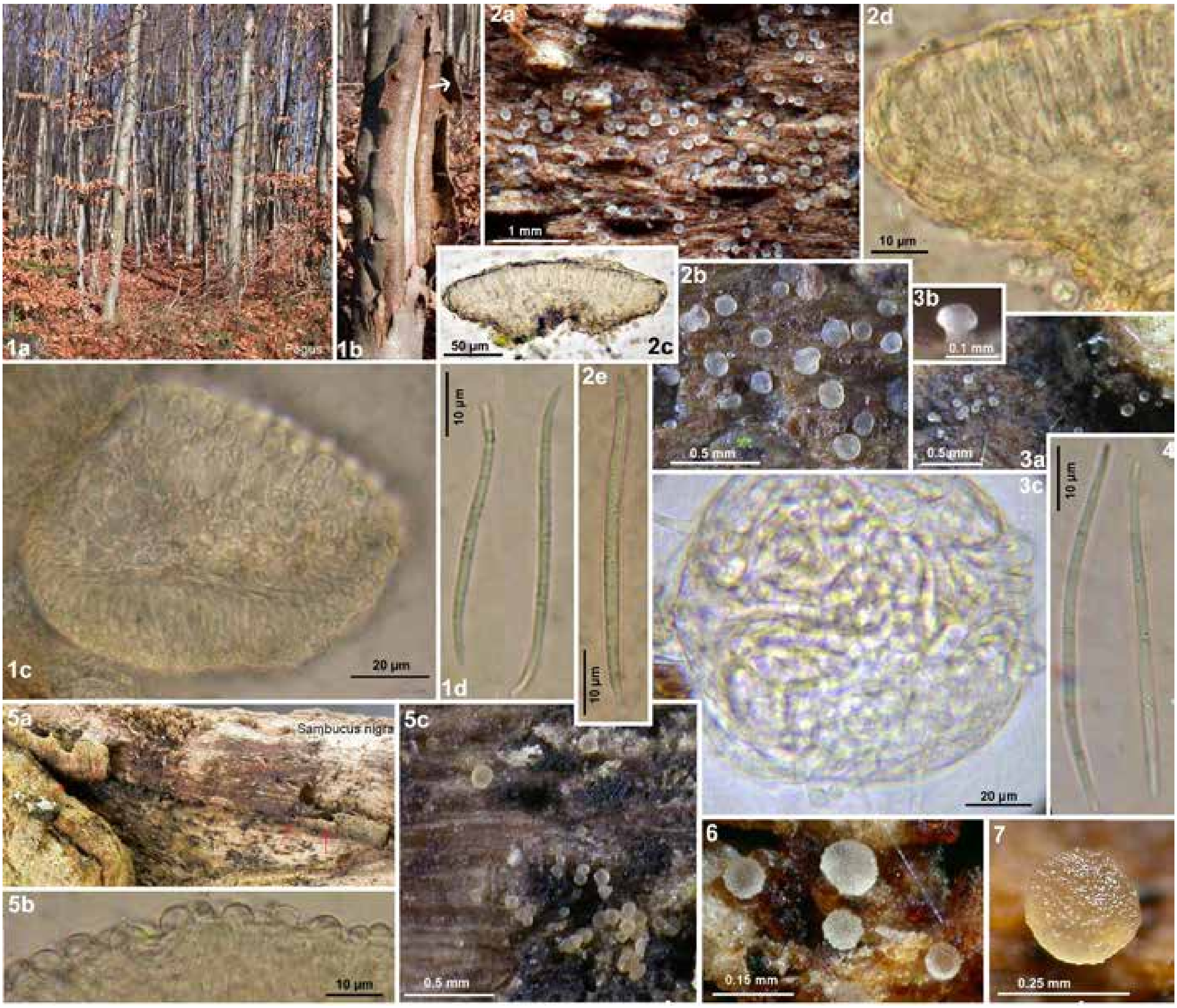


Plate 146. **1–7**: *Hyalorbilia rotifera*. – **1a**. young beech forest; **1b**. living *Fagus* with large wound; **5a**. decorticated xeric branch of *Sambucus nigra*; **2a–b**, **6**, **7**, **5c**. rehydrated apothecia; **3a–b**. fresh apothecia; **2c–d**. apothecia in median section; **1c**. apothecium in top view; **5b**. margin in top view; **1d**, **2e**, **4**. conidia from substrate; **3c**. dead rotifer colonized by assimilative hyphae. – Living state (in **1c** & **2d** only some asci and spores alive) except for **1d** (in H_2O); **4**, **5b** (in KOH). — **1a–d**. H.B. 7627b: Luxembourg, Walferdange, on *Fagus*; **2a–e**. H.B. 7620a: ibid., on *Fagus*; **3a–c**. H.B. 7507a (holotype): Great Britain, Suffolk, on *Ulex*; **4**. H.B. 6988b: Luxembourg, Ettelbruck, on *Salix*; **5a–c**. H.B. 6908b: Belgium, on *Sambucus*; **6**. 3.I.2010: Luxembourg, Waldhaff, on *Fagus*; **7**. 3.II.2007: ibid., Echternach, on *Fagus*.

wood of *Sambucus* a minute SB was present at each spore end and the asci were extraordinarily long. Here and in samples on bark of *Cornus* and *Salix* the spores were consistently straight and homopolar. In the type collection 4 free spores were figured by E. Batten (IVV: H.B. 7507a), all with a single elongate spore body ~0.8 × 0.2 µm in the wider end, but no such body could be observed when the material was received in the fresh and living state.

Among the samples from which sequences were gained, only that on *Corylus* bark was microscopically studied (IVV: 22.I.2019). It fits in ascus (*24–29 × 5.2–5.3 µm) and spore size (*4–5 × 1.7–2 µm inside living asci, indistinctly heteropolar, without SBs), but the conidia are with *62–77.5 × 2.1–2.3 µm longer than in the other four samples in which conidia were seen, although they show the same number of septa (3–6).

Anamorph. The flexuous, slender conidia of the presumed anamorph of *H. rotifera* (Pl. 145: 1f; 146: 1d, 2e, 4; see also IVV) resemble those of *B. helminthodes*, which differs in larger, more straight conidia (53–84 × 2.8–3.7 µm) and is known to infect oo- and zygospores.

In the type collection of *H. rotifera* a single infected rotifer was found close to an apothecium. The interior of the rotifer was colonized by *5–8 µm wide assimilative hyphae similar as in *Lecophagus*, but the emerging and external hyphae being much narrower (*2.5–3.5 µm) than in *Lecophagus*. Very probably these hyphae belong to the adjacent *Hyalorbilia* apothecia. That they belong to an orbiliaceous fungus is supported by the fact that their wall surface stains lilac in CRB.

Phylogeny. Sequences of *H. rotifera* were obtained from apothecia of two samples from Luxembourg, on *Salix* and *Corylus*, comprising ITS and LSU, one also SSU (V7–9). In the ITS they fully concur except for 1 nt in ITS2, but they differ in 1 nt in LSU D1 and 3 nt in LSU D2 (0.7 %). Another sequence was made from an undocumented sample (G.M. 2014-11-28.1) which by microscopy belonged to *H. subfusispora* (G.M. 2014-11-28.2). This deviates from the above by 5.2–5.4 % in

ITS but only 0.3–0.7 % in LSU. We presume here a mixture of two *Hyalorbilia* species. In all three sequences the S1506 intron is absent.

In our combined analysis (Phyl. 6), *H. rotifera* clustered in the strongly supported *Vermispora* clade, and here with boreal to subarctic North American environmental clones (V11–12) in a likewise strongly supported subclade. The three *H. rotifera* sequences formed a supported clade in NJ analyses of ITS, LSU, or ITS+LSU (not shown), which clustered sister to most of the environmental clones which include also some from alpine central Europe. *H. rotifera* shows to all these clones an 8–10.5 % ITS distance, but also among the clones a distance of up to 6.5–13.5 % occurs. When analysing LSU (D1–D2), *H. rotifera* showed a 1–3 % distance to these clones. Its ITS distance to *H. hergiswiliana* lies at ~30 %, and to *H. subfusispora* at 33–34 %.

Ecology. The sparse to abundant apothecia of *Hyalorbilia rotifera* were found on ± rotten bark (rarely wood) of dead xeric branches of various angiosperm trees and shrubs, also on the inner surface of bark detaching from large wounds of living trunks of *Fagus*. The collections are from cold-temperate humid, planar to colline areas in atlantic northwestern and subcontinental central Europe.

Specimens included. **GREAT BRITAIN**: **East England**, **Suffolk**, 4 km ESE of Halesworth, 0.4 km NNW of Wenhaston, Bicker's Heath, 15 m, branches of *Ulex europaeus*, on bark, 27.III.2004, S.M. Francis & E. Batten (E.B. 4504, ex H.B. 7507a, M-0276417, **holotype**). — **BELGIUM**: **Wallonie**, **Luxembourg**, 8 km SE of Arlon, 0.7 km SE of Sterpenich, 325 m, branch of *Sambucus nigra*, on wood & bark, 23.IV.2001, H.O. Baral (H.B. 6908b, anam. substr.). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 10 km W of Ettelbruck, 1.8 km NW of Grosbous, Bruch (an der Wark), 380 m, branch of *Salix ?cinerea*, on bark, 27.V.2001, G. Marson (H.B. 6988b, anam. substr.). – **Gutland**, **Capellen**, 6.5 km ESE of Arlon, 1.3 km NW of Steinfort, Aechels, 330 m, branch of *Salix caprea*, on bark, 5.V.1998, H.O. Baral (ø). – **Luxembourg**, 6 km NNE of Luxembourg, 2 km E of Walferdange, Gréngewald, Croix de la Femme Morte, 412 m, trunk of *Fagus sylvatica*, on bark, 20.XI.2004, G. Marson (H.B. 7620a, anam. substr.). – ibid., trunk of *F. sylvatica*, on bark, 25.XI.2004, G. Marson (H.B. 7627b, anam. substr.). – 7 km NE of Luxembourg, Waldhaff, 417 m, trunk of *F. sylvatica*, on bark, 3.I.2010, G. Marson (ø). – 5.3 km NE of Luxembourg, 3 km NE of Kirchberg, 347 m, trunk of *Fagus sylvatica*, on bark, 28.XI.2014, G. Marson (G.M. 2014-11-28.1, non vid., sq.: MN15140). – 5 km SE of Luxembourg, 1.5 km E of Itzig, Reimeschbaach, 297 m, branch of *Salix*, on bark, 17.X.2015, G. Marson (G.M. 2015-10-17.1, non vid., sq.: MK493151). – ibid., branch of *Corylus ?colurna*, on bark and old pyrenomycete, 22.I.2019, G. Marson (G.M. 2019-01-22.1, sq.: MN151405). – **Echternach**, 10 km WNW of Echternach, 1.2 km SW of Beaufort (Befort), Längt, 340 m, trunk of *F. sylvatica*, on bark, 3.II.2007, G. Marson (ø). — **GERMANY**: **Baden-Württemberg**, 3 km NE of Tübingen, 1 km NE of Lustnau, Stauden, 400 m, branch of *Cornus ?sanguinea*, on bark, 15.IX.2001, H.O. Baral (ø).

Hyalorbilia fusarina (Burghouts & W. Gams) E. Weber & Baral, **comb. nov**., MB 830794 — Pl. 24: b

Basionym: *Vermispora fusarina* Burghouts & W. Gams, Mem. N. Y. bot. Gdn 49: 58 (1989) (Pl. 24: b)

Etymology: named after the phragmoconidia reminiscent of macroconidia of *Fusarium*.

Typification: Netherlands, Assen, on eggs of *Globodera pallida*, I.1984, Th. Burghouts (CBS 382.84, ex-type culture; dried material: holotype)

Description: — **TELEOMORPH**: unknown. — **ANAMORPH**: vermispora-like (data from Burghouts & Gams 1989 and Chen et al. 2007c: fig. 4). **Mycelial hyphae** 1–3 µm wide, hyaline. **Conidiophores** not differentiated from mycelial hyphae, arising mostly as lateral branches, simple or branched, repeatedly geniculate by proliferating in a sympodial manner, 17–80 µm long, 2.5–3 µm wide near the base, ending in a truncate, 1.5–2.5 µm wide scar. **Conidia** fusiform, curved and slightly beaked at the apex, 30–50(–55) × (3.5–)4–4.5(–5) µm, (2–)3(–4)-septate. Chlamydospores absent.

Habitat: Agricultural soil, isolated from nematode eggs of *Globodera pallida*. Known only from temperate subatlantic Europe.

Phylogeny. ITS sequences from three strains of the type collection were available for *H. fusarina*. A distance of 1.5–2 % is found among them although they were all gained from the same isolate. Considering this infraspecific variation which might include sequencing errors, the distance of 2.5–4.5 % between *H. fusarina* and *H. leguminacea* is comparatively low. In contrast, *H. fusarioides* differs from these three species by ~21–24 % and various gaps which cause strong optical divergence in the alignment. The 5.8S distance between the *Vermispora* clade and other clades of *Hyalorbilia* or other genera is surprisingly high, e.g., 3 % to *Lilapila*, 4.5–5 % to *Amphosoma*, 5–7 % to *Hyalorbilia* p.p.maj., and 6.5–7.5 % to *Lecophagus*.

Sequences of two strains of *H. fusarina* (CBS 382.84, 383.84A) comprise LSU D1–D4 and are identical in the D1–D3. Their D1–D3 distance to *H. leguminacea* is 0.9 % and to *H. spermatophaga* 2.5 %.

Specimens included. **NETHERLANDS**: **Drenthe**, Assen, isolated from eggs of *Globodera pallida* buried in agricultural soil, I.1984, Th. Burghouts (CBS 382.84, ex-type culture, conid. isol., doc. vid.; dried material: **holotype**; CBS 383.84A, CBS 383.84B), sq.: DQ494377– DQ494379, HQ110699–HQ110700.

Hyalorbilia leguminacea (Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu) E. Weber & Baral, **comb. nov**., MB 830795 — Pl. 24: a

Basionym: *Vermispora leguminacea* Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu, Fungal Diversity 26(1): 136 (2007)

Etymology: named after the pod-shaped conidia resembling fruits of legumes.

Typification: China, Fujian, soil, 2003, X.Z. Liu (HMAS 140512, holotype; ex-type culture: CGMCC 6.0291)

Description: — **TELEOMORPH**: unknown. — **Anamorph**: vermispora-like (data from Chen et al., 2007c: fig. 6). **Mycelial hyphae** 1.5–3 µm wide, hyaline. **Conidiophores** simple, ± straight, slightly geniculate by sympodial proliferation, 26–104 µm long, 1.5–3 µm wide near the base, gradually narrowed to 1–1.5 µm towards the apex. **Conidia** hyaline, cylindric-fusoid, pod-shaped, straight to slightly curved, *20–34 × 4–5 µm, (1–)3(–5)-septate.

Habitat: Isolated from soil. Known only from China.

H. leguminacea resembles *H. fusarina* but has distinctly shorter, more pod-shaped conidia. The scale bars in Chen et al. (2017c) are sometimes highly erroneous, those in fig. 6 E–F being probably the most reliable ones.

Phylogeny. ITS Sequences of the holo- and paratype of *H. leguminacea* were gained by Liu et al. (2005b, as *V. fusarina*) and also by Chen et al. (2007a), partially misidentified as *V. fusarina*. The five available ITS Sequences derive very probably from only three strains; also one sequence of LSU D1–D3 exists for one strain (AS6.0291). A distance of 0.5–1.2 % is found among the five strains, although the *H. leguminacea* strains derive from only three isolates. The S1506 intron is absent in two sequences of *H. leguminacea* (AY776169, AY776170), according to the used ITS5 primer.

Specimens included. **CHINA**, **Fujian**, from soil, 2003, X.Z. Liu (HMAS 140512, **holotype**; ex-type culture: CGMCC 6.0291, conid. isol., doc. vid., sq.: DQ494376, HQ110701). – ibid. (HMAS 140513, **paratype**; CGMCC 6.0290; sq.: DQ494375). (strains 786 = AY776169 and 333 = AY776170 probably also from holo-/paratype). – ?**Beijing**, undated, Yang et al. 2007 (CGMCC 3.6757, YXJ13-5, non vid., sq.: AY773447).

Hyalorbilia spermatophaga (Drechsler) E. Weber & Baral, **comb. nov.**, MB 830796 — Pl. 24: d

Basionym: *Dactylella spermatophaga* Drechsler, Phytopathology 28(1): 91 (1938)

≡ *Vermispora spermatophaga* (Drechsler) Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu, Fungal Diversity 26(1): 124 (2007)

Etymology: named after the habit of the fungus to consume oospores of oomycetes ('eating seeds').

Typification: USA, Maryland, Beltsville and Virginia, Arlington, on decaying plant remains, undated, C. Drechsler (holotype: illustration in Drechsler 1938)

Description: — **TELEOMORPH**: unknown. — **ANAMORPH**: vermispora-like (data from Drechsler 1938 and Chen et al. 2007c: fig. 7). **Mycelial hyphae** 1–2 µm wide, hyaline. **Conidiophores** hyaline, septate, simple or somewhat branched, slightly geniculate by sympodial proliferation, 27–75 µm long, 2.5–4 µm wide at the base, tapering to 1–2 µm at the apex. **Conidia** hyaline, fusiform, truncate at the base, straight or often slightly to medium curved at narrowly rounded apex, *(25–)35–65 × 3.5–5.5 µm, (2–)3(–4)-septate.

Habitat: Isolated from decaying plant remains or soil, parasitizing many species of *Pythiaceae* (mostly *Pythium* and *Phytophthora*).

Phylogeny. A sequence of the ITS and LSU region was available for a non-type strain of *H. spermatophaga* (CBS 255.76), which shows an ITS distance of 12.5–13 % to *H. fusarina* and 13 % to *H. leguminacea*. In *H. spermatophaga* the presence or absence of the intron is unknown because the ITS1 primer was used.

Specimens included. **USA**: **Maryland**, Beltsville, and **Virginia**, Arlington, decaying plant remains, on hyphae, conidia, zoosporangia, oogonia, and oospores of *Pythium* and *Phytophthora*, undated, C. Drechsler (**holotype** [illustration in C. Drechsler 1938], conid. isol., doc. vid.). – **Michigan**, East Lansing, on oospores of *Phytophthora megasperma* var. *sojae*, isol. by B. Sneh (CBS 255.76, non vid., sq.: DQ494374, HQ110698).

Hyalorbilia fusarioides (D.C. Harris) E. Weber & Baral, **comb. nov.**, MB 830797 — Pl. 17

Basionym: *Microdochium fusarioides* D.C. Harris, Trans. Br. mycol. Soc. 84(2): 358 (1985)

≡ *Microdochiella fusarioides* (D.C. Harris) M. Hern.-Restr. & Crous, in Hernández-Restrepo, Groenewald & Crous, Persoonia 36: 62 (2015) [2016]

Etymology: named after the conidium shape resembling macroconidia of *Fusarium*.

Typification: Great Britain, Kent, East Malling Research Station, *Malus* leaves on and in soil, on oospores of *Phytophthora syringae*, X.1980, D.C. Harris (IMI 218715, holotype; ex-type culture CBS 741.83).

Description: — **TELEOMORPH**: unknown. — **ANAMORPH**: vermispora-like (data from Harris 1995 and Hernández-Restrepo et al. 2015). **Mycelial hyphae** 1–2 µm wide, hyaline. **Conidiophores** simple or branched, septate, geniculate by sympodial proliferation, ~7–100(–150) µm long, 2–3 µm wide, ~1.5 µm at apex. **Conidia** hyaline, narrowly fusiform, tapered towards narrowly rounded apex and truncate base, slightly to medium curved (falcate), *30–60 × 2–3 µm, (1–)3(–5)-septate, dry but with a droplet of moisture at the mid-point of each conidium. **Chlamydospores** subglobose to ellipsoid, forming intercalary chains.

Habitat: Isolated from apple leaves on and in soil, parasitic on oospores of oomycetes (Harris 1985); DNA extract from maize roots. Known from temperate humid Great Britain and Germany.

Phylogeny. Sequences of three CBS cultures of the type isolate from apple leaves in East Malling (Kent, Great Britain) were gained by Hernandez-Restrepo et al. (2015), comprising ITS and LSU (D1–D3). Three 'uncultured *Vermispora*' DNA extracts from roots of maize near Göttingen (Niedersachsen, Germany) comprise ITS and LSU (D1). The S1506 intron is absent in all six sequences which are identical in their overlapping part, except for 1 nt in the ITS1 in two of the DNA extracts, therefore, they belong to *H. fusarioides*. Three further uncultured clones from the same maize field clustered also in the *Vermispora* clade but distant from the above: two (V1) in a clade with the three former *Vermispora* spp. (*H. fusarina*, *H. leguminacea*, *H. spermatophaga*), and one (V13) in a clade with clones V11–V12 and *H. rotifera* (see Phyl. 6, see also S6 & S7).

H. fusarioides shows a high ITS distance to the three former *Vermispora* species, ranging at ~21–24 %, compared to 2.5–13 % among the latter, although in the 5.8S region it differs from them by only 1 nt (pos. 142, Tab. 18). In the LSU D1–D3 *H. fusarioides* differs from the three former *Vermispora* species by 6.5–7.3 % (8.2–8.7 % in D1–D2), compared to 0.9–2.5 % or 1.2–2.6 % among the latter, respectively.

Specimens included. **GREAT BRITAIN**: **South East England**, **Kent**, 6 km WNW of Maidstone, East Malling Research Station, apple orchard, 25 m, *Malus* leaves on and in soil, on oospores of *Phytophthora syringae*, X.1980, D.C. Harris (IMI 218715, **holotype**, CBS 740.83, 741.83 [ex-type], 742.83, sq.: KP858975, KP858976, KP858977, KP859039, KP859041). — **GERMANY**: **Niedersachsen**, 4.5 km NW of Göttingen, Holtensen, 158 m, maize field, soil around roots of *Zea mays*, 2010–2011 (as Uncultured *Vermispora*, HG936894, HG936895, HG936896).

Orbilia Fr., Fl. Scan.: 343 (1836)

Lectotype species: *Peziza xanthostigma* Fr. (≡ *Orbilia xanthostigma*, series *Orbilia*), designated by Bachman (1909)

≡ *Peziza* section *Orbilia* (Fr.) P. Karst., Not. Sällsk. Fauna et Fl. Fenn. Förh., 10: 106 (1869)

?= *Dactylium* Nees, Syst. Pilze: 58 (1816) [1816–1817]; Fr., Syst. Mycol. 3: 382, 412 (1832) [nom. utique rej., Art. 56.1] – Type species: *D. candidum* Nees [but identity unquestionable for *Dactylium candidum* s. Drechsler 1937a: 523]

= *Arthrobotrys* Corda, Pracht-Fl. Europ. Schimmelbild.: 43 (1839) – Type species: *A. superbus* Corda [= *Orbilia* ?*auricolor* (A. Bloxam) Sacc., series *Arthrobotrys*]

= *Trinacrium* Riess in Fresenius, Beitr. Mykol. 2: 42 (1852) – Type species: *T. subtile* Riess [(?)series *Hemiorbilia*]

= *Habrostictis* Fuckel, Jahrb. Nassau. Ver. Naturkd. 23–24: 249 (1870) – Lectotype species: *H. rubra* Fuckel [= *Orbilia carpoboloides* (P. & H. Crouan) Baral] (series *Habrostictis*, non *Habrostictis* Clem.), designated by Höhnel (1917: 330)

= *Dactylella* Grove, J. Bot. 22: 199 (1884) – Type species: *D. minuta* Grove (?series *Neodactylella*)

= *Dicranidion* Harkn., Bull. Calif. Acad. Sci. 1: 163 (1885) – Type species: *D. fragile* Harkn. [= *Orbilia eucalypti* (W. Phillips & Harkn.) Sacc., series *Orbilia*]

= *Cheilodonta* Boud., Bull. Soc. Mycol. Fr. 1: 114 (1885) – Lectotype species: *Peziza carpoboloides* P. & H. Crouan [≡ *Orbilia carpoboloides* (P. & H. Crouan) Baral, series *Habrostictis*], indirectly designated by Höhnel (1917: 333)

= *Hyalinia* Boud., Bull. Soc. Mycol. Fr. 1: 114 (1885), nom. illegit., ICN Art. 53.2 – Type species: *Helotium crystallinum* Quél. [= *Orbilia crenatomarginata* (Höhn.) Sacc. & Trotter, series *Hyalinia*]

= *Monacrosporium* Oudem., Ned. Kruidk. Arch., Ser. 2,4: 250 (1885) – Lectotype species: *M. elegans* Oudem. [≡ *Orbilia elegans* (Oudem.) Baral et al., series *Arthrobotrys*], designated by Clements & Shear (1931)

= *Helicoon* Morgan, J. Cincinnati Soc. Nat. Hist. 15: 49 (1892) – Lectotype species: *H. sessile* Morgan [= *Orbilia luteorubella* (Nyl.) P. Karst., series *Helicoon*], designated by Linder (1929)

= *Pedilospora* Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 111: 1047 [61 of repr.] (1902) – Type species: *P. parasitans* Höhn. [?= *Orbilia eucalypti* (W. Phillips & Harkn.) Sacc., ?series *Orbilia*]

= *Anulosporium* Sherb., Mycologia 25: 262 (1933) – Type species: *A. nematogenum* Sherb. [nom. dub., identity unclear at the species level]

= *Radotinea* Velen., Monogr. Discom. Bohem.: 298 (1934) – Type species: *R. caudata* Velen. [= *Orbilia* ?*aristata* (Velen.) Velen., (?)series *Hemiorbilia*]

= *Orbiliella* Kirschst., Ann. Mycol. 36: 374 (1938) – Type species: *Orbiliella armeniaca* Kirschst. [= *Orbilia auricolor* (A. Bloxam) Sacc., series *Arthrobotrys*]

= *Didymozoophaga* Soprunov & Galiulina, Mikrobiologiya 20: 493 (1951), nom. inval., ICN Art. 39.1; nom. illegit., ICN Art. 52.1 – Lectotype species: *D. superba* (Corda) Soprunov & Galiulina (≡ *A. superbus*, series *Arthrobotrys*), designated by Schenck et al. (1977)

= *Orbiliaster* Dennis, Kew Bull. 9: 294 (1954) – Type species: *Orbiliaster pilosus* Dennis [≡ *Orbilia pilosa* (Dennis) Baral, series *Drechslerella*]

= *Drechslerella* Subram., J. Indian bot. Soc. 42: 299 (1964) ['1963'] – Type species: *D. acrochaeta* (Drechsler) Subram. (series *Drechslerella*)

= *Candelabrella* Rifai & R.C. Cooke, Trans. Br. Mycol. Soc. 49(1): 160 (1966) – Type species: *C. javanica* Rifai & R. C. Cooke [≡ *A. javanicus* (Rifai & R.C. Cooke) Jarow., series *Arthrobotrys*]

= *Genicularia* Rifai & R.C. Cooke, Trans. Br. Mycol. Soc. 49: 153 (1966) nom. illegit., ICN Art. 53.1 [non *Genicularia* Rouss. 1806] – Type species: *G. cystosporia* (Dudd.) Rifai & R.C. Cooke (see *Geniculifera*)

= *Dactylariopsis* Mekht., Mikol. Fitopatol. 1: 278 (1967) – Type species: *D. brochopaga* (Drechsler) Mekht. [≡ *Orbilia brochopaga* (Drechsler) Baral et al., series *Drechslerella*]

= *Dactylosporium* Mekht. (1967), Mikol. Fitopatol. 1: 277 (1967) nom. illegit., ICN Art. 53.1 [non *Dactylosporium* Harz 1871] – Type species: *D. leptosporum* (Drechsler) Mekht. [≡ *Dactylellina leptospora* (Drechsler) M. Morelet, series *Dactylellina*]

= *Golovinia* Mekht., Mikol. Fitopatol. 1: 275 (1967) – Type species: *G. bembicodes* (Drechsler) Mekht. [≡ *Orbilia bembicodes* (Drechsler) E. Weber & Baral et al., series *Drechslerella*]

= *Dactylellina* M. Morelet, Bull. Soc. Sci. Nat. Archéol. Toulon et du Var 178: 6 (1968) – Type species: *D. leptospora* (Drechsler) M. Morelet (series *Dactylellina*)

= *Duddingtonia* R.C. Cooke, Trans. Br. Mycol. Soc. 53: 316 (1969) – Type species: *D. flagrans* (Dudd.) R.C. Cooke [≡ *A. flagrans* (Dudd.) Mekht., series *Arthrobotrys*]

= *Geniculifera* Rifai, Mycotaxon 2: 214 (1975) – Type species: *G. cystosporia* (Dudd.) Rifai [≡ *A. cystosporius* (Dudd.) Mekht., series *Arthrobotrys*]

= *Nematophagus* Mekht., Mikol. Fitopatol. 9(2): 250 (1975) – Type species: *N. azerbaijanica* Mekht. [≡ *A. azerbaijanicus* (Mekht.) Oorschot, series *Arthrobotrys*]

= *Laridospora* Nawawi, Trans. Br. Mycol. Soc. 66: 344 (1976) – Type species: *L. appendiculata* (Anastasiou) Nawawi [≡ *Dactylellina appendiculata* (Anastasiou) M. Scholler et al., series *Dactylellina*]

= *Drechsleromyces* Subram., Kavaka 5: 93 (1978, '1977') – Type species: *D. atractoides* (Drechsler) Subram. [≡ *Dactylella atractoides* Drechsler, series *Neodactylella*]

= *Gangliophragma* Subram., Kavaka 5: 94 (1978, '1977') – Type species: *G. rhopalota* (Drechsler) Subram. [≡ *Dactylella rhopalota* Drechsler, series *Neodactylella*]

= *Kafiaddinia* Mekht. Mikol. Fitopatol. 12: 8 (1978) – Type species: *K. fusarispora* Mekht. [= *Dactylellina leptospora* fide Rubner 1996, series *Dactylellina*]

= *Monacrosporiella* Subram., Kavaka 5: 94 (1978, '1977') – Type species: *M. megalospora* (Drechsler) Subram. [≡ *A. megalosporus* (Drechsler) M. Scholler et al., series *Arthrobotrys*]

?= *Tripoconidium* Subram., Kavaka 5: 95 (1978) – Type species: *T. aphanopagum* (Drechsler) Subram. (as '*aphanophagum*', ?section *Arthrobotrys*)

= *Woroninula* Mekht., Khishchnye Nematofagovye Griby – Gifomitsety: 109 (1979) – Type species: *W. polycephala* (Drechsler) Mekht. [≡ *A. polycephalus* (Drechsler) Rifai, series *Arthrobotrys*]

?= *Descalsia* A. Roldán & Honrubia, Mycol. Res. 92: 494 (1989) – Type species: *D. cruciata* A. Roldán & Honrubia (?series *Hemiorbilia*)

= *Roigiella* R.F. Castañeda, Revta Jardín bot. Nac., Univ. Habana 5(1): 62 (1984) – Type species: *R. lignicola* R.F. Castañeda (= *Arthrobotrys* sp. fide Seifert et al. 2011, series *Arthrobotrys*)

= *Gamsylella* M. Scholler, Hagedorn & A. Rubner, Sydowia 51(1): 108 (1999) – Type species: *G. arcuata* (Scheuer & Webster) M. Scholler et al. (series *Gamsylella*)

= *Pseudotripoconidium* Z.F. Yu & K.Q. Zhang, in Yu et al., Mycologia 103(1): 168 (2011) – Type species: *P. sinense* Z.F. Yu & K.Q. Zhang (series *Pseudotripoconidium*)

Etymology: see under the respective series.

Description: — **TELEOMORPH**: **Apothecia** hydrated ((0.07–)) (0.1–)0.2–2(–4)((–7.5)) mm diam., variously reddish-coloured (often orange or brick-red, also rose to pink), more rarely hyaline, yellow, blood-red, brownish or olive-black, translucent or not, round, sometimes ellipsoid or with undulating margin, soft-fleshed, rarely distinctly gelatinous, superficial to erumpent; disc ± flat, often also concave or convex, margin usually distinct, not or slightly, sometimes strongly protruding, smooth or finely crenulate, sometimes with short to long whitish teeth or hairs, developing gymnohymenial or sometimes cleistohymenial; exterior ± concolorous, broadly sessile to subsessile, also with an obconical to cylindrical stipe which is very rarely higher than wide. **Asci** *(24–)30–100(–140) × (2.8–)4–11(–15.3) µm, 8- up to 128-spored, spores uni- up to multiseriate, usually most or all asci with a varying percentage of the spores with an inverse orientation, usually the lower spores inverted, rarely the upper spores; **apex** (†) ± hemispherical in all viewing directions, or strongly truncate in front view (often with ± distinct shoulders) while hemispherical in profile view, thin-walled or with a distinct apical wall thickening †(0.4–)0.7–3(–6) µm thick (mostly with apical chamber), spores at maturity dehydrated and agglutinated to form a single body that is forcibly ejected through a slit-like apical pore; **base** ± narrowed to a thin or thick, often ± flexuous stalk of very variable length, usually forked at the base into 2(–3) branches (Y-, T-, L-, h- or H-shaped), some asci seemingly non-furcate (with one branch reduced to a septum at the lateral part of the ascus stalk). **Ascospores** *(1.8–)2.5–20(–30) × (0.6–)1–4(–6) µm, homopolar or slightly to strongly heteropolar in shape, sometimes with a distinct basal tail, highly diverse in shape (cylindrical, subulate, clavate, fusiform, ellipsoid, ovoid, globose, triangular, heart-shaped, sperm-shaped), straight or slightly to very strongly curved (reniform, falcate, geniculate, or helicoid), hyaline, smooth (very rarely warted), non-septate and uninucleate (very rarely 1–2-septate inside living asci); each spore containing a medium to strongly refractive **spore body** (SB) attached to the spore apex (rarely at subapex or lateral wall), SBs variously shaped (lens- to plug-shaped, globose, tear-shaped, ampulliform, rod-shaped, vermiform, filiform), either broadly attached to spore wall or apically narrowed to a wide or small point, sometimes with a fine, short to long, partially very delicate and then ± invisible filum, straight or flexuous to helicoid, sometimes uncinate; usually with a few small LBs (lipid content very low to low, very rarely medium); overmature spores 0–1-septate, vermiform SBs then strongly contracted and inflated, sometimes with a high lipid content (multiguttulate). **Paraphyses** apically uninflated or slightly to very strongly capitate or clavate, sometimes spathulate, lageniform, mammiform, or lanceolate, terminal cells either of ± equal length (desiccation-tolerant taxa), or distinctly or much longer than lower cells (predominantly desiccation-sensitive taxa), usually equalling or ± exceeding the dead asci, but often surmounted by the living asci; generally branched in their lower part, unbranched in upper part if with long terminal cells but rarely or frequently branched if with short terminal cells, anastomoses usually frequent in lower part, always absent in upper part. **Subhymenium** rarely clearly separated from the medullary excipulum, composed of anastomosing basal cells of paraphyses tightly woven with the branches of the furcate ascus bases. **Medullary excipulum** hyaline or very pale reddish, rarely olivaceous-brown, 10–20 up to 70–150(–200) µm thick, of loose to dense, thin-walled, rarely distinctly gelatinized textura intricata, composed of *(1.5–)2–3(–4)((–6)) µm wide hyphae, intermingled with some or many inflated globose to prismatic cells *5–15(–20)((–30)) × (4–)6–10(–16)((–27)), either sharply delimited from ectal excipulum or indistinctly so (if inflated cells very abundant), at lower or at least mid flanks sometimes forming a thin delimiting layer of t. porrecta. **Ectal excipulum** hyaline to very pale reddish, of non- or sometimes slightly to medium gelatinized, usually vertically or indistinctly oriented t. globulosa-angularis(-prismatica), either extending from base to margin, or replaced at mid flanks or margin by t. prismatica-porrecta oriented at a 0–50° angle to the surface, or rarely from base to margin of horizontally oriented t. (globulosa-)angularis(-prismatica), (10–)15–25 or usually 30–60 or up to 70–120(–220) µm thick near base, 10–30(–50) µm thick near margin, marginal cells thin- or sometimes thick-walled; **glassy processes** absent, less often present, 1–10 up to 30–100(–200) × (2–)3–4(–5) µm, often stratified, low- to high-refractive, solid, **hairs** rarely present, 10–100 or up to 200(–300) × (3–)4–7(–9.5) µm, cylindrical or slightly moniliform, thin- or thick-walled, septate, processes and hairs free or ± coherent to form a fimbriate to lacerate or dentate margin. **Anchoring hyphae** sparse to abundant, sometimes seen around each apothecium as a white subiculum (in dry state), *(1.5–)2–4(–6) µm wide, walls *0.2–0.4(–1.2) µm thick, sometimes forming a dense, hyaline, sometimes gelatinized t. intricata below apothecia. **SCBs** in paraphyses and ectal excipulum frequently present, either globose, hyaline, 1–3(–5) µm diam., low-refractive, or ring- to keyhole-shaped, medium refractive, hyaline to pale orange, 2–7(–11) µm diam. (often both types occurring mixed); **VBs** in desiccation-sensitive taxa often present as very low- to rather high-refractive, globose to elongate, hyaline, rarely yellowish or reddish vacuoles (1–)1.5–20(–25) × (1–)1.5–3(–4) µm, in strongly desiccation-tolerant taxa consistently absent; **carotenoids** in **LBs** [0.2–1(–2) µm diam.] of paraphyses, subhymenium and ectal excipulum (at flanks and especially margin) present in many taxa, pale to bright yellow-orange. **Exudate** over paraphyses, margin and flanks either sparse to absent (especially in desiccation-sensitive taxa), or abundant (especially in desiccation-tolerant taxa), forming a covering layer which is either ± continuous or broken into clods or granules, loosely adhering to a thin invisible gel layer, or firmly attached, sometimes forming thick glassy caps on each paraphysis, (medium to) strongly refractive, hyaline or pale to light yellow, 0.2–2(–5) µm thick over paraphyses, margin and flanks; paraphyses and asci usually more or less separable by pressure; gel between cells and on anchoring hyphae mostly distinctly lilac in **CRB**. — **ANAMORPH**: anguillospora-like, arthrobotrys-like, dactylella-like, dactylellina-like, descalsia-like, dicranidion-like, drechslerella-like, dwayaangam-like, gamsylella-like, helicoon-like, pseudotripoconidium-like, tridentaria-like, trinacrium-like, vermispora-like. **Mycelial hyphae** *2.5–7.5 µm wide, hyaline. **Colonies** hyaline/whitish to cream, yellowish, orange, rose, salmon or reddish-brownish. **Conidiophores** emerging from mycelial hyphae, rarely aggregated in synnemata, branched or unbranched in lower, middle or upper part, gradually narrower towards apex, (1.5–)7–400(–1500) µm long. **Conidiogenous cells** monoblastic or sympodial, partially with denticles or nodules. **Conidia** either unbranched, cylindrical, ellipsoid, clavate, fusoid to fusiform, inversely pyramidal (with nipple-shaped protuberances, pseudotripoconidium-like), straight or slightly to strongly curved, also vermiform (anguillospora-like) or strongly coiled (barrel-shaped, helicoon-like), (0–)1–17(–21)-septate; or branched (descalsia-, dicranidion-, dwayaangam-, tridentaria-, trinacrium-like), mostly multiseptate, arms cylindrical or ± tapering, straight or curved. — Living cells containing small, rarely large **LBs**; large **glycogen** regions partially present (in unbranched conidia); wall surface mostly distinctly lilac in **CRB**. **Trapping organs**: some species with adhesive branches and arches (gamsylella-like), adhesive knobs and non-constricting rings (dactylellina-like), adhesive networks (arthrobotrys-like), or constricting rings (drechslerella-like).

Habitat: Saprobiontic on dead bark and wood (including resin), woody fruits, herbaceous stems of mono- and dicots, textile, fruitbodies of perennial basidiomycetes or pyrenomycetes, exceptionally on dung or bones, the substrate being usually decomposed (optimal to often final stage) or sometimes very undecayed; substrate permanently moist (hygric) or periodically dry (xeric, then frequently in tight association with green algae and black yeasts); sometimes capturing nematodes, rarely arthropods or rotifers, occasionally parasitic on pollen. **Desiccation tolerance**: mature asci intolerant or tolerating a few weeks up to ~3.5 years; excipular cells and ascospores between a few days and several years. **Distribution**: worldwide, in arctic-alpine, boreal-montane, temperate, subtropical and tropical, humid to arid climates, with the highest species number in the (sub)tropical (semi)arid regions.

Recognized subgenera: *Habrostictis*, *Hemiorbilia*, *Orbilia* (see also Tab. 62), with 434 recognized species plus 7 with provisional name and 74 unnamed species ('affinis'); numbers referring to species with known teleomorph.

Generic concept. In the here applied wide circumscription, the genus *Orbilia* includes about 90 % of the species of *Orbiliomycetes* with a known teleomorph. Unlike *Hyalorbilia*, *Orbilia* forms a very diverse though likewise monophyletic group. The genus is sharply delimited from *Hyalorbilia* by a large number of more or less consistent characteristics (see also Tab. 59). The most important are: (1) only 1 spore body (SB) in each ascospore (mostly in the spore apex), (2) apex of dead asci either hemispherical and thick-walled or truncate and thin-walled (only exceptionally hemispherical and thin-walled), (3) ascus base usually ± furcate, croziers consistently absent or exceptionally present in a few taxa, (4) paraphyses often capitate but also spathulate-mammiform to lanceolate or uninflated, not embedded in ample gel, and (5) an ectal excipulum at the lower flanks generally of textura angularis, often with vertically elongated prismatic cells. As a very rare exception, a few abnormal spores with 2 spore bodies, one at each end, were seen in some species of *Orbilia* (series *Lentiformes*, *Hesperideae*, *Serpentinae*, see p. 71). Such abnormal spores appear to reveal the origin of the genus from an ancestor which showed SBs at both spore ends (see p. 79).

The genus *Orbilia* is applied here in the circumscription as proposed by Baral (1994), Baral & Marson (2001), and Baral et al. (2017b). Prior to this, a different concept was in use in which the genus *Hyalorbilia* was included in *Orbilia*. On the other hand, some of the species assigned in the present study to *Orbilia* have been segregated hereof into three different genera: species with uninflated paraphyses in combination with a hairy or dentate margin were segregated in the genera *Hyalinia* (hairs solid, glassy) and *Orbiliaster* (hairs septate), whereas those with protruding spathulate paraphyses and a hairy margin were referred to *Habrostictis*.

The previous inclusion of *Hyalorbilia* in *Orbilia* is astonishing since this genus differs in several respects from the generally accepted key characteristics of *Orbilia* which comprise capitate paraphyses, furcate ascus bases, and isodiametric excipular cells. On the other hand, *Hyalorbilia* possesses strongly conglutinate hymenial elements, a feature which is often stressed as typical of *Orbilia* though being actually absent in most species of that genus.

A total of six teleomorph-typified genera and a large number of anamorph-typified genera are considered to be synonymous with *Orbilia* in the present circumscription. Among the teleomorph-typified genera, the type species of *Orbiliaster* and *Orbiliella* belong to section *Arthrobotrys* of subgenus *Orbilia*, that of *Radotinea* probably falls in section *Hemiorbilia* of subgenus *Hemiorbilia*, that of *Hyalinia* belongs to section *Aurantiorubrae* of subgenus *Habrostictis*, while *Habrostictis* (= *Cheilodonta*) is reduced here to a subgenus and emended to include a large group (section *Habrostictis*) of predominantly newly described species. Prior to about 1950, quite a few species here accepted in *Orbilia* were considered to belong to helotialean genera, such as *Calloria*, *Helotium*, *Laetinaevia*, and *Mollisia*. For a history of the genus and its varying circumscription see p. 192 ff.

Considering the vast number of species recognized in this monograph and the high diversity in character combinations, a subdivision into several genera instead of subgenera and sections would be worth taking into consideration. However, according to our molecular phylogenetic analyses, several of the morphologically important characteristics occur scattered in rather distant groups within *Orbilia*, which complicates the preparation of keys to these infrageneric groups. As a consequence of a subdivision of *Orbilia* into several genera, molecular data would be required in order to place a species in one of these genera. Many of the microscopic characteristics did not clearly correlated with a phylogenetic group, hence do not permit recognition of the group by morphology alone. Therefore, we have accepted paraphyletic groups in several cases, based on striking morphological traits, for instance, we have defined section *Hemiorbilia* by a thick-walled hemispherical ascus apex although the group is only moderately supported, or series *Lentiformes* and *Phanosomates* are recognized based on the lens-shaped vs. lantern-shaped spore bodies, although our molecular data do not suggest such a split.

Diversity of teleomorph. Macroscopically, *Orbilia* encompasses a rather high diversity in both colour and shape. Most of desiccation-tolerant species show different shades of reddish colours (including orange, rosaceous and lilaceous), while some are yellow or ochraceous, and a few black. The margin is usually smooth or only slightly roughened, but in some species it is crenulate or fringed with whitish teeth or hairs. Desiccation-sensitive species are often whitish to pale cream, but also here yellow, orange, red, or rosaceous-lilaceous colours occur; the margin is usually smooth, but also here in some species hairy or toothed.

Particularly the microscopic features of the genus encompass a very high morphological diversity. Apart from differences in the apices of asci and paraphyses, a high variation in spore and SB shape and size is noted, the number of spores per ascus varies between 8 and 128, also the mentioned marginal fringe in some groups made up of septate hairs or glassy processes is remarkable. Organelles of the living cells of paraphyses and excipulum, i. e. vacuolar bodies (VBs) and cytoplasmic bodies (SCBs), play an important role in the classification, especially at the species or series level.

Nomenclature of teleomorph. When Fries (1836: 343) erected the genus *Orbilia* he provided little more than a reference to the two included species described by him earlier (Fries 1815: 165, 1822: 146). The brief statements that concern the new genus run as follows: '[apothecia] membranaceous-gelatinous, asci moniliform = *Orbilia*', and 'to *Orbilia* belong *P. leucostigma* and *P. xanthostigma* which much resemble the genus *Ascobolus*'. *Calloria*, a genus which was thought to be closely related to *Orbilia* during the following hundred years, was simultaneously described by Fries in the same paragraph as having a 'smooth hymenium and unchangeably persistent, clavate asci'. Fries' concept of *Calloria* must have been rather large, as he stated that 'to *Calloria* belong most of the small and gelatinous members of *Peziza*'.

The 'Dictionary of Fungi' (Hawksworth et al. 1996, Kirk et al. 2008) gives the year of valid publication of the genus *Orbilia* as 1849. In fact, Fries provided valid combinations into *Orbilia* only in 1849, whereas in 1836 he merely stated that the two species *Peziza leucostigma* and *P. xanthostigma* belong to the new genus. However, the same applies to *Calloria*, and that genus is listed in that Dictionary as 1836. According to ICN Arts 40.1, 40.3 (Turland et al. 2018), also *Orbilia* was validly described by Fries in 1836, because before 1958 the indication of a type was not necessary, and there is no requirement in the Code for making valid combinations into the new genus (P. Kirk pers. comm.).

Type material of the two species originally included in *Orbilia* by Fries has obviously not survived. His purely macroscopical diagnoses (see p. 1401) might even include the genus *Hyalorbilia*, but Fries' (1836, 1849) statement of moniliform asci as a generic character of *Orbilia* excludes *Hyalorbilia*. The word 'moniliform' should either refer to dead collapsed asci with a moniliform outline around the included 8 uniseriate spores, or to rows of spores inside disintegrated asci at an overmature stage. Either of these cases can only be provoked by short and thick spores as occur, e. g., in *O. eucalypti* and *O. leucostigma* or *O. xanthostigma*, but were never seen in *Hyalorbilia*, even in those taxa with subglobose spores. Species of *Orbilia* with cylindrical to filiform spores, such as *O. auricolor*, *O. epipora*, or *O. cardui*, can also be excluded from being used as neotypes of *Peziza leucostigma* and *P. xanthostigma*.

Clements & Shear (1931) were commonly believed to be the first having designated a lectotype of *Orbilia*. Their selection of *P. leucostigma* was followed by Nannfeldt (1932: 253) and later authors, although Nannfeldt did not mention Clements & Shear in this context. It was, therefore, a surprise to learn that in the rather unknown paper of Bachman (1909) on discomycetes of Ohio a number of genera were lectotypified. On p. 57 of this study, *O. xanthostigma* was given as the 'type species' of *Orbilia*, without further explanation. The interpretation of this species by Bachman was apparently that of *O. eucalypti*, but this does not affect the herewith effectuated lectotypification.

Because of the difficulty to interpret Fries' two originally included taxa, Nannfeldt selected *P. leucostigma* in the interpretation of Nylander (1869: 54) as 'neotypus' of *Orbilia*, but he did not designate a neotype specimen. In the present reexamination, material under the name *P. leucostigma* in the herbarium of P.A. Karsten was found to comprise four different species of *Orbiliaceae* (*H. inflatula*, *O. epipora*, *O. eucalypti*, *O. leucostigma*). Judging from the identification as *O. leucostigma*, all of them should have had colourless apothecia, which is no more evident after such a long time. Also *O. xanthostigma* was interpreted in the past century in quite different ways. In the present monograph two recent collections are designated as neotypes of *O. leucostigma* and *O. xanthostigma*.

Anamorph. Various anamorph-typified genera so far known to be connected to *Orbilia* contribute to the high morphological diversity of the genus. Previously, such genera have been defined by their conidial morphology and the type of conidiophore. In comparison with *Hyalorbilia* a much higher diversity of conidial types occur in *Orbilia*, which is the reason why in the past so many different genera have been recognized. These were based on conidial characters such as unbranched or branched, straight or curved, 0–1- or multiseptate, or presence vs. absence of a strongly enlarged middle cell. Also conidiophore morphology was used to define a genus, which included differences in conidiophore length and apical branching, such as presence of distinct denticles or nodules aggregated in nodes, or simple unbranched apices with a single conidiogenous locus at the tip (see p. 109 ff.).

Based on molecular data, so far only one group of anamorphs was modified in its generic circumscription within *Orbilia*. This group comprises predatory, mainly nematode-trapping taxa and is included here in section *Arthrobotrys* of subgenus *Orbilia*. The new circumscription typifies genera by their type of trapping organs, which were found to provide a more reliable morphological marker. The remaining anamorph-typified genera were continued to be characterized by conidial characters up to now, because trapping organs are unknown in almost all of them. Most of these genera are quite heterogeneous in their rDNA data, but they are difficult to redefine, because a purely molecular classification would make little sense in regard to application of their names. Merely *Pseudotripoconidium* was found to constitute a natural monophyletic group, based on its peculiar conidia and its long conidiophores with denticles at the tip. With the new nomenclatural rules (ICN, Turland et al. 2018) these genera are now considered as synonyms of *Orbilia* in the broad concept of the genus. They are mostly difficult to define regarding their type species for which authentic DNA data is usually unavailable.

A striking correlation between morphology and desiccation tolerance of the anamorph can be noted: intolerant species generally have unbranched straight conidia being usually formed on long conidiophores, whereas tolerant species have either branched or unbranched conidia formed on more or less short conidiophores, the conidia being mostly curved when unbranched (C-shaped). However, the two ecological groups form taxonomic entities only to a certain degree, mainly because intolerance to drought appears to be an apomorphy within the genus that developed in different evolutionary lines.

A simplified survey on the anamorphs of *Orbilia* can be given as follows (for a detailed report of the genera and species see p. 214 ff.): long conidiophores characterize section *Arthrobotrys*, C-shaped conidia (vermispora-like) are typical of section *Aurantiorubrae* but also occur in section *Lentiformes*, scolecosporous conidia (anguillospora- and helicoon-like) are mainly found in section *Helicoon*, Y-shaped conidia (trinacrium-like) are very common in sections *Habrostictis* and *Hemiorbilia* and in series *Piliferae* of section *Aurantiorubrae*, but also occur in section *Lentiformes* and other groups, dicranidion-like conidia occur in sections *Lentiformes*, *Aurantiorubrae* and *Orbilia*, and higher-branched conidia occur especially in series *Hemiorbilia* of section *Hemiorbilia* (dwayaangam-like) and series *Microsomates* of section *Orbilia* (arachnoid type) (see Baral et al. 2017b fig. 1).

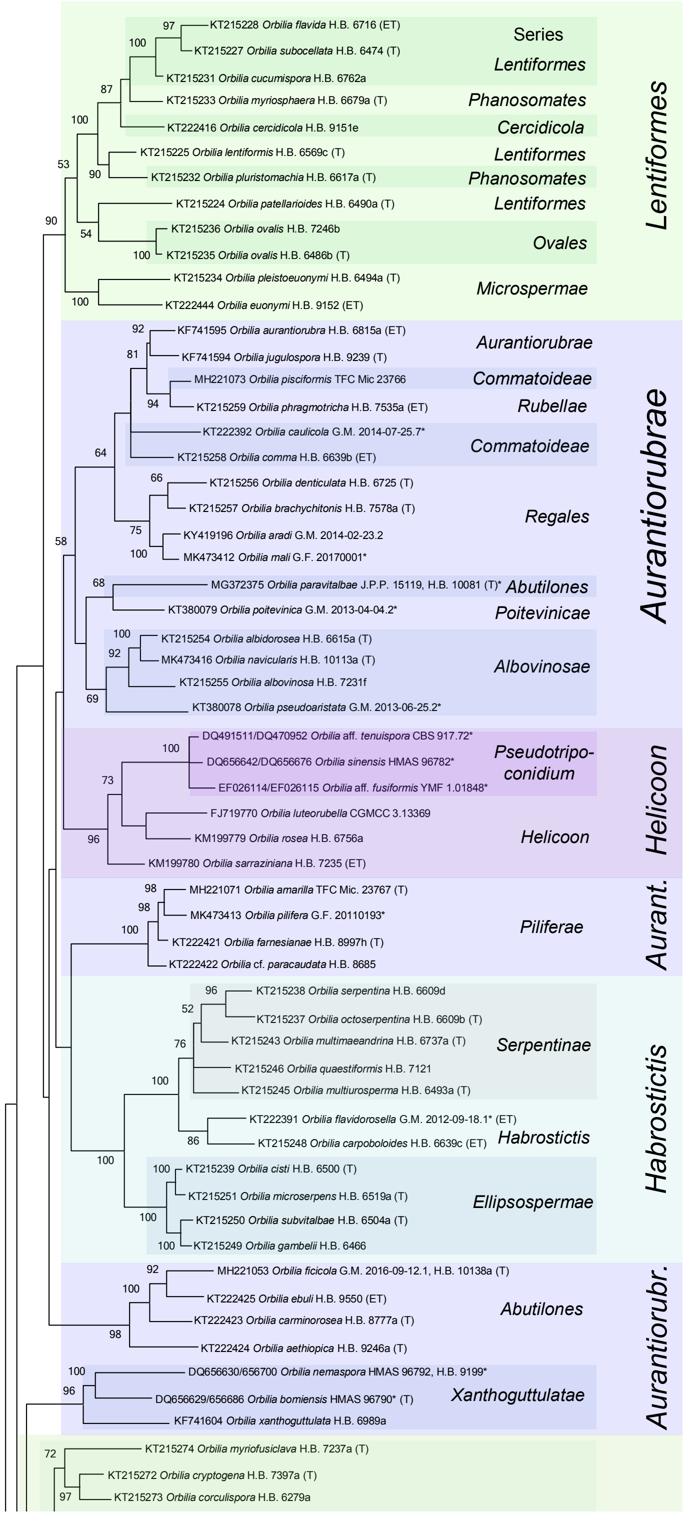
Despite a high conidial diversity within *Orbilia*, groups of clearly recognizable teleomorph-typified species often possess very similar or even indistinguishable anamorphs, mainly with trinacrium- and vermispora-like conidia. For instance, a frequently recorded anamorph is *Trinacrium robustum* agg., which we found to be connected to about 36 different teleomorph-typified species of *Orbilia*, mainly of section *Habrostictis*, but also of sections *Hemiorbilia* and *Lentiformes*. Some of these connections remain to be proved by pure culture, but evidence for a connection exists for all three mentioned infrageneric groups. Due to the frequent lack of type cultures, molecular data from authentic specimens could be gained only in some cases, therefore, the identity of many of these anamorph-typified species remains unsettled.

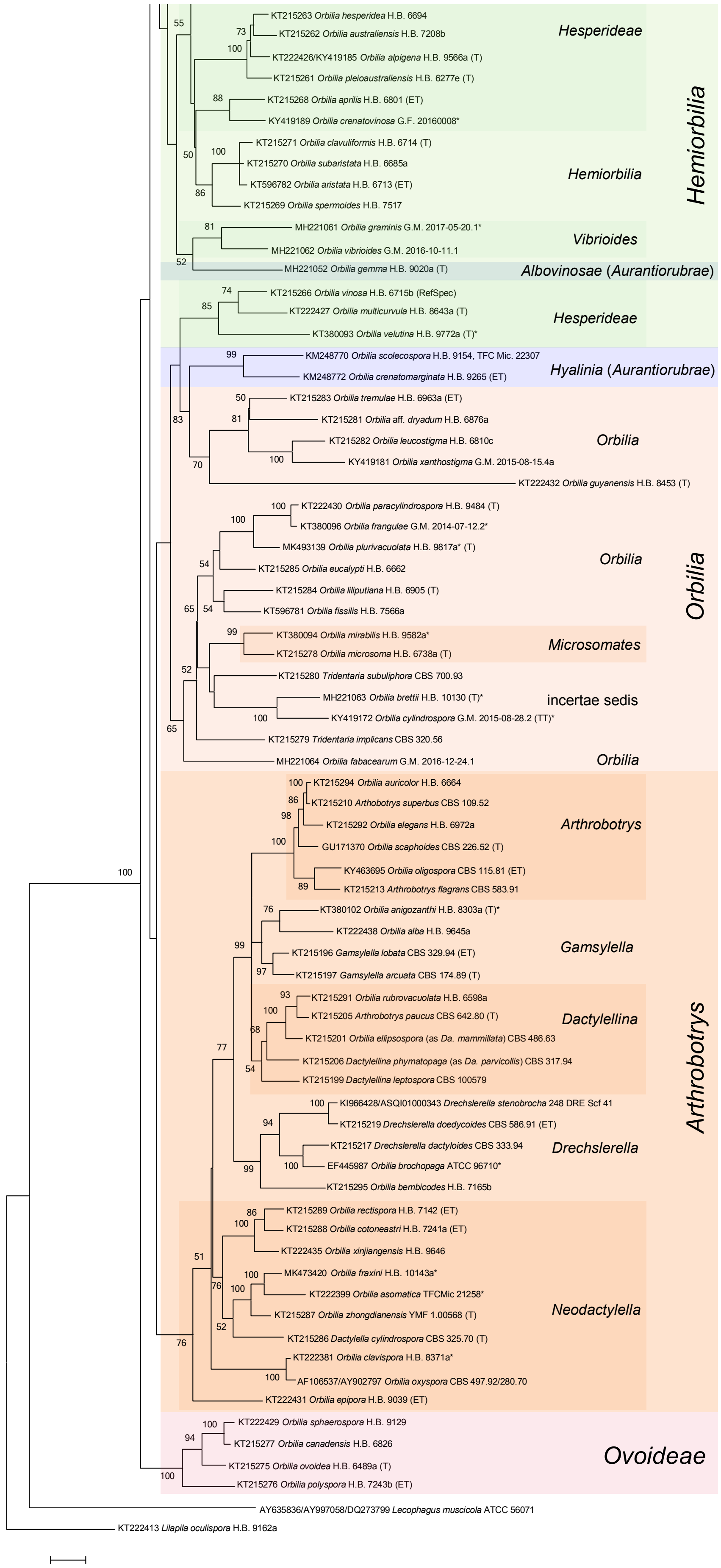
The frequent occurrence of different types of conidia in one isolate complicates the application of names of anamorphs as well as the use of anamorphs as markers of infrageneric groups. For example, trinacrium-like anamorphs often form some unbranched conidia which resemble those of *Dactylella*, except that they are formed on short conidiophores. Also higher-branched conidia (descalsia- and dwayaangam-like) may occur mixed with trinacrium-like conidia in one isolate. Similar problems are caused by the inconsistent presence of microconidia in anamorphs with unbranched conidia. In some taxa, microconidia are not sharply differentiated from macroconidia, and they may sometimes constitute the predominant or only conidia formed in pure culture.

Phylogeny within *Orbilia*. Most published molecular phylogenetic analyses of the genus *Orbilia* are focused on members of section *Arthrobotrys* and particularly nematode-trapping species. Various such analyses, e.g., by Hagedorn & Scholler (1999) and Yu et al. (2011), include a maximum of only two further sections of *Orbilia*, *Helicoon* and *Orbilia*. Some studies provide a more balanced data set in regard to the sections that they represent. For instance, Zhang et al.'s (2015) neighbour joining ITS tree of ~30 species regarding the position of *O. laevimarginata* includes five more or less supported clades: sections *Arthrobotrys*, *Aurantiorubrae*, and *Helicoon*, and series *Hyalinia* and *Xanthoguttulatae*. Liu et al. (2006a) present analyses of ITS (parsimony, ~30 spp.) and LSU (neighbour joining, ~20 spp.), which include members of seven or six sections, respectively. Here, it was mainly section *Helicoon* which received high support in the ITS tree, and the nematode-trapping taxa of section *Arthrobotrys* which were well-supported in the LSU tree. The analysis of Magyar et al. (2017a) comprises 20 *Orbilia* species in eight sections, all of which forming monophyletic clades. However, except for the highly supported section *Arthrobotrys* which here included only nematode-trapping taxa, bootstrap values were low within *Orbilia* and, therefore, not shown at most nodes.

As already stated under the class *Orbiliomycetes*, about 100 species of *Orbilia* have been included in the ML analysis of SSU+ITS+LSU done with RAxML (Baral et al. 2017b, erroneously as 'SSU+5.8S+LSU'). Comparable to the entire class, the backbone phylogeny within the genus remained unresolved and the question unanswered which subgenus or section is the ancestral one. The main tree topology actually changed among the different best trees of this analysis. Six strongly supported clades were recognized that represent six sections within the genus *Orbilia*: *Arthrobotrys*, *Habrostictis*, *Helicoon*, *Lentiformes*, *Ovoideae*, and *Orbilia*. Two further sections, *Hemiorbilia* and *Aurantiorubrae*, were not supported: the former formed a monophyletic clade and the latter was paraphyletic, being composed of six strongly supported subclades. These six clades were included in one section for morphological reasons, although they clustered unresolved without any supported affinities between them. Five of them were recognized at the series level: *Abutilones*, *Albovinosae*, *Hyalinia*, *Piliferae*, and *Xanthoguttulatae*. The sixth clade included four series: *Aurantiorubrae*, *Regales*, *Rubellae*, each with only 1–2 species, and the paraphyletic series *Commatoideae*.

The present ML analysis of the same gene region done with MEGA6 (Phyl. 7) shows largely a similar tree topology, with one main exception: series *Hyalinia* clustered medium supported sister to a clade of section *Orbilia* (with *O. leucostigma*, *O. xanthostigma* and *O. tremulae*), whereas in Baral et al. (2017b) it clustered unresolved in the highly paraphyletic section *Aurantiorubrae* of subgenus *Habrostictis*.





Phylogenetic analysis 7. Phylogram of genus *Orbilia* inferred from ML analysis of SSU (V8–V9)+ITS1-5.8S-ITS2+LSU (D1–D2) rDNA dataset (131 sequences, 2000 positions, aligned with MAFFT), using the GTR+G+I model in MEGA6 (100 replicates). The tree is rooted with *Lilapila oculispora* and *Lecophagus muscicola*. RefSpec = reference specimen, T = type, ET = epitype, TT = topotype, * = SSU ± absent.

Table 62. Synoptic table of selected characters for the infrageneric groups of *Orbilia* (for futher details see Tab. S3): **ascus apex**: h = hemispherical, t = truncate, – = thin-walled, + = thick-walled (often with ocular chamber); **dome**: – = thin-walled, + = thick-walled; **ascus base**: T-shaped, Y-shaped, H-shaped (with one blindly ending branch), etc.; **spore number**: high numbers are estimated; **inverse orientation**: lmh = low/medium/high number of spores inverted; **inverted spores**: L = lower spores inverted, U = upper spores inverted; **VBs**: + = vacuolar bodies present; **SCBs**: g = globose, c = crystalloid; **glassy processes**: + = present at margin; **septate hairs**: + = present at margin; **SBs**: g = globose, l = lens-shaped, t = tear-shaped, v = vermiform/filiform, p = plug-shaped, f = with filum, r = rod-shaped; **SB attachment**: a = apical, s = subapical, l = lateral; **spore shape**: g = (sub)globose, e = ellipsoid, cy = cylindrical, cl = clavate, f = fusoid/fusiform, o = ovoid/

Genus *Orbilia*	Ascus apex	Dome	Ascus base	Spore number	Inverse orientation	Inverted spores	VBs	SCBs	Glassy processes	Septate hairs	SBs
Subgenus *Hemiorbilia*											
Section *Lentiformes*											
Series *Lentiformes*	h/(t)	+/–	LTYh(H)	8–64	l m	L	–	g	–	–	l p
Series *Ovales*	t	–	Th	8	m	L	–	g	–	–	t r
Series *Cercidicola*	t	–	LY	8	m	L	–	g c	–	–	r f
Series *Phanosomates*	h/(t)	+/–	LTYh	8–128	(l) m	L	–	g	–	–	g t p f
Series *Microspermae*	h	+	LTYh	16–128	–	–/(L)	–	g	–	–	g t f
Section *Hemiorbilia*											
Series *Hesperideae*	h	+/++	LTYh	8–128	(l) m	L	–	g c	–/+	–/(+)	g t p r v
Series *Hemiorbilia*	h	+/++	LTYh	8	l m	L	–	g c	–/+	–/(+)	t r v
Series *Vibrioides*	h	++	LTYh	8–128	m		–	g	–	–	r t
Subgenus *Habrostictis*											
Section *Aurantiorubrae*											
Series *Regales*	t	–	LTYh(H)	8	m	L	–	g	–/+	–	g t (p)
Series *Commatoideae*	t	–	LTYh	8	m	L	–/(+)	g c	–/+	–	g t
Series *Rubellae*	t	–	LTY	8	m	L	–	g c	–/+	+	g t
Series *Aurantiorubrae*	t	–	LYh	8	m	L/(U)	–	g c	–/+	–	t (+f) v
Series *Xanthoguttulatae*	t	–	LTYh	8	m	L/U	–/+	g c	–/+	–	t v (g)
Series *Hyalinia*	t	–	LTYh	8	m	L	–	g c	–/+	–	t
Series *Abutilones*	t	–	LTYh	8	m	L/U	–/(+)	g c	–/(+)	–/(+)	v t
Series *Poitevinicae*	t	–	LY	8	m	L	–	g c	+	–	t
Series *Piliferae*	t	–	LTYh	8	m	L	–	(g) c	–/(+)	+	g t r
Series *Albovinosae*	t	–	LTYh	8–32	(l) m	L	–	g c	+	–/+	(g) t
Section *Helicoon*											
Series *Helicoon*	t	–	LTY(H)	8	m	L/U	+/–	g	–/(+)	–	v t
Series *Pseudotripoconidium*	t	–	LTY	8	m	L/(U)	+/(–)	g	–	–	v
Section *Habrostictis*											
Series *Habrostictis*	t	–	LTYh	8–16	m	L	–	g c	–	+/–	v
Series *Serpentinae*	t	–	LTYh(H)	8–64	m	L	–	g c	–	–	v
Series *Ellipsospermae*	t	–	LTYh	8–128	m	L	–	g c	–	–	v t+f
Subgenus *Orbilia*											
Section *Ovoideae*	t/h	–/+	LTYh(H)	8–128	l m	L	–	g (c)	–/+	–/(+)	g t
Section *Orbilia*											
Series *Microsomates*	t	–	LTYh(H)	8–64	m	L	–	g c	+	–	(t) p (l)
Series *Orbilia*	t	–	LTYhH	8–16	m	L	+/–	g	–/+	–	g
Section *Arthrobotrys*											
Series *Neodactylella*	t	–	LTYhH	8	m	L	+/–	g	–/+	–/(+)	g t
Series *Arthrobotrys*	t	–	LTYhH	8	m	L	+/–	g	–/+	–	g t (r)
Series *Dactylellina*	t	–	LYThH	8	(l)m	L/(U)	+/–	g	–/+	–	r t g
Series *Gamsylella*	t	–	YThH	8	(l)m	L/U	–	g	–	–	g r
Series *Drechslerella*	t	–	(LT)YhH	8	(?l)m	L	+/–	g	+/(–)	–(+)	r t
Genus *Orbilia*	Ascus apex	Dome	Ascus base	Spore number	Inverse orientation	Inverted spores	VBs	SCBs	Glassy processes	Septate hairs	SBs

Specific nucleotide positions. Only a few positions in the rDNA have been found that are more or less characteristic for the genus *Orbilia*. The combination of 2 adjacent nucleotides in the SSU V8 region is unique: pos. 141–142 is AT**AT**CT, whereas other orbiliaceous taxa with available SSU have AT**TC**CT or rarely AT**A**CCT (Tab. 60). In the 5.8S and LSU D1–D2 domain no characteristic nucleotide positions have been found.

In the region of the '*Orbiliales*-specific' primers (Smith & Jaffee 2009), a majority of *Orbilia* spp. either concur with a majority of *Hyalorbilia* spp. (Orb5.8s1F), or with *Lilapila* and *Mycoceros* (Orb5.8s3F) or *H. erythrostigma* and *H. orbiliicola* (Orb28S2R). However, a small minority of *Orbilia* spp. deviate in the latter two regions, where they mainly provide unique motifs. Also in stem-loop B8 near the 3'-end of 5.8S the motifs occurring in *Orbilia* are very diverse and without a nucleotide characteristic for the genus, although all these motifs do not occur in other orbiliaceous genera, except for a few *Orbilia* spp. which concur with some members of the *oviparasitica-multiguttulata* clade of *Hyalorbilia* (Tabs 18–19).

Plesiomorphic characters in *Orbilia*. Hypotheses on the plesio- or apomorphy of characters are given under each organ in the two morphology chapters about teleomorphs and anamorphs. A summary is presented under the class (p. 253). To establish sound hypotheses on the evolution of characters is still premature and must await more comprehensive molecular studies.

Ecology. The large genus *Orbilia* exhibits a very wide ecological diversity. The inhabited substrate includes bark and wood, herbaceous stems, perennial basidiomycetes, pyrenomycetes, exceptionally on dung or other residues of obovoid, t = with a tail, h = heart-shaped or triangular; **spore tail**: + = present, – = absent; **spore curvature**: 0 = straight, 3 = strongly curved; **spore apex**: r = rounded, o = obtuse, a = (sub)acute to acuminate; **paraphysis apex**: 0 = uninflated, 4 = very strongly inflated; **paraphysis shape**: c = capitate/clavate, s = spathulate/lageniform/lanceolate, m = mammiform; **apothecial colour**: hy = hyaline/white, red = reddish (orange, rose), yel = yellow, li = lilaceous, bl = black-olivaceous; **desiccation tolerance of apothecia**: t = desiccation-tolerant, s = desiccation-sensitive, a = semiaquatic; **anamorph**: an = anguillospora-like, ar = arthrobotrys-like, art = arthropod-like, d = dactylella-like, da = dactylellina-like, de = descalsia-like, di = dicranidion-like, dw = dwayaangam-like, ga = gamsylella-like, h = helicoon-like, ps = pseudotripoconidium-like, td = tridentaria-like, tr = trinacrium-like, v = vermispora-like.

SB attachment	Spore shape	Spore tail	Spore curvature	Spore apex	Paraphysis apex	Paraph. shape	Apoth. colour	Desicc. toler.	Anamorph	Genus *Orbilia*
										Subgenus *Hemiorbilia*
										Section *Lentiformes*
a	cl cy e o	–	0–3bas	r o	0–2(3)	c	red/bl	t	tr v	Series *Lentiformes*
	cl e f o	–	0–1bas	r o	1–3	c	red	t	Di	Series *Ovales*
a	cy	–	1–3bas	r	0–2	c	red	t	v?	Series *Cercidicola*
a	e cl o	–/(+)	0–1bas	r o	0–2	c	red	t	tr	Series *Phanosomates*
a	g e cl o	–	0–1(2)	r o	0–1	(c)	hy/red	t	V	Series *Microspermae*
										Section *Hemiorbilia*
(s) (l)	e cy cl h f o	–/(+)	0–4	r o a	0–2(3)	c	red	t	tr v dw	Series *Hesperideae*
a	cy e f t	+	0–1	r o a	0–1(2)	c	red	t	tr de dw	Series *Hemiorbilia*
s a	cy cl	–	0–4	r o	0–1	c	yel/red	t	?dw	Series *Vibrioides*
										Subgenus *Habrostictis*
										Section *Aurantiorubrae*
a	cy cl f	–	0–3	r o	0–3	c s m	red/yel	t	v	Series *Regales*
a	cy e f t	–/+	0–3	o a	(0)1–3	c	red/(yel)	t (s)	an v	Series *Commatoideae*
a	cy e f cl t	–/+	0–3	(r) o a	1–3	s m	red	t	v	Series *Rubellae*
a	f t	–/+	1–3	a	1–2	c	red/yel	t	v	Series *Aurantiorubrae*
a	f	–/(+)	2–3	(o) a	(0)1–3	c s	hy/red/yel	t s	d di	Series *Xanthoguttulatae*
a	f t	(–)/+	3	r o a	0–1	(c)	hy/yel	s	d	Series *Hyalinia*
a	cy f cl	–/(+)	0–3	(o) a	1–3	c s	red/yel	t	di	Series *Abutilones*
a	cl f	–	0	r (o)	0–2	c	red	t	v	Series *Poitevinicae*
a	cy e f	–/+	0–3	r o (a)	1–3	c s m	red/yel	t	tr	Series *Piliferae*
a	f (cy)	–/+	0–1	(r o) a	0–2	(c) s	red	t	dw tr	Series *Albovinosae*
										Section *Helicoon*
a	cy f cl g	–	0–1(3)	(r) o a	1–4	c	hy/li/red	(t) s a	an d h v	Series *Helicoon*
a	cy f (g)	–	0–1(3)	r o a	0–4	c	hy/red/yel	s	ps	Series *Pseudotripoconidium*
										Section *Habrostictis*
a	cl f e	–	0–2bas	r o a	1–4	s m	red/yel	t	v	Series *Habrostictis*
a	cl cy f e t o	–	0–3	r o a	1–4	c s	red	t	tr td	Series *Serpentinae*
a s	cl f e o	–	0–1(3)	r o (a)	1–4	c	red	t	tr	Series *Ellipsospermae*
										Subgenus *Orbilia*
a (l)	g e cl cy f o	–/(+)	0–2	r o (a)	0–3	c (s)	red/(hy)/(bl)	t	v(?)	Section *Ovoideae*
										Section *Orbilia*
a	cy cl e f	–	0–3	r o (a)	0–2(3)	c s	red	t	tr de art	Series *Microsomates*
a(s)l	g cy cl e f o	–/(+)	0–4	r o	(0)1–4	c s	hy/yel/red/(lil)	s t	d di v	Series *Orbilia*
										Section *Arthrobotrys*
a	cy f cl	–/(+)	0–3	r o	0–2(3)	c (s)	hy/yel	t s	d (v an)	Series *Neodactylella*
a	f cy cl	–/(+)	(0)2–3	r o	1–3	c (s)	hy/yel	s t	ar	Series *Arthrobotrys*
a	f cy cl	–/(+)	0–3	r o	0–2	c (s)	hy/red	s	da	Series *Dactylellina*
a	cy f cl	–	0–3	r o	0–2	c s	hy/yel	s t	ga	Series *Gamsylella*
(a) s	e cy cl f o	–	0(1)	r o	0–3	c (s)	hy/yel/(red)	s (t)	dr	Series *Drechslerella*
SB attachment	Spore shape	Spore tail	Spore curvature	Spore apex	Paraphysis apex	Paraph. shape	Apoth. colour	Desicc. toler.	Anamorph	Genus *Orbilia*

animals, and soil. A wide range of climatic regions is colonized, and a majority of taxa are found in semiarid to arid vegetation types. In contrast to *Hyalorbilia*, desiccation tolerance of apothecia is, therefore, often much higher. Parasitism on other fungi is not known with certainty, but parasitism on eggs and adults of various invertebrates (nematodes, rotifers, arthropods) is typical of four series of section *Arthrobotrys*, but as yet unknown with certainty in any other infrageneric group of *Orbilia*. Taxa being predacious on testaceous rhizopods might occur in series *Orbilia*: *Dicranidion dactylopagum* is possibly connected to the *O. leucostigma* aggregate, while some other predacious species currently placed in *Dactylella*, *Tridentaria*, and *Trinacrium* are of unclear phylogenetic relationship. Species of the latter three genera are also known to prey on oospores (see p. 214 ff.). Finally, parasitism on pollen seems to be a common feature of *Orbilia*.

Subgenus *Hemiorbilia*

Orbilia subgenus ***Hemiorbilia*** Baral, Syst. Ascomycetum 13: 118 (1994) – Type species: *Orbilia occulta* (Rehm) Sacc.

Description: — **TELEOMORPH**: **Apothecia** hydrated rose to (ochraceous-)orange or brick-red, also olivaceous-black, margin glabrous or crenulate, denticulate to dentate, or hairy, sessile or short-stipitate. **Ascus apex** (†) hemispherical to slightly (rarely medium to strongly) truncate, with apical wall thickening, rarely thin-walled, often with distinct apical chamber; **base** T-, L-, Y-, or h-, exceptionally H-shaped; **Ascospores** and **SBs** variously shaped. **Paraphyses** apically uninflated or slightly, rarely strongly capitate-clavate. — **ANAMORPH**: descalsia-like, dicranidion-like, dwayaangam-like, trinacrium-like, vermispora-like. **Trapping organs**: unknown.

Key to subgenera, sections (and series) of *Orbilia*

1. Spore bodies (SBs, only visible in living ascospores) lens- to plug-shaped, wider than tall (rarely distinctly taller than wide due to a basal prolongation), widest part above where they are affixed to the spore wall, here (0.7–)1–2(–3) µm wide; spores ellipsoid-oblong or clavate, apex rounded; SCBs never crystalloid; apothecial margin always without glassy processes; apothecia always desiccation-tolerant
series *Lentiformes* (section *Lentiformes*, subgenus *Hemiorbilia*), p. 459

1. SBs globose, tear-shaped, rod-shaped, vermiform, only exceptionally wider than tall (rarely absent), either not visibly connected to the spore wall, or narrowly attached, i.e., apically attenuated (if not attenuated then SBs max. 0.8 µm wide at their widest part 2

2. Apex of dead asci hemispherical to slightly truncate, shape only slightly depending on the viewing direction, thick-walled (min. †0.5–1 µm), especially when immature, rarely also some asci thin-walled and strongly truncate; apex of paraphyses uninflated but also slightly to medium inflated, never uniformly spathulate to mammiform; apothecia always desiccation-tolerant .... (subgenus *Hemiorbilia*) 3

2. Apex of dead asci usually medium to strongly truncate in front view (sometimes centrally indented and/or laterally inflated by forming 2 shoulders), hemispherical in profile view, thin-walled (†~0.2–0.4 µm) 5

3. SBs ± abruptly divided into an inflated, mostly tear- to stomach-shaped, also vermiform, rod-shaped or nearly globose lower part and a fine (rarely thick) filum of about the length of the inflated part (but also much shorter); crystalloid SCBs present only in series *Cercidicola*; apothecial margin always without glassy processes or hairs ....
.... **series *Phanosomates*** (p. 505), ***Cercidicola*** (p. 501), **and *Microspermae*** (p. 528, section *Lentiformes*)

3. SBs vermiform, subulate, tear-shaped, ampulliform, rarely globose, apically gradually narrowed to a small or wide point, filum absent or very short; crystalloid SCBs present or absent................4

4. Ascus apical wall immature †(2–)3–4(–6) µm thick; rough exudate often provoking a warted hymenium and radial ribs at the margin; crystalloid SCBs absent; asci (32–)64–128-spored; Australia................ **series *Vibrioides* p.p.** (p. 746)

4. Ascus apical wall immature †0.5–2.5(–3.5) µm thick (if 2.5–4.8 µm then asci < 32-spored); exudate never forming warts on the hymenium; crystalloid SCBs present or absent; asci 8–128-spored (if SBs ± globose see also section *Ovoideae*) ....
.... **section *Hemiorbilia***, **series *Vibrioides* p.p.**

5. SBs filiform to vermiform or subulate, apically narrowed to a small point, sometimes divided into an inflated lower part and a long filum, often flexuous to curled, total length of SBs min. 1/3 of spore length, length/width ratio ~4–10(–20) ....(subgenus *Habrostictis*) 6

5. SBs globose, ellipsoid, tear-, plug- or rod-shaped (rarely absent), apically narrowed to a small or wide point, filum either invisible or absent to very short, total length of SBs max. 1/3 of spore length, length/width ratio ~1–4 8

6. Apothecia ± desiccation-sensitive, white, pale lilaceous-rosaceous, yellow- to ochre-orange, with a smooth, rarely crenulate margin; asci 8-spored; crystalloid SCBs absent, VBs usually present; spores *2.6–17 × 0.8–2.2 µm; paraphyses clavate-capitate, terminal cells 2.5–6 × longer than lower cells .... **section *Helicoon*** (p. 953)

6. Apothecia desiccation-tolerant, pale to bright yellowish-ochraceous to usually orange-red or rose(-lilaceous), with a smooth or ± hairy margin; asci 8–128-spored; crystalloid SCBs present or absent, VBs mostly absent; spores *3.3–19.5 × 0.9–5 µm; paraphyses clavate-capitate or spathulate-lageniform, mammiform, or lanceolate, terminal cells (0.2–)0.5–1.5(–3)× longer than lower cells 7

7. Asci 8–128-spored; spores *(3.3–)4–17(–19.5) × (1.3–)1.6–4(–5) µm; terminal cells of paraphyses (0.2–)0.5–1.5(–3)× as long as lower cells................ **section *Habrostictis*** (p. 1012)

7. Asci 8-spored; spores *4.8–11 × 0.9–2.3 µm; terminal cells of paraphyses (1–)2–3 × as long as lower cells................
................**series *Abutilones*** (section *Aurantiorubrae*), p. 885

8. SBs apically narrowed to a usually wide point, rod- to pear-shaped or ampulliform, 1.2–2(–4) × 0.4–1.3 µm; asci 8-spored; apothecia rose-orange, desiccation-tolerant................9

8. SBs apically narrowed either to a small point, with or without a very short, often invisible filum, or to a wide point and then SBs max. 1.2(–1.4) µm long, or absent................10

9. Spores *3.7–7.5 × 2.2–3.3 µm, ellipsoid-ovoid to broadly fusoid-clavate, l:w ratio < 3; anamorph dicranidion-like ....
................**series *Ovales*** (section *Lentiformes*), p. 498

9. Spores *5–11 × 1–3 µm, fusoid-clavate, l:w ratio > 3 or spores with a tail; anamorph trinacrium-like with curved-down arms....
.... **series *Piliferae*** (section *Aurantiorubrae*), p. 915

10. SBs plug-shaped, also tear- to dumbbell-shaped or ampulliform, rarely subglobose, 0.3–1.2(–1.4) × 0.25–0.8(–1.2) µm, attached by a wide point, rarely by a filum; glassy processes and exudate caps on paraphyses mostly present; asci 8–64-spored; apothecia orange to rose, always desiccation-tolerant .... **series *Microsomates*** (section *Orbilia*), p. 1295

10. SBs (if present) globose to broadly tear-shaped, with or without short, ± thin or invisible filum 11

11. Spores *(1.3–)1.7–3.8(–4.3) µm wide, globose to ovoid, ellipsoid-fusoid, clavate, or subcylindrical, straight or curved only near base; SBs globose to broadly ellipsoid-ovoid, (0.6–)0.7–1.5(–1.9) µm wide; terminal cells of paraphyses (0.5–)1–2(–3)× as long as lower cells; asci 8–128-spored; apothecia orange to rose or lilaceous, rarely ochraceous, always desiccation-tolerant .... **section *Ovoideae*** (p. 1241)
If paraphyses ± mammiform, spores ± clavate, with or without tail, anamorph trinacrium-like see *O. pilifera* (p. 918) and *O.* aff. *farnesianae* (p. 925, series *Piliferae*, section *Aurantiorubrae*).

11. Spores *0.8–2.5(–3) µm wide; SBs (0.2–)0.3–0.8(–1.3) µm wide, sometimes absent; terminal cells of paraphyses (1–)2–4(–6)× as long as lower cells................12

12. Spores predominantly < *6.5 µm long................13

12. Spores predominantly > *6 µm long................14

13. SBs globose to broadly tear-shaped, centrically oriented in spore apex (or absent); asci 8(–16)-spored; conidia unbranched (dactylella-like) or branched (dicranidion-like), never with inflated cells ..... **section *Orbilia*** (p. 1292, see also series *Neodactylella*, section *Arthrobotrys*)

13. SBs globose to rod-shaped, often ± eccentrically oriented in spore apex; conidia unbranched, often with inflated cells .... **series *Drechslerella*** (p. 1623), ***Gamsylella*** (p. 1610), and ***Dactylellina*** (p. 1584, section *Arthrobotrys*)

14. Spores consistently distinctly helicoid (curved in 3 dimensions), apex subacute to acute, rarely rounded to obtuse; SBs 1.5–4.5 µm long, broadly to narrowly tear-shaped or subulate to filiform, rarely ellipsoid to globose and without visible connection to spore wall 15

14. Spores straight to falcate (curved in 2 dimensions), sometimes with basal appendage or slightly helicoid.. 16

15. Apothecia desiccation-tolerant, with yellow to orange-red colours (rarely whitish), margin smooth to crenulate; anamorph vermispora- or dicranidion-like (with curved, C-shaped or U-shaped conidia, conidiophores very short)... ....**series *Aurantiorubrae*** (p. 833) and ***Xanthoguttulatae*** (p. 848, *xanthoguttulata-succulenticola* clade, section *Aurantiorubrae*)

15. Apothecia desiccation-sensitive or only slightly tolerant, whitish, yellowish or brownish, margin smooth to distinctly dentate; anamorph dactylella-like (with ± straight conidia, conidiophores short to very long) .... **series *Hyalinia*** (p. 868) and ***Xanthoguttulatae*** (p. 856, *nemaspora-vermiformis* clade, section *Aurantiorubrae*)

16. Spores consistently slightly to strongly falcate (C-shaped), rarely very indistinctly helicoid, *(6–)7–13(–15) × (0.8–)1–1.5(–1.7) µm, apex rounded to obtuse; SBs (0.8–)1–2.3(–2.6) µm long, globose to filiform; apothecia predominantly desiccation-sensitive...... .... **section *Arthrobotrys*** (p. 1432)

16. Not with this combination of characters, if spores falcate then ± constricted or geniculate in basal part and/or with acute apex 17

17. Apothecia desiccation-tolerant, with yellow, orange or rose to lilaceous colours; spores *6–15(–19) × (0.6–)1–2.5(–2.8) µm, apex rounded to acute.. **section *Aurantiorubrae*** (p. 769)
If SBs absent see *O. asomatica* (p. 1487, series *Neodactylella* of section *Arthrobotrys*), if SBs eccentrical and rod-shaped see *O. anigozanthi* (p. 1619, series *Gamsylella* of section *Arthrobotrys*); if apothecia desiccation-sensitive see also section *Helicoon* (p. 953).

17. Apothecia predominantly ± desiccation-sensitive, whitish, yellowish or brownish, rarely orange; spores *6–11.5 × 1–1.7(–2) µm, apex rounded to obtuse, rarely subacute .... **section *Arthrobotrys*** (p. 1432)

Habitat: xeric wood and bark of gymno- and angiosperms (including resin), also caulicolous or foliicolous, from subarctic to tropical, humid to arid climates. All species desiccation-tolerant.

Recognized sections: *Lentiformes* and *Hemiorbilia*, with 111 recognized species plus 2 with provisional name and 16 unnamed species (‘affinis’).

General remarks. The present circumscription of subgenus *Hemiorbilia*, which is mainly based on morphological criteria, includes two sections: *Lentiformis* and *Hemiorbilia*. The main feature common to most of its members is the more or less thick-walled, hemispherical to slightly truncate ascus apex (often with apical chamber) when studied in the dead state. However, this type also occurs in a few members of section *Ovoideae* of subgenus *Orbilia*. All members of subgenus *Hemiorbilia* have desiccation-tolerant apothecia with a reddish, rarely black colour. The paraphyses are usually not or only slightly inflated at the apex, and are never spathulate-mammiform or lanceolate-lageniform. Frequently they are covered by a thick layer of exudate. H-shaped ascus bases were only very rarely seen. Ascospore and SB shape are highly diverse.

Although series *Ovales* shows the characteristics of series *Orbilia* of subgenus *Orbilia*, including thin-walled truncate ascus apices, capitate paraphyses, and a dicranidion-like anamorph, the single species of this series, *O. ovales*, is included in section *Lentiformes* owing to its molecular data. Also section *Ovoideae* appears to form a transition between the two subgenera. It is characterized by predominantly globose to broadly tear-shaped, rarely ampulliform SBs, and predominantly or exclusively thin-walled ascus apices, but includes a few aberrant species in which thick-walled apices predominantly or exclusively occur (*O. clavipisca*, *O. lilacina*, *O. eremaeae*). On the other hand, we have included some members with ampulliform to globose SBs in section *Hemiorbilia* (e.g., *O. myriomuscula* and *O. sarothamni*). Molecular data are required in order to clarify relationships of such critical taxa in the future.

Section delimitation. Section *Lentiformes* is characterized by the consistent absence of crystalloid SCBs (except for *O. cercidicola*) and glassy processes. Most of its members possess quite characteristic, either lens- or lantern-shaped SBs. Series *Vibrioides* of section *Hemiorbilia* concurs in the absence of crystalloid SCBs and glassy processes. It differs in a strongly thickened ascus apical wall and (in some taxa) subapically inserted SBs, and is macroscopically more or less recognizable by a pruinose to prominently warted hymenium and exterior due to a sulphur-yellow exudate on the protruding paraphyses and excipular cells. In the rest of the large section *Hemiorbilia* crystalloid SCBs and glassy processes are often present, the spores tend to have a basal tail, and the SBs similarly tend to be subapically or laterally inserted in some species.

Anamorphs. Members of sections *Lentiformes* and *Hemiorbilia* form either stauroconidia (predominantly trinacrium-like, in *Lentiformes* also dicranidion-like, in *Hemiorbilia* also descalsia- and dwayaangam-like) or curved phragmoconidia (vermispora-like). Taxa with predatory capabilities are unknown within subgenus *Hemiorbilia*.

Phylogeny. Subgenus *Hemiorbilia* as proposed by Baral (1994) is adopted here based on the hypothesis that the striking morphology of the hemispherical, thick-walled ascus apex observed in sections *Lentiformes* and *Hemiorbilia* represents a character of high taxonomic importance which could be plesiomorphic within *Orbilia*. It would appear logical that these two sections form different lineages of more basal, ancient relationships, forming a paraphyletic group which nevertheless traces back to a common ancestor. This hypothesis implies that the thin-walled truncate ascus apex of subgenus *Orbilia* developed by reduction from the hemispherical thick-walled ascus apex of subgenus *Hemiorbilia*. Section *Ovoideae* represents an intermediate assemblage of taxa that morphologically stands somewhat between these two groups, and series *Ovales*, which shares most characters of series *Orbilia*, appears to represent a convergent lineage that emerged within section *Lentiformes*,

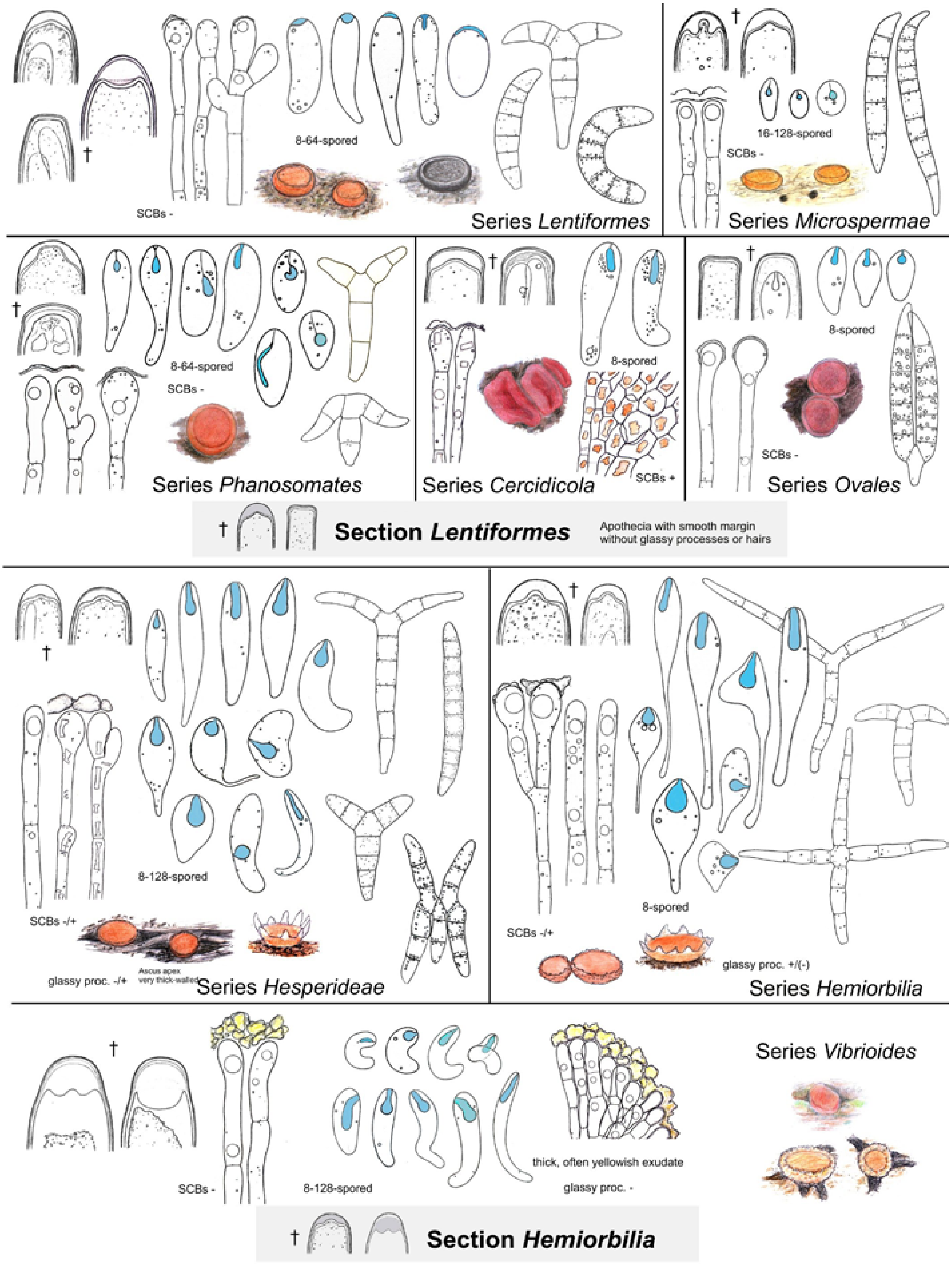


Plate 147. *Orbilia* subgenus *Hemiorbilia*, comprising sections *Lentiformes* and *Hemiorbilia*.

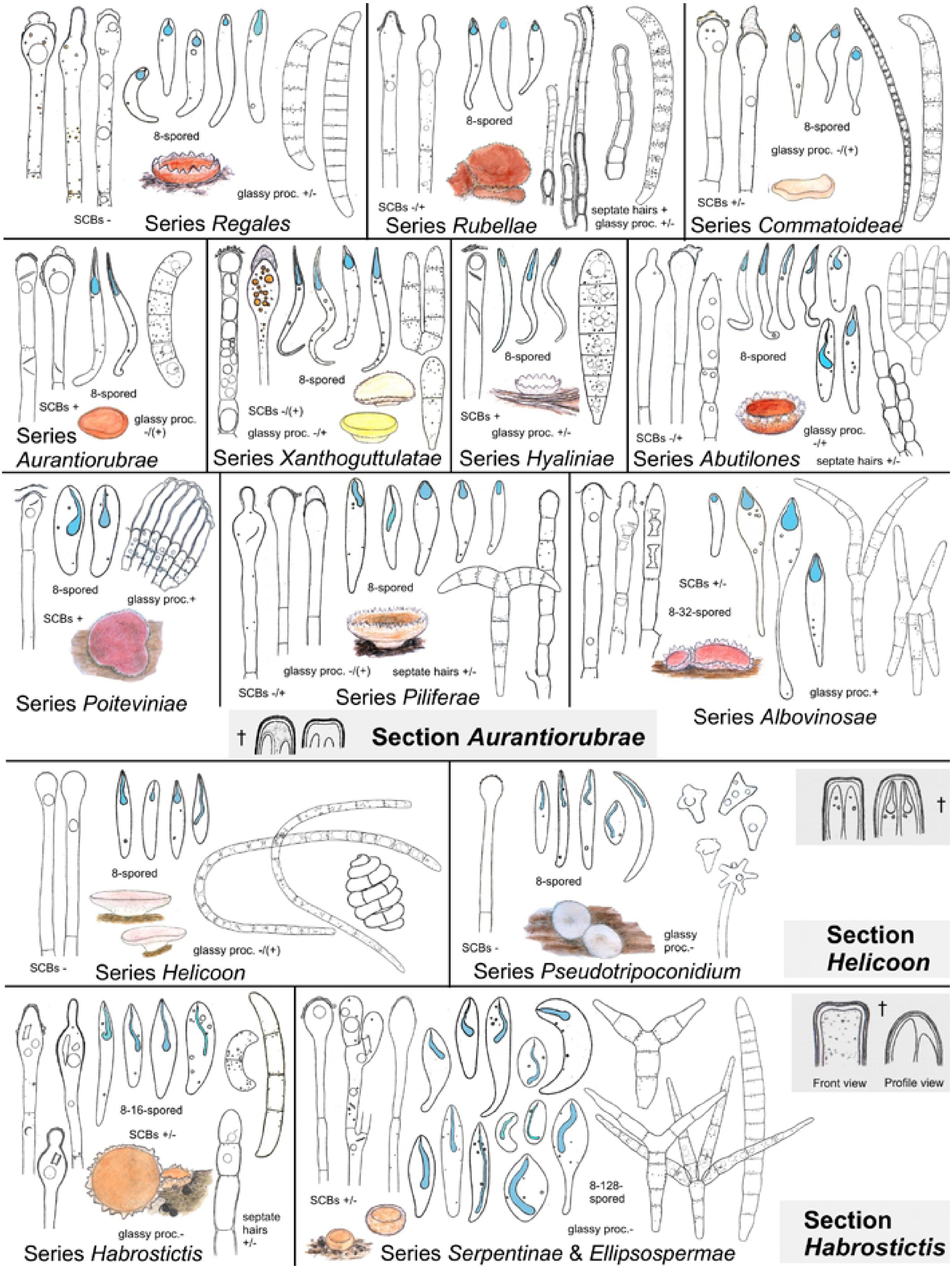


Plate 148. *Orbilia* subgenus *Habrostictis*, comprising sections *Aurantiorubrae*, *Helicoon*, and *Habrostictis*.

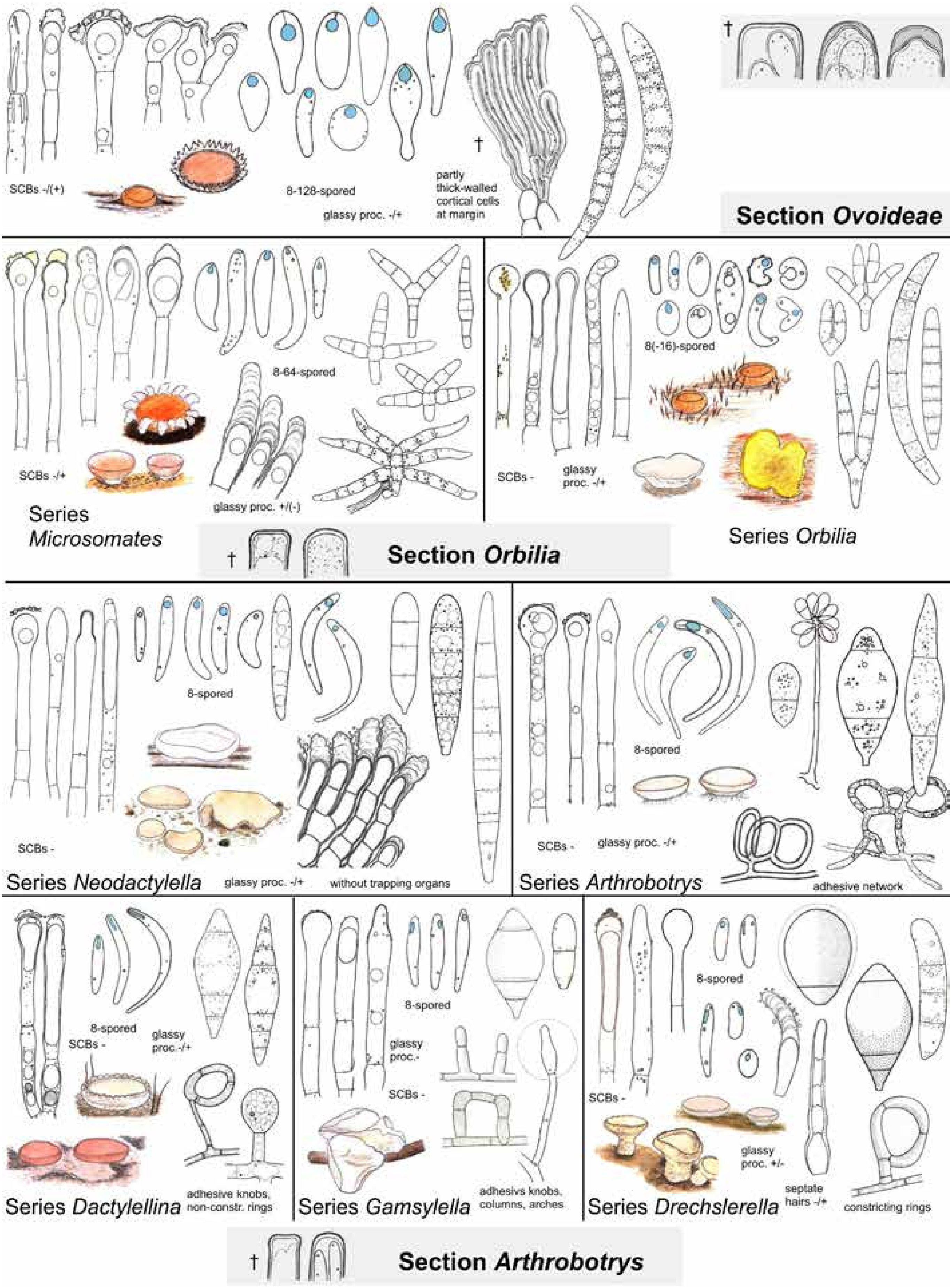


Plate 149. *Orbilia* subgenus *Orbilia*, comprising sections *Ovoideae*, *Orbilia*, and *Arthrobotrys*.

whereas series *Orbilia* appears to show closer molecular affinities with section *Hemiorbilia*.

In the phylogenetic analysis of rDNA presented in Baral et al. (2017b) the two sections of subgenus *Hemiorbilia* (*Lentiformes* and *Hemiorbilia*) appear in a paraphyletic position. Subgenus *Orbilia* formed a more basally positioned paraphyletic group, and subgenus *Habrostictis* a more terminally positioned paraphyletic group. However, the bootstrap support of this arrangement is absent to low, therefore, the result varies from one tree to another.

Specific nucleotide positions. No molecular motifs being characteristic of subgenus *Hemiorbilia* have been discovered in any of the frequently recorded regions of nuclear rDNA. However, the two included sections with DNA data show a few rather consistent nucleotide positions by which they can be distinguished from each other (see there).

Ecology. All species of subgenus *Hemiorbilia* are desiccation-tolerant and grow on xeric substrate from arctic-alpine to tropical and from humid to arid regions.

Section *Lentiformes*

Orbilia subgenus ***Hemiorbilia*** section ***Lentiformes*** Baral & E. Weber, **sect. nov.**, MB 814998 – Type species: *Orbilia lentiformis* Baral & G. Marson

Latin diagnosis: *Apothecia sessilia vel subsessilia, rosea ad aurantiaca vel atroolivacea, margine laevi, raro parum crenulato. Asci 8- ad 128-spori, apice in statu emortuo hemisphaerico, interdum truncato, tenui- vel crassitunicato, basi stipite bifurcato. Ascosporae subglobosae, ovoideae, ellipsoideae, cylindricae vel clavatae, apice rotundato vel obtuso, in statu vivo prope apicem corpusculum refringens lenti-, obturamenti-, bacilli- vel lanterniformem continentes. Paraphyses non vel leniter, raro valde clavato-capitatae. Excipulum ectale marginem versus cellulis vivis plerumque corpuscula globosa continentibus, absque processis vitreis.*

Description: — **TELEOMORPH**: **Apothecia** (0.08–)0.15–0.9(–1.3) mm diam., rose to orange, also olivaceous-black, (sub)sessile, disc ± flat, margin smooth, rarely slightly crenulate. **Asci** *(26–)40–100(–140) × (4–)5–11(–15.3) µm, 8- up to 128-spored, (0–)1/8–**1/4–1/2**–3/4(–4/4) of lower spores inversely oriented; **apex** (†) ± hemispherical (irrespective of viewing direction) or sometimes rather strongly truncate, rarely distinctly shouldered (series *Ovales*), thin-walled or with apical wall thickening [immature †0.8–2(–4) µm thick] with apical chamber; **base** L-, T-, Y- or h-, exceptionally H-shaped. **Ascospores** *(2.2–)3–17(–22) × 1.5–5(–6) µm, ovoid to subglobose, cylindric-ellipsoid, or ellipsoid- to fusoid-clavate, apically rounded to obtuse, sometimes with a thick tail, straight to slightly, rarely strongly curved (especially near base); **SBs** apically attached, either lens- to plug- or calotte-shaped, or ± lantern-shaped, sometimes of an intermediate type. **Paraphyses** uninflated or only slightly clavate-capitate at the apex, rarely strongly so (mainly series *Ovales*), terminal cells (0.3–)0.5–1.5(–2)× longer than lower cells. **Ectal excipulum** at flanks of textura (globulosa-) angularis(-prismatica), cells isodiametric or vertically elongated, near base *(5–)7–20(–26) × (3–)5–13(–20) µm, (†) thin-walled to slightly or rarely strongly gelatinized, common walls †0.4–1(–2) µm thick, near margin of t. angularis-prismatica to t. porrecta oriented at a high to low angle; **glassy processes** or **hairs** consistently absent. **Anchoring hyphae** (1.5–)2–3.5(–5) µm wide, walls 0.2–0.4(–1) µm thick. **SCBs** globose, rarely crystalloid (series *Cercidicola*); **VBs** consistently absent; **carotenoids** in **LBs** not observed. **— ANAMORPH**: vermispora-, trinacrium- or dicranidion-like. **Conidiophores** unbranched, hyphoid or forming chains of short inflated cells, *3–35 µm long. **Conidiogenous cells** monoblastic or sympodial, often with denticles. **Conidia** septate, unbranched (phragmosporous), often ± curved, or branched (staurosporous), with two arms and one stipe. **Trapping organs**: none observed.

Habitat: lignicolous, caulicolous, foliicolous, all taxa desiccation-tolerant.

Recognized series: *Cercidicola*, *Lentiformes*, *Microspermae*, *Ovales*, and *Phanosomates*, with 30 recognized species plus 2 with provisional name and 1 unnamed species ('affinis').

Taxonomic remarks. In the present concept, section *Lentiformes* includes five series: *Lentiformes*, *Ovales*, *Cercidicola*, *Phanosomates*, and *Microspermae*. It comprises almost exclusively taxa with hemispherical ascus apices, often with a slight or distinct, congophilous apical wall thickening. However, considerable variation in the ascus apex was noted in quite a few species of series *Lentiformes* and *Phanosomates*, even within a population: although the apices typically were hemispherical or only slightly truncate and with a distinctly thickened wall, sometimes with apical chamber, in some of the examined apothecia the apices were medium to strongly truncate, though never shouldered, and often also without an apical wall thickening.

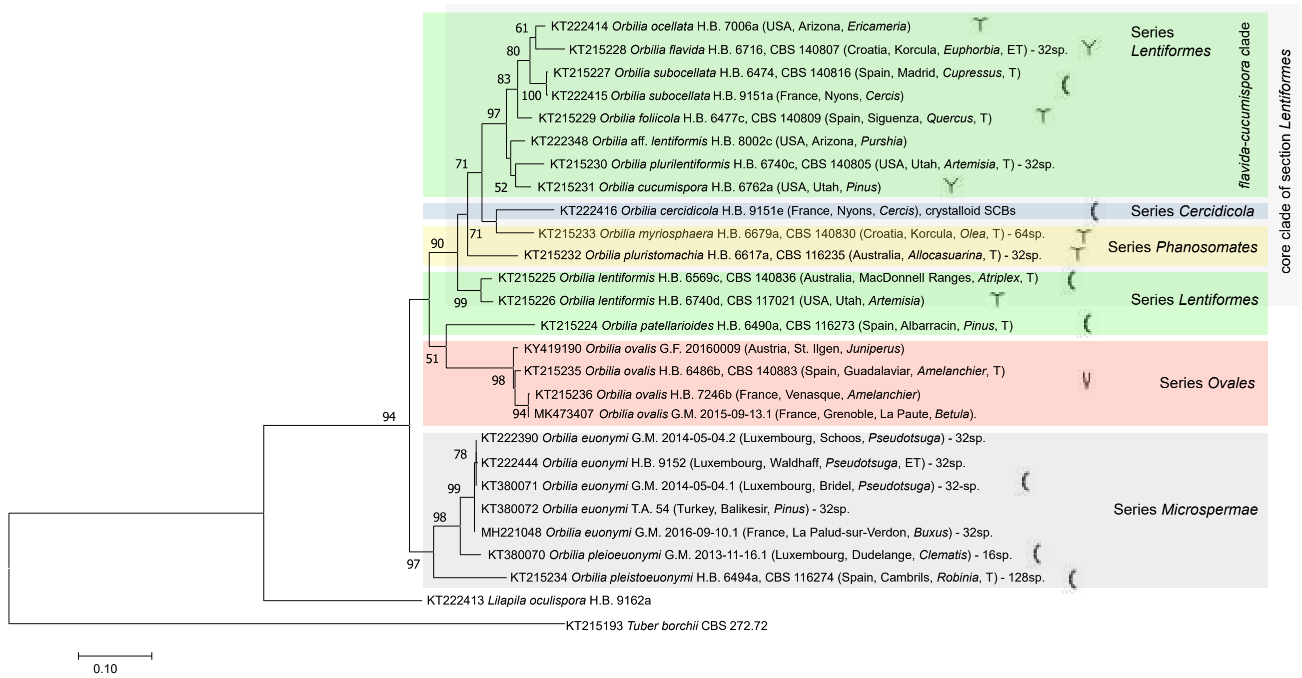
Further characteristics include paraphyses with a more or less equal cell length and usually uninflated apices, the absence of both crystalloid SCBs and glassy processes, and reddish or sometimes black, consistently desiccation-tolerant apothecia. Only two species sharply deviate from this set of characteristics: series *Ovales* with the single species *Orbilia ovalis* shows strongly truncate, shouldered, thin-walled ascus apices and capitate paraphyses with the terminal cells often longer than the lower cells, and series *Cercidicola* with the single species *O. cercidicola* deviates from all others in the presence of striking crystalloid SCBs.

Series delimitation. Two very different main types of SBs occur within section *Lentiformes*, according to which we distinguish the two more species-rich series of this group. Accordingly, series *Lentiformes* is characterized by quite unique lens-shaped, very broadly attached spore bodies (a species with very similar but smaller SBs, *O. microlentiformis*, is tentatively placed in series *Microsomates* of subgenus *Orbilia*), whereas members of series *Phanosomates* possess completely different, lantern-shaped SBs, which are narrowly attached by a short to long, very thin filum. Four species with ascospores and SBs similar to series *Phanosomates* but smaller are affiliated in series *Microspermae*.

O. cucumispora, *O. macroasca*, *O. cercidicola* and *O. ovalis* form a morphological transition between these two types of SBs: *O. cucumispora* shows a tendency to the lens-shaped type and is, therefore, assigned to series *Lentiformes*. The latter three resemble more the lantern-shaped type, deviating by SBs with a rather thick connecting part, but are placed in three different series. The very thin, calotte-shaped SBs in *O. pileosoma* (series *Lentiformes*) represent an extreme variant of the lens-shaped type.

Anamorph. Conidial diversity within section *Lentiformes* includes unbranched, phragmosporous (vermispora-like) and branched, staurosporous conidia (trinacrium-, rarely dicranidion-like). In series *Lentiformes* both vermispora- and trinacrium-like anamorphs occur, whereas in series *Phanosomates* only trinacrium-like conidia are known and in series *Microspermae* exclusively large phragmoconidia. In series *Ovales* a dicranidion-like anamorph and in series *Cercidicola* a vermispora-like anamorph are presumed (both series only with one species).

Phylogeny. Sequences were gained from 18 taxa that clustered in section *Lentiformes*, comprising ITS and LSU (D1–D2, rarely



Phylogenetic analysis 8. Phylogram of section *Lentiformes* inferred from combined ML analysis of SSU (V8–V9)+ITS1-5.8S-ITS2+LSU (D1–D2) rDNA dataset (27 sequences, 1720 positions, aligned with MUSCLE) using the K2+G model in MEGA7 (500 replicates). The tree is rooted with *Lilapila oculispora* and *Tuber borchii*. Asci 8-spored except when otherwise stated; T = type, ET = epitype.

D3 or more) and mostly also SSU (V8–V9, exceptionally also V1–V7). The S1506 intron is absent in all of them, except for *O. myriosphaera* of series *Phanosomates* and most sequences of series *Microspermae*. Based on analyses of SSU+ITS+LSU, section *Lentiformes* forms a strongly supported monophyletic clade (Baral et al. 2017b, Phyl. 7). The phylogenetic placement of the clade within the large genus *Orbilia* never received any support. In some trees it was found at the base of the genus in sister position to all remaining groups, while in that in Baral et al. (2017b) it diverged rather terminally after most other sections.

Phyl. 8 gives a combined phylogenetic analysis of section *Lentiformes* based on the three available gene regions. Seperate analyses of the ITS and LSU are added as supplementary information (Phyls S9 [ITS] and S11 [LSU]). All these analyses suggest that different types of ascus apices and spore bodies occur within this group. A close relationship between series *Lentiformes* and series *Phanosomates* was already presumed based on a similar shape of ascus apex, ascospores, paraphyses, and SCBs. However, despite the sharp morphological difference between lens- and lantern-shaped SBs in the two series, strains representing these two types did not cluster in distinct clades. Instead, species with lens-shaped SBs occur intermingled in a clade with those with lantern-shaped SBs. Moreover, *O. patellarioides* (with lens-shaped SBs) always clustered distant from the other taxa with this spore body type. Also *O. lentiformis* formed with a majority of series *Lentiformes* only in the combined analysis a strongly supported clade, which is referred to as 'core clade of section *Lentiformes*' here. Although the two morphologically defined groups turned out to be paraphyletic in all of our analyses of different rDNA gene regions, we prefer to maintain our classification system of two larger series based on spore body morphology, because it would seem here more logical that evolution went in one direction, i. e., at a single event from one spore body type to another. This circumscription has at least the advantage of easy series recognition without molecular data. However, it requires living ascospores because the lantern-shaped SBs are impossible to see in herbarium material.

Placement of *O. ovalis* (series *Ovales*) in section *Lentiformes* is surprising, as its microscopic characteristics, including the presumed anamorph, would refer it to subgenus *Orbilia*, in particular to series *Orbilia*. However, compared to the high molecular distance between *O. patellarioides* and the core clade of section *Lentiformes*, *O. ovalis* is not more distantly related to those and even shows a tendency to cluster with *O. patellarioides*. However, its morphology is very different from any member of section *Lentiformes*, including its thin-walled truncate ascus apex. Because of the high molecular distance to any member of the genus *Orbilia*, *O. ovalis* is here recognized here in a series of its own. On the other hand, we have retained *O. patellarioides* in series *Lentiformes* because it shows the typical morphology of that series.

In all mentioned analyses, series *Microspermae* formed a ± well-supported clade of its own that stands distant from the core of section *Lentiformes*. This placement was unexpected, as it closely resembles series *Phanosomates* in spore body shape, except for much smaller ascospores and SBs. Mainly because of our molecular data we here recognize a separate series for it.

A majority of series *Lentiformes* clustered in a ± strongly supported clade, here referred to as *flavida-cucumispora* clade, which comprises six species with lens-shaped SBs but also *O. cucumispora* which has elongate, plug-shaped SBs intermediate to series *Phanosomates*. However, *O. lentiformis*, which is morphologically difficult to delimit from *O. ocellata*, surprisingly clustered in a clade of its own distant from the *flavida-cucumispora* clade, though still in the core clade of section *Lentiformes* (in Phyl. S9 it formed a medium supported clade with *O. pluristomachia*).

The two species of series *Phanosomates* with available sequences clustered as a paraphyletic group within the core clade of section *Lentiformes*, though monophyletic in a weakly supported clade in Phyl. S8. *O. cercidicola* resembles series *Phanosomates* in SB morphology and actually clustered in a ±

Key to series of section *Lentiformes*

1. SBs often wider than tall, broadly affixed to apical spore wall, here (0.6–)1–2(–3) µm wide, lens-, calotte-, or plug-shaped, never apically distinctly narrowed; asci 8- up to 64-spored .... **series *Lentiformes***, p. 459
1. SBs never wider than tall, rod- to lantern-shaped, apically narrowed to a small or max. 0.5 µm wide point 2

2. Asci 8-spored, apices (†) thin-walled, strongly truncate in front view, ± distinctly shouldered; terminal cells of paraphyses 1.5–2(–3)× longer than lower cells, apically slightly to strongly inflated .... ***O. ovalis*** (**series *Ovales***), p. 498
2. Asci 8- up to 128-spored, apices (†) thick- or thin-walled, hemispherical or truncate in front view but never with shoulders; terminal cells of paraphyses (0.3–)0.5–1.5(–2)× longer than lower cells, apically not or slightly, rarely strongly inflated 3

3. Living paraphyses and excipular cells containing crystalloid SCBs (orange in excipulum); asci 8-spored; ascospores *(11–)12.5–17(–18.7) × (3.5–)3.7–4.5(–5) µm, often distinctly curved; bark of *Cercis* & *Ulmus*, semihumid, mediterranean or continental Europe .... **series *Cercidicola***, p. 501
3. Paraphyses and excipular cells only with globose, hyaline SCBs; asci 8- up to 128-spored 4

4. Spores *(2.2–)2.5–4(–5.5) × 1.5–2.5(–3) µm (exceeding 2.5 µm in width only when 16-spored); SBs mainly 1–1.8 × 0.2–0.6 µm; asci 16- up to 128-spored, apex (†) hemispherical, with apical thickening .... **series *Microspermae***, p. 528
4. Spores *(3.7–)4.5–15(–17.3) × (2.4–)2.8–4.8(–6) µm (< 3.2 µm wide only when 32–64-spored); SBs mainly 2–4 × 0.5–1.3 µm; asci 8- up to 64-spored, apex thin- or thick-walled, hemispherical or sometimes truncate .... **series *Phanosomates***, p. 505

weakly supported clade with *O. myriosphaera* in Phyls 8, S9. Yet, we prefer to place it in a series of its own because it has conspicuous reddish crystalloid SCBs unlike any other member of section *Lentiformes*, and a different excipulum texture.

Specific nucleotide positions. Molecular motifs in the SSU V8–V9, ITS, or LSU D1–D3 specific to the entire section *Lentiformes* have not been found. Two positions in the LSU separate it from a majority of remaining *Orbilia* spp. (see also under section *Hemiorbilia*, p. 544), but concur with most basal orbiliaceous genera, suggesting a common ancestry for these groups and an apomorphy for the remaining *Orbilia* spp.: all members of section *Lentiformes* have TGCAGCTC**T**AA at pos. 292 of D1 and GAGG**A**CCGCG at pos. 591 of D2, whereas most remaining members of *Orbiliomycetes* have TGCAGCTC**A**AA (including *Hyalorbilia* p.p.maj.) and GAGG**T**CCGCG (including *H. erythrostigma*, *H. orbiliicola*, *H. tortuosa*, and *Mycoceros*), respectively. As an exception, *O. xanthoguttulata*, *O. succulenticola*, and *Gamsylella arcuata* concur with section *Lentiformes* at pos. 292, and *O. pseudoaristata* at pos. 591. In the SSU V8–V9 pos. 70 is unique for series *Lentiformes, Phanosomates*, and *Cercidicola* (AGG**G**TTG), except for *O. patellarioides* which has AGG**T**CTG like other *Orbilia* spp., especially of section *Hemiorbilia*, series *Abutilones*, and series *Orbilia*, while most remaining *Orbilia* spp. have AGG**T**TTG.

Series *Lentiformes*

Orbilia subgenus ***Hemiorbilia*** section ***Lentiformes*** series ***Lentiformes* –** Type species: *Orbilia lentiformis* Baral & G. Marson

Etymology: named after the lens-shaped spore bodies.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.12–)0.2–0.5(–1) mm diam., either orange to rose or black-olivaceous, sessile, ± smooth. **Asci** *(47–)55–120(–138) × (5.5–)6.5–12(–13) µm, 8- up to 64-spored, about half or often only 1/8–1/3 of lower spores inverted; **apex** (†) hemispherical to rather strongly truncate, never indented nor laterally inflated, hemispherical in profile view, thin-walled or often with an (immature) †0.8–2(–4) µm thick dome, then often with apical chamber; **base** L-, T-, Y-, h-, rarely H-shaped. **Ascospores** *5–19 × 1.7–4.5 µm, ovoid, ellipsoid, cylindrical or often clavate, straight to ± strongly curved near base; **SBs** *(0.3–)0.5–1.2(–1.6) × (0.6–)1–2(–3) µm, rarely 0.2–0.4 or 2–3.5 µm high, lens- to broadly plug-shaped, also with a central prolongation (T-shaped) or rod-shaped, rarely forming a very thin calotte-shaped layer, broadly affixed to apical wall, never narrowed towards apex; frequently with 2 groups of **LBs**. **Paraphyses** uninflated at the apex or only slightly to medium, rarely strongly clavate-capitate, terminal cells 0.4–1.5(–2)× longer than lower cells, sometimes branched near apex. **SCBs** always globose. **Exudate** (0.2–)0.5–2(–6) µm thick, continuous, rough-cloddy or granular, loosely to firmly attached, hyaline to pale yellowish, also dark (bluish-)olive(-brown). — **ANAMORPH**: vermispora-like, trinacrium-like. **Conidiophores** ~7–30 µm long, partially branched. **Conidia** *(11–)15–54 × 4–7.5 µm (in situ and actual length) when phragmosporous, (1–)3–7(–11)-septate, straight or slightly to strongly curved; *20–56 × 10–64 µm when staurosporous, Y/T-shaped, arms straight or slightly bent downwards. **Conidiomata** only observed in *O. purshiae* (uncertain).

Habitat: wood and bark of both gymno- and angiosperms (including resin), foliicolous, or caulicolous, temperate to subtropical, humid to semiarid, always desiccation-tolerant.

Recognized species: 13, plus 1 unnamed species (‘affinis’).

Taxonomic remarks. Series *Lentiformes* is easily recognized by its very broadly attached, usually lens-shaped spore bodies in the ascospore apex, which are often also visible in herbarium material (in water or MLZ, in water sometimes retaining their refractivity). Four of the included species sharply differ from the remaining in very dark, blackish-olivaceous apothecia, therefore, they can easily be confused by macroscopy with lichenized fungi, or members of *Patellariales*. *O. cucumispora* is exceptional in its T- to rod-shaped SBs, whereas *O. pileosoma* has a very special type of SB that forms a very thin and broad, calotte-like layer. Variation in the ascus apex between hemispherical/thick-walled and truncate/thin-walled was noted in *O. lentiformis*, *O. pleiolentiformis*, *O. ocellata*, and *O. foliicola.*

Species delimitation. High variation in spore size and curvature is noted in most of the here accepted species. This variation is even seen within a population, and particularly within a single ascus, and makes species delimitation quite difficult. Also the SBs vary somewhat within a given population, especially in height. Species of the *O. lentiformis* complex (including *O. ocellata*, *O. subocellata*, and *O. foliicola*) are very difficult to separate based on teleomorph morphology, but appear to be separable by their anamorph and by molecular data.

Anamorph. Either unbranched or branched conidia are formed in culture. The former are mostly vermispora-like,

Key to species of series *Lentiformes*

1. Apothecia dark olivaceous or black due to a blue-green-olivaceous, ~1–5 µm thick exudate 2
1. Apothecia pale to bright orange or rose, exudate hyaline to pale yellowish 5

2. Asci 16-spored; spores ellipsoid-obovoid, *4.8–7(–8) × (3.2–)3.5–4.5 µm; SBs forming a thin (0.2–0.4 µm) hemispherical callotte at the spore apex; wood of gymnosperms, boreal to cold-temperate humid western North America .... ***O. pileosoma***, p. 468
2. Asci 8-spored; spores more elongate; SBs lens- to plug-shaped, 0.4–1.6 µm tall 3

3. Asci *8.5–10 µm wide (†7.3–9.5 µm), apical wall of immature asci †1.5–3.3 µm thick; SBs 0.8–1.6 µm tall, plug-shaped, with very prominent edges at the inner prolongation; spores *(8.3–)12–16(–17) × (2.8–)3–3.8(–4.2) µm, base mostly tapered and curved; wood of *Purshia* (*Rosaceae*), temperate subhumid to semiarid western North America .... ***O. purshiae***, p. 466
3. Asci *6–8 µm wide (†5–7.2 µm), apical wall of immature asci †0.9–1.5 µm thick; SBs 0.4–1.2 µm tall; wood of gymnosperms (mostly *Pinus*) 4

4. Spores *(7.5–)9–13(–14.5) × (2.6–)3–3.6(–3.8) µm, mostly strongly clavate, with a short, ± curved tail; SBs lens-shaped, 0.4–1 µm tall; orosubmediterranean humid Europe, mesomediterranean semihumid Macaronesia .... ***O. patellarioides***, p. 461
4. Spores *(9–)10–13.5 × (1.8–)2–2.6 µm, cylindrical, base not or only slightly narrowed and curved; SBs predominantly plug-shaped, 1–1.2 µm tall; boreal humid western North America .... ***O. atrolentiformis***, p. 464

5. SBs rod- to plug-shaped (T-shaped), taller than wide (1.5–3.5 × 0.6–1 µm), apically mostly abruptly widened; spores *(11–)13–19(–22) × 4–5.2(–5.7) µm, often ± dumbbell-shaped; asci 8-spored; apothecia pinkish-rose; bark & wood of gymnosperms, (oro)temperate (sub)humida western North America .... ***O. cucumispora***, p. 494
5. SBs lens-shaped, wider than tall (0.2–1.8 × 1–2.5 µm) 6

6. Asci 64-spored, *120–138 × 10.7–12.5 µm; spores *7–12 × 2.8–3.7 µm; apothecia 0.5–1 mm diam.; bark of *Cercis*, mesosubmediterranean semihumid southern Europe .... ***O. myriolentiformis***, p. 494
6. Asci max. 32-spored, mainly *60–105 × 7–11 µm; apothecia 0.15–0.65 mm diam. 7

7. Asci 32-spored 8
7. Asci 8–16-spored 9

8. Spores *(3.8–)5–8(–9.7) × (2–)2.2–2.8(–3) µm; asci *(54–)60–84(–92) × (6.7–)7–8.8(–9.3) µm; herbaceous stems, also bark & wood of angiosperms, temperate to thermomediterranean (semi)humid Europe and cool-maritime northwestern North America .. ***O. flavida***, p. 487
8. Spores *7–10.5(–11.3) × (2.8–)3–3.6(–4) µm; asci *(60–)70–105(–120) × (8.4–)9–11(–12) µm; bark & wood of angiosperm shrubs, boreal humid to temperate semiarid western North America .... ***O. plurilentiformis***, p. 492
If SBs only partly broadly attached and ± subglobose, compare *O. multicreosoteris* (section *Ovoideae*, p. 1275).

9. Asci 16-spored; spores *(6–)7–12(–15) × (2.4–)2.7–3.7(–4.4) µm; wood & bark of angiosperms, herbaceous stems, temperate to subtropical, humid to arid southern Europe, western North America and central Australia .... ***O. pleiolentiformis***, p. 484
9. Asci 8-spored 10

10. Spores *5.7–12.3 × 1.7–2.4 µm; asci *~4.5–5.5 µm wide, apex strongly truncate, without dome; marginal excipulum with short glassy processes .... see ***O. microlentiformis*** (series *Microsomates*), p. 1300
10. Spores *2.8–5.5 µm wide; asci *(6–)7–10(–11.5) µm wide, apex hemispherical to slightly truncate, with ± distinct dome (usually †0.5–1.4 µm thick); marginal excipulum without glassy processes 11
If spores *2.3–3.2 µm and asci *5–6 µm wide, see *O.* cf. *ocellata* on inflorescence of *Asteraceae* (p. 480).

11. Spores predominantly strongly tapered at base, here either tail-like or strongly curved 12
11. Spores predominantly slightly to medium tapered at base, here rarely tail-like, straight to slightly curved 13

12. Spores straight to slightly curved, often with tail-like base, *8.8–12.8 × 3–3.5 µm; SBs lens-shaped; ascus apical dome †0.8–1.2 µm thick; wood of *Pinus*, southern Europe .... ***O. patellarioides*** (rare reddish form), p. 461
12. Spores strongly curved at base, not tail-like, *11–17.5 × 3–4 µm; SBs plug-shaped; ascus apical dome †1.5–2 µm thick; wood of *Purshia*, western North America .... ***O. purshiae*** (rare reddish form), p. 466

13. On leaves of *Quercus ilex* agg.; spores *(7–)8–12.5(–15.5) × 3.3–4.2 µm; mediterranean Europe .... ***O. foliicola***, p. 482
13. On wood and bark of angiosperms (rarely gymnosperms) 14

14. Spores *(7–)8–12(–13) × (2.8–)3.2–4(–4.5) µm; asci *(47–)54–68(–76) × (6.5–)7–8.5(–9.2) µm; conidia trinacrium-like; subarctic to subtropical humid to semiarid Europe, North America, Asia .... ***O. ocellata***, p. 476
14. Asci *(8–)8.5–9.5 µm wide or wider 15

15. Spores *(9–)10–13(–14) µm long; asci up to *9(–9.7) µm wide; conidia vermispora-like; (sub)mediterranean Europe ......***O. subocellata***, p. 481
15. Spores *(10–)12–17(–19) µm long; asci up to *10.5(–11.5) µm wide; conidia vermispora- or trinacrium-like; boreal to subtropical, humid to arid, worldwide but absent in central Europe .... ***O. lentiformis***, p. 470

slightly to strongly curved phragmoconidia, the latter Y-shaped, trinacrium-like stauroconidia. In one case vermispora-like conidia were observed in orange ?sporodochia on the natural substrate (*O. purshiae*). The two types of conidia appear to characterize species of the above-mentioned *O. lentiformis* complex (see Tab. 63).

Phylogeny. Our combined phylogenetic analyses of SSU+ITS+LSU (Phyls 7–8) and separate analyses of ITS or LSU (S11) show that series *Lentiformes* is paraphyletic. Nevertheless we maintain it here because of the striking similarity in SB morphology among the species (see under Section *Lentiformes*, p. 458). The two species with black apothecia, for which sequences were available (*O. patellarioides*, *O. purshiae*), clustered separate from those with reddish apothecia but did not form a supported clade.

Specific nucleotide positions. No specific molecular motifs could be detected that are unique for members with lens-shaped SBs. When including series *Phanosomates* and *Ovales*, however, the group deviates in the ITS1 at pos. 1 as ATCATTA**A** vs. ATCATTA**C** in series *Microspermae* and ATCATTA**T** in series *Cercidicola*.

Ecology. Thirteen of the 14 taxa known within series *Lentiformes* occur on ligneous substrate (wood and bark), but some of them may also grow on herbaceous substrates or leaves. Four species were exclusively recorded on gymnosperms (*O. patellarioides*, *O. cucumispora*, *O. atrolentiformis*, *O. pileosoma*), though the latter two were only 1–2 × collected. *O. lentiformis* and *O. subocellata* grow mainly on angiosperms, but occasionally on gymnosperms. Within Europe, *O. flavida* is the most commonly recorded species of this series. It is the only one which was predominantly collected on herbaceous stems. *O. lentiformis*, *O. ocellata*, and *O. pleiolentiformis* were occasionally found on herbaceous substrate. Several species were recorded from different continents, including Europe, Macaronesia, North America, Asia, and Australia. *O. lentiformis* and *O. ocellata* also occur in Asia and northern Africa, moreover *O. lentiformis* and *O. pleiolentiformis* in Australia. Five species were so far only found in the Rocky Mountains and Colorado Plateau of North America and three only in the mediterranean belt of Europe. Among the latter is *O. foliicola* which is exceptional in growing on coriaceous leaves of *Quercus ilex* agg.

Species with blackish-olivaceous apothecia

Orbilia patellarioides Baral & G. Marson, **sp. nov**., MB 814370 — Pls 150–151, Map 21

Etymology: referring to the macroscopical similarity to species of the genus *Patellaria*.

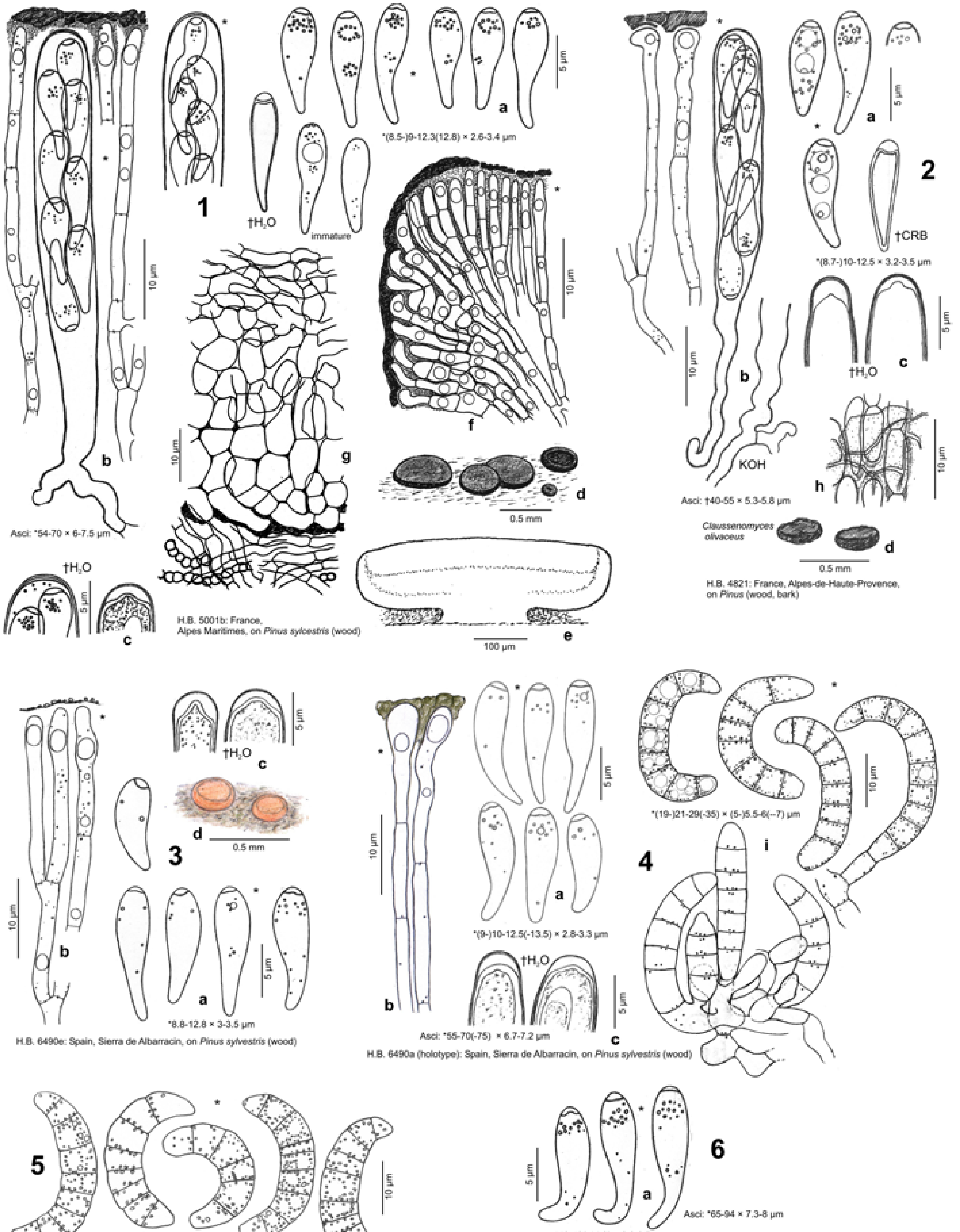
Typification: Spain, Teruel, Frías de Albarracín, branch of *Pinus sylvestris*, 26.IX.1999, G. Marson & H.O. Baral (ex H.B. 6490a, M-0276552, holotype; ex-type culture: CBS 116273; sq.: KT215224).

Latin diagnosis: *Apothecia in statu rehydratata atroolivacea, 0.25–0.85 mm diam. Asci 8-spori, apice rotundati, leniter crassitunicati. Ascosporae *7.5–14.2 × 2.6–3.7 µm, profunde clavatae, ad basim valde attenuatae, plus minusve curvatae, in statu vivo prope apicem corpusculum refringens lentiformem, perlate affixum continentes. Paraphyses ad apicem non vel modice inflatae, exsudato valido atroolivaceo tectae. Habitat ad lignum putridum, raro corticem, ramorum siccorum arborum coniferarum in zona orosubmediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.85(–1.3) × 0.25–0.75(–0.9) mm, 0.14–0.23 mm high, black (rarely bright orange), round to elliptical, large apothecia sometimes somewhat lobate, scattered to densely gregarious; disc flat (to slightly convex), somewhat shining though finely rough, margin thin or thick, 0–10 µm protruding, (very) finely rough; sessile or subsessile with an indistinct pseudostipe ~20–50 × 170–200 µm immersed in algal layer, superficial, sometimes erumpent from small slits; dry with thicker, distinctly protruding margin. **Asci** *54–90(–105) × 6–7.5(–8) µm {7}, †(40–)50–73(–85) × 5.3–7.2 {4}, 8-spored, spores 2(–3)-seriate, (0–)1–3(–5) lower spores inversely oriented {10} (rarely mixed), pars sporifera *(27–)29–39 → 25–26 µm long, †(32–)38–50 µm; **apex** (†) ± hemispherical irrespective of the viewing direction, dome *0.4–0.7 µm thick, †1–1.5 → 0.8–1.4 µm thick {4}, often with apical chamber, emptied asci sometimes with an olivaceous (in KOH more ochraceous) apical wall; **base** with short to very long, flexuous, ± thick stalk, L- to Y-shaped. **Ascospores** *(7.5–)9–13(–14.5)((–17)) × (2.6–)3–3.6(–3.8) µm {10}, †7.5–13.5 × 2.4–3.6 µm {2}, free spores rarely with a septum close to the apex {1}, clavate, apex rounded (to obtuse), base mostly strongly attenuated, often with a distinct tail 1–3(–5) × 1.3–1.8 µm, straight or often slightly to strongly curved or geniculate in lower part, rarely hooked; **SBs** 0.4–1 × 1.4–2 µm {6}, lens-shaped, apically broadly attached; with 2–12 subapically grouped **LBs** 0.1–0.4(–0.7) µm) diam. and a few ones towards base. **Paraphyses** apically uninflated or slightly (to medium) capitate, some sublageniform, partially flexuous, terminal cell *9.5–27(–31) × 1.7–4 µm {4}, †1.6–3.5 µm wide, lower cells *(4–)6–20(–23) × 1.5–2.3(–2.5) µm {4}, †1.2–1.6 µm wide; rarely branched at upper septum, apices somewhat glued together, hymenium light olive. **Medullary excipulum** hyaline to pale rose, 30–50 µm thick, of dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a pale olive or hyaline, ~4–15 µm thick layer of subparallel hyphae. **Ectal excipulum** of (*) thin-walled to slightly, (†) distinctly gelatinized, pale to light olivaceous-brown or bluish-olivaceous, dark olive towards margin, of vertically oriented t. globulosa-angularis(-prismatica) from base to lower flanks, 20–90 µm thick near base, cells *5–16 × 4–11 µm {4}, common walls †0.5–1.5 µm thick, appearing glassy-gelatinous in dead state; 20–50 µm thick at lower flanks; 20–35 µm at mid flanks, of t. (angularis-)prismatica(-porrecta) oriented at a 45–90° angle, cells *5–14 × 3–7 µm {3}, at margin 25–30 µm thick, oriented at 20–45(–90)°, marginal cortical cells *4–11(–15) × 2–4(–7) µm {3}. **Anchoring hyphae** sparse to abundant, hyaline, *1.5–4 µm wide, wall 0.2–0.4 µm thick {3}, forming a dense, hyaline t. intricata ~10–100 µm thick. **SCBs** in paraphyses (0–)1(–2), rarely many globose or ellipsoid, 1–2 µm diam., at mid flanks and margin 2–2.8 µm diam. **Exudate** over paraphyses dark olive to bluish-olive, cloddy, 1–5 µm thick, ± loosely attached; over margin and flanks bright to dark (brass-)olive or blue-green, rough-cloddy, 1–6 µm thick, more olive-brown with age; especially in outer region of ectal excipulum with dark brass-olive, very finely granular intercellular exudate; dark olive clods KOH-resistant, turning deep yellowish-(brass-)grey-brown, ample acetic acid restores blue-green pigment in full strength. — **ANAMORPH**: vermispora-like (from ascospore isolate {2} and natural substrate {4}). **Conidiophores** strongly reduced, repeatedly branched. **Conidiogenous cells** *~7–10 × 3–3.5 µm. **Conidia** unbranched, strongly to very strongly curved (C-shaped), rarely slightly helicoid, *(17–)21–30(–35) × (4.5–)5–6.5(–7.5) µm (~25–45 µm actual length) {5}, †20–28 × 5–6 µm {1}, 3–9(–11)-septate, often germinating to form further conidia.

Habitat: collected 1.5–3 m above the ground, on dead, mostly decorticated, 10–80 mm thick, still-attached branches of *Larix ?decidua* {1}, *Pinus* sp. {4}, *P. canariensis* {1}, *P. sylvestris* {8/3}, on 0.1–0.5 mm deep slightly to often strongly decayed wood {17}, rarely bark {1}, sometimes broken (splitted) areas, often in beetle galleries, also close to cankers with sparse resin flow but not clearly associated with resin, wood covered by a layer of sparse to abundant green algae and brown hyphae. **Associated**: *Ciliolarina laricina* {1}, *Claussenomyces olivaceus* {1}, *Coniochaeta malacotricha* {1}, *Dacrymyces* sp. {2}, *Hypogymnia physodes* {1}, *Lophium mytilinum* {1}, *Melanelia glabratula* {1}, *Mytilinidion ?gemmigenum* {1}, *Orbilia aristata* {1}, *O. coniferarum* {1}, *O. cylindrospora* {2}, *O. delphinus* {1}, *O. euonymi* {2}, *O. ?ocellata* {1}, *O. sphaerospora* {3}, *O. subcylindrospora* {1}, *O. subtrapeziformis* {1}, *O. subvinosa* {11}, *O. trapeziformis* {1}, *O. vinosa* {2}, *Parmelia* sp. {3}, *Pseudevernia furfuracea* {1}, *Pseudohelotium sordidulum* {2}, *Sarea resinae* {1}, *Usnea* sp. {1}. **Desiccation tolerance**: fully viable for at least 3 months; after 12 months some mature asci and many ascospores still intact. **Altitude**: 860–1830 m a.s.l. **Geology**: Middle & Upper Jurassic and Cretaceous marl & limestone, Pleistocene silt & gravel; trachybasalt. **Phenology**: II, IV, VII–X (throughout the year, long-lived).

Taxonomic remarks. *Orbilia patellarioides* is easily recognized by its dark olive exudate and clavate ascospores



H.B. 5001b: France, Alpes Maritimes, on *Pinus sylcestris* (wood)

H.B. 4821: France, Alpes-de-Haute-Provence, on *Pinus* (wood, bark)

H.B. 6490e: Spain, Sierra de Albarracin, on *Pinus sylvestris* (wood)

H.B. 6490a (holotype): Spain, Sierra de Albarracin, on *Pinus sylvestris* (wood)

H.B. 6729b: France, Var, Verdon, on *Pinus sylvestris* (wood)

H.B. 5321a: France, Hautes Alpes, on *Pinus sylvestris* (wood)

Plate 150. **1–6**: *Orbilia patellarioides*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia (rehydrated; **3**: orange colour variant, **2d**: dry, left with very similar rehydrated *Claussenomyces olivaceus*); **e**. apothecium in median section; **f**. marginal ectal excipulum in median section; **g**. id., near base; **h**. marginal ectal excipulum in surface view; **i**. conidia and conidiophores (**4i**. from culture, **5i**. from substrate).

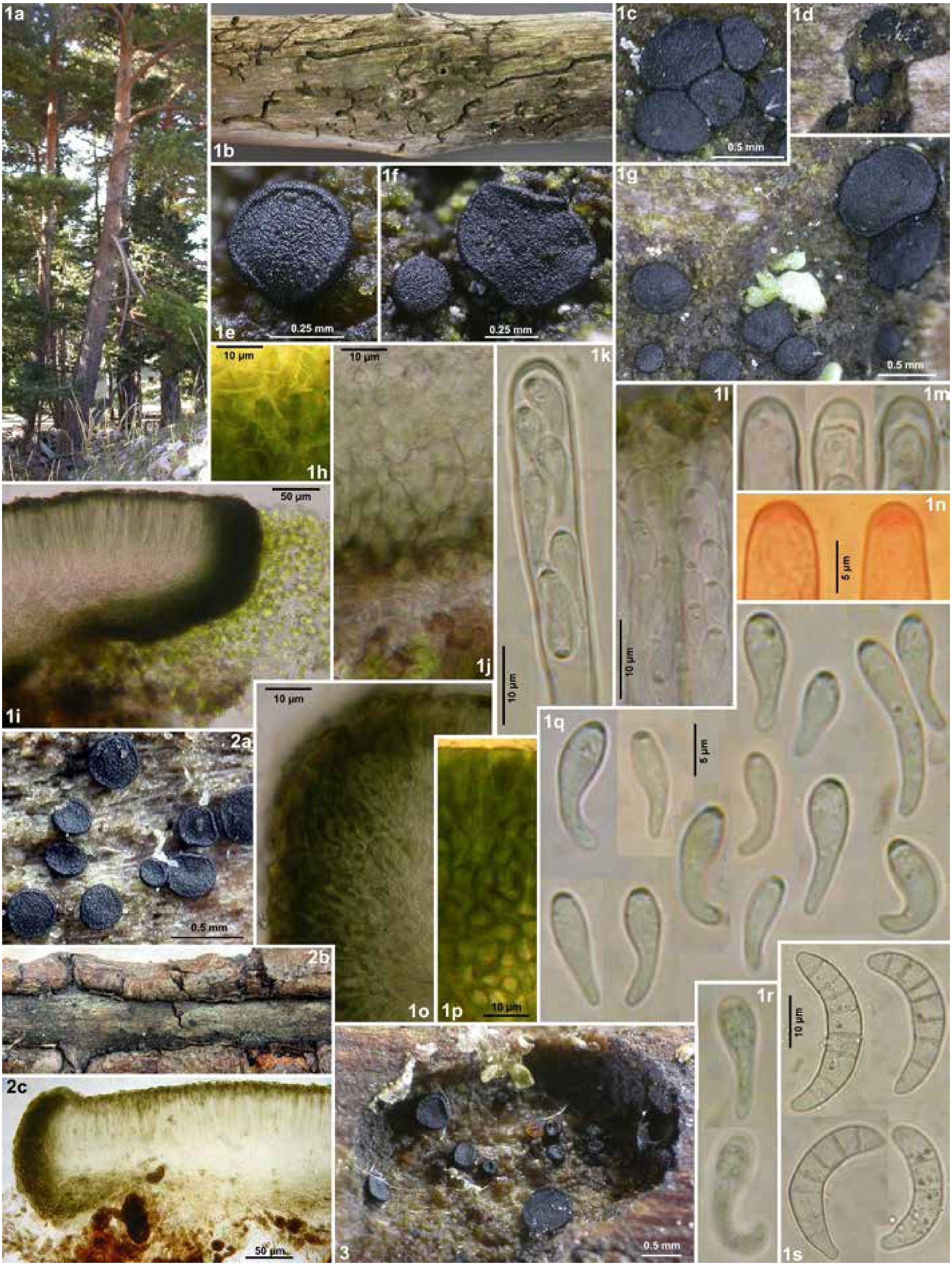


Plate 151. **1–3**: *Orbilia patellarioides*. – **1a**. open pine forest at northern slope of Mont Ventoux; **1b**, **2b**. dead branches of *Pinus sylvestris*; **1c–g**, **2a**, **3**. rehydrated apothecia (**3** with *O. vinosa*); **1i**, **2c**. apothecia in median section; **1o**. marginal ectal excipulum in median section; **1h**. id., external view, showing cloddy exudate; **1p**, id., showing cortical cells; **1j**. excipulum near base in median section; **1k–l**. asci; **1m–n**. ascus apices (**1n** in CR-SDS); **1q–r**. ascospores; **1s**. conidia from substrate. – Living state, except for **1m–p**, **r** (in water), **2c** (in PVA). — **1a–s**. H.B. 9173h: France, Mont Ventoux, on *Pinus*; **2a–c**. H.B. 5001b: France, Gréolières les Neiges, on *Pinus*; **3**. H.B. 6490a (holotype): Spain, Sierra de Albarracín, on *Pinus*.

with lens-shaped spore bodies. The ascospores resemble those of *O. ocellata* but differ in their attenuated, tail-like base. Two other North American species with black apothecia resemble *O. patellarioides* even microscopically: *O. atrolentiformis* differs in narrower, basally scarcely attenuated spores with more plug-shaped SBs, *O. purshiae* in somewhat larger spores with distinctly plug-shaped SBs, and in thicker ascus apical domes.

Variation. Little variation could be observed among the collections of *O. patellarioides*, except for the spores which strongly vary in their actual length, also from slightly to strongly curved. A few spores were seen in which the basal tail looked like a hook, being curved by almost 180° (Pl. 151: 1r). In a single collection (Pl. 150: 4, holotype) the black apothecia grew in close association with what is perhaps only a colour variant of *O. patellarioides* (Pl. 150: 3): minute apothecia (0.2–0.3 mm) showed the orange colour of *O. ocellata* but the spore shape of *O. patellarioides*. The microfeatures between black and orange apothecia closely concurred except that, in the orange variant, the exudate formed merely a ~1 µm thick, refractive, very pale yellowish, granular layer lying over hyaline gel. Possibly, these orange apothecia belong instead to *O. ocellata* in which basally tapered spores sometimes occur, though not in that frequency. Similar colour variants were noted in *O. purshiae* and *Amphosoma atroolivaceum*.

Anamorph. The curved (C-shaped) conidia of *O. patellarioides* are not untypical within section *Lentiformes*, but show an extraordinary width coupled with a strong curvature. Only in *O. pileosoma*, *O. subocellata* and series *Microspermae* were similar ± curved phragmoconidia observed. The conidia of *O. patellarioides* resemble those of *Lecophagus navicularis* in shape, being only slightly smaller. Yet, mycelium and conidia of *O. patellarioides* did not contain cubical SCBs, also the mycelial hyphae of *Lecophagus* are about three times as wide.

Phylogeny. Sequences were taken from an ascospore isolate (ex-type culture) from Frías de Albarracín (SSU V8–V9, ITS, LSU D1–D2) and from apothecia of a sample from Le Labouret (SSU V7–V9, ITS, LSU D1–D6). In the overlapping gene regions the two strains are fully identical, although the two sites are 730 km apart.

O. patellarioides clustered unresolved and outside the core clade of section *Lentiformes* (Phyls S9 [ITS], S11 [LSU]) or in our combined analysis (Phyl. 8) weakly supported with *O. ovalis*, with a very high ITS/LSU D1–D2 distance to other members of series *Lentiformes*, the lowest percentage being to *O. lentiformis* s.l. (~19%/3.8–4.3%) and *O. ovalis* (19–20%/4.3–5%), that to *O. purshiae* 22%. Molecular affinities between *O. patellarioides* and *O. ovalis* (series *Ovales*) appear to exist also in the very conservative 5.8S region, where the two species are fully congruent, whereas other members of section *Lentiformes* show 1–2 deviating nucleotides.

Ecology. *O. patellarioides* grows, often in abundance, on ± rotten wood of dead, decorticated, still-attached branches of gymnosperms, predominantly *Pinus sylvestris*. The macroscopically hardly different *Claussenomyces olivaceus* was once found in association. *O. patellarioides* seems to be rather common in calcareous altimontane mountain ranges of southern Europe, with a humid, orosubmediterranean, rarely orotemperate (Savoie) or nearly suprasubmediterranean climate. The vegetation includes more or less open pine forests at north-exposed slopes or plateaus, sometimes with *Buxus sempervirens*, *Genista*, and *Juniperus oxycedrus*. In Tenerife (Macaronesia) it was found in a south-exposed, lower mesomediterranean semihumid *Pinus canariensis* forest (*Sideritido solutae-Pinetum canariensis*, L. Quijada pers. comm.).

Map 21. Known distribution of *O. patellarioides* in Europe and Macaronesia.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Savoie**, 40 km NNE of Briançon, 3.8 km SSW of Termignon, Le Châtel, 1270 m, branch of *Pinus* (?) *sylvestris*, on wood, 5.VIII.1995, G. Marson (H.B. 5321a). – **Drôme**, 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branch of *Pinus sylvestris*, on wood, 23.VIII.1996, G. Marson (ø). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 20 km NW of Gap, 0.7 km E of Les Coutières, Col du Festre, 1390 m, branch of *Larix* ?*decidua*, on wood, 23.VIII.2000, G. Marson (H.B. 6761a). – **Alpes-de-Haute-Provence**, 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *Pinus*, on wood & bark, 24.X.1992, G. Marson (H.B. 4821 ø, G.M. 4924). – 1.4 km NNE of Le Labouret, 1350 m, branches of *P. sylvestris*, on wood, 30.VIII.2015, G. Marson (G.M. 2015-08-30.2, sq.: MH091027). – 8 km SE of St.-Julien-du-Verdon, 3 km NW of Soleilhas, Vauplane, 1600 m, branch of *Pinus*, on wood, 16.VII.1994, G. Marson (H.B. 5132a). – 10.5 km E of St.-André-les-Alpes, 2.3 km WNW of Annot, 2.6 km NE of Col de l'Iscle, 1145 m, branch of *P. sylvestris*, on wood, 16.VIII.2001, G. Marson (H.B. 7061b). – 6.5 km SE of Castellane, 0.8 km NW of La Bâtie, Col de Luens, 1080 m, branch of *P.* (?)*sylvestris*, on wood, 5.X.1993, G. Marson (ø). – **Alpes Maritimes**, 28 km N of Monte Carlo, ~2 km NE of Col du Turini, l'Authion, ~1830 m, branch of *Pinus*, on wood, 3.X.1993, G. Marson (H.B. 5143). – 19 km NNE of Grasse, 4 km NNE of Gréolières, Gréolières les Neiges, 1405 m, branch of *P. sylvestris*, on wood, 1.X.1993, G. Marson (H.B. 5001b, anam. substr. & cult.). – 24 km N of Nizza, 1.5 km WSW of Utelle, Madone d'Utelle, 1150 m, branch of *P. sylvestris*, on wood, 3.X.1993, G. Marson (H.B. 5142a). – **Var**, 11 km SSE of Moustiers-Ste.-Marie, 3 km SSE of Aiguines, Grand Plan de Canjuers, 860 m, branch of *P.* (?)*sylvestris*, on wood, 5.VIII.1999, G. Marson (H.B. 6729b, anam. substr.). – **Vaucluse**, 9.5 km NE of Bedoin, 1.5 km NW of Mont Ventoux, Mt. Serein, 1385 m, branch of *P. sylvestris*, on wood, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9173a, anam. substr.). – **Hautes-Alpes**, 27 km SE of Gap, 2.5 km NE of Montclar, Col St.-Jean, 1335 m, branch of *Pinus*, on wood, 6.X.1993, G. Marson (H.B. 5016b, anam. substr.). — **SPAIN**: **Aragón**, **Teruel**, Sierra de Albarracín, 40 km W of Teruel, 4.5 km W of Frías de Albarracín, 1615 m, branch of *P. sylvestris*, on wood, 26.IX.1999, G. Marson & H.O. Baral (M-0276552, **holotype**; **isotype** in H.B. 6490a; anam. cult., CBS 116273; sq.: KT215224; H.B. 6490e orange variant). – Sierra de Javalambre, 23 km SSE of Teruel, 1.8 km E of Camarena de la Sierra, 1585 m, branch of *P. sylvestris*, on wood, 1.IV.2012, R. Tena (R.T.L. 12040101). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Vilaflor, 0.6 km ENE of Vilaflor, Las Lajitas, 1445 m, branch of *P. canariensis*, on wood, 19.II.2012, L. Quijada (TFC Mic. 23352, doc. vid.).

Orbilia atrolentiformis Baral & G. Marson, **sp. nov.**, MB 813483 — Pls 152–153

Etymology: referring to the black colour of apothecia and the ± lens-shaped spore bodies.

Typification: USA, Montana, Yellowstone, branch (or root?) of *Pinus contorta*, 5.VI.1996, G. Marson (ex H.B. 5741a, M-0276437, holotype).

Latin diagnosis: *Similis* Orbiliae patellarioidi *sed ascosporae angustiores*, *ad basim haud vel parum attenuatae*, *ad apicem corpusculo refringente magis incrassato*, *plerumque obturamentiforme*, *angulato*. *Habitat ad lignum putridum rami sicci* Pini contortae *in zona boreali humidi Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.8(–1) × 0.2–0.7 mm, 0.19–0.24 mm thick (receptacle 0.07–0.12 mm),

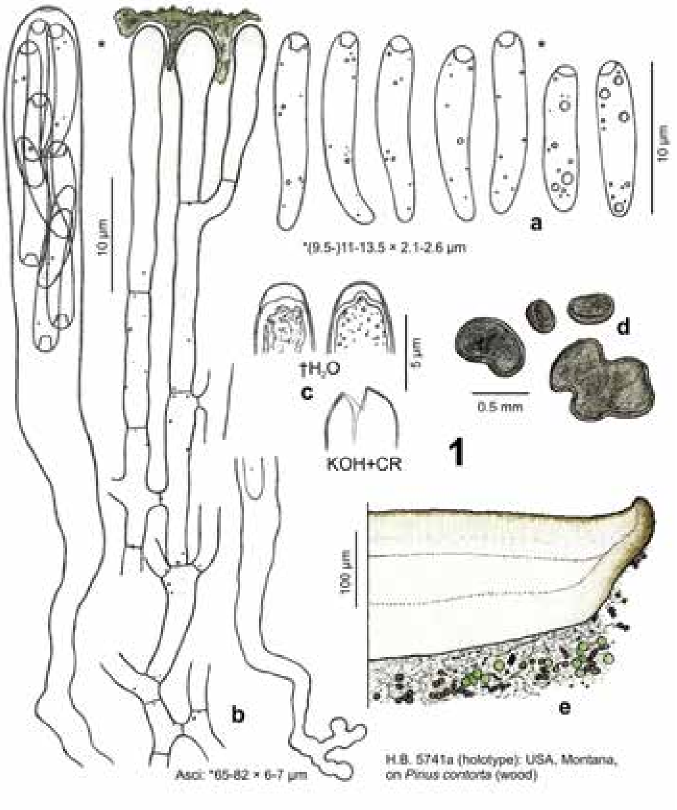


Plate 152. **1**: *Orbilia atrolentiformis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section.

olivaceous-black, young round to elliptical, ± undulating when large, scattered to gregarious in small groups; disc slightly concave to flat, finely rough, margin distinctly rising above disc, even; broadly sessile, sometimes with a distinct stipe 0.1–0.12 × 0.15–0.18 mm hidden in detritus, externally glabrous, shining, superficial to somewhat erumpent; dry with only slightly inrolled margin, disc remaining exposed. **Asci** *63–82 × 5.5–7 µm, †55–65 × 5–6 µm, 8-spored, spores 2–3-seriate, 2–3(–4) lower spores inversely oriented (rarely mixed), pars sporifera *25–35 µm long; **apex** (†) hemispherical to slightly truncate, dome immature †0.9–1.1 → 0.4–0.7 µm thick, sometimes with distinct apical chamber; **base** with long, thin, flexuous stalk, T-, L- to Y-shaped. **Ascospores** *(9–)10–13.5 × (1.8–)2–2.6 µm, †8–10.5 × 2.1–2.6 µm, (sub)cylindrical or (cylindric-)clavate, ends rounded, slightly attenuated near base, straight to slightly (or medium) curved towards the not or only slightly attenuated base; **SBs** 1–1.2 × 1.3–1.5 µm, lens- or often strongly plug-shaped, sometimes with inner edges, apically broadly attached; **LBs** sparse, minute, later increasing in size. **Paraphyses** apically uninflated to medium clavate, terminal cell 11–28 × 2.2–3.7 µm, lower cells 10–17 × 1.7–2.6 µm, sometimes branched near apex. **Medullary excipulum** hyaline, 60–110 µm thick, upper layer 40 µm thick, of dense small-celled texture, lower layer 20–70 µm thick, of a horizontal textura porrecta or loose t. intricata with inflated cells, sharply delimited. **Ectal excipulum** hyaline, of (*) thin-walled, (†) medium gelatinized (common walls 0.5–1 µm thick), vertically oriented t. angularis-prismatica from base to lower flanks, 30–80 → 20–40 µm thick, cells *9–23 × 8–12 µm, †5–10 × 5–9 µm, cortical cells very pale brownish; 20–25 µm thick near margin, at mid flanks of ± gelatinized t. prismatica oriented at a 30–70° angle to the surface, at margin of t. prismatica-porrecta oriented at 20–30°, bright to dark grey-brown-olive (mainly at the cortex), marginal cortical cells †7–11 × 2–5 µm. **Anchoring hyphae** sparse to abundant, hyaline, †2–3(–3.5) µm wide, walls 0.2 µm thick, forming a dense t. intricata. **SCBs** partially present in paraphyses, globose. **Exudate** over paraphyses, margin and flanks dark olive-brown, KOH-resistant, in young apothecia dark olive, turning greyish- or ochre-brown in KOH; 1–2 µm thick, broken in large clods or small granules, ± loosely attached. **— ANAMORPH**: unknown (but see under *O. pileosoma*, p. 469).

Habitat: collected on dry ground, decorticated, 35–40 mm thick projecting branch (or root?) of *Pinus contorta*, on wood, often in beetle galleries or hidden at the border of deep clefts, 0.3–0.5 mm deep very rotten, strongly greyed, with some green algae. **Associated**: '*Chlorosplenium*' *viridulum*, *Odontotrema oregonensis*, *Orbilia pileosoma*, various crustose lichens (*Amandinea*, *Lecanora*). **Desiccation tolerance**: fully viable for at least 13 months. **Altitude**: 2035 m a.s.l. **Geology**: Quaternary felsic volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia atrolentiformis* differs from the macroscopically similar *O. patellarioides* in narrower, subcylindrical ascospores lacking tails, also in the often strongly plug-shaped SBs. *O. purshiae* differs in much broader spores.

Ecology. *O. atrolentiformis* is only known from a single population of about 25 apothecia. It grew on rotten wood of a dead xeric branch (or root?) of *Pinus contorta* (lodgepole pine) in the boreal humid, upper montane lodgepole pine

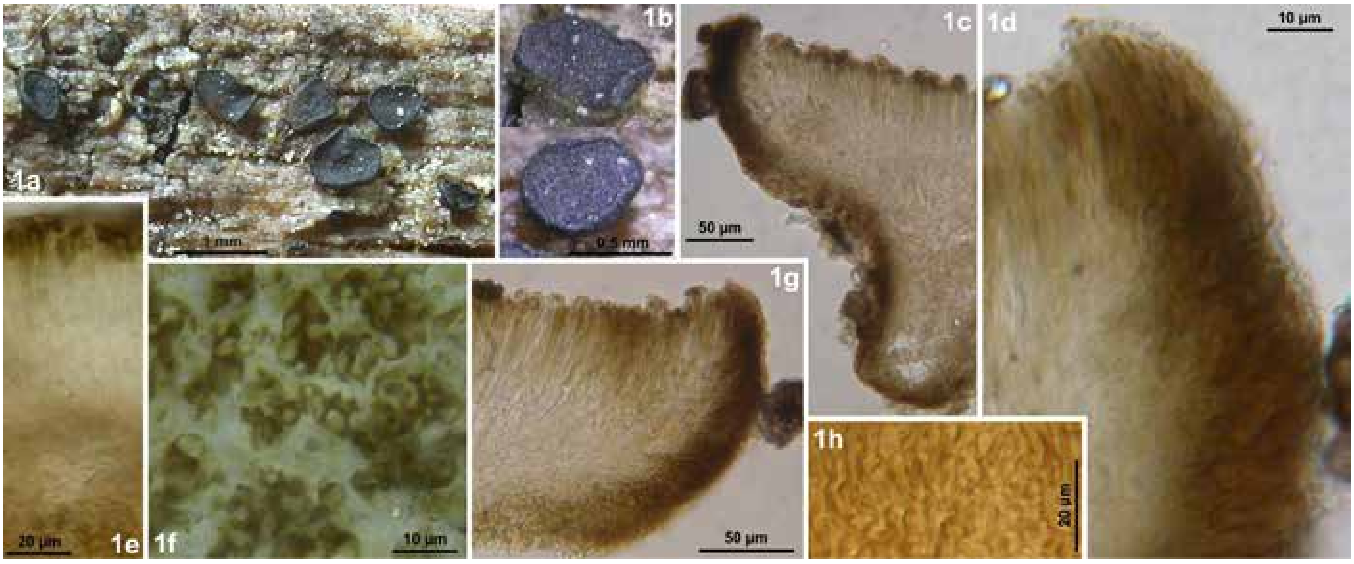


Plate 153. **1**: *Orbilia atrolentiformis*. – **1a–b**. apothecia in rehydrated state; **1c**. apothecium in median section; **1d**, **g**. id., near margin; **1h**. id., in external view; **1e**. hymenium and medullary excipulum in median section; **1f**. top view on hymenium. – Dead state (KOH, except for **1c**, **g**: H$_2$O). — **1a–h**. H.B. 5741a (holotype): USA, Montana, on *Pinus*.

forest at the northern end of the Middle Rocky Mountains in western North America. Black apothecia of an *Amandinea* sp. grew in association which much resemble the *Orbilia* but have more convex hymenia and are clearly connected to a thallus. The smaller-sized but otherwise macroscopically very similar apothecia of the associated *O. pileosoma* grew in a separate small population.

Specimens included. **USA**: **Montana**, Middle Rocky Mountains, SE of West Yellowstone, 2035 m, branch (?root) of *Pinus contorta*, on wood, 5.VI.1996, G. Marson (ex H.B. 5741a, M-0276437, **holotype**).

Orbilia purshiae Baral & G. Marson, **sp. nov.**, MB 814378 — Pls 154–155, Map 22

Etymology: named according to the predominant host plant, *Purshia stansburyana.*

Typification: USA, Arizona, Jacob Lake, branch of *Purshia stansburyana*, 17.V.1995, G. Marson (ex H.B. 5295a, M-0276573, holotype).

Latin diagnosis: *Similis* Orbiliae patellarioidi *sed corpuscula ascosporarum obturamentiformia, elongato-angulata, asci latiores, tunica apicali magis incrassata*. Habitat ad *lignum putridum ramorum siccorum* Purshiae *vel* Cercocarpi *in zona orotemperata subhumida ad semiarida Americae septentrionalis*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.7(–1) × 0.2–0.5(–0.7) mm, 0.13–0.18(–0.24) mm thick (receptacle 0.11–0.18 mm), black (rarely associated by some abnormal bright orange apothecia), round to often ± elongate in direction of the wood fibres, somewhat undulating when large, scattered or gregarious in small or larger groups; disc flat, finely rough, margin thin, not rising above disc, even; externally glabrous, sessile; margin dry not inrolled, more distinct, partially navicular like a *Hysteropatella*, ± immersed among wood fibres. **Asci** *55–75(–82) × 8.5–10 µm {3}, †(47–)60–80(–95) × (7.3–)7.8–8.8(–9.5) µm {3}, 8-spored, spores 3–4-seriate, (1–)3–5(–6) lower spores inversely oriented (not or partially mixed) {3}, pars sporifera *32–42(–45) µm long; **apex** (†) always hemispherical, dome †1.5–3.3 → 1–2 µm thick {3}, with very prominent apical chamber, exterior sometimes olivaceous by a thin layer of exudate; **base** with short to medium long, thick, flexuous stalk, T-, L-or Y-shaped. **Ascospores** *(8.3–)12–16(–17) × (2.8–)3–3.8(–4.2)((–5)) µm {3}, †10–14.3 × 2.7–3.2(–3.6) µm {2}, clavate to cylindric- or ellipsoid-clavate, apex rounded, base medium to often strongly attenuated, rarely tail-like (exceptionally with a short tail), straight or mostly slightly to strongly curved near base; **SBs** *(0.8–)1–1.6 × 1.2–1.8 µm {3}, plug-shaped with prominent inner edges, apically broadly attached; **LBs** sparse, minute. **Paraphyses** apically ± cylindrical to very slightly clavate or sublageniform, terminal cell */†8.5–15(–19) × 1.8–3 µm {2}, straight to ± flexuous, often with brownish-olivaceous, slightly roughened wall, lower cells *(4.5–)8–15 × 1.7–2.8 µm {2}; frequently branched near apex. **Medullary excipulum** ± hyaline, 30–50(–100) µm thick, of dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a hyaline to pale amber t. porrecta, dead cells with light yellow-ochre cytoplasm. **Ectal excipulum** ± hyaline, cortex black-brown-olivaceous, of (*) slightly to medium gelatinized, ± vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 15–100 µm thick near base, cells *6–15 × 4.5–10 µm {3}; 15–25 µm thick near margin, of t. prismatica-angularis oriented at a 70–80° angle to the surface, or t. prismatica-porrecta at a 30° angle, marginal cortical cells */†6–15 × 2–4 µm {2}. **Anchoring hyphae** hyaline, †2–3.5 µm wide, wall 0.2–0.3(–0.7) µm thick {1}, forming a loose or dense, not or medium gelatinized t. intricata at the base. **SCBs** absent. **Exudate** dark olive-brownish, rough-cloddy, over paraphyses 2–4 µm thick, ± firmly attached, KOH-resistant (turning reversibly brass-amber-brown); over margin and flanks rough-cloddy, in KOH turning reddish-brown, near base fox-ochre. — **ANAMORPH**: vermispora-

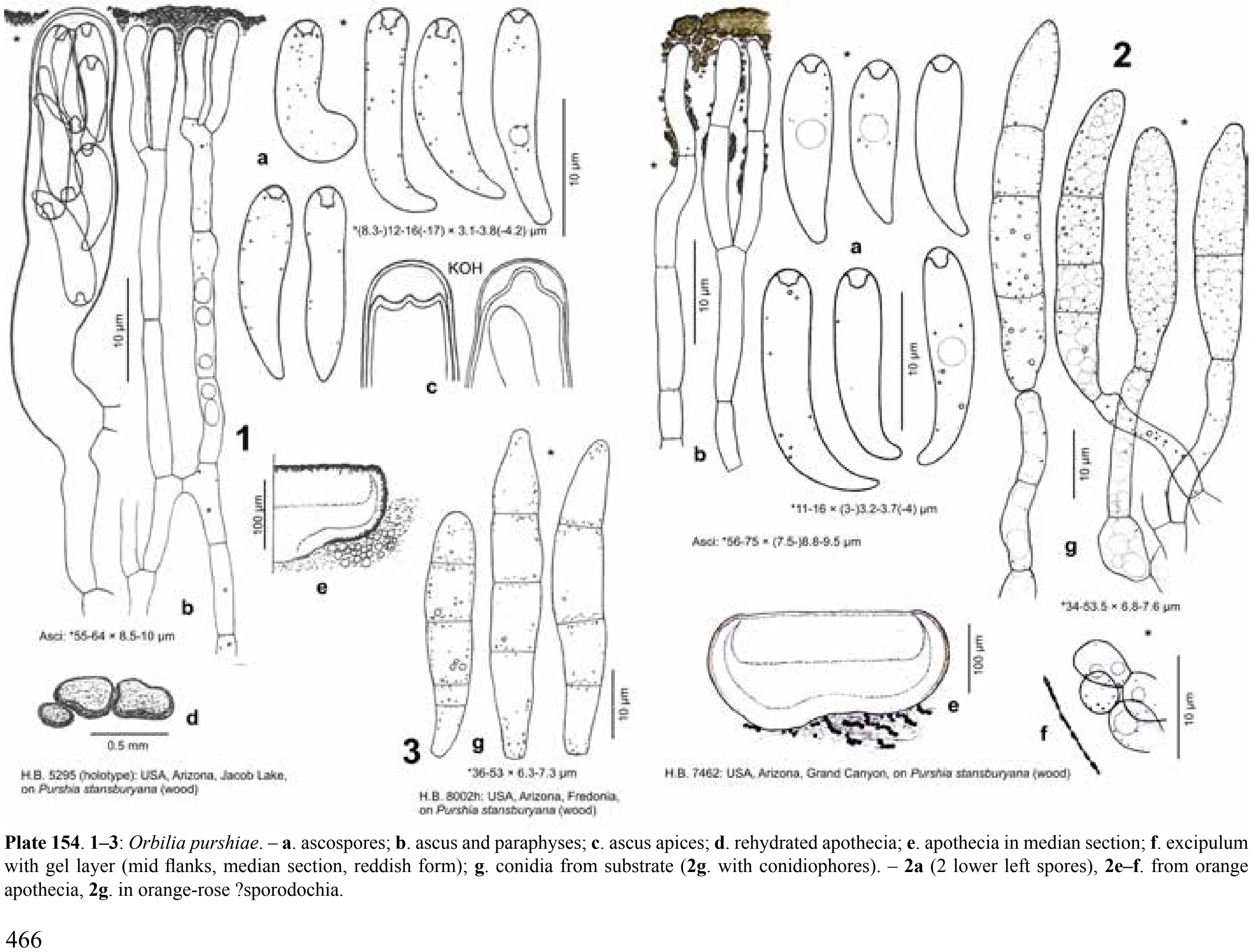


Plate 154. **1–3**: *Orbilia purshiae*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. excipulum with gel layer (mid flanks, median section, reddish form); **g**. conidia from substrate (**2g**. with conidiophores). – **2a** (2 lower left spores), **2e–f**. from orange apothecia, **2g**. in orange-rose ?sporodochia.

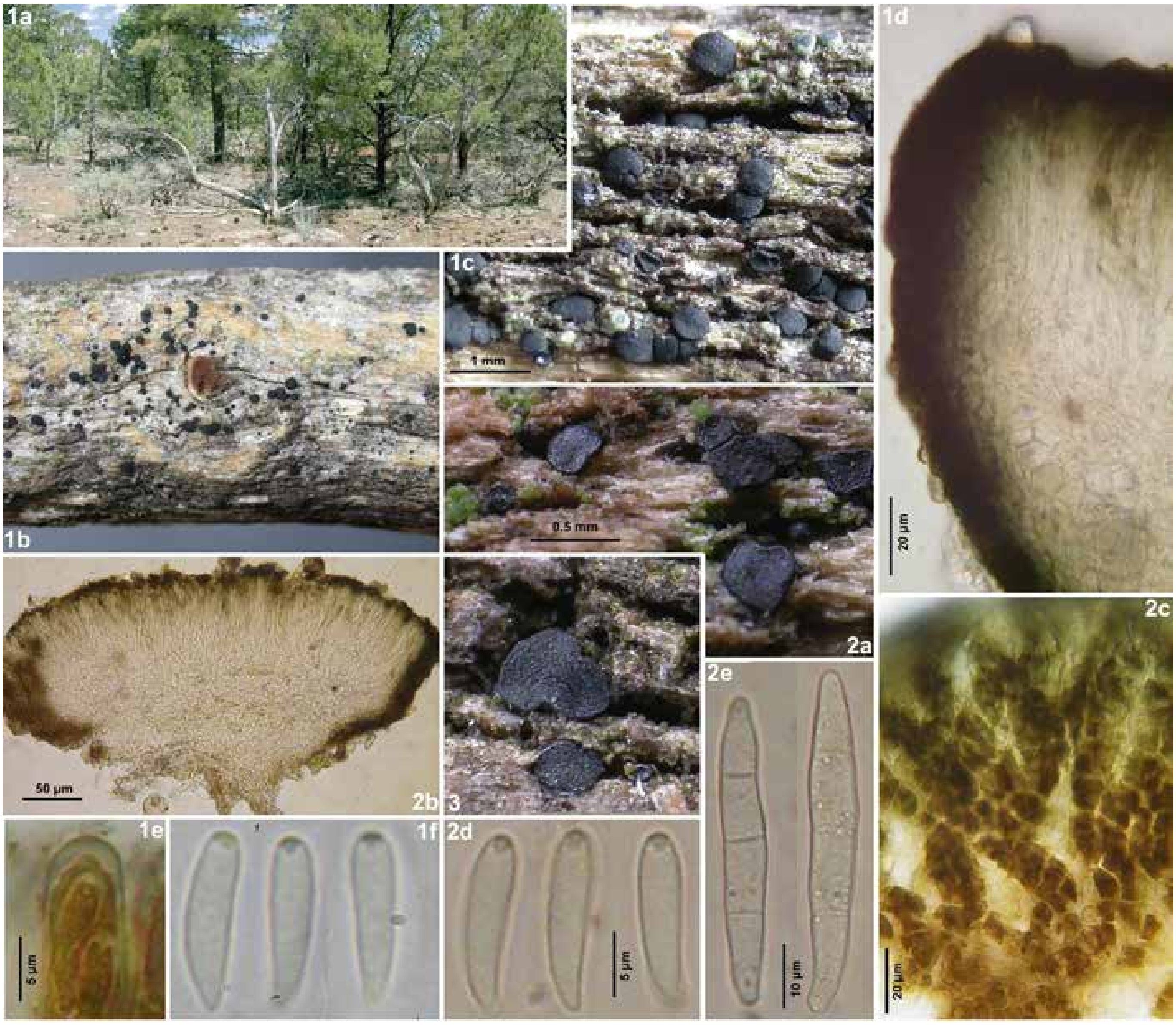


Plate 155. **1–3**: *Orbilia purshiae*. – **1a**. subhumid pinyon-juniper woodland on high plateau near South Rim of Grand Canyon, with *Pinus edulis* and dead *Purshia*; **1b–c**, **2a**, **3**. rehydrated apothecia; **2b**. apothecium in median section; **1d**. ectal excipulum in median section (flanks and margin); **2c**. cloddy exudate (external view); **1e**. ascus apex; **1f**, **2d**. ascospores; **2e**. conidia from substrate. – Living state, except for **1e**. — **1a–f**. H.B. 7462a: USA, Arizona, Grand Canyon, on *Purshia*; **2a–e**. H.B. 8002h: USA, Arizona, Fredonia, on *Purshia*; **3**. H.B. 8059a: USA, Utah, on *Purshia*.

like (presumed, from natural substrate {3}). (?)**Conidiomata** ~0.3–0.4 mm diam., ?sporodochial, bright orange-rose, inner tissue of textura angularis, thin-walled, small-celled, without a differentiated ectal layer {1}. **Conidiophores** short, sometimes branched. **Conidiogenous cells** *~12–25 × 3.3–4 µm. **Conidia** unbranched, almost straight to slightly (rarely medium) curved, narrowly fusoid, *(30–)35–45(–53.5) × 6.3–7.6 µm {2}, †33–43 × 5.3–6.3 µm {1}, (1–)3(–4)-septate.

Habitat: collected 0.5–2.5 m above the ground, on decorticated, (4–)6–16 mm thick twigs and branches of *Purshia stansburyana* {5}, *Cercocarpus ledifolius* {1}, on 0.3–1.5 mm deep strongly decayed wood {5}, slightly to strongly greyed, with a few or quite many green algae. **Associated**: *Caloplaca* sp. {1}, *Candelariella* sp. {1}, *Durella* sp. {1}, *Odontotrema oregonensis* {1}, *Orbilia arizonensis* {4}, *O. calyptrata* {1}, *O. delphinus* {1}, *O. euonymi* {1}, *O. flexisoma* {1/3}, *O.* ?*gambelii* {1}, *O.* ?*lentiformis* {3}, *O. macrodelphinus* {2}, *O. maeandrina* {4}, *O. multimaeandrina* {1}, *O. serpentina* {1}, *O. subovoidea* {1}, ?*Schizoxylon* sp. {1}, *Symbiotaphrina desertorum* {1}, foliose and crustose *Lecanorales*. **Desiccation tolerance**: fully viable for at least 7 months, after 28 months spores and some excipular cells still viable, conidia after 6 months. **Altitude**: 1880–2500 m a.s.l. **Geology**: Permian and Jurassic (red) sand- & limestone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia purshiae* differs from *O. patellarioides* in wider asci with a thicker apical dome, slightly larger ascospores which usually lack a tail, distinctly plug-shaped SBs, and in the substrate (*Rosaceae* vs. gymnosperms). The also conifericolous *O. atrolentiformis* has much narrower spores, but similar plug-shaped SBs.

A few bright orange-coloured apothecia in H.B. 7462a are microscopically indistinguishable (Pl. 154: 2a, lower left 2 spores, e–f) and appear to represent a colour variant of *O. purshiae*. Comparable rare cases of pigment loss were noted in *O. patellarioides* and *Amphosoma atroolivaceum*.

Anamorph. A few bright orange apothecioid fructifications (?sporodochia) without asci resembled the orange colour variant of *O. purshiae*, but were found in close association with the black apothecia in H.B. 7462a. The conidia formed in them (Pl. 154: 2g) coincide with those found on the natural substrate of another collection (Pl. 154: 3g). The wall surface of the conidiophores stained pale lilac with CRB, a character typical of *Orbiliomycetes*. The question remains open whether

Map 22. Known distribution of *O. purshiae* in North America.

these fructifications are host apothecia of another *Orbilia*, or conidiomata of *O. purshiae*.

Phylogeny. A sequence was taken in Feb. 2020 from apothecia on branches from Coconino Plateau (SSU V9, ITS, LSU D1 and part of D2). In our combined analysis of section *Lentiformes* (not shown) *O. purshiae* clustered unresolved among *O. patellarioides*, the core clade of section *Lentiformes*, *O. ovalis*, and series *Microspermae*. In the ITS it showed a distance of 22 % to *O. patellarioides*, while the lowest distance was 19.5 % to *O. lentiformis* s.l.

Ecology. *O. purshiae* was found on rotten wood of dead xeric branches of two genera of *Rosaceae* shrubs, *Purshia* (Stansbury's cliffrose) and *Cercocarpus* (mountain mahogany) in the Colorado Plateau (southwest of Northern America): in cold-temperate subhumid pinyon-juniper woodlands, partially adjacent to warm-continental semiarid or cold-temperate subhumid sagebrush desert scrubs, in the Grand Canyon section (Kaibab and Coconino Plateau) and at the foothills of Utah mountains.

Specimens included. **USA**: **Utah**, Utah Mts., 16 km SSW of Boulder, 1920 m, branch of *Purshia stansburyana*, on wood, 11.VI.2003, G. Marson (H.B. 8059a, anam. substr.). – 19 km ENE of Springdale, 11 km WNW of Mt. Carmel Junction, 1880 m, branch of *P. stansburyana*, on wood, 14.VI.2003, G. Marson (ø). – **Arizona**, Grand Canyon, Kaibab Plateau, 28 km ESE of Fredonia, 13 km NNW of Jacob Lake, 2115 m, branch of *P. stansburyana*, on wood, 17.V.1995, G. Marson (ex H.B. 5295a, M-0276573, **holotype**). – ibid., branch of *P. stansburyana*, on wood, 15.VI.2003, G. Marson (H.B. 8002h, anam. substr.). – 93 km SSE of Fredonia, S of North Rim, 2500 m, branch of *Cercocarpus ledifolius*, 17.V.1995, G. Marson (ø). – Coconino Plateau, 7.5 km ESE of Grand Canyon Village, close to South Rim, 2205 m, branch of *Purshia stansburyana*, on wood, 16.VI.2003, G. Marson (H.B. 7462a, G.M. 2003-06-16.1, anam. substr., sq.: MT356590).

Orbilia pileosoma Baral & G. Marson, **sp. nov.**,
MB 813484 — Pls 156–157

Etymology: referring to the extraordinarily thin, calotte-shaped spore bodies (resembling a pileolus).

Typification: USA, Utah, Panguitch, branch of *Abies concolor*, 20.VI.2000, G. Marson (ex H.B. 6998c, M-0276553, holotype).

Latin diagnosis: *Apothecia in statu rehydratata atroolivacea, 0.15–0.5 mm diam. Asci 16-spori, apice rotundati, in statu emortuo crassitunicati. Ascosporae *4.8–8 × 3.2–4.5 µm, late ellipsoideae vel obovoideae, intus prope apicem calotta refringente leniter incrassata. Paraphyses ad apicem haud inflatae, exsudato valido atroolivaceo tectae. Habitat ad lignum putridum ramorum siccorum arborum coniferarum in zona orotemperata ad boreali humida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.4(–0.5) × 0.12–0.4 mm, 0.11 × 0.18 mm thick, black, round, sometimes broadly elliptical, scattered or subgregarious in small groups; disc flat,

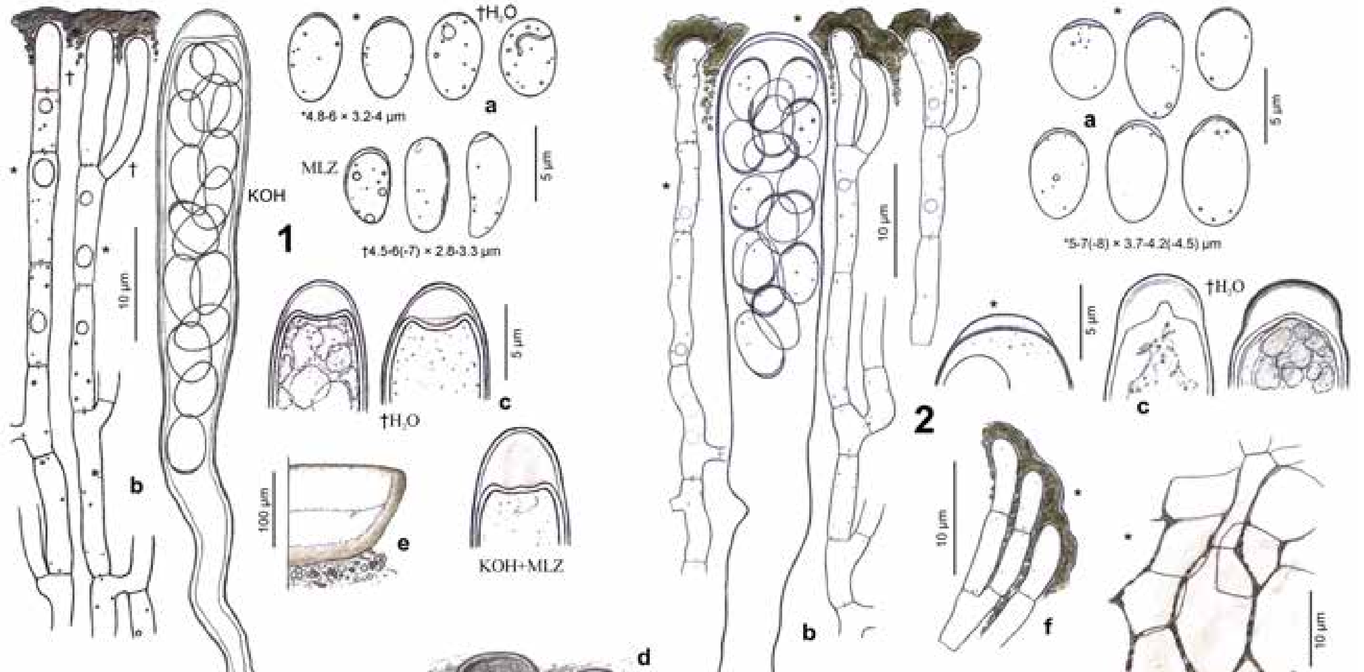


Plate 156. **1–2**: *Orbilia pileosoma*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apex (on **1c** dextrinoid in MLZ); **d**. rehydrated apothecia. **e**. apothecium in median section; **f**. ectal excipulum (margin, median section); **g**. id., near base.

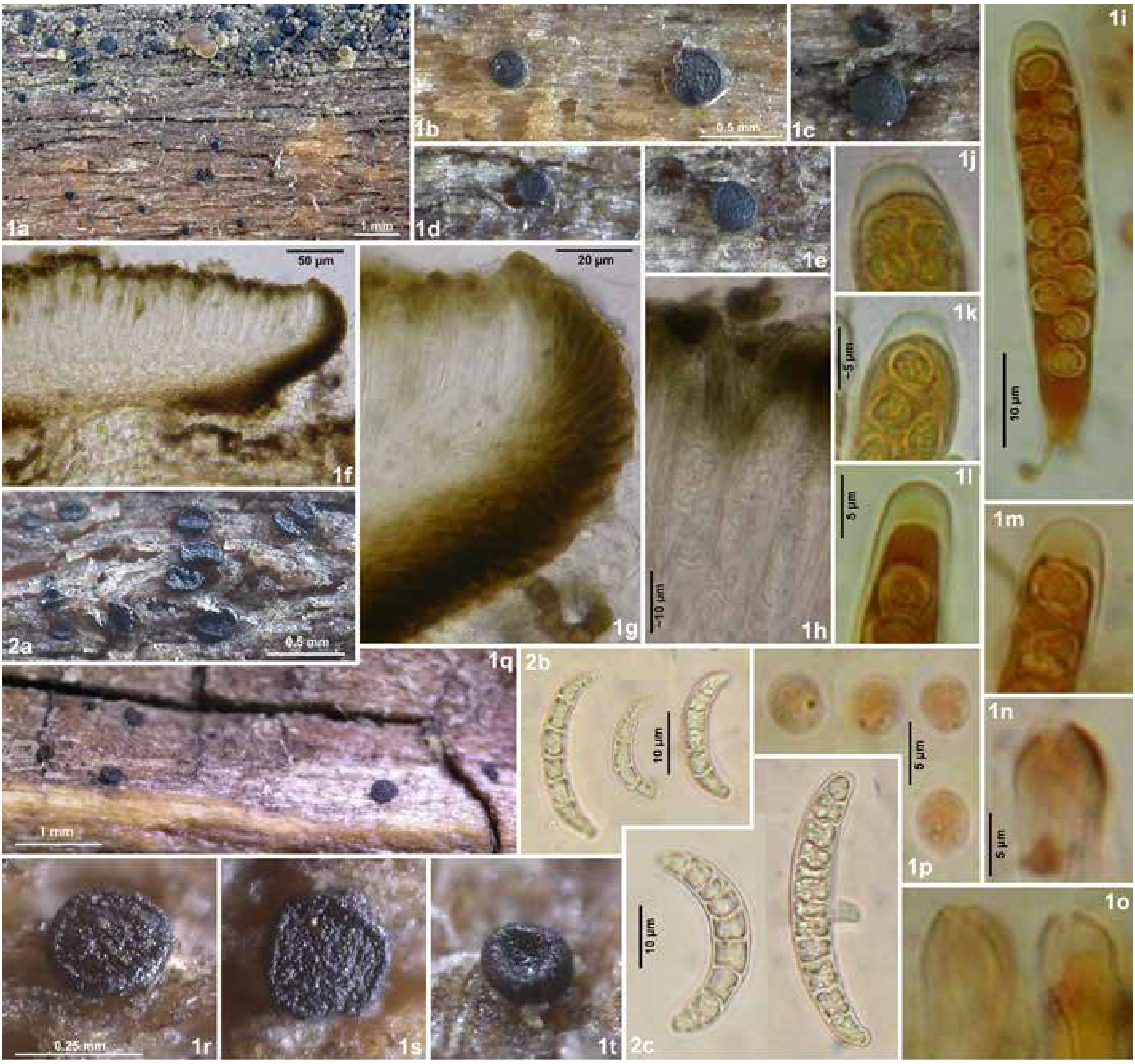


Plate 157. **1–2**: *Orbilia pileosoma*. – **1a–e**, **q–t**, **2a**. rehydrated apothecia (**1a**: crustose lichens in upper part); **1f**. apothecium in median section; **1g**. marginal region in median section; **1h**. detail of hymenium showing olive exudate; **1i**. ascus; **1j–o**. ascus apices (**n–o** emptied via apical slit); **1p**. ascospores (SBs located where plasma looks as being detached); **2b–c**. conidia from substrate. – All in dead state: **1f**, **h**, **2b–c** (in water); **1g** (in KOH); **1j–k** (in KOH+IKI); **1i**, **l–o** (in KOH+CR+IKI); **1p** (KOH+CR). — **1a–t**. H.B. 6998c (holotype): USA, Utah, on *Abies*; **2**. H.B. 5741b: USA, Montana, on *Pinus*.

eventually slightly convex, finely rough, margin ± thick, distinct, 0–10 µm protruding, shining; sessile, superficial or slightly immersed in detritus or wood fibres. **Asci** *(50–)55–69(–77) × 9–10.2(–13) µm {1}, †45–70 × (7–)7.5–9 µm {2}, 16-spored, spores 3–4-seriate, about half of the lower spores inversely oriented (strongly mixed, some horizontally oriented), pars sporifera *30–45 µm long, †24–46 µm; **apex** (†) hemispherical to distinctly subconical or subtruncate, dome immature †2–3(–4) µm thick, mature ~2–2.5 µm, sometimes with distinct apical chamber, dome in KOH+MLZ partially pale to light red (± ring-shaped) {2}, emptied asci especially in older apothecia often with bright olive-brown periascus; **base** with short to medium long, thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *4.8–7(–8) × (3.2–)3.5–4.5 µm {1}, †4.3–6(–7) {2} × 2.8–3.3 {1} or 3.8–4.2 {1} µm, broadly ellipsoid to obovoid, rarely clavate, straight; **SBs** 0.2–0.4 × 1.5–3 µm, forming a thin calotte-shaped layer very broadly attached to the apical wall. **Paraphyses** apically ± uninflated, terminal cell */†(6–)7–10(–13) × (1.6–)1.8–2.4(–3.3) µm {2}, lower cells *5–15 × 1.7–2.7(–4) µm {2}; quite frequently branched near apex. **Medullary excipulum** hyaline, 30–50 µm thick (50–70 µm in centre), of dense textura intricata with many inflated cells, (†) somewhat gelatinized, sharply or very indistinctly delimited. **Ectal excipulum** of (*) thin-walled, (†) strongly gelatinized, ± vertically oriented t. (globulosa-)angularis from base to mid flanks, 20–40 µm thick near base, cells *8–18 × 6–10.5 µm; near margin 15–20 µm thick, of t. porrecta oriented at 30–45°, cortical cells *5–9 × 2–2.2 µm {1}. **Anchoring hyphae** ± sparse, hyaline, †1.7–3 µm wide, walls †0.2–0.5 µm thick {1}. **SCBs** in paraphyses ± globose. **Exudate** over paraphyses cloddy (to granular), 1–3 µm thick, bright to deep olive-brown, in KOH turning light olive-amber-brown, ± firmly attached; over marginal excipulum cloddy(-granular), 1–2 µm thick, bright to dark olivaceous-brown (KOH more reddish-brown, acetic acid recovers the olive colour), also present between the cells, gradually paler towards medullary excipulum. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {1}). **Conidiophores** not seen. **Conidia** unbranched, slightly to strongly curved, †16–27 × 3.8–4 µm, 4–5-septate, or 29–45 × 6.3–6.5 µm, 8–11-septate (observed in the same sample).

Habitat: collected ~0.2–2 m above the ground, decorticated, 15–35 mm thick branches (and roots?) of *Abies concolor* {1}, *Pinus contorta* {1}, close to or in old beetle galleries, on 0.2–1 mm deep very rotten wood {2}, strongly greyed, with some green algae. **Associated**: *Amandinea* sp. {2}, '*Chlorosplenium*' *viridulum* {1}, *Claussenomyces* sp. {1}, *Lachnellula* sp. {1}, *Lecanora* sp. {1}, *Melaspilea emergens* {1}, *Odontotrema oregonensis* {1}, *Orbilia atrolentiformis* {1}, *O. concoloris* {1}, *O. phanosoma* {1}. **Desiccation tolerance**: fully viable after min. 17 months. **Altitude**: 2035–2775 m. **Geology**: Upper Cretaceous calcareous sandstone, (Tertiary to) Quaternary volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pileosoma* is easily distinguished from the other species with black apothecia by 16-spored asci and extraordinary, very thin and wide, calotte-like SBs in the mature living ascospores. The SBs resemble the apical wall thickenings of living asci, but they stain light blue in CRB, and loose refractivity without getting inflated when adding KOH (Pl. 157: 1p).

Variation. In the sparse *Pinus* collection, the ascus apical dome reacted distinctly pale red in MLZ though it was negative in IKI or KOH+IKI. After KOH-treatment the MLZ-reaction was light red in all asci (Pl. 156: 1c, lower ascus). The abundant *Abies* collection was iodine-negative in either treatment (the stain in Pl. 157: 1l–m is probably due to presence of CR). This difference might be accidental, and further collections should be tested for the feature.

Anamorph. Two types of vermispora-like phragmoconidia were observed on the substrate of the *Pinus* collection (Pl. 157: 2b–c). Whether both of them belong to *O. pileosoma*, or perhaps one to the associated *O. atrolentiformis*, remains unclear.

Ecology. *O. pileosoma* grew on rotten wood of decorticated xeric branches of *Abies concolor* (white fir) in the boreal humid Douglas fir mixed forest at the southern end of Dixie Forest (Utah Mountains) and of *Pinus contorta* (lodgepole pine) in the boreal humid lodgepole pine forest at the northern end of Middle Rocky Mountains (Yellowstone). Black apothecia of an *Amandinea* grew in association in both collections; they much resemble those of the *Orbilia* but are generally larger, with more convex hymenia, and clearly connected to a thallus. The associated *O. atrolentiformis* differed macroscopically merely in larger apothecia.

Specimens included. **USA**: **Montana**, Middle Rocky Mountains, SE of West Yellowstone, 2035 m, branch (or root?) of *Pinus contorta*, on wood, 5.VI.1996, G. Marson (H.B. 5741b, anam. substr.). – **Utah**, Utah Mts., Bryce Canyon, 42 km SSE of Panguitch, Rainbow Point, 2775 m, branch of *Abies concolor*, on wood, 20.VI.2000, G. Marson (M-0276553, **holotype**; **isotype** in H.B. 6998c).

Species with reddish apothecia

Orbilia lentiformis Baral & G. Marson, **sp. nov.**, MB 814369 — Pls 158–162, Map 23

Etymology: named according to the lens-shaped spore bodies.

Typification: Australia, Northern Territories, Alice Springs, branches of *Atriplex nummularia*, 9.X.1998, G. Marson (ex H.B. 6569c, MEL 2389210, holotype; ex-type culture: CBS 140836; sq.: KT215225, MH878193).

Latin diagnosis: *Apothecia in statu rehydratata aurantiaca vel rosea, 0.1–0.7 mm diam. Asci 8-spori, apice in statu emortuo parum vel modice truncati, partim crassitunicati. Ascosporae *11–19 × 3–5.5 µm, clavatae, in statu vivo prope apicem corpusculum refringens lentiformem, perlate affixum continentes. Paraphyses ad apicem non vel modice inflatae, exsudato tenui hyalino tectae. Habitat ad lignum vel corticem putridum ramorum siccorum fruticum vel arborum angiospermarum, raro coniferarum, in locis borealis ad subtropicis, humidis ad aridis Europae, Asiae, Americae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.15–0.5(–0.7) mm diam., 0.12–0.23 mm high, pale to bright orange or rose, scarcely translucent, round, scattered to subgregarious; disc medium concave to slightly convex, margin indistinct to distinct, thin, 0–25 µm protruding, smooth; broadly sessile, superficial to deeply immersed, erumpent between fibres; dry bright to deep orange-red. **Asci** *((50–))61–90(–103)((–110)) {11} × (8–)8.5–9.7 {6} or 9–10.5(–11.5) µm {6}, †(50–)60–90(–105) × ((6–))(6.5–)7–10(–11)((–12)) µm {16}, 8-spored, spores *biseriate, (0–)1–6(–8) lower spores inverted {11} (not to strongly mixed), pars sporifera *32–52 µm long; **apex** (†) slightly to medium truncate, hemispherical in profile view, dome distinct, also nearly absent, †0.8–1.7(–2.7) → (0.3–)0.5–1(–1.5) µm thick {11}, some with distinct apical chamber; **base** with short to sometimes long, thick, flexuous stalk, unbranched or T-, L-, Y- to h-shaped. **Ascospores** *((8.3–))(10–)12–17(–19)((–21)) × (3–)3.3–4.5(–5.5) µm {22}, †((8–))(10–)11–15.5(–17) × (2.8–)3.2–4.2(–4.5) µm {11}, ellipsoid-clavate, often also cylindric-ellipsoid, apex rounded (to obtuse), base slightly to strongly attenuated, sometimes tail-like, straight to slightly, sometimes rather strongly curved; overmature up to 3-septate {1}; **SBs** *(0.3–)0.6–1.3(–1.6) × (1.5–)1.7–2.2(–2.5) µm {6}, lens- to sometimes plug-shaped, apically broadly attached; with some minute, scattered or grouped **LBs** in each half, 1–2 glycogen bodies 1–2 µm diam. per spore; very rarely a single spore 1-septate within the living ascus {1}, in dead asci 1-septate spores sometimes frequent {2}. **Paraphyses** apically uninflated to slightly or medium, sometimes strongly clavate-capitate, terminal cell *(3–)5–15(–20) × (2–)2.5–4.5(–5.5) µm {6}, †10–20 {1} × 2–4.5 µm {2}, lower cells *(3.5–)7–15(–23) × 1.4–2.5(–3.5) µm {4}, †1.3–1.7 µm wide {1}; rarely {2} or frequently {9} branched at upper septum, hymenium pale rose. **Medullary excipulum** pale rose, 30–60 µm thick, of dense textura intricata with some or many inflated cells, not sharply delimited. **Ectal excipulum** pale rose, of thin-walled to slightly gelatinized, irregularly or vertically oriented t. angularis from base to mid flanks or margin, 20–40 µm thick near base, cells *6–15 × 5–11 µm {4}, †4–8 × 4–6 µm {1}; 20–30(–40) µm thick near margin, of t. prismatica to t. porrecta oriented at a 0–30° angle to the surface, marginal cortical cells *6–13 × 3–5 µm {3}. **Anchoring hyphae** sparse to abundant, *2.5–3.5 µm wide, walls 0.2 µm {2} or 0.3–0.8 µm thick {1}, sometimes covering flanks and margin by an up to 25 µm thick layer. **SCBs** globose, in paraphyses (0.5–)1–2(–2.8) µm diam., in ectal excipulum (near margin) (1–)1.8–3.3 µm diam. **LBs** in basal ectal excipulum sometimes present, pale yellowish. **Exudate** over paraphyses 0.2–0.5(–1.5) µm thick, granular-cloddy or continuous, hyaline, loosely attached, rarely lacking; over margin and flanks ~0.2–0.5 µm thick, ± continuous. — **ANAMORPH**: vermispora-like {T/2} or trinacrium-like {1/4} (from ascospore isolate/natural substrate). **Conidiophores** not seen. Different strains produced different types of **conidia**: **(1)** phragmosporous, cylindric(-fusoid), mostly slightly curved at upper end, *18–25 × 5–6 µm {T}, †19–25 × 4–5 µm {2}, (1–)3(–4)-septate {3}; **(2)** Y-(or T-)shaped, total size *20–33 × (13–)18–21(–25) µm {3}, stipe *12–23 × 5.2–7.5 µm, 1–4-septate, arms *8–13 × 4–5.2 µm, 1–2-septate, straight or slightly curved downwards.

Habitat: collected 0.5–3 m above the ground, decorticated or corticated, 3.5–32 mm thick twigs and branches of *Abies lasiocarpa* {1}, *Amelanchier utahensis* {1}, *Artemisia tridentata* {1}, *A. filifolia* {1}, *Atriplex nummularia* {1}, *A.* cf. *polycarpa* {1}, ?*Chrysothamnus* sp. {1}, ?*C. viscidiflorus* {1}, *Ericameria nauseosa* {1}, *Fraxinus excelsior* {1}, ?*Glossopetalon spinescens* {1}, *Larrea tridentata* {2}, *Mahonia fremontii* {1}, *Picea abies* {1}, ?*Prunus* sp. {1}, *Pseudotsuga menziesii* {1}, *Purshia stansburyana* {1}, *Quercus robur* {1}, *Ribes cereum* {1}, *Salix* sp. {2}, *S. rhamnifolia* {1}, *Sarcobatus vermiculatus* {2}, *Thymelaea lythroides* {1}, indet. angiosperm {1}, on 0.3 mm deep strongly decayed wood {19} and bark {6} (bast, in clefts of periderm, bark partially detaching), strongly greyed, covered by green algae or not; inflorescence stems of *Yucca gloriosa* {1}, *Y. elata* {1}. **Associated**:

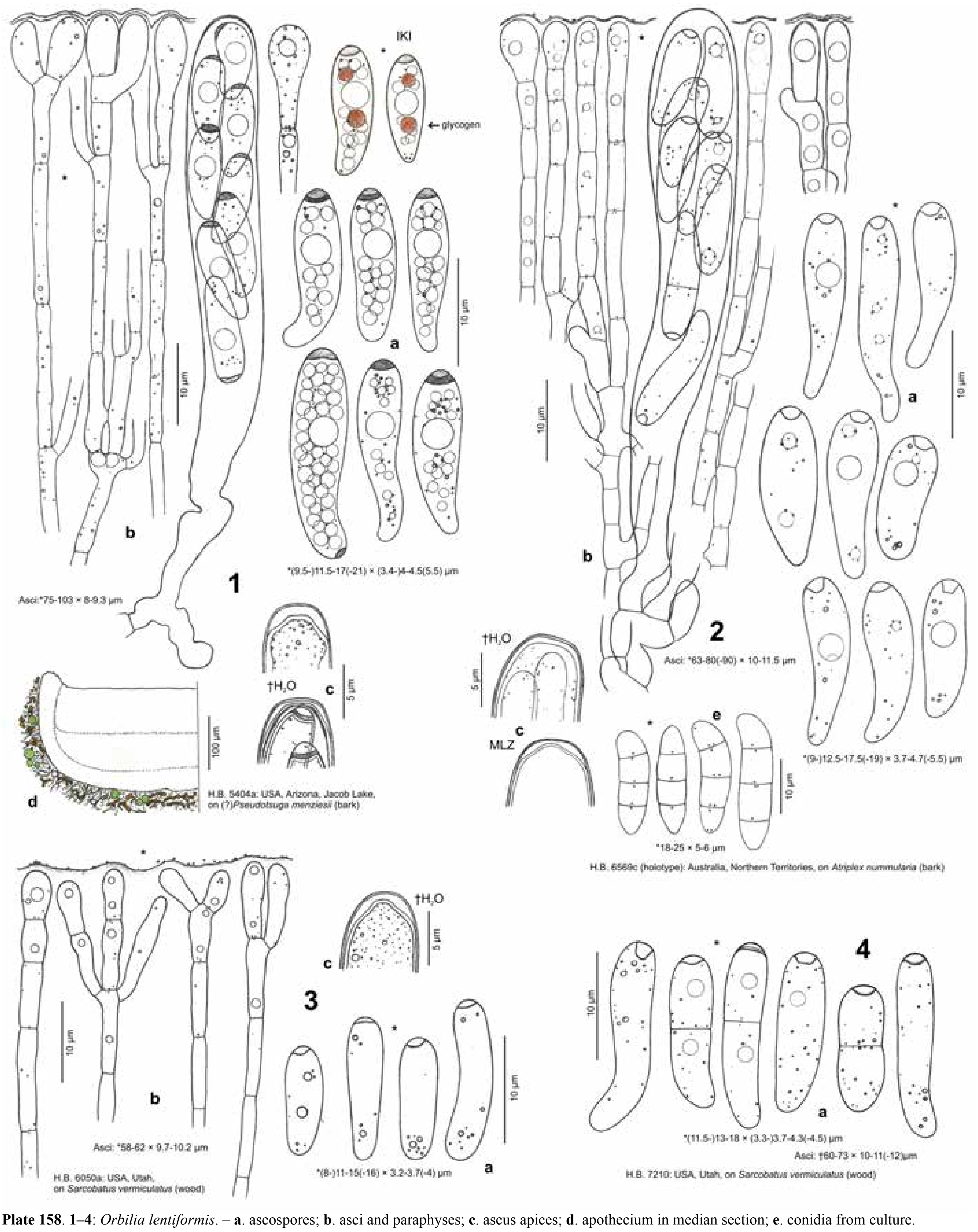
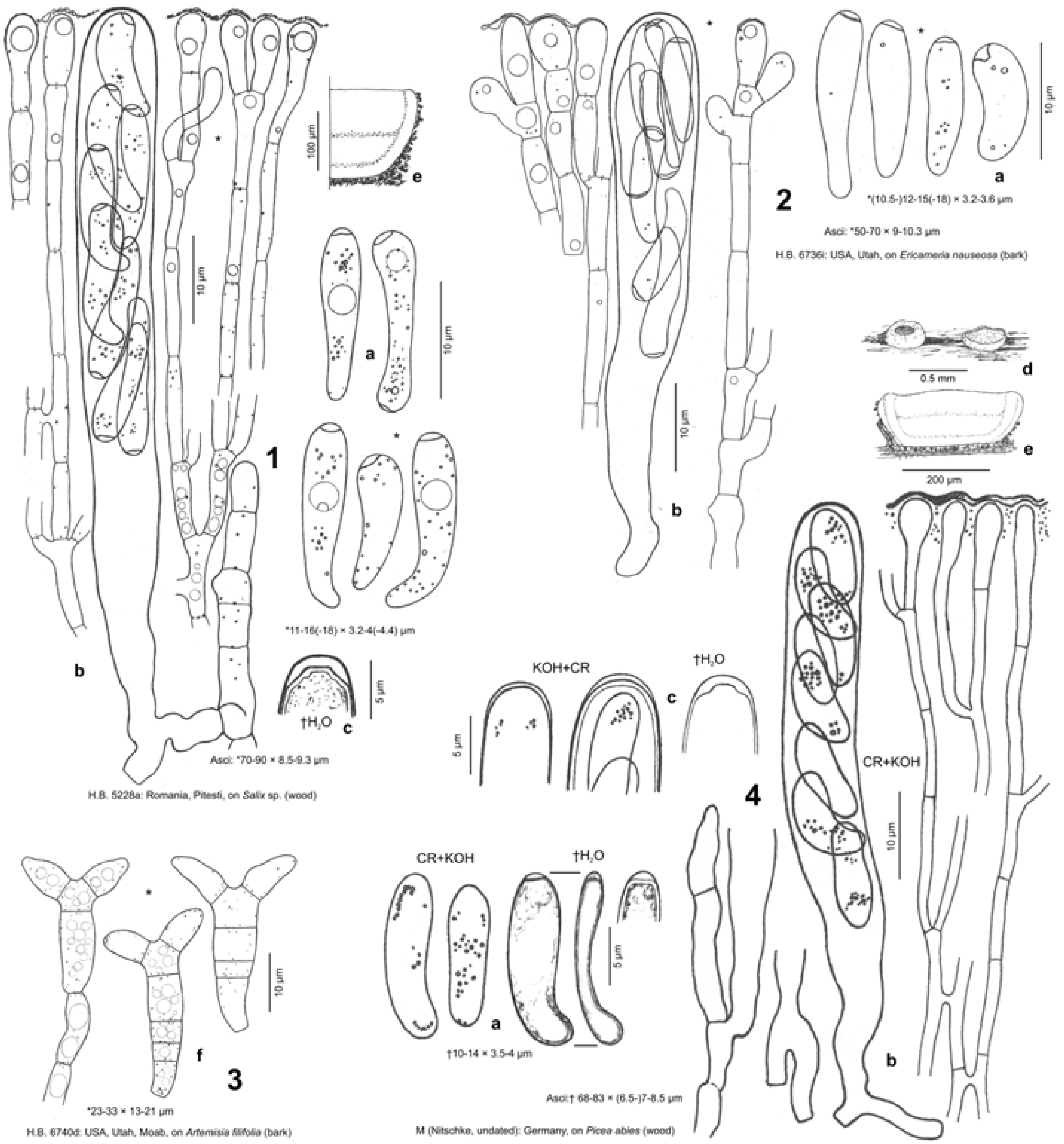


Plate 158. **1–4**: *Orbilia lentiformis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. conidia from culture.

Caloplaca sp. {2}, *Candelariella* sp. {1}, *Carestiella schizoxyloides* {1/2}, *Crumenulopsis* sp. {1}, ?*Durella* sp. {1}, *Gloniopsis* aff. *praelonga* {1}, *Hysteropatella* spp. {3}, *Lachnellula* sp. {1}, *Lecanora caesiorubella* {1}, *Melanohalea subolivacea* {2}, *Melaspilea emergens* {2}, *Mellitiosporiella pulchella* {1}, *Odontotrema* sp. {1/1}, *Odontura rhaphidospora* {1}, *Orbilia aristata* {1}, *O. atriplicis* {1}, *O. bicknellensis* {2}, *O. calyptrata* {2}, *O.* ?*carpoboloides* {1}, *O. delphinus* {3/1}, *O. denticulata* {1}, *O. dixiensis* {1}, *O. flavida* {1}, *O.* ?*flexisoma* {1}, *O. macroserpens* {1}, *O.* ?*macrotrapeziformis* {3}, *O. maeandrina* {2}, *O. magnifica* {2}, *O. mesaverdiana* {1}, *O.* ?*multidelphinus* {1}, *O. multigambelii* {1}, *O. multimaeandrina* {4}, *O. multiphanosoma* {2}, *O. multitrapezoidea* {2/1}, *O. myriophanosoma* {1}, *O. myriostomachia* {1}, *O. myriourosperma* {2}, *O.* ?*navajoana* {1}, *O. ocellata* {2}, *O. paradoxoides* {1}, *O. pleiocreosoteris* {1}, *O.*



H.B. 5228a: Romania, Pitesti, on *Salix* sp. (wood)

H.B. 6736i: USA, Utah, on *Ericameria nauseosa* (bark)

H.B. 6740d: USA, Utah, Moab, on *Artemisia filifolia* (bark)

M (Nitschke, undated): Germany, on *Picea abies* (wood)

Plate 159. **1–4**: *Orbilia lentiformis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. conidia from culture.

pleiolentiformis {2}, *O. pleiomesaverdiana* {1/2}, *O.* ?*pleionavajoana* {1}, *O. pleiourosperma* {1}, *O. plurilentiformis* {2}, *O. pluristomachia* {2}, *O. pubescens* {1}, *O. sonorensis* {2}, *O. vermiculati* {1}, *Ostropales* {1}, *Perrotia flammea* {1}, *Pragmopora* sp. {1}, *Psiloglonium lineare* {1}, *Stictis* sp. {1}, *Symbiotaphrina desertorum* {1}, *S. larreae* {2}, *Teichospora* sp. {1/2}, *Teichosporella dura* {2}, ?*Unguiculariopsis* sp. {1}. **Desiccation tolerance**: fully tolerant for at least 1.5 years, submature asci still viable after 27 months, paraphyses even after 39 months. **Altitude**: 600–2800 m a.s.l. (southwest of Northern America), 1–275 m (Europe and northern Africa), 1600–1772 m (Asia), 586 m (Australia). **Geology**: USA: Paleo- to Mesozoic lime- & sandstone; basaltic or felsic lava, gneiss; France: mica schist; Australia: Neoproterozoic sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia lentiformis* is characterized by 8-spored asci and comparatively large, cylindric-clavate ascospores with lens- to sometimes plug-shaped SBs. Among those 8-spored species of series *Lentiformes* with reddish apothecia, *O. lentiformis* forms together with *O. ocellata*, *O. subocellata*, and *O. foliicola* a difficult species complex. Our molecular analysis of the ITS rDNA show that the latter three species are rather similar and form a clade with high distance to *O. lentiformis*. Different conidial types (phragmo- vs. staurosporous) occur in both clades, however. This suggests that at least four species occur in this complex, while their recognition by features of asci and ascospores is hardly possible (see Tab. 63). Because sequence data were available only for a very small part of our collections, and anamorph data also only in about half of them, only premature taxonomic conclusions can be drawn at present. A number of collections are with hesitation referred to *O. lentiformis*. Specimens with both types of conidia are included in *O. lentiformis* here because of a low molecular distance between the North American strain with trinacrium-like conidia and the Australian type strain with vermispora-like conidia (Phyl. 8) and because characteristic morphological traits in the teleomorph could not be found.

Variation. A sharp delimitation between *O. lentiformis* and *O. ocellata* was impossible because of a rather high variation in both ascus and spore size as observed between or even within populations of both taxa. In three collections (Pls 158: 1; 159: 2 & 164: 2; 159: 3 & 164: 4) the two species grew in association apparently on the same branches, though in separate populations. In these cases, a differentiation was rather easily possible concerning every apothecium examined. The distinguishing features are mainly seen in the width of the living asci and the length of the living ascospores (see Tab. 63). Although in some of the collections the obtained values strongly overlap, many specimens could be assigned to one of the two taxa because usually either only ascus width or spore length overlapped, but not both. Extraordinarily long asci were observed in a collection from Morocco (Pl. 160) with consistently thin-walled ascus apices; also here spore size is intermediate to *O. ocellata*, despite the long asci.

Further variation within *O. lentiformis* concerns, e. g., the shape of SBs which are ± plug-shaped in some spores of some collections (Pls 158: 2, 4; 159: 2), and the thickness of the apical dome, being exceptionally thick in a collection on *Larrea* (Pl. 161: 5, KOH 2–2.7 → 1–1.5 µm). Those North American collections of *O. lentiformis* which tend to plug-shaped SBs may be confused with the reddish variant of the North American *O. purshiae*, which appears to be separable by strongly tapered and curved spore bases.

Not included collections. Three samples from western North America on *Purshia* (Pl. 162: 1–2, IVV: H.B. 8059b) are intermediate between *O. lentiformis* and *O. ocellata* because of their rather short spores (Tab. 63). Therefore, and because of deviating molecular data (see below), they are not included in either description. Their long asci appear to exclude *O. ocellata*, while spores and asci would fit *O. subocellata* rather well. The latter species is characterized by a vermispora-like anamorph (Pl. 166) and is likewise intermediate in spore length between *O. lentiformis* and *O. ocellata*.

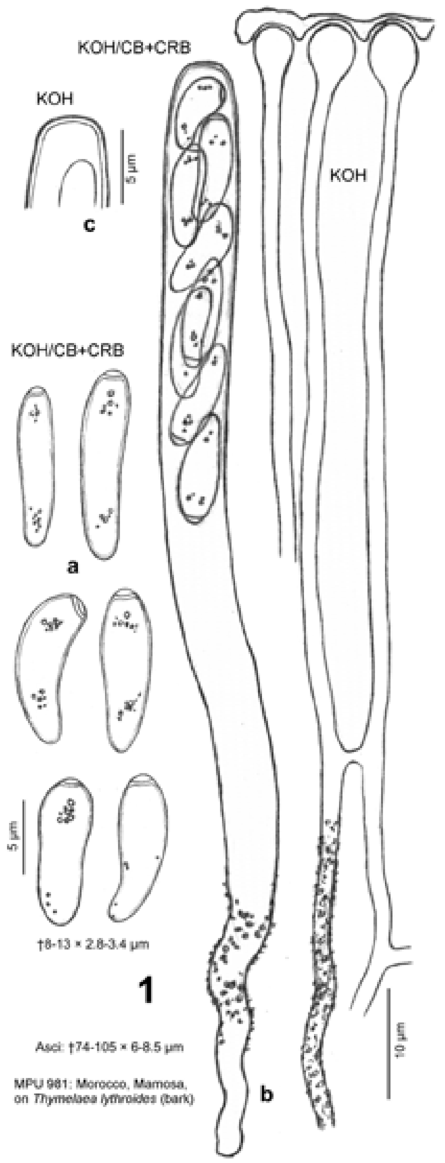


Plate 160. **1**: *Orbilia lentiformis*. – **a**. ascospores; **b**. ascus and paraphyses (septa invisible in KOH); **c**. ascus apex.

Anamorph. Striking differences in conidial morphology were noted among the collections tentatively referred here to *O. lentiformis*. In five collections we have observed conidia on the natural substrate, and in two further ones we obtained them in pure culture. In three of these seven samples the conidia were Y-shaped (staurosporous), with the two arms sometimes slightly bent downwards, resembling *Trinacrium incurvum*, Pls

Table 63. Tentative differences in ascus and ascospore size (in µm) within the *O. lentiformis* complex (taxa with 8-spored asci). The observed conidial types appear to be characteristic at the species level but differed between populations of *O. lentiformis* as circumscribed at present.

	O. lentiformis	*O.* **aff.** *lentiformis*	*O. subocellata*	*O. foliicola*	*O. ocellata*
Asci	*61–90(–103) × (8–)8.5–10.5(–11.5) †(50–)60–90(–105) × (6.5–)7–10(–11)	*68–95 × (7.5–)8.2–9(–9.3) †70–90(–105) × 7.2–8.5 µm	*57–85(–91) × (8.2–)8.5–9(–9.7) †(55–)62–82(–94) × 7–8.5	*(41–)46–70(–77) × (8.2–)8.5–9.5(–10.5) †48–65 × 7–8.5(–9.7)	*(47–)54–68(–76) × (6.5–)7–8.5(–9.2) †(37–)45–63(–68) × (5.2–)6–7(–7.5)
Spores	*(10–)12–17(–19) × (3–)3.3–4.5(–5.5)	*(8–)9–12(–13) × 3.8–4.5(–5)	*(9–)10–13(–14) × (3.3–)3.5–4.3(–5)	*(7–)8–12.5(–15.5) × 3.3–4.2	*(7–)8–12(–13) × (2.8–)3.2–4(–4.5)
Anamorph	vermispora-like, trinacrium-like	trinacrium-like	vermispora-like	trinacrium-like	trinacrium-like
Host	gymno- & angiosperms	*Purshia*	gymno- & angiosperms	*Quercus ilex* agg. (leaves)	angiosperms
Distribution	Europe, Africa, Asia, Australia, America	America	Europe	Europe	Europe, Africa, Asia, America

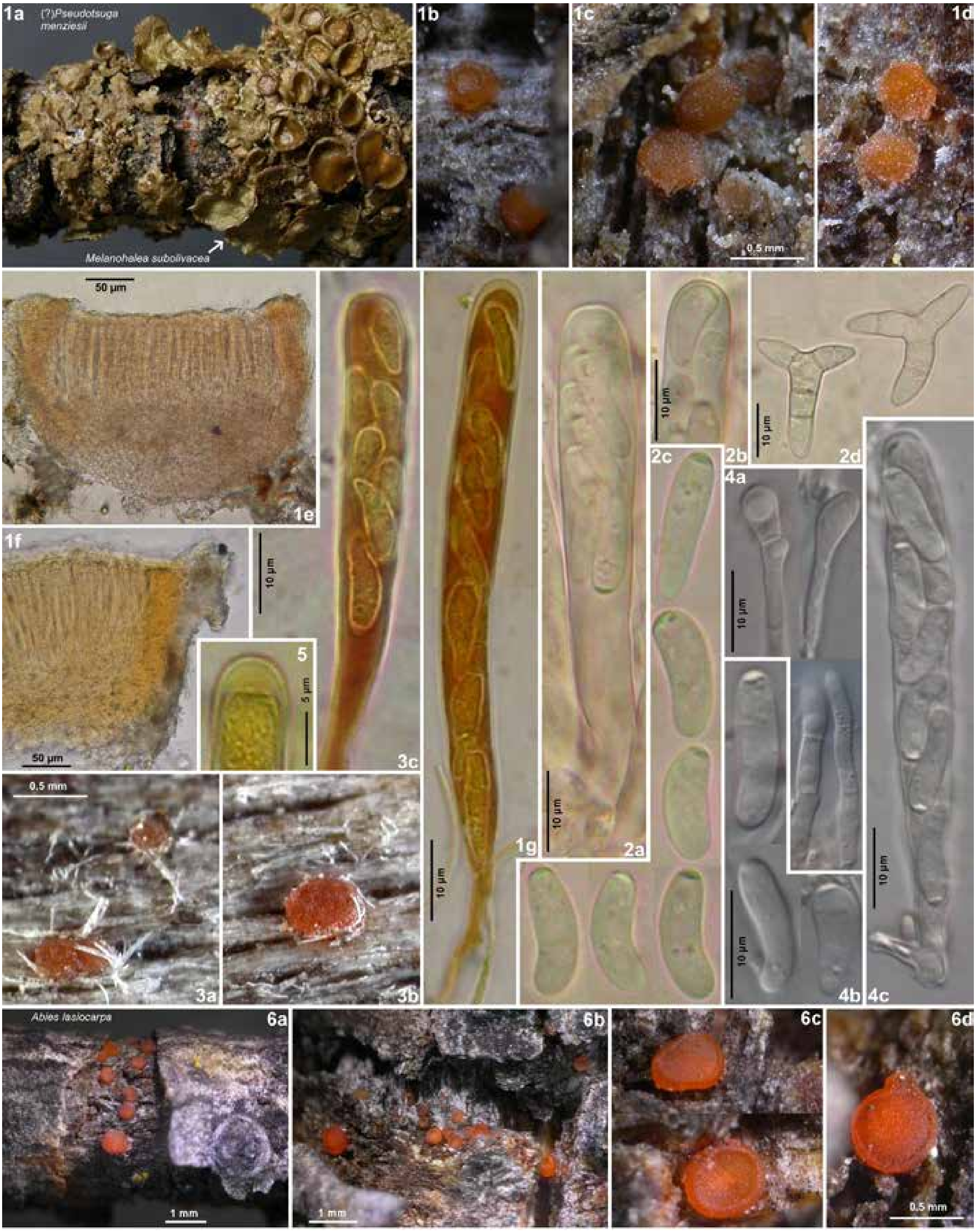


Plate 161. **1–6**: *Orbilia lentiformis*. – **1a**, **6a**. dead xeric corticated conifer branches; **1a–d**, **3a–b**, **6a–d**. rehydrated apothecia; **4e–f**. apothecia in median section; **4a**. paraphyses; **1g**, **2a–b**, **3c**, **4c**. asci (**1g**, **3c** in IKI); **2c**, **4b**. ascospores; **2d**. conidia from substrate. – Living state, except for **1g**, **3c** (in IKI), ascus in **4c**. – **4a–c**: phot. E.S. Popov. — **1a–g**. H.B. 5404a: USA, Arizona, on (?)*Pseudotsuga*; **2a–d**. H.B. 7891b: Mongolia, Ulaanbaatar, on *Salix*; **3a–c**. H.B. 5705c: USA, Colorado, on *Ribes*; **4a–c**. LE 247245: Russia, Altay, on *Salix*; **5**. H.B. 8477a: USA, Nevada, on *Larrea*; **6a–d**. H.B. 9578a: USA, Arizona, on *Abies*.

159: 3; 161: 2d, H.B. 7210), whereas in the other four they were unbranched (phragmosporous) and slightly curved (vermispora-like, Pl. 158: 2e, H.B. 5228a, 5705c, 8059b). These two types of conidia were also obtained in the two ascospore isolates: in one isolate (H.B. 6740d) stauro- and phragmoconidia were formed, while the other (H.B. 6569c) produced merely phragmoconidia.

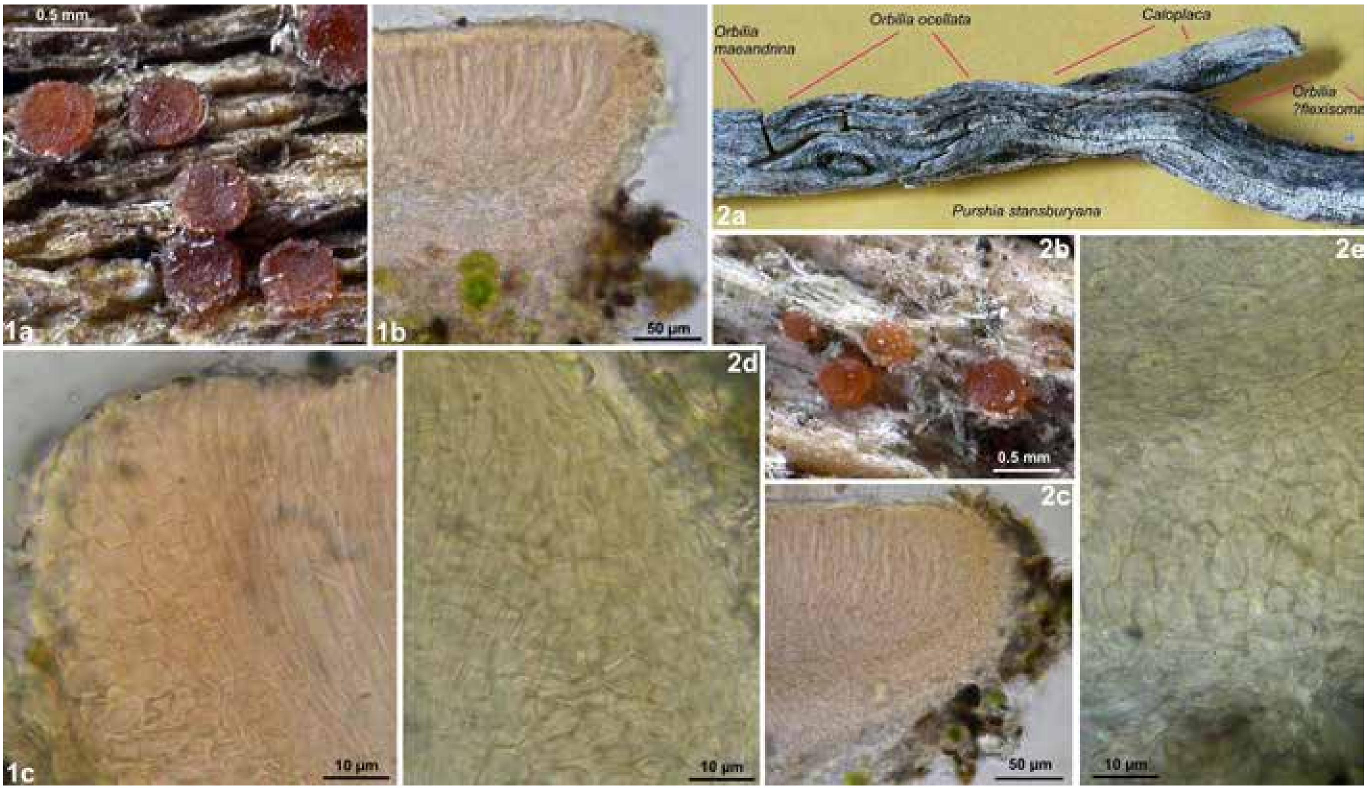


Plate 162. **1–2**: *Orbilia* aff. *lentiformis*. – **1a**, **2b**. rehydrated apothecia; **1b**, **2c**. apothecia in median section; **1c**, **2d**. id., ectal excipulum at margin; **2e**. id., at base. – Living state. — **1a–c**. H.B. 8002c: USA, Arizona, Fredonia, on *Purshia*; **2a–e**. H.B. 8061b: USA, Utah, Mt. Carmel, on *Purshia*.

In a not included collection (IVV: H.B. 8059b) the curved vermispora-like conidia were formed in abundance in the hymenium of a single apothecium which contained only empty asci. The associated mature apothecia are intermediate to *O. ocellata* in spore size (see above), suggesting a relation to the European *O. subocellata*, while the conidia were distinctly smaller (†14–17 × 4–4.3 µm).

Because anamorph data were not available in a majority of collections, and trinacrium-like anamorphs are generally known to produce also some unbranched conidia, these observations need further investigation. As the type of *O. lentiformis* we have selected an Australian collection which solely formed a vermispora-like anamorph in culture (Pl. 158: 2). A similar diversity in conidial morphology was observed between *O. ocellata*/*O. foliicola* and *O. subocellata* (Tab. 63).

Phylogeny. From two strains of *O. lentiformis* with different anamorphs, SSU+ITS+LSU sequences were taken from pure culture: holotype from Australia on *Atriplex*, vermispora-like (Pl. 158: 2); paratype from USA on *Artemisia*, trinacrium-like (Pl. 159: 3). From a further sample (*O.* aff. *lentiformis*), being intermediate to *O. ocellata*, an ITS sequence was taken from apothecia: from USA on *Purshia*, anamorph unknown (Pl. 162: 1). Our molecular analyses showed that the two typical strains always clustered in a strongly supported clade but with a 5 % distance in the ITS region (0.5 % in the LSU). This clade did not fall near *O. ocellata* as expected, but showed a high distance to any species of series *Lentiformes* and *Phanosomates* (10.5–15 % in the ITS and 3.5–5 % in the LSU). The lowest distance of 10.5–11 % was to *O. pluristomachia* (series *Phanosomates*), with which *O. lentiformis* formed a medium supported clade (Phyl. S9). The distance to *O.* aff. *lentiformis* ranged at 12–12.5 %, although the ascus size of that sample matched that of *O. lentiformis* (see Tab. 63). Only the intermediate collection nested in the *flavida-cucumispora* clade by showing a 6 % ITS distance to *O. ocellata*.

The above result indicates that pronounced molecular differences correlate with differently sized asci and ascospores, but less so with differently shaped conidia. The conidial types did not correlate with the observed clades (see also under *O. ocellata*/*O. subocellata*). We here distinguish *O. lentiformis* from *O. ocellata* based on ascus and spore size, supported by molecular data. Whether the observed 5 % distance between the trinacrium- and the vermispora-forming strain of *O. lentiformis* merits recognition at some taxonomic level should be investigated from sequences of further collections. Molecular data from one of the intermediate samples on *Purshia* (*O.* aff. *lentiformis*) points to a species of its own, although these samples did not markedly differ from *O. lentiformis* or *O. ocellata* in their hymenial features (see Tab. 63).

Ecology. *O. lentiformis* occurs on rotten wood and bark of dead xeric branches of various trees and shrubs of angiosperms (rarely gymnosperms). It was found to occur widespread in the southwest of Northern America in the subtropical to cold-temperate, arid to semiarid (to subhumid) creosotebush, sagebrush, salt bush, paloverde mixed cacti desert scrub, and mixed grass-scrubland in the Chihuahuan, Sonoran, and Mojave Desert, and in warm-continental semiarid pinyon-juniper woodlands of the Canyonlands section and boreal humid Engelmann spruce forests of the Mogollon Rim and Southern Rocky Mountains. Single collections are from subtropical semihumid (thermomediterranean) northwestern Africa (Morocco), mesosubmediterranean atlantic western Europe, supratemperate (almost suprasubmediterranean) Romania, hemiboreal to warm-continental (sub)humid eastern Europe (Russia), orotemperate (sub)humid (winter-dry), orotemperate (altimontane to subalpine) continental central Asia (Altay, western Mongolia), and subtropical arid central Australia (acacia open shrubland northeast of MacDonnell Ranges). The three not included North-American samples are from cold-temperate subhumid to warm-continental semiarid pinyon-juniper woodlands of the Colorado Plateau (Utah Mountains and Grand Canyon).

Specimens included (conidia: C = vermispora-like, Y = trinacrium-like): **FRANCE**: **Pays-de-la-Loire**, **Loire-Atlantique**, 2 km NE of Piriac-sur-Mer, NNE of Port au Loup, Plage Pors Er Ster, 9 m, inflorescence stem of *Yucca gloriosa*, 13.XI.2016, J.P. Priou (J.P.P. 16314a, doc. vid.). — **MOROCCO**: **Gharb-Chrarda-Béni Hsen**, ~23 km NE of Rabat, ~13 km SW of Kénitra, Sidi Taibi, 'Mamosa', ~20 m, twig of *Thymelaea lythroides*, on bark, XII.1934, G. Malençon (MPA 981, Malençon Champ. Maroc 185, H.B. 5459 ø). — **ROMANIA**: **Argeş**, 100 km WNW of Bucureşti, ~8 km SE of Piteşti, A1 motorway, ~275 m, branch of *Salix*, on wood, 12.XII.1994, R. Reuter (H.B. 5228a, anam. substr. C). — **RUSSIA (West)**, **Pskov**, **Loknya**, 41 km NW of Velikiye Luki, 8 km N of Nasva, SW of Bashovo, 130 m, branch of *Fraxinus excelsior*, on wood, 27.IV.2011, E.S. Popov (LE 247564, ESP-11-0049, unpres., doc. vid.). – **Astrakhan**, **Akhtubinsk**, 189 km ESE of Volgograd, 35 km ENE of Bolkhuny, WNW of Zeleny Sad, S of Baskunchak salt lake, 1 m, branch of *Quercus robur*, on wood, 27.IV.2009, E.S. Popov (LE 294874, anam. substr. Y, doc. vid.). – **Rostov**, **Sholokhovsky**, 230 km WNW of Volgograd, SW of Veshenskaya, 57 m, branch of (?)*Prunus*, on wood, 9.VI.2002, Y.A. Rebriev, vid. E.S. Popov (LE 294858, anam. substr. Y, doc. vid.). — **Russia (East)**: **Altay**, **Kosh-Agachskiy**, 240 km SE of Gorno-Altaysk, 64 km WNW of Kosh-Agach, SW of Kuray, valley of Tyute river, 1772 m, branch of *Salix*, on wood, 7.VIII.2008, E.S. Popov (LE 247245, doc. vid.). — **MONGOLIA**: **Ulaanbaatar**, Khenti Mts., 25 km SE of Ulaanbaatar, 8 km W of Nalayh, Bogd Khan Uul Mt., ~1600 m, branch of *Salix rhamnifolia*, on wood, 1.VIII.2005, P. Karasch (P.K. 01082005-1, H.B. 7891b, anam. substr. Y). — **AUSTRALIA**: **Northern Territories**, MacDonnell Ranges, 15 km WNW of Alice Springs, N of Honey Moon Gap, 586 m, branches of *Atriplex nummularia*, on wood, 9.X.1998, G. Marson (ex H.B. 6569c, MEL 2389210, **holotype**, anam. cult. C, CBS 140836; sq.: KT215225, MH878193). — **USA**: **California** (border to Nevada), Mojave Desert, 20 km SW of Beatty, 16 km SW of Rhyolite, Daylight Pass E of Death Valley, 1315 m, branch of indet. angiosperm, on wood, 2.V.1995, G. Marson (H.B. 8528d ø). – **Nevada**, Mojave Desert, 6 km SW of Beatty, 2.6 km SSE of Rhyolite, 1030 m, branch of *Atriplex*, on wood, 2.V.1995, G. Marson (H.B. 8676b). – 18.5 km WSW of Las Vegas, 4.5 km ESE of Blue Diamond, 960 m, branch of *Larrea tridentata*, on wood, 1.V.1995, G. Marson (H.B. 8477a). – **Utah**, Utah Mts., ~1.5 km ESE of Torrey, ~2075 m, branch of *Artemisia tridentata*, 15.V.1995, G. Marson (ø). – Bryce Canyon, 30 km SE of Panguitch, 7.5 km WNW of Tropic, near Visitor Center, 2410 m, branches of (?)*Chrysothamnus viscidiflorus*, on bark, 24.VIII.1994, G. Marson (H.B. 5243c ø). – **Canyonlands**, Arches, 20 km NNW of Moab, Salt Valley Wash, 1427 m, branch of *Artemisia filifolia*, on bark, 18.VI.2000, G. Marson (H.B. 6740d, CBS 117021, anam. cult. Y; sq.: KT215226). – 7 km NW of Moab, 1390 m, branch of *Sarcobatus vermiculatus*, on wood, 1.VI.1996, G. Marson (H.B. 6050a). – Canyonlands, 35 km WSW of Moab, Upheaval Dome, Whale Rock, 1745 m, branch of *Mahonia fremontii*, on wood, 17.VI.2000, G. Marson (H.B. 6735b). – 20 km SW of Moab, Dead Horse Point, 1810 m, branch of *Purshia stansburyana*, on wood, 10.VI.2003, G. Marson (H.B. 8079a). – 36 km S of Moab, 5 km WNW of Hatch Rock, 1813 m, branch of *Ericameria nauseosa*, on bark, 16.VI.2000, G. Marson (ex H.B. 6736i, in M-0276532 [H.B. 6736f, type of *O. myriophanosoma*]). – 50 km SSW of Moab, Needles Visitor Center, Salt Creek, near Cave Spring Trail, 1475 m, branch of *Sarcobatus vermiculatus*, on wood, 15.VI.2000, G. Marson (H.B. 7210, anam. substr. Y). – **Arizona**, Grand Canyon, Kaibab Plateau, 37 km SE of Fredonia, S of Jacob Lake, 2415 m, branches of (?)*Pseudotsuga menziesii*, on bark, 17.V.1995, G. Marson (H.B. 5404a). – Mogollon Rim, 83 km SSE of Vernon, 9.5 km SSW of Hannagan Meadow, Rte. 191 (Coronado Trail), 2800 m, branches of *A. lasiocarpa*, on bark & wood, 2.VI.2003, G. Marson (H.B. 9578a). – 31 km ENE of Safford, 20 km SSE of Clifton, Rte. 191, 1510 m, stem of *Yucca elata*, 1.VI.2003, G. Marson (ex H.B. 7880f, in M-0276551 [H.B. 7880a, holotype of *O. paradoxoides*]). – Sonoran Desert, 200 km NW of Phoenix, Wikieup, ~600 m, branch of ?*Chrysothamnus*, on wood, 3.V.1995, G. Marson (H.B. 5716c ø). – 17.5 km NNE of Lukeville, Organ Pipe National Monument, Ajo Mountain Trail, ~700 m, branch of ?*Glossopetalon spinescens*, 5.V.1995, G. Marson (H.B. 5809f ø). – ibid., branch of *Larrea tridentata*, 5.V.1995, G. Marson (H.B. 5687i ø). – **Colorado**, Southern Rocky Mountains, 64 km SW of Denver, Hwy 285, Santa Maria, ~2600 m, branch of *Ribes cereum*, on wood, 14.VI.1996, G. Marson (H.B. 5705c, anam. substr. C). – Canyonlands, 15.5 km SSE of Cortez, Mesa Verde, 5 km NNW of Spruce Tree House, 2290 m, branch of *Amelanchier utahensis*, on wood, 31.V.1996, G. Marson (ø). – **Unlocalized**: [?Germany, ?log of] *Picea abies*, on wood, XII.1865, [T.R.J. Nitschke] (M, H.B. 5073 ø).

Not included. **USA**: **Utah**, Utah Mts., 16 km SSW of Boulder, 1920 m, branch of *P. stansburyana*, on wood, 11.VI.2003, G. Marson (H.B. 8059b ø, anam. substr. C). – 19 km ENE of Springdale, 11 km WNW of Mt. Carmel Junction, 1880 m, branch of *Purshia stansburyana*, on wood, 14.VI.2003, G. Marson (H.B. 8061b). – **Arizona**, Grand Canyon, Kaibab Plateau, 28 km ESE of Fredonia, 13 km NNW of Jacob Lake, Rte. 89, 2115 m, branch of *P. stansburyana*, on wood, 15.VI.2003, G. Marson (H.B. 8002c; sq.: KT222348).

Orbilia ocellata Baral, G. Marson & E. Weber, **sp. nov.**, MB 813485 — Pls 163–165, Map 24

Etymology: referring to the lens-shaped spore body resembling a transect of an ocular lens.

Typification: Luxembourg, Esch-sur-Alzette, branch of *Quercus*, 12.VI.1994, G. Marson (ex H.B. 5104, M-0276540, holotype).

Latin diagnosis: Orbiliae lentiformi *persimilis sed asci leniter angustiores et ascosporae breviores.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.13–0.4(–0.5) mm diam., 0.11–0.13 mm high, pale to light (to bright) orange(-rose), slightly translucent, round, scattered to (sub)gregarious in small groups; disc slightly concave to flat, margin thin, 0–20 µm protruding, smooth or very finely crenulate; broadly sessile, slightly erumpent between fibres, immersed in detritus; dry bright orange-red(-apricot). **Asci** *(47–)54–68(–76)((–87)) × (6.5–)7–8.5(–9.2) µm {10}, †(37–)45–63(–68) × (5.2–)6–7(–7.5) µm {8}, 8-spored, spores *biseriate, (0–)1–4(–5) lower spores inverted {13} (± mixed or not), pars sporifera *(25–)28–40 µm long; **apex** (†) slightly to ± strongly (conico-)truncate, hemispherical in profile view, thin-walled {4} or with dome †0.3–1.4 → 0.3–0.6 µm thick {5}, sometimes variable

Map 23. Known distribution of *O. lentiformis* in North America and Eurasia (yellow = not included collections on *Purshia*).

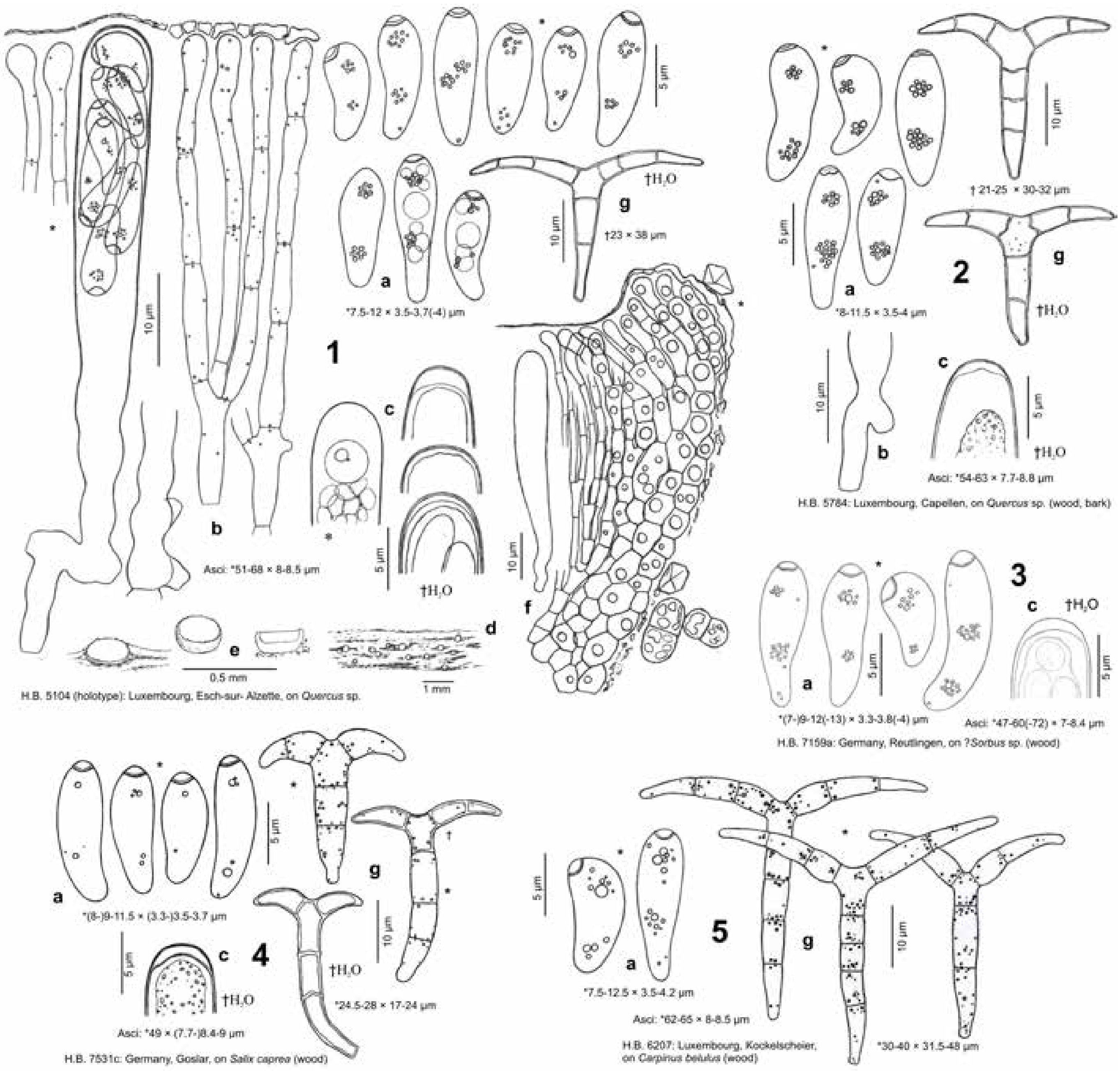


Plate 163. **1–5**: *Orbilia ocellata*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices (**1c** left: young ascus with large fusion nucleus); **d**. apothecia on substrate; **e**. apothecia (rehydrated, one in median section); **f**. ectal excipulum (margin and mid flanks, median section); **g**. conidia from substrate.

within a population, rarely with very slight apical chamber; **base** with very short to medium long, thick, ± flexuous stalk, unbranched or L-, H- or Y-shaped. **Ascospores** *(7–)8–12(–13)((–14)) × (2.8–)3.2–4(–4.5)((–5)) µm {15}, †(6–)7–11(–12.6) × 2.8–3.5 µm {4}, ellipsoid-clavate, sometimes subcylindrical or ellipsoid-fusoid, apex rounded to obtuse, slightly to strongly attenuated near base, straight to slightly curved (upper spores often strongly curved); **SBs** *0.4–1(–1.3) × 1.4–2 µm {6}, lens-shaped, apically broadly attached; often with some small **LBs** grouped in each half; overmature spores non-septate. **Paraphyses** apically uninflated or slightly (to medium) clavate-capitate, terminal cell *(4–)6–18(–23) × 1.8–3.5(–4.5) µm {2}, †1.5–3.8 µm wide {2}, lower cells *7–15.5 × 1.5–2.5(–3) µm {5}, †1–2 µm wide {1}; sometimes branched near apex. **Medullary excipulum** 30–40 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** pale to light rose, of thin-walled, vertically or indistinctly oriented t. angularis(-prismatica) from base to mid flanks, sometimes with pale yellowish LBs, 30–35 µm thick near base, cells *7–15 × 5–6 or 8–11 µm {2}; 20–30 µm thick near margin, of t. prismatica-angularis to prismatica-porrecta oriented at a 0–20(–80)° angle to the surface, marginal cortical cells *6.5–13 × (3–)4–5(–7) µm {2}, †10–14 × 2–3 µm {1}. **Anchoring hyphae** rather abundant, *1.8–2.7 or 2.5–4 µm wide, walls 0.2–0.6(–1) µm thick {2}, forming a rather dense hyaline t. intricata up to 40 µm thick, sometimes forming a thin layer up to the margin. **SCBs** globose, in paraphyses 1–2(–2.5) µm diam., sometimes absent, in ectal excipulum (1.5–)2–3(–4) µm diam. **Exudate** over paraphyses 0.4–1.5 µm thick, cloddy, hyaline, loosely attached; over margin and flanks 0.5–3 µm thick. **— ANAMORPH**: trinacrium-like (from ascospore isolate {1}, ascocarp on agar {1}, and natural substrate {7}). **Conidiophores** short. **Conidia** Y/T-shaped, the two arms often bent somewhat downwards, conidia from central Europe somewhat larger, total size */†21–30(–40) × (17–)25–52 µm, arms tapering */†(8–)15–25 × 3–4.5 µm, (1–)2–3-septate, stipe */†16–32 × 3.2–4.5(–5.5) µm, 2–4-septate; from southern Europe and USA: total size *22.5–32 × (10–)12–22.5 µm, arms *5–13 × 4.5–6.5 µm, 0–2(–3)-septate, stipe *15–2 4 × 5–7 µm, 2–4(–5)-septate, in pure culture (H.B. 6475b, 25.VIII.94) also unbranched, more or less straight phragmoconidia seen: *24–30 × 5.5–6.5 µm, 3–7-septate.

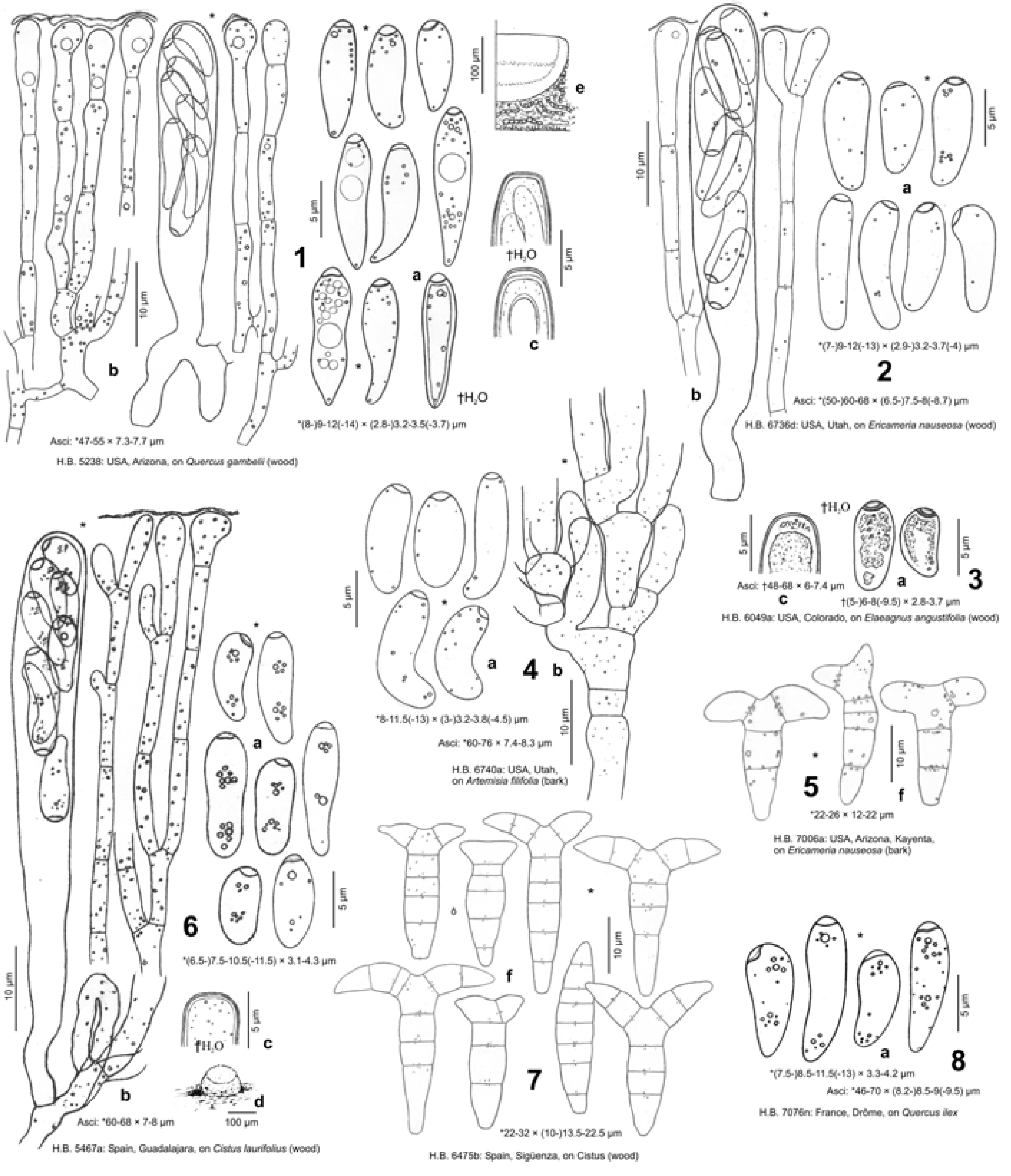


Plate 164. **1–8**: *Orbilia ocellata.* – **a**. ascospores (**3a**. refractive SBs in dead spores); **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium (rehydrated); **e**. apothecium in median section; **f**. conidia (**7f**. from culture, **5f**. from substrate).

Habitat: collected 0.1–3.5 m above the ground, ± corticated to decorticated, (2–)4–35(–60) mm thick twigs and branches (rarely ~15–20 cm thick trunk) of *Amelanchier utahensis* {1}, *Artemisia filifolia* {2}, *Baccharis salicifolia* {1}, *Carlina xeranthemoides* {1}, *Carpinus betulus* {1}, *Cercocarpus betuloides* {1}, *Chrysothamnus viscidiflorus* {1}, *Cistus* sp. {1}, *C. laurifolius* {1}, *Coleogyne ramosissima* {1}, *Elaeagnus angustifolia* {1}, *Ericameria nauseosa* {3}, *Fagus sylvatica* {1}, *Juglans major* {1}, *Lonicera altaica* {1}, *Malus domestica* {1}, *Pyrus communis* {1}, *Quercus* sp. {2}, *Q. gambelii* {1}, *Q. rotundifolia* {1}, *Rosa* sp. {3}, *Rhamnus myrtifolia* {1}, *Salix* sp. {2}, *S. caprea* {1}, *Sorbus* sp. {1}, on 0.1–0.5 mm deep medium to strongly decayed wood {22} and bark {12} (bast {6} or periderm {3}), rarely on leaves of *Yucca* sp. {2}, petioles of *Carlina xeranthemoides* {1}, often strongly greyed, with many green algae or not. **Associated**: ?*Calloria* spp. {2}, ?*Chaetoplea umbilicata* {1}, *Claussenomyces* sp. {1}, *Coniochaeta subcorticalis* {1}, *Durella* ?*atrocyanea* {1}, ?*Exarmidium* sp. (apothecioid) {1}, ?*Hypoxylon* sp. {1}, *Hysterium* ?*angustatum* {1}, ?*Laetinaevia* sp. {1}, *Melanelia glabratula* {1}, *Melanohalea*

Plate 165. **1–10**: *Orbilia ocellata*. – **1a**. clearing in beech forest with fallen trunk; **6a**. xeric branch of *Malus*; **2a–d**, **3**, **4a**, **5a**, **c**, **6b–e**, **7b–e**, **8a**. rehydrated apothecia; **5b**, **7a**, **f**, **8b**. dry apothecia; **2e**. apothecium in median section; **2f**. ectal excipulum in median section (flanks and margin); **4b**. globose SCBs in excipular cells; **1b**, **4e**. asci; **1c**, **4c–d**, **5d**. ascospores (inversely oriented spores with detached cytoplasm and SBs that remained refractive); **9**, **10**. conidia from substrate. – Living state, except for asci in **4d–e**, ascus and spores in **5d** (in IKI). – **1a–c**, **2c**, **6a–e**, **7a–f**, **8a–b**: phot. P. Perz; **4a–e**: R. Tena; **5b**: L. Quijada. — **1a–c**. P.P. 20080803: Poland, Szczecin, Osetno, on *Fagus*; **2a–f**. H.B. 8309a: Poland, Kłodzko, Szczytna, on *Salix*; **3**. H.B. 6049a: USA, Colorado, on *Elaeagnus*; **4a–e**. 27.VIII.2011: Spain, Teruel, on *Rhamnus*; **5a–c**. H.B. 9224: Tenerife, on *Carlina*; **6a–e**. P.P. 20060808: Poland, Kłodzko, Szczytna, on *Malus*; **7a–f**. P.P. 20060811: Poland, Kłodzko, on Pyrus; **8a–b**. P.P. 20060621: Poland, Kłodzko, Wolany, on *Rosa*; **9**. H.B. 7531c: Germany, Goslar, on *Salix*; **10**. H.B. 7159a: Germany, Reutlingen, on *Sorbus*.

subolivacea {1}, *Mellitiosporiella* sp. {1}, *M. pulchella* {1}, *Orbilia aristata* {2/1}, *O.* ?*barrowensis* {1}, *O. bicknellensis* {2/1}, *O. caulicola* {1}, *O.* ?*commarosa* {1}, *O. delphinus* {4}, *O. dixiensis* {1}, *O. filiformis* {1}, *O. flavida* {2}, *O. flexisoma* {1}, *O. gambelii* {1}, *O. lentiformis* {2}, *O. macrodelphinus* {1}, *O. maeandrina* {1}, *O. mesaverdiana* {2}, *O. microserpens* {1}, *O. mongolica* {1}, *O. multimaeandrina* {5}, *O. multiphanosoma* {4}, *O. multitrapezoidea* {2}, *O. myriophanosoma* {1}, *O. pleiolentiformis* {1}, *O. plurilentiformis* {4}, *O. serpentina* {3}, *O.* ?*sonorensis* {1}, *O. subsiculispora* {1}, *O. subaristata* {1}, *O. subovoidea* {1}, *Patellaria* ?*atrata* {2}, *Perrotia flammea* {1}, *Physcia* sp. {1}, *Pragmopora* sp. {1}, *Schizoxylon* sp. {1}, ?*Stictis* sp. {1}, ?*Teichospora* sp. {1}, *Teichosporella dura* {1}, *Tryblidaria* sp. {1}, *T. fenestrata* {1}, *Xanthoria* sp. {1}. **Desiccation tolerance**: fully tolerant for at least 6 months, conidia partially viable after 3 months. **Altitude**: 1200–2410 m a.s.l. (western North America), 150 m a.s.l. (Alaska), 8–1250 m (Europe), 2161 m (Macaronesia), 2200 m (Mongolia). **Geology**: Lower Carboniferous sediment, Pennsylvanian-Permian sandstone, Triassic, Jurassic & Cretaceous sand-, marl-, mud- & limestone, Quaternary marine sand; rhyolite, dacite, trachytic basalt. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia ocellata* is characterized by 8-spored asci and medium-sized, cylindric-clavate ascospores with striking lens-shaped SBs. For the delimitation from *O. lentiformis* see p. 473. Without the anamorph, delimitation from *O. subocellata* is quite difficult (see p. 482), due to only gradual differences and rather high variation among the collections (Tab. 63). *O. ocellata* may also be confused with a rare reddish colour variant of the typically black-olivaceous conifer-inhabiting *O. patellarioides* (Pl. 150: 3). This variant seems to be separable from *O. ocellata* by consistently tapering, tail-like spore bases. *O. foliicola* concurs with *O. ocellata* in morphology of the teleomorph, but grows on coriaceous leaves and is separated for molecular reasons (see under *O. foliicola*, p. 483).

Variation. Specimens here assigned to *O. ocellata* vary in spore length, especially within a single ascus, also in ascus size and spore width. Further variation was noted in the apical domes which were entirely absent in some collections (Pl. 164: 1, 3, 6). For variation in the anamorph see below.

Not included collections. A Spanish sample on inflorescences of *Achillea millefolium* (see IVV: E.R.D. 7175) and another on undetermined *Asteraceae* deviate by distinctly narrower spores of *7.5–10.3 × 2.3–3 µm or *9.5-11.2 × 2.8-3.2 µm and asci †42–60 × 5–6 µm or *5.5–6 µm wide, respectively (E. Rubio pers. comm.).

Anamorph. In seven collections of *O. ocellata*, trinacrium-like conidia were observed on the natural substrate (Pls 164: 5; 165: 9–10). In two further samples, corresponding conidia were obtained on agar, one in pure culture from USA (IVV: 25.VIII.1994) and one from apothecia on agar from Spain (Pl. 164: 7). The latter culture was unintentionally obtained due to macroscopic confusion with associated apothecia of *O. subovoidea*. This culture is assumed to belong to *O. ocellata* because of the conidia that resemble those observed on the natural substrate in other collections. In the North American strain numerous unbranched straight conidia developed together with the short-armed trinacrium-like conidia, whereas such phragmoconidia were only rarely seen in the culture from Spain. There is a tendency to larger conidia (mainly longer-armed) in collections from temperate regions (Luxembourg, Germany), in comparison with those from warmer regions (southern Europe and western North America). The largest conidia were found in a collection from Luxembourg (H.B. 6207), with a total size of *30–40 × 31.5–48 µm (Pl. 163: 5).

Phylogeny. The single available sequence of *O. ocellata* (Arizona, on *Ericameria*, conidia trinacrium-like, IVV: H.B. 7006a) was gained from apothecia and comprises SSU, ITS, and LSU. It clustered in vicinity of *O. subocellata* (Phyl. 8) but with a minimum distance of 3.5 %, and with much higher distance to other members of series *Lentiformes* (see under *O. subocellata*, p. 482, and *O. foliicola*, p. 483). The *flavida-cucumispora* clade which comprises strains of seven species received medium (S11) or strong (Phyls 8, S9) support in our analyses.

Ecology. *O. ocellata* grows on rotten wood and bark of dead xeric branches of various angiosperm trees and shrubs (rarely herbaceous substrate) and shows also a high ecological amplitude regarding the climate. It is widespread in southwestern USA, being recorded in the Colorado Plateau (Uinta Basin, Utah Mountains, Grand Canyon, Canyonlands and Navajo section) and Chihuahuan desert in cold- to warm-temperate, subhumid to semiarid pinyon-juniper woodlands and sagebrush (and blackbrush) desert scrubs, also in a ponderosa pine forest adjacent to pinyon-juniper woodland (*Chrysothamnus*) and a riparian angiosperm woodland (*Juglans*). It was also recorded from boreal (or subarctic) Alaska, supramediterranean semihumid Macaronesia (*Spartocytisetum supranubiae*), and orotemperate (sub) humid (winter-dry), continental Mongolia (*Laricetum* with *Betula*, *Lonicera*, *Salix*). Various collections are from very diverse vegetation types in atlantic to subcontinental central, western, and southern Europe, including shady angiosperm forests, solitary trees and shrubs in open agricultural areas, and xerophytic shrublands in supra- (to oro-)temperate to suprasub- or mesosubmediterranean humid and supra- to thermomediterranean semihumid climates.

Specimens included. **POLAND**: **West Pomerania**, 20 km SE of Szczecin, ~2 km E of Dobropole Gryfiński, Osetno, ~70 m, trunk of *Fagus sylvatica*, on wood, 3.VIII.2008, G. Domian, vid. P. Perz (P.P. 20080803-GD-Osetno-1, doc. vid.). – **Lower Silesia**, Kłodzko, garden of Z. Perz, 400 m, branch of *Pyrus communis*, on wood, 11.VIII.2006, P. Perz (P.P. 20060811-1). – 3 km NNW of Polanica Zdrój, W of Wolany, ~400 m, branch of *Rosa*, on wood, 21.VI.2006, P. Perz (P.P. 20060621-1, doc. vid.). – Góry Bystrzyckie, 16 km W of Kłodzko, 1.5 km NW of Szczytna, Polna ulica, 480 m, branch of *Malus domestica*, on wood, 8.VIII.2006, P. Perz (P.P. 20060808-3). – ibid., branch of *Salix*, on wood, 8.VIII.2006, P. Perz (P.P. 20060808-4, H.B. 8309a). — **GERMANY**: **Niedersachsen**, Goslar, Oberharz, Goslar, Granestausee, 320 m, branch of *Salix caprea*, on wood, 2.VI.2004, H.O. Baral (H.B. 7531c, anam. substr.). – **Baden-Württemberg**, Schwäbische Alb, 5.3 km ESE of Eningen, 1.8 km NW of Würtingen, S of Mutschlenbühl, 705 m, branch of *Rosa*, on bark, 30.X.2001, H.O. Baral (ø). – 11 km SE of Reutlingen, 1.6 km ENE of Holzelfingen, Hohrot 785 m, branch of *Sorbus*, on wood, 28.VI.2002, G. Marson (H.B. 7159a, anam. substr.). — **LUXEMBOURG**: **Gutland**, **Capellen**, 4 km WNW of Capellen, 2 km E of Steinfort, Treisch, 325 m, branch of *Quercus*, on wood & bark, 8.V.1997, G. Marson (H.B. 5784, anam. substr.). – **Esch-sur-Alzette**, 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 380 m, branch of *Quercus*, on bark, 12.VI.1994, G. Marson (ex H.B. 5104, M-0276540, **holotype**; G.M. 5191 **isotype**: anam. substr.). – 5 km SSW of Luxembourg, 0.5 km W of Kockelscheier, Houbësch, 320 m, branches of *Carpinus betulus*, on wood, 11.VIII.1998, G. Marson (H.B. 6207, anam. substr.). — **FRANCE**: **Aquitaine**, **Gironde**, – 8 km SW of Royan, 6 km NE of Soulac-sur-Mer, 8 m, leaves (Wedel) of *Yucca*, 20.XI.2011, J.P. Priou (J.P.P. 11217, non vid.). – 20 km SW of Royan, 6 km SSW of Soulac-sur-Mer, l'Amélie, Arrière dune, 12 m, leaves of *Yucca*, 20.XI.2011, O. Priou (J.P.P. 11206, doc. vid.). — **SPAIN**: **Castilla-La Mancha**, **Guadalajara**, 18 km SW of Sigüenza, 2.5 km NE of Almadrones, NW of E-90, 1065 m, branch of *Cistus*, on wood, 24.IX.1999, H.O. Baral & G. Marson (H.B.

Map 24. Known distribution of *O. ocellata* in North America, Europe, and Macaronesia.

6475b, anam. apoth.). – 55 km NNW of Guadalajara, NW of Majaelrayo, Arroyo La Matilla, 1180 m, branch of *Salix*, on wood, 14.V.1996, H.O. Baral (H.B. 5472b). – ibid., branch of *Cistus laurifolius*, on wood, 14.V.1996, H.O. Baral (H.B. 5467a). – **Aragón**, **Teruel**, 21 km WSW of Montalbán, W of Pancrudo, 1250 m, branch of *Rhamnus myrtifolia* subsp. *myrtifolia*, on wood, 27.VIII.2011, R. Tena (R.T.L. 11082701, doc. vid.). – 25 km WNW of Teruel, 5 km ENE of Albarracín, 1090 m, branch of *Rosa*, on wood, 16.V.2015, J.P. Priou (J.P.P. 15141, doc. vid.). – **Com**. **Valenciana**, **Castellón**, 13.5 km NNW of Castellón, 3.2 km WSW of Vilafamés, Camí de Costur, 400 m, branch of *Quercus rotundifolia*, on wood, 27.IX.1999, H.O. Baral (ø). — **MACARONESIA**: **Canary Islands**, **Tenerife**, La Orotava, Las Cañadas del Teide, 7 km E of Teide, close to Montaña Mostaza, 2161 m, twigs & leaves (petioles) of *Carlina xeranthemoides*, on bark & wood, 13.II.2009, L. Quijada, J. Diaz Armas & E. Beltrán-Tejera (TFC Mic. 21491, H.B. 9224). — **MONGOLIA**: **Bayan Ölgii**, Altay Mts., 10 km SW of Tsengel, Khovd river valley, 2200 m, branch of *Lonicera altaica*, on bark, 9.VIII.2005, P. Karasch (H.B. 7893c ø). — **USA**: **Alaska**, Fairbanks, University Campus, 150 m, on indet. tree, VIII.2011, D.H. Pfister, vid. B. Liu (B.L., doc. vid.). – **Colorado**, Uinta Basin, 50 km ESE of Vernal, 6 km NE of Dinosaur, 2100 m, on *Cercocarpus betuloides*, 12.VI.1996, G. Marson (ø). – Canyonlands, ~31 km NW of Cortez, Pleasant View, 2110 m, branches of *Elaeagnus angustifolia*, on wood, 1.VI.1996, G. Marson (H.B. 6049a). – 15.5 km SSE of Cortez, Mesa Verde, 5 km NNW of Spruce Tree House, 2290 m, branch of *Artemisia filifolia*, on bark, 31.V.1996, G. Marson (H.B. 6276c ø). – **Utah**, Canyonlands, Capitol Reef, 40 km WSW of Hanksville, 23 km E of Torrey, 1557 m, branch of *Baccharis salicifolia*, on bark, 19.VI.2000, G. Marson (H.B. 6741f). – Natural Bridges, 41 km W of Blanding, 2090 m, branch of *Amelanchier utahensis*, on wood, 14.VI.2000, G. Marson (ø). – Arches, 20 km NNW of Moab, Salt Valley Wash, 1427 m, twigs & branches of *A. filifolia*, on bark, 18.VI.2000, G. Marson (H.B. 6740a). – near Valley of the Gods, 25 km NNW of Mexican Hat, 10 km N of Mokee Dugway, Cedar Mesa, 1990 m, branch of *Ericameria nauseosa*, on bark, 14.VI.2000, G. Marson (ø). – Canyonlands, 36 km S of Moab, 5 km WNW of Hatch Rock, 1813 m, branch of *E. nauseosa*, on bark & wood, 16.VI.2000, G. Marson (H.B. 6736d). – Utah Mts., Bryce Canyon, 30 km SE of Panguitch, 7.5 km WNW of Tropic, 2410 m, branch of ?*Chrysothamnus viscidiflorus*, on bark, 25.VIII.1994, G. Marson (ø, anam. cult.). – **Arizona**, Navajo, 85 km SW of Mexican Hat, 27 km SW of Kayenta, Rte. 160, Klethla Valley, 2015 m, branch of *Ericameria nauseosa*, on bark, 13.VI.2000, G. Marson (H.B. 7006a, anam. substr.; sq.: KT222414). – Canyonlands, 45 km SW of Page, 26 km SW of Marble Canyon, 1522 m, branch of *Coleogyne ramosissima*, on wood, 16.VI.2003, G. Marson (ø). – Grand Canyon, Coconino Plateau, 3 km N of Tusayan, 2068 m, branch of *Quercus gambelii*, on wood, 28.VIII.1994, G. Marson (H.B. 5238, anam. substr.). – **New Mexico**, Chihuahuan Desert, 30 km SW of Carlsbad, ?4 km NW of Whites City, ~3 km NE of Carlsbad Caverns, 1200 m, branch of *Juglans major*, on wood, 24.V.1996, G. Marson (H.B. 5673a).

Not included. **SPAIN**: **Asturias**, 12 km NW of Villablino, 1.7 km NW of Puerto de Leitariegos, ESE of Braña de Arriba, 1445 m, inflorescence of *Achillea millefolium*, 11.IX.2017, J. Linde, vid. E. Rubio (E.R.D. 7175). – id., on indet. *Asteraceae* (non vid.).

Orbilia subocellata Baral & E. Weber, **sp**. **nov**.,
MB 813486 — Pls 166–167

Etymology: named after the resemblance to *O. ocellata*.

Typification: Spain, Madrid, Alcalá de Henares, branch of *Cupressus sempervirens*, 23.IX.1999, G. Marson & H.O. Baral (ex H.B. 6474, M-0276596, holotype; ex-type culture: CBS 140816; sq.: KT215227, MH878186).

Latin diagnosis: Orbiliae ocellatae *persimilis, sed asci et ascosporae leniter latiores, conidia non ramosa, ab* O. lentiforme *in sequentia nucleotidium differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.15–0.3(–0.5) mm diam., 0.13–0.14 mm thick, light to deep (rose-)orange-red, round, subgregarious in small groups; disc slightly flat, margin finely crenulate; broadly sessile, slightly erumpent between fibres. **Asci** *57–67 {1} or 70–85(–91) {1} × (8.2–)8.5–9(–9.7) µm {2}, †(55–)62–82(–94) × 7–8.5 µm {2}, 8-spored, 1–2(–3) lower spores inverted {2} (rarely mixed), pars sporifera *35–39 µm long; **apex** (†) slightly to medium truncate, hemispherical in profile view, with dome †0.8–1 µm thick {1}; **base** T-shaped. **Ascospores** *((8–))(9–)10–13(–14)((–15.3)) × (3.3–)3.5–4.3(–5) µm {3}, †10–13 × 3–3.8 µm {1}, ellipsoid-clavate to subcylindrical, apex rounded to obtuse, slightly to medium attenuated near base, straight to slightly curved (upper spores often strongly curved); **SBs** *0.8–1 × 2–2.4 µm {2}, lens-shaped, apically broadly attached; mostly with some small **LBs** grouped in each half. **Paraphyses** apically uninflated to slightly, rarely medium clavate, sometimes curved at apex, terminal cell */†7–19 × 2–2.8 µm {1}, lower cells */†8–18 × 1–1.6 µm {1}; sometimes branched near apex. **Medullary excipulum** pale rose, 35–45 µm thick, of dense t. intricata-globulosa, indistinctly delimited. **Ectal excipulum** pale rose, 15–20 µm thick near base, of thin-walled t. globulosa(-prismatica), cells *7–13 × 5–8 µm {1}, 12 µm at flanks and margin, near margin of t. porrecta oriented at 0°, marginal cortical cells *7–9 × 2.5–3.5 µm. **Anchoring hyphae** medium abundant, *2–3.5 µm, wall 0.2 µm {1}. **SCBs** not observed. **Exudate** over paraphyses 1.5–3 µm thick, cloddy-continuous, loosely attached, at margin 0.5–1 µm thick. — **ANAMORPH**: vermispora-like (from ascospore isolate {2} and natural substrate {2}). **Conidiophores** short. **Conidia** phragmosporous, cylindric-fusoid, often apically or entirely slightly to medium, rarely strongly curved, *(17.7–)19–29(–35.5) × 5.5–6.5(–7.2) µm {2, culture}, *26.3–29.5 × ~5.5 µm {1, natural substrate}, (2–)3(–5)((–6))-septate, containing a few minute LBs and WBs, and numerous medium-sized non-refractive vacuoles, also many small, 1(–3)-septate conidia *11–16 × 4.2–4.5 µm observed in pure culture {1}.

Habitat: collected (0–)1–2 m above the ground, corticated to partially decorticated, 4–20 mm thick twigs and branches of *Cercis siliquastrum* {1}, *Cupressus sempervirens* {1}, *Rosa* sp. {2}, on 0.1 mm deep

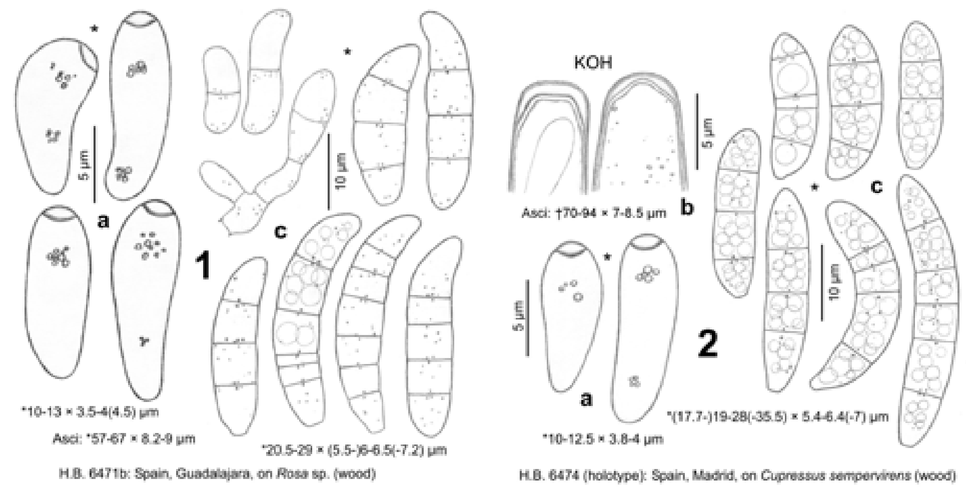


Plate 166. **1–2**: *Orbilia subocellata*. – **a**. ascospores; **b**. ascus apices; **c**. conidia (from culture).

medium to strongly decayed wood {4} and bark {2}, strongly greyed, wood splitted or with ± deep clefts. **Associated**: *Claussenomyces* sp. {1}, *Nitschkia broomeana* {1}, *Orbilia cercidicola* {1}, *O. flagellispora* {1}, *O. gambelii* {1}, *O. myriolentiformis* {1}, *O. myriosphaera* {1}, *O. subaristata* {2}, *O. subclavuliformis* {1}, *O. trapeziformis* {1}, *O. ?tremulae* {1}, *Unguiculariopsis ?rehmii* {1}, small lichen thalli. **Desiccation tolerance**: fully tolerant for at least 5 months, ascospores after 6.5 months. **Altitude**: 460–1060 m a.s.l. **Geology**: Cretaceous & Miocene calcareous clay, gravel & sandstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia subocellata* is somewhat intermediate between *O. ocellata*/*O. foliicola* and *O. lentiformis* in both spore length and ascus width (see Tab. 63). *O. ocellata* and *O. foliicola* differ in trinacrium-like conidia, the former also in narrower asci. *O. lentiformis* tends to larger asci and longer ascospores compared to *O. subocellata*, but there is actually no sharp difference, including conidial morphology. A collection on *Cercis* (Pl. 167) was without conidia but clustered with *O. subocellata*; also its asci and spores are too large to be included in *O. ocellata*.

Anamorph. We here segregate *O. subocellata* from *O. ocellata* mainly because of its vermispora-like conidia which were abundantly formed in pure culture in the holotype and a paratype. Because of the close microscopical similarity in the teleomorph, we assume that some of the specimens with insufficient morphological data and unavailable anamorph or sequence data, assigned by us to *O. lentiformis* or *O. ocellata*, might in fact belong to *O. subocellata*, especially those with an intermediate ascus and ascospore size. The conidia of *O. subocellata* closely concur with those of *O. lentiformis*, except for being slightly larger and more curved. In pure culture (Pl. 166: 1) also smaller conidia (possibly microconidia) were observed, which look as being immature but which were found detached from the conidiophores in abundance.

Not included collections. A Spanish sample on wood of *Quercus rotundifolia* with spores *11.5–14 × 3.7–4 µm and asci *57–80 × 9.2–9.4 µm (IVV: H.B. 5498) and a further collection on *Rosa* (J.P.P. 15124) might belong here, but any evidence is lacking

Phylogeny. Molecular data comprising SSU, ITS, and LSU were gained from the holotype of *O. subocellata* on *Cupressus* (from pure culture) and from a paratype on *Cercis* (from apothecia). The two strains differ by 0.5% in the ITS and 0% in the LSU. *O. subocellata* clustered in the *flavida-cucumispora* clade (Phyls 8, S9, S11) by showing to *O. ocellata* a distance of 3.5% in the ITS (1% in LSU), to *O. foliicola* 6.5/1.5–2%, and to *O. lentiformis* 15–16/4–5%.

Ecology. The four collections included in *O. subocellata* were found on wood and bark of xeric branches of *Cercis*, *Cupressus* and *Rosa*, in suprasub- to mesomediterranean, semihumid areas of central and northeastern Spain and southern France.

Specimens included. **SPAIN**: **Madrid**, 3.5 km NE of Alcalá de Henares, University Campus, 0.6 km NW of botany building, 610 m, branch of *Cupressus sempervirens*, on wood, 23.IX.1999, G. Marson & H.O. Baral (ex H.B. 6474, M-0276596, **holotype**, anam. cult., CBS 140816; sq.: KT215227, MH878186). – **Castilla y León**, **Soria**, 22 km NE of Sigüenza, NNE of Estación Medinaceli, 1013 m, branch of *Rosa*, on wood, 21.IX.1999, H.O. Baral (H.B. 6471b, anam. substr. & cult.). – **Aragón**, **Huesca**, central Pyrenees, 15 km N of Jaca, N of Canfranc, Puente de Arriba, 1060 m, branch of *Rosa*, on bark & wood, 13.X.2010, J.P. Priou (J.P.P. 10169, anam. substr., doc. vid.). — **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1.5 km N of Nyons, Forêt Domaniale de Veaux, le Devés, 460 m, twigs of *Cercis siliquastrum*, on wood & bark, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9151a; sq.: KT222415).

Not included. **SPAIN**, **Castilla-La Mancha**, **Guadalajara**, 0.9 km SSW of Los Santos de la Humosa, 875 m, branch of *Quercus rotundifolia*, on wood, 23.V.1996, H.O. Baral (H.B. 5498). – **Aragón**, **Teruel**, Sierra de Albarracín, 25 km WNW of Teruel, 5 km ENE of Albarracín, 1090 m, branch of *Rosa*, 16.V.2015, J.P. Priou (J.P.P. 15124, doc. vid.).

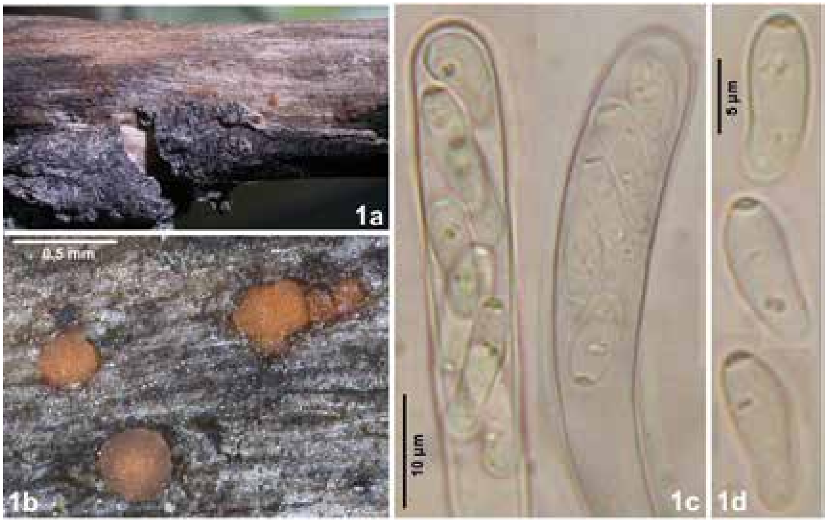


Plate 167. **1**: *Orbilia subocellata*. – **1a**. xeric branch of *Cercis siliquastrum*; **1b**. rehydrated apothecia; **1c**. asci; **1d**. ascospores. – Living state. **— 1a–d**. H.B. 9151a: France, Rhône-Alpes, on *Cercis*.

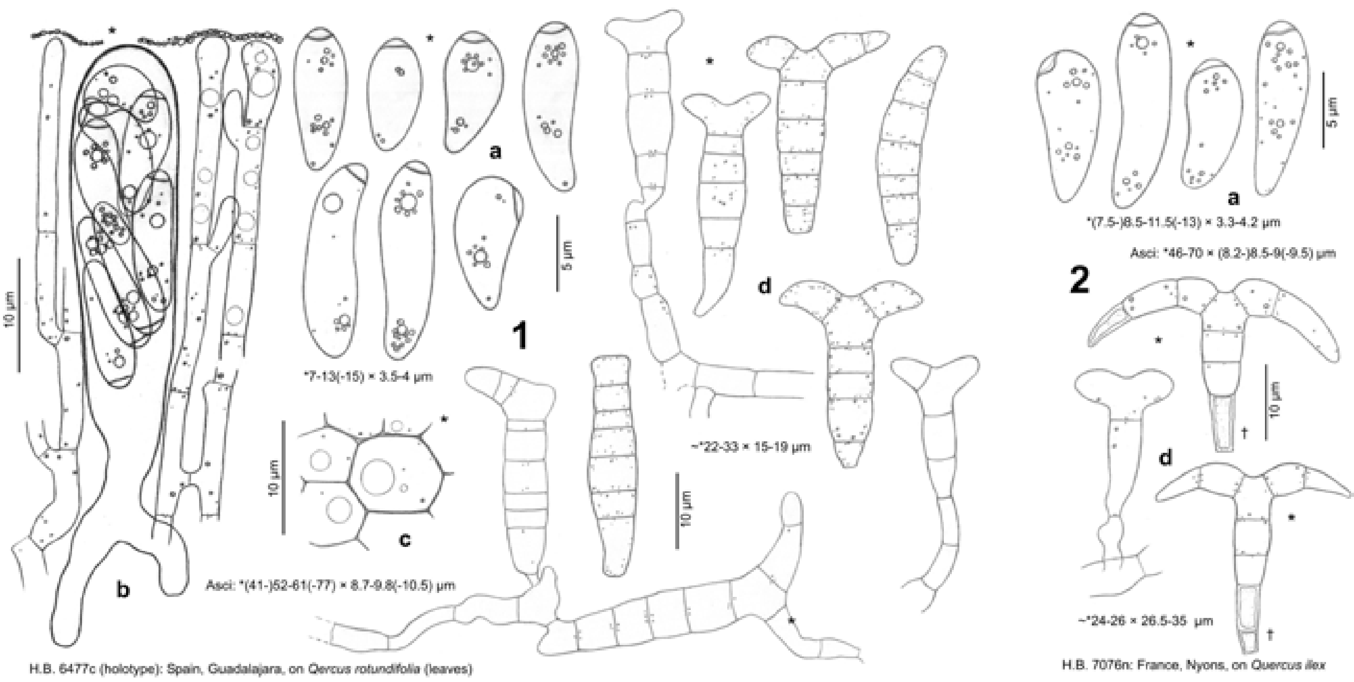
Orbilia foliicola Baral & E. Weber, **sp. nov.**, MB 813487 — Pls 168–169

Etymology: named after the habitat, leaves of *Quercus*.

Typification: Spain, Guadalajara, Almadrones, leaves of *Quercus rotundifolia*, 24.IX.1999, H.O. Baral (ex H.B. 6477c, M-0276484, holotype, ex-type culture: CBS 140809; sq.: KT215229, MH878181).

Latin diagnosis: Orbiliae ocellatae *persimilis sed apothecia in foliis* Quercus ilicis *crescunt, etiam in sequentia nucleotidium differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.12–0.25 mm diam., 0.11–0.13 mm high,



H.B. 6477c (holotype): Spain, Guadalajara, on *Qercus rotundifolia* (leaves)

H.B. 7076n: France, Nyons, on *Quercus ilex*

Plate 168. **1–2**: *Orbilia foliicola*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ectal excipulum near margin in surface view, cells containing globose SCBs; **d**. conidia (**1d**. from culture, **2d**. from substrate).

pale to light orange-rose, slightly translucent, round, very scattered to subgregarious; disc flat, margin thin, 0–5 µm protruding, smooth; broadly sessile, superficial; dry bright apricot. **Asci** *(41–)46–70(–77) × (8.2–)8.5–9.5(–10.5) µm {2}, †48–65 × 7–8.5(–9.7) µm {2}, 8-spored, spores *3–4-seriate, 1–3(–5) lower spores inverted {2} (rarely mixed), pars sporifera *30 µm long; **apex** (†) slightly to rather strongly (conico-)truncate, hemispherical in profile view, varying within a population between thin-walled {2} or mostly with a †0.3–1.4 → 0.3–0.6 µm thick dome {2}, without apical chamber; **base** with very short to medium long, thick, ± flexuous stalk, L-, h- or Y-shaped. **Ascospores** *(7–)8–12.5(–15.5) × 3.3–4.2((–5)) µm {2}, †(7.5–)8.5–10(–12.5) × 3.1–3.4 µm {1}, ellipsoid-clavate, sometimes subcylindrical or ellipsoid-obovoid, apex rounded to obtuse, slightly to strongly attenuated near base, straight to slightly curved (upper spores often strongly so); **SBs** *0.5–1.2 × 1.8–2.1(–2.4) µm {2}, lens-shaped, apically broadly attached; often with some small **LBs** grouped in each half. **Paraphyses** apically uninflated to medium clavate, terminal cell *7.5–18.5 × 1.8–3.8 µm {2}, lower cells *5.5–12 × 1.5–3 µm {2}, rarely branched at upper septum. **Medullary excipulum** pale orange, 15–20 µm thick, of dense textura intricata-angularis, medium sharply delimited. **Ectal excipulum** subhyaline, of slightly gelatinized, indistinctly oriented t. angularis-prismatica from base to margin, 25–30 µm thick near base, cells †6–14 × 4–8.5 µm {1}; 15–20 µm thick near margin, oriented at a 20–30° angle to the surface, marginal cortical cells †6–10 × 3.5–4.7 µm {1}. **Anchoring hyphae** rather sparse, †2–3.5 µm wide, walls 0.2–0.5 µm thick {1}. **SCBs** globose, in paraphyses 1–2 µm diam., in ectal excipulum (1–)2–3 µm. **Exudate** over paraphyses 0.3–0.6 µm thick, cloddy-granular, hyaline, loosely attached; over margin and flanks 0.5–3 µm thick. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** *~7–30 × 2–3.8 µm, 1–3-septate, usually branched, conidia formed terminally. **Conidia** branched, Y/T-shaped, the two arms always bent downwards, total size *22–33 {2} × 15–19 {1} or 26–33 {1} µm, stipe *14–25 × 4.5–6.5 µm, 2–5-septate, arms tapering, *(5–)6–13(–19) × 4–4.5 µm, 0–3-septate, some conidia unbranched, straight to slightly curved, */†~24–38 × 4–6 µm, 3–6-septate.

Habitat: collected 0.4–1.5 m above the ground, on lower surface of dead leaves of *Quercus ilex* {1}, *Q. rotundifolia* {1}, strongly greyed, green algae sparse. **Associated**: *Calycellina* aff. *albida* {2}, ?*Micraspis* sp. {1}, *Micropeziza mollisioides* {1}, *Mollisia nervicola* {1}, ?*Mycosphaerella* sp. {1}, *Orbilia quercus-ilicis* {1}, *Rutstroemia coracina* {1} etc. **Desiccation tolerance**: fully tolerant for at least 3 months. **Altitude**: 460–1065 [–1435] m a.s.l. **Geology**: Cretaceous & Miocene calcareous clay, marl, gravel & sandstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia foliicola* very closely concurs with the lignicolous *O. ocellata* and *O. subocellata* in apothecial characteristics (ascus and spore size, spores basally ± attenuated), and with *O. ocellata* also in the trinacrium-like conidia. It is separated here because of its peculiar ecology, coriaceous leaves of *Quercus ilex* agg., but mainly since our molecular data indicate that it is different from the all sequenced collections on ligneous substrate here assigned to *O. lentiformis* s.l., *O. ocellata*, and *O. subocellata*.

The only further *Orbilia* which we have found growing on coriaceous leaves of *Quercus* (*O. quercus-ilicis*, section *Habrostictis*) is macroscopically indistinguishable and even microscopically similar. It is mainly recognizable by a very different type of spore body and, therefore, difficult to segregate when dealing with dead material (only in *O. foliicola* the SBs remain indistinctly perceptible in dead spores).

Anamorph. The conidia of *O. foliicola* obtained in pure culture (Pl. 168: 1d) closely resemble those of *O. ocellata* from mediterranean regions (Pl. 164: 7), so that morphological distinction of the two taxa is impossible. Conidia found on the natural substrate differed in longer arms, but this might be a matter of maturity. Conidia of *O. quercus-ilicis* sharply differ in being tridentaria-like with straight arms.

Phylogeny. A sequence was gained from pure culture of the holotype of *O. foliicola*, comprising SSU, ITS, and LSU. A DNA isolate (partial 5.8S and entire ITS2) from *Pinus heldreichii* needles in Montenegro differs by only 1 nt in the ITS2. In our analyses *O. foliicola* clustered in the *flavida-cucumispora* clade (Phyls 8, S9, S11), with a 7% distance in the ITS region to *O. ocellata*, *O. subocellata*, and *O.* aff. *lentiformis*, and 11.5–12.5% to *O. lentiformis*.

Ecology. *O. foliicola* was collected on the greyed lower surface of dead, xeric, leathery leaves of *Quercus ilex* and *Q. rotundifolia* in the mesosub- to supramediterranean semihumid

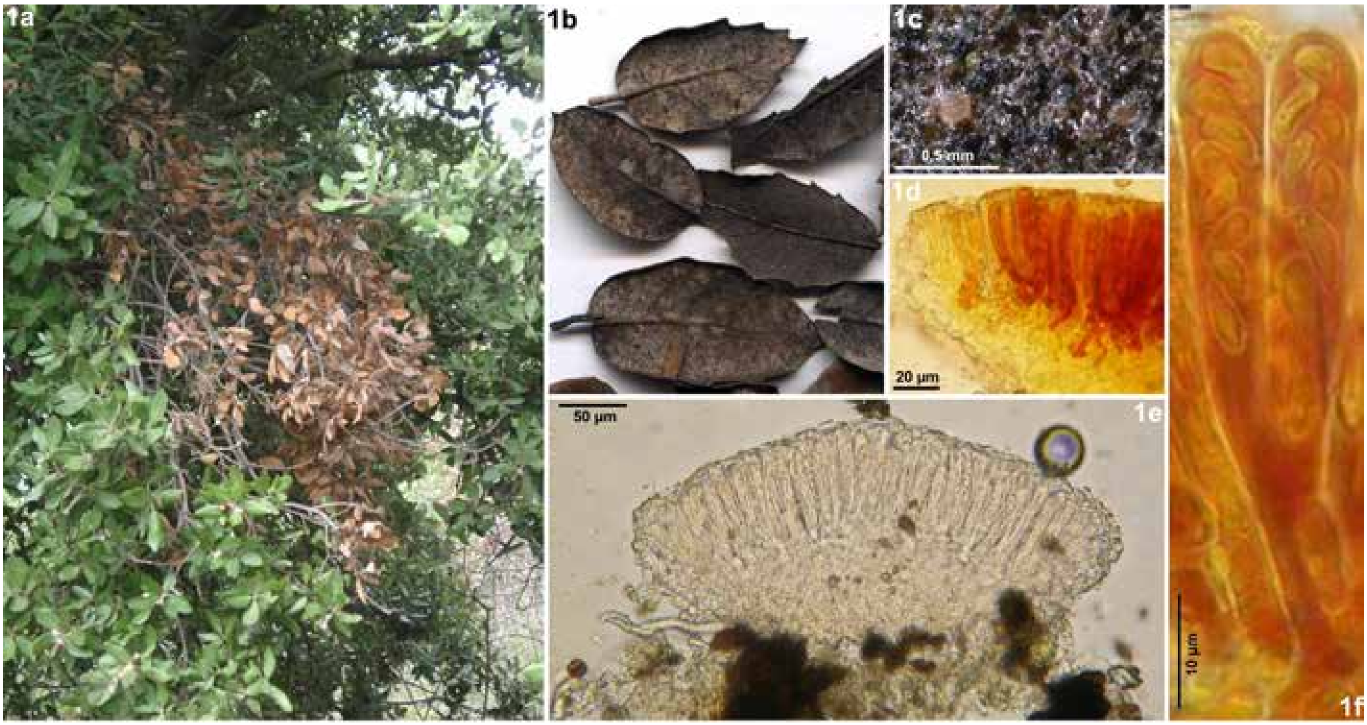


Plate 169. **1**: *Orbilia foliicola*. – **1a**. *Quercus ilex* shrub with partially dead twigs; **1b**. dead leaves of *Quercus ilex* (lower surface); **1c**. apothecia in rehydrated state; **1d–e**. apothecia in median section; **1f**. asci. – Dead state (KOH, KOH+IKI). — **1a–f**. H.B. 7076b: France, Nyons, on *Quercus*.

maquis (*Quercetum ilicis*) of southern Europe. Like *O. quercus-ilicis*, with which it grew together in the holotype (though on separate leaves), *O. foliicola* was so far only found on still-attached leaves but not on those lying on the ground.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1 km N of Nyons, Col du Pontias, 460 m, leaves of *Quercus ilex*, 18.VIII.2001, G. Marson (H.B. 7076b, anam. substr.). — **SPAIN**: **Castilla-La Mancha**, **Guadalajara**, Sistema Central, 18 km SW of Sigüenza, 2.5 km NE of Almadrones, 1065 m, leaves of *Quercus rotundifolia*, 24.IX.1999, H.O. Baral (M-0276484, **holotype**; **isotypes** in H.B. 6477c, probably also in K(M) 64409 and J.T.P. (with *Rutstroemia coracina* & *O. quercus-ilicis*); anam. cult., CBS 140809; sq.: KT215229, MH878181). — **MONTENEGRO**: ~23 km ENE of Podgorica, Kučka korita, 1435 m, isolate from needles of *Pinus heldreichii*, V.2015 (2814_133, Lazarević & Menkis 2020, mol. extr., sq.: MT242046).

Orbilia pleiolentiformis Baral & G. Marson, **sp. nov.**, MB 813488 — Pls 170–171

Etymology: named according to 16-spored asci and a lens-shaped spore bodies.
Typification: USA, Utah, Bears Ears, branch of *Populus tremuloides*, 14.VI.2000, G. Marson (ex H.B. 7181a, M-0276559, holotype).

Latin diagnosis: *Similis* Orbiliae lentiformi *et* O. ocellatae *sed ascis 16-sporis differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.18–0.5 mm diam., 0.11–0.17 mm high, pale carneous-rose to bright orange-rose or orange, round, singly to ± gregarious; disc slightly concave to flat, also medium convex, margin thin, 5–10 µm protruding, even; broadly sessile, superficial to deeply immersed. **Asci** *(58–)65–88(–92)((–128)) × (7–)8–10(–10.6) µm {7}, †(50–)60–80(–90) × (5.5–)6–8.3 µm {6}, 16-spored, spores obliquely 2–3(–4)-seriate, (1–)2–8(–12) lower spores inversely oriented {7} (strongly mixed or not), pars sporifera *(35–)38–49(–58) µm long, †48–70 µm; **apex** (†) hemispherical to slightly or medium (rarely strongly) truncate, rarely indented, dome (†) absent {2} or 1–1.2 → 0.5–0.7(–1.2) µm thick {6}; **base** with medium long, thick, ± flexuous stalk, T-, L- or Y-shaped. **Ascospores** *((5–))(6–)7–12(–13)((–17)) × (2.4–)2.7–3.7(–4.4) µm {8}, †6–13 × 2.7–3.3 µm {2}, subcylindrical to ellipsoid or ellipsoid-clavate, apex rounded to obtuse, slightly to medium attenuated near base, straight to medium (upper spores strongly) curved or geniculate near base; **SBs** *(0.2–)0.3–0.7(–1) × (1.3–)1.5–1.8(–2) µm {6}, lens-shaped, apically broadly attached; **LBs** sparse or often forming 2 groups, germinating spores 1-septate {1}. **Paraphyses** apically slightly to medium clavate-capitate, sometimes irregularly deformed, rarely lageniform, terminal cell *(5.5–)7–15(–21) × (2.2–)2.8–4.5(–5) µm {6}, lower cells *(6–)9–19 × 1.3–2.5(–3) µm {6}, near base or apex 3–4 µm wide; rarely or often frequently branched near apex. **Medullary excipulum** hyaline, 10–60 µm thick, of dense textura globulosa-intricata, sharply delimited (mainly towards margin). **Ectal excipulum** hyaline, of vertically or irregularly oriented t. angularis(-prismatica), 20–60 µm thick near base, cells *6–26 × 5–14 µm {3}; from lower flanks to submargin 15–30 µm thick, cells *7–12 × 6–11 µm; at margin 15–30 µm thick, of t. prismatica(-porrecta) oriented at 10–50°, marginal cortical cells *5–15 × 3–5 µm {3}, thick-walled; no glassy caps. **Anchoring hyphae** sparse to ± abundant, */†2–3.5(–4) µm wide, walls 0.2–0.4 µm thick {3}. **SCBs** absent or present, globose, in paraphyses 1–3 µm diam., in marginal excipular cells 2–3.5 µm. **Exudate** over paraphyses 0.3–2 µm thick, continuous to granular-cloddy, loosely adhering; over margin 1–3 µm thick. **— ANAMORPH**: unknown.

Habitat: collected ± on the ground or still-attached in 1–3 m above the ground, corticated or decorticated, 6–40 mm thick branches of *Allocasuarina decaisneana* {1}, *Chrysothamnus viscidiflorus* {1}, *Ericameria nauseosa* {1}, *Ficus carica* {1}, *Populus tremuloides* {1}, *Salix* sp. {1}, on 0.2–0.5 mm deep medium to mostly strongly decayed wood {3} or bark (bast) {2}, slightly to strongly greyed, green algae absent or sparse; on herbaceous stems of ?*Cichorium intybus* {1}, *Yucca elata* {1}. **Associated**: *Carestiella schizoxyloides* {1}, *Eutypella* ?*scoparia* {1}, *Lachnella alboviolascens* {1}, ?*Nectria* sp. {1}, *Orbilia albovinosa* {1}, *O. bicknellensis* {2}, *O. caulicola* {1}, *O. cylindrosoma* {1}, *O. denticulata* {1}, *O. flavida* {1}, *O. lentiformis* {2}, *O. macrotrapeziformis* {1}, *O. multiphanosoma* {1}, *O. multivinosa* {1}, *O. ocellata* {1}, *O. paradoxoides* {1}, *O. phanosoma* {1}, *O. pleioobtusispora* {1}, *O. pleiovitalbae* {1}, *O. pluristomachia* {1}, *O. serpentina* {2}, *O. ungulata* {1}, *O. vitalbae* {1}, *Patellaria atrata* {1}, *Peniophora* ?*violaceolivida* {1}, *Pragmopora* sp. {1}, *Symbiotaphrina desertorum* {1}, ?*Teichospora* sp. {1}, *Teichosporella dura* {1}, *Trichopeziza* ?*perrotioides* (immature) {1}. **Desiccation tolerance**: fully viable for at least 14 months, after 27 months still some asci,

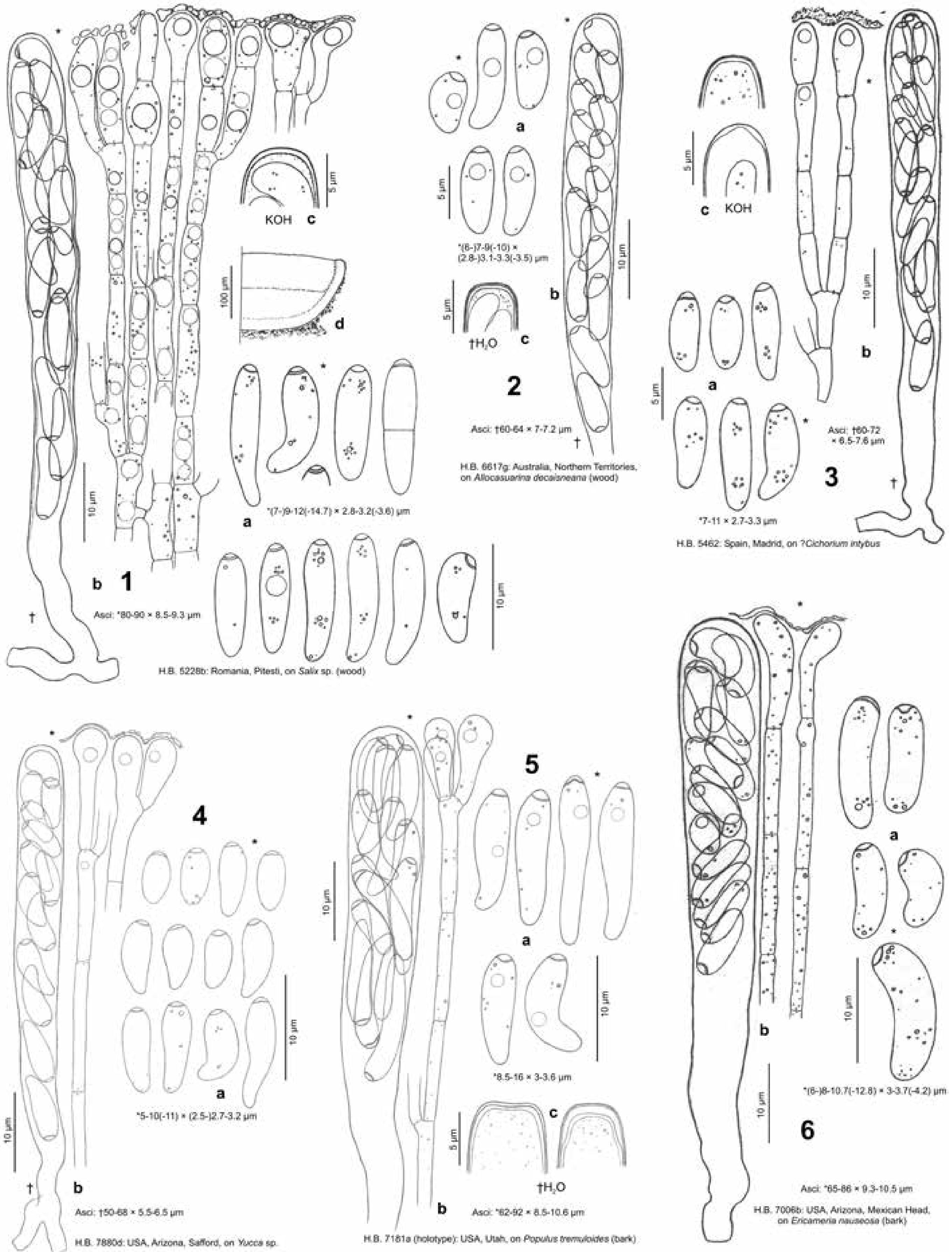


Plate 170. **1–6**: *Orbilia pleiolentiformis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section.

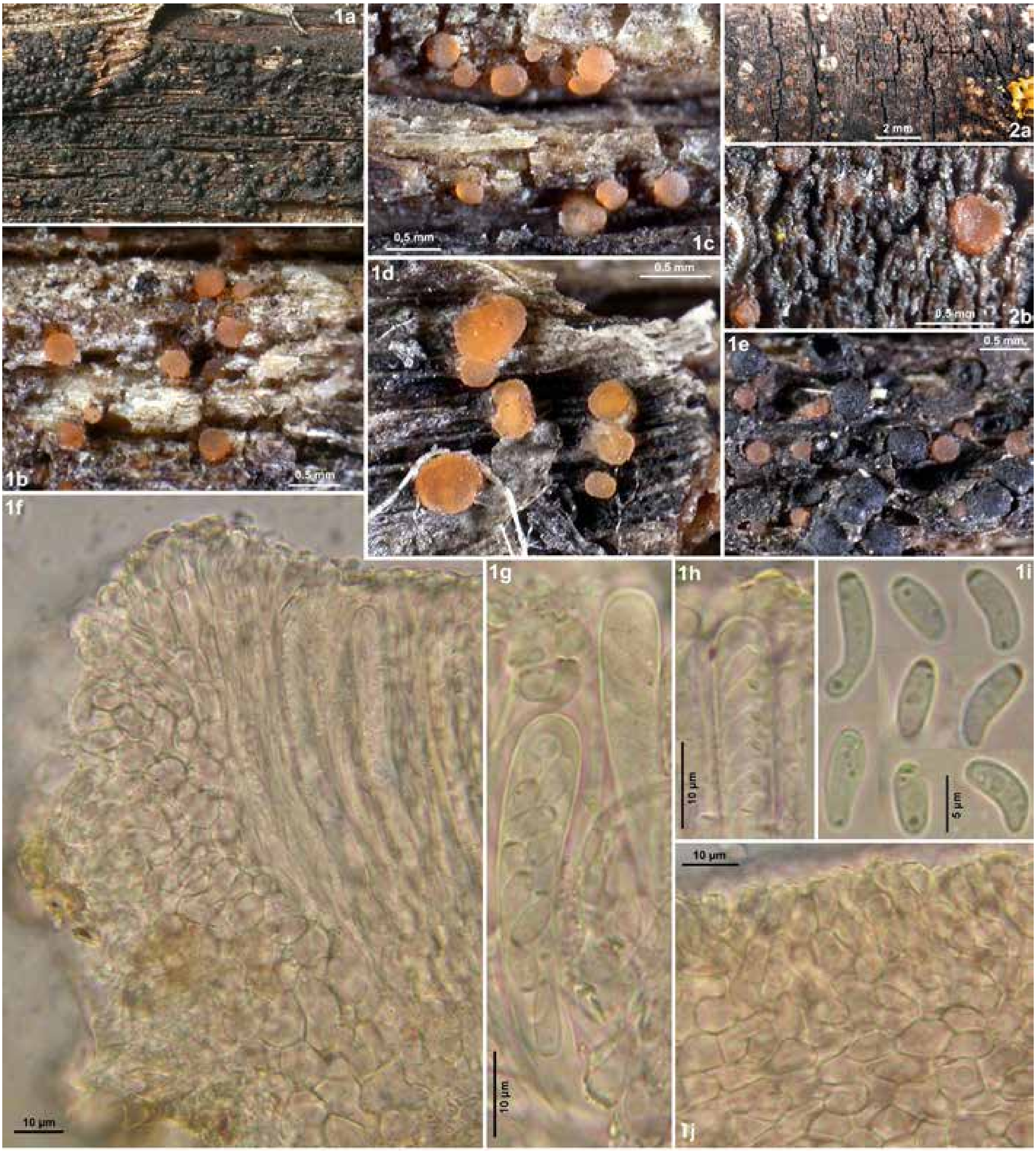


Plate 171. **1–2**: *Orbilia pleiolentiformis*. – **1a–e**, **2a–b**. rehydrated apothecia (**1a**, **e**. associated with ?*Teichospora* sp.); **1f**. ectal excipulum in median section (mid flanks and margin); **1j**. margin in surface view; **1g–h**. asci; **1i**. ascospores. – Living state. — **1a–j**. H.B. 7880d: USA, Arizona, on *Yucca*; **2a–b**. H.B. 7181a (holotype): USA, Utah, on *Populus*.

paraphyses and many excipular cells alive. **Altitude**: 275–600 m a.s.l. (Europe), 1510–2600 m (western North America), 500 m (Australia). **Geology**: USA: Triassic-Jurassic-Cretaceous (red) sandstone, volcanic rock (basalt, andesite, rhyolite); France: Miocene sandstone, gravel & clay; Australia: Cenozoic regolith (sand). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleiolentiformis* differs from *O. ocellata* and *O. lentiformis* only in spore number. In three collections, 8- and 16-spored populations grew together on the same branch, either intermingled or in separate groups at a distance of, e. g., 12 cm, which might suggest that the two spore numbers belong to one and the same population. In another collection of *O. pleiolentiformis*, however, *O. flavida* grew in association which has 32-spored asci and smaller spores, and which rarely shows a few 16-spored asci among the typical ones. On the other hand, apothecia of *O. pleiolentiformis* were never found to contain asci with a spore number higher than 16 (see also p. 56–57).

Variation. Considerable variation in ascus and spore dimensions was noted among the collections. Three of the four North American collections showed extraordinarily wide asci and ascospores. Whether this difference is more than accidental should be clarified from further collections. Specimens from herbaceous substrates but also those on *Allocasuarina* and *Ficus* showed rather short spores, whereas those on *Ericameria* and *Salicaceae* differed in rather long spores. One of the *Ericameria* samples (IVV: 24.VIII.1994) deviated in extraordinarily long asci (*112–128 × 8–9.5 µm) and spores (*13–15(–17) × 3.2–4(–4.4) µm). However, ascus and spore length also varied considerably within an apothecium, and measurements overlap too much, therefore, we preferred not to split our collections into different taxa.

Ecology. *O. pleiolentiformis* was found on ± rotten wood and bark of dead, xeric branches of angiosperm trees and shrubs, more rarely on herbaceous stems. The collections are from mesosub- and mesomediterranean semihumid southwestern Europe, e.g., ruderal places with *Foeniculum vulgare* and *Eryngium campestre*, and cold-temperate, almost suprasubmediterranean (sub)humid southeastern Europe. From the Sonoran Desert and Colorado Plateau (Canyonlands and Navajo section, Utah Mountains, Mogollon Rim) in western North America are samples in a warm-temperate semiarid mixed grass-scrubland, cold-temperate subhumid to almost semiarid sagebrush desert scrub and pinyon-juniper woodland, and cold-temperate humid Douglas fir forest, and from central Australia one from the Ayers Rock area in a subtropical arid acacia open shrubland.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1 km N of Nyons, W of Col du Pontias, 415 m, branch of *Ficus carica*, on wood, 11.X.2002, G. Marson (H.B. 7231d). — **SPAIN**: **Madrid**, Meseta Central, 31 km ENE of Madrid, 2.8 km NE of Alcalá de Henares, SW of University Campus, Calle de Severo Ochoa, 600 m, stem of ?*Cichorium intybus*, 12.V.1996, H.O. Baral (H.B. 5462). — **ROMANIA**: **Argeş**, 100 km WNW of Bucureşti, ~8 km SE of Piteşti, A1 motorway, ~275 m, branch of *Salix*, on wood, 12.XII.1994, R. Reuter (H.B. 5228b). — **USA**: **Utah**, Utah Mts., Dixie Forest, 1.5 km ESE of Cedar City, 1815 m, on branch of *Chrysothamnus viscidiflorus*, 24.VIII.1994, G. Marson (ø). – Canyonlands, 33 km W of Blanding, 2 km NNE of Bears Ears East, 2600 m, branch of *Populus tremuloides*, on bark, 14.VI.2000, G. Marson (M-0276559, **holotype**; **isotype** in H.B. 7181a). – **Arizona**, Navajo, 85 km SW of Mexican Hat, 27 km SW of Kayenta, Klethla Valley, 2015 m, branch of *Ericameria nauseosa*, on bark, 13.VI.2000, G. Marson (H.B. 7006b ø). – Mogollon Rim, 31 km ENE of Safford, 20 km SSE of Clifton, Rte. 191, 1510 m, stem of *Yucca elata*, 1.VI.2003, G. Marson (H.B. 7880d). — **AUSTRALIA**: **Northern Territories**, Great Sandy Desert, 11.5 km ENE of Yulara, 14 km NNE of Ayers Rock (Uluru), Lasseter Hwy, 500 m, branch of *Allocasuarina decaisneana*, 12.X.1998, G. Marson (H.B. 6617g).

Orbilia flavida Feltgen, Rec. Mém. Trav. Soc. Bot. G.-D. Luxemb. 16 [‘15’]: 43 (1903) — Pls 172–174, Map 25

(?)= *Orbilia paradoxa* Ade, Mitt. Bad. Landesvereins Naturk. (Naturschutz, Freiburg), N.F. 1: 331 (1924) [non *Orbilia paradoxa* Velen. 1934, = *O. xanthostigma*]

?= *Orbilia uvispora* Mouton, Bull. Soc. R. Bot. Belg. 39 (2): 51 (1900)
  ≡ *Hyalinia uvispora* (Mouton) Boud., Hist. Class. Discom. Eur.: 104 (1907)

Etymology: *flavida*: from the yellowish colour of the apothecia in the holotype (though recent samples are consistently reddish); *paradoxa*: probably referring to the remarkable spore bodies; *uvispora*: indicating resemblance of the ascospores to seeds of *Vitis*.

Typification: Luxembourg, Brandenbourg, stem of *Seseli libanotis*, 7.VIII.1902, J. Feltgen (LUX 42552, holotype of ***Orbilia flavida***); Croatia, Dubrovnik-Neretva, Korčula island, Pupnat, stem of *Euphorbia wulfenii*, 11.VI.2000, H.O. Baral (ex H.B. 6716, M-0291761, epitype, designated here, MBT385111, ex-epitype culture: CBS 140807; sq.: KT215228). — Germany, Baden-Württemberg, Tauberbischofsheim, bracts of *Cichorium intybus*, 27.IX.1923, A. Ade (type of ***O. paradoxa***, not located). — Belgium, Wallonie, Liège, stem of *Angelica sylvestris*, undated, collector unknown (BR 090713-18, holotype of ***O. uvispora***).

Misapplied name: Feltgen (1901: 37, p.p.: on *Knautia*), as ‘*Orbilia* sp., aff. *O. rosella*’.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.4(–0.5) mm diam., 0.09–0.18 mm high, (pale to) light (to bright) rose to orange, very rarely with a shade of yellow (but pale yellow in the type, according to Feltgen), often translucent, round or sometimes broadly elliptical, very scattered to medium gregarious, hymenium slightly concave to flat; disc often finally slightly to medium convex, margin 0–5 µm protruding, irregularly finely crenulate, rarely smooth, thick in young apothecia, exterior glabrous; broadly sessile, erumpent between fibres, also seemingly superficial; dry apothecia light to deep orange. **Asci** *(54–)60–85(–109) × (6.7–)7–8.8(–9.3) µm {15}, †49–73(–82) × (5.7–)6–7(–7.5) µm {10}, 32-spored, very rarely some asci with only ~16 spores {2}, pars sporifera *(28–)33–49 µm long, †36–46 µm {type}, 10–16 lower spores inversely oriented {7}, usually mixed in the middle part only; **apex** (†) slightly to medium (to strongly) (conico-)truncate, hemispherical in profile view, dome †0.5–0.8(–1) → 0.3–0.4 µm thick {5}, with a low apical chamber; **base** with short or ± long undulating stalk, T-, L-, h- or rarely H-shaped. **Ascospores** *(3.8–)5–8(–9.7)((–10.5)) × (2–)2.2–2.8(–3)((–3.2)) µm {24}, †4–7 × 1.7–2.5 µm {5}, ellipsoid to often ellipsoid-clavate, also subcylindrical or fusoid, apex rounded to obtuse, rarely with a tail-like base, straight or quite often slightly to strongly curved near base (comma-shaped); **SBs** 0.4–0.7(–0.9) × 1.2–1.6 µm {7}, lens-shaped, apically broadly attached; with a few minute **LBs**. **Paraphyses** apically uninflated or often slightly to medium or even strongly clavate-capitate, often irregular in shape, terminal cell *(5–)7–17(–22) × (2–)2.5–5(–5.5) µm {13}, †1.5–3.5(–4.5) µm wide {4}, lower cells *8–14.5(–18) × 1.2–2(–3) µm {6}, †8–12 × 0.8–1.5 µm {2}, enlarged to *2–2.5(–2.8) µm near base and apex, quite often di(-tri)chotomously branched near apex. **Medullary excipulum** pale rose, 20–30 µm thick, of dense textura angularis, indistinctly delimited. **Ectal excipulum** very pale rose, of thin-walled t. globulosa-angularis from base to mid flanks or margin, 25–40(–55) µm thick near base, cells *5–15(–21) × 5–13(–18) µm {4}, oriented irregular or horizontal (though cells vertically elongate); 15–30 µm thick at flanks and margin, oriented at a 0–10° or up to 80° angle, cells *6–9 × 6–10 µm, slightly to strongly thick-walled (common walls †0.5–1(–1.5) µm thick), marginal cortical cells elongate, *5–15 × 3–4.5 µm {4}, cylindric-clavate. **Anchoring hyphae** especially near base, at flanks forming a thin appressed layer, */†2–3.5(–4) µm wide, walls 0.2–0.4(–0.8) µm thick {3}. **SCBs** globose, in terminal cells of paraphyses 1.5–3.5 µm diam., low-refractive, 1(–2) per cell; in marginal cortical cells 1.5–3(–4) µm diam. **Exudate** pale yellowish(-amber), over paraphyses 0.3–0.8 up to 1–2(–3) µm thick, continuous or ± cloddy, loosely attached; over margin thin. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1}). **Conidiophores** not observed. **Conidia** Y-shaped, total size *30–36 × 17.5–30.5 µm {1}, stipe *17.5–25 × 4.3–5.5 µm, 2–3-septate, arms tapering, *9–16.5 × 3–4.3 µm, 1–2-septate, a single unbranched phragmoconidium seen: *37 × 4.5 µm, 4-septate.

Habitat: collected on dry ground or 0.05–5 m above the ground, 1(?–2) years old, 6–35 mm thick herbaceous stems, rarely petioles of *Aeonium arboreum* {1}, *Agave americana* {1}, *Apiaceae* {2}, *Arecales* {1}, *Echinops sphaerocephalus* {4}, *Echium vulgare* {1/2}, *Epilobium* ?*angustifolium* {1}, *Euphorbia wulfenii* {1}, *Foeniculum vulgare* {3}, *Heracleum mantegazzianum* {1}, *H. sphondylium* {2}, *Knautia arvensis* {1}, *Melilotus* sp. {4}, *M. albus* {2}, *Rubus fruticosus* {1}, ?*Rumex* {1}, *Sambucus ebulus* {2}, *Seseli libanotis* {1}, *Tanacetum vulgare* {1/1}, *Urtica dioica* {1}, *Verbascum* sp. {1}, *V. densiflorum* {1}, *V. lychnitis* {1}, *Yucca* sp. {3}, *Y. gloriosa* {1}, on epidermis or often on areas devoid of epidermis; or on 5–40 mm thick, partially decorticated branches of *Acacia* sp. {1}, *Clematis vitalba* {1}, *Cytisus scoparius* {1}, *Ficus carica* {1}, *Mahonia dictyota* {1}, *Parthenocissus quinquefolia* {1}, *Salix* sp. {3}, *S.* (?)*caprea* {1}, also on textile {1}, on wood {9} or bark (bast) {5}, outer 0.1–0.3 mm slightly to strongly decayed, slightly to strongly greyed and covered with green algae, sometimes in old beetle galleries. **Associated**: *Bulbillomyces* sp. {1}, ?*Calloriopsis* sp. {1}, *Cistella grevillei* {4}, ?*Cucurbitaria* sp. {1}, *Cyathicula cacaliae* {1}, *C. cyathoidea* {1/1}, *C. nigrofusca* {1}, ‘*Dasyscyphus*’ *castaneus* {1}, *Diaporthe* sp. {1}, *D. arctii* {1}, *Eutypella*

?*scoparia* {1}, *Hydropisphaera arenula* {1}, *Karstenia rhopaloides* {1}, *Lachnella alboviolascens* {3}, *L. villosa* {7}, ?*Laetinaevia* sp. {1}, *Lecanora* sp. {1}, *Leptospora rubella* {1}, *Lewia scrophulariae* {1}, *Mollisia ligni* {1}, *Nectria* sp. {1/1}, *Neodasyscypha cerina* {1}, *Olla millepunctata* {1}, *O. scrupulosa* {1}, *Orbilia albovinosa* {1}, *O. aristata* {2}, *O. bicknellensis* {2}, *O. caulicola* {8}, *O. cylindrosoma* {5}, *O. eucalypti* {1}, *O. flavidorosella* {2}, *O. lentiformis* {1}, *O. ?obtusispora* {1}, *O. ocellata* {2}, *O. pleiolentiformis* {1}, *O. quaestiformis* {12}, *Orbilia serpentina* {1}, *O. subclavuliformis* {2}, *O. ungulata* {4}, *O. vibrioides* {1}, *O. ?vinosa* {1}, *O. vitalbae* {4/1}, *Patellaria atrata* {3}, ?*Phoma* sp. {3}, *Phyllactinia guttata* {1}, *Pseudolachnea hispidula* {1}, *Pyrenopeziza ?escharodes* {1}, *P. ?rubi* {1}, ?*Ramichloridium schulzeri* {1}, *Stictis ?stellata* {1}, *Trichopeziza* aff. *mollissima* {3}, *T. lizonii* {1}, *T. ?perrotioides* (immature) {1}, *T. sulphurea* {1}, *Unguiculariopsis ilicincola* {1}, *Urceolella crispula* {1}, *U. ?pani* {1}, *Xanthoria parietina* {1}. **Desiccation tolerance**: fully viable for at least 5 months. **Altitude**: 196–435 m a.s.l. (cold-temperate Europe), 1–1017 m (subatlantic to mediterranean Europe), 1195 m (Macaronesia). **Geology**: Devonian slate, Buntsandstein, Keuper (marl & sandstone, Minette), Lower to Upper Jurassic shale, sand- & limestone, Quaternary sand, loess; mica schist, basaltic flow. **Phenology**: (II–)IV–XI (long-lived).

Phenology of *O. flavida*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
0	2	1	2	4	8	11	7	7	4	6	0

Taxonomic remarks. *Orbilia flavida* is characterized by 32-spored asci and rather small, ellipsoid-clavate, partially curved ascospores. It differs from the similar North American *O. plurilentiformis* in smaller spores. Small-spored populations of *O. pleiolentiformis* differ from *O. flavida* mainly in 16-spored asci. *O. myriolentiformis* deviates in 64-spored asci, also in larger spores and, therefore, much larger asci.

The multispored asci of *O. flavida* and its characteristic SBs were overlooked by J. Feltgen who studied the species only in the dead state (see below). We here designate a Croatian specimen (Korčula, on *Euphorbia*, ex H.B. 6716, Pl. 172: 4), from which a sequence was gained, as **epitype** of *O. flavida*.

Variation. The examined collections of *O. flavida* showed little variation among each other. Even the two samples from North America match the European ones very well. However, as in the other species of series *Lentiformes*, spore length varies rather strongly within a single ascus. Only the collection from Asturias studied by E. Rubio (pers. comm.) showed unusually broad spores (7–8 × 2.8–3.2 µm, size evaluated from scale), appearing intermediate to the North American *O. plurilentiformis*.

Type studies. The holotype of ***O. flavida*** in LUX contained three apothecia when reexamined, contrary to Hein (1976) who suspected the material to be empty. Although the asci of the two tested apothecia were 32-spored (Fig. 172: 2), *O. flavida* was originally described as '8-spored, spores 1½–2-seriate'. Apart from this and the sporoplasm, which Feltgen figured and described with 'one oil drop in each end', protologue and Feltgen's drawing on the label (Fig. 152) fully concur with the present documentation regarding paraphysis and ascospore shape and size (see Tab. 64).

Sections of the two apothecia possessed asci with a spore number of at least 25–30. The lens-shaped SBs at the broader end of the spores were clearly visible as a slightly refractive region that is clearly separated from the detached cytoplasm, but only when adding ample MLZ or IKI to the KOH mount (Pl. 172: 2a–b).

Feltgen described the apothecia as 'pale yellow, yellow when dry'. Another collection from Luxembourg (on *Knautia*), being referable to *O. flavida* according to our reexamination, was identified by Feltgen (1901: 37) as '*Orbilia* sp., related to *O. rosella*' and described by him as 'pale yellowish-reddish' and again with 8-spored asci (IVV: H.B. 7305). We have almost never noticed a yellow tint in *O. flavida*, but instead a pale rose or orange colour. Possibly, the report of a yellowish component is due to examination under sunlight or a light source with a high yellow proportion.

We have never encountered 8-spored asci in *O. flavida* and only very exceptionally a few with 16 spores. Feltgen obviously overlooked polyspory in this species, perhaps as a consequence of his preparation method which killed the asci, with the result that spores were difficult to discern inside. On the other hand, we frequently found *O. flavida* growing in association with other species of *Orbilia*, mainly such with 8-spored asci, therefore, the possibility cannot be excluded that the holotype was a mixture, and Feltgen's description refers at least partially to an 8-spored taxon. Candidates which more or less fit his drawing are *O. ungulata*, *O. vitalbae*, *O. caulicola*, or *O. cylindrosoma*. However, when comparing measurements taken from the two collections studied by him (Tab. 64), it seems clear that he was dealing with the same fungus as now found in his voucher specimens.

Höhnel (1906: 1276) examined the type material of *O. flavida* and found only a single 'immature' pale reddish apothecium which he confirmed to belong to the genus *Orbilia*. Possibly, the asci he saw were mature and the spores inside masked by the refractive ascoplasma, in the case he did not apply staining agents. Based on Feltgen's description, Höhnel could not see major differences to *O. flavidorosella*, a species which is treated in the present study in section *Habrostictis*, and which seriously differs from *O. flavida* in truncate ascus apices and fusoid spores with subulate SBs.

Not included collections. Type material of ***O. paradoxa*** could not be located in S. In the protologue, Ade (1924) reported the apothecia to grow very sparsely at the base of dry rotten bracts of the flower heads of *Cichorium intybus*, 'am Apfelberg zwischen Hochhausen und Gamburg auf dem linken Tauberufer, 27. Sept. 1923'. Ade's description regrettably lacks any illustration, but strongly suggests identity with *O. flavida*. The main part of the description runs as follows: 'asci 16–24-spored, rounded above, 70–75 × 6–7 µm, spores comma-shaped, mostly curved, 7–9 × 3–4 µm, at the rounded and broader upper end

Table 64. *Orbilia flavida* in Feltgen's herbarium as described by Feltgen and reexamined in the present study.

Specimen	Element	Feltgen	Present study
holotype LUX 042552	Asci	†55–62 × 7–8 µm	†60–63 × 5.7–6.5 µm
	Ascospores	4–8 × 2.5–3 µm	†4–6.2 × 1.7–2.1 µm
	Spore number	8	32
'*Orbilia*. sp. aff. *rosella*' LUX 042439	Asci	†45 54 × 5–6 µm	†52–65 × 5.7–6.5 µm
	Ascospores	†5–6 × 2 µm	†4.5–6 × 2–2.4 µm
	Spore number	8	32

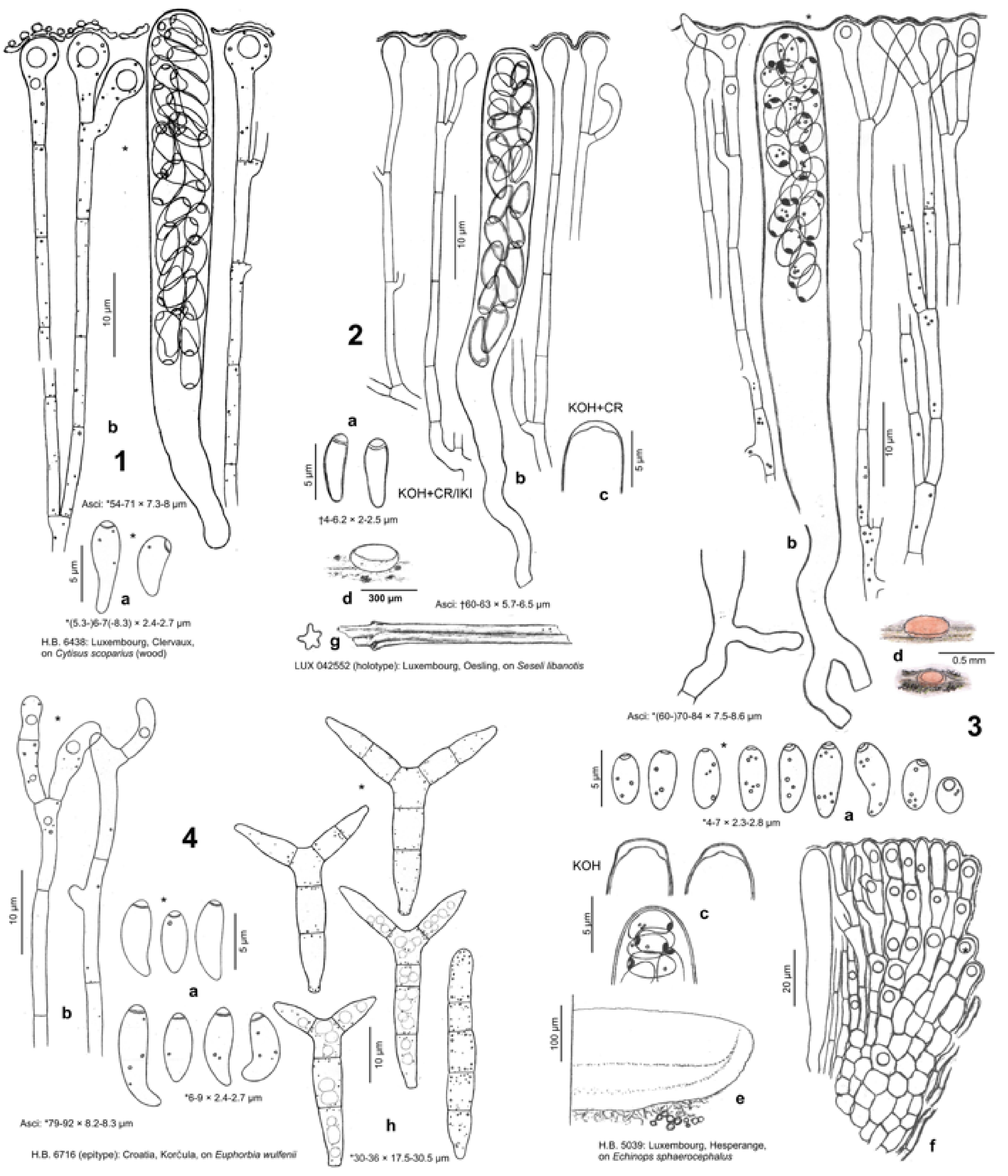


Plate 172. **1–4**: *Orbilia flavida*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. dead herbaceous stem (on the left in cross section); **h**. conidia from culture.

always provided with a strongly refractive polar spot.' The report of a striking apical spore body indicates that Ade studied living material. The spore width is larger than in our description of *O. flavida*. It might either be erroneous, although the ascus size fits perfectly, or it is due to the formation of oversized spores combined with a reduced spore number.

The holotype of ***O. uvispora*** in BR (Belgium, Liège, on stems of *Angelica*, BR 090713-18) was reexamined by both Dennis and Spooner, and found to be devoid of apothecia that resemble an *Orbilia*, according to their revision labels. In the present examination, a single apothecium (rehydrated 0.15 mm diam) was found, which undoubtedly belongs to the described taxon, but only immature asci were seen (Pl. 173: 5). The observed microscopic features confirm Mouton's (1900) placement in *Orbilia*. The asci have a hemispherical (truncate-conical), distinctly thick-walled (0.7–0.8 µm) apex, hence the species

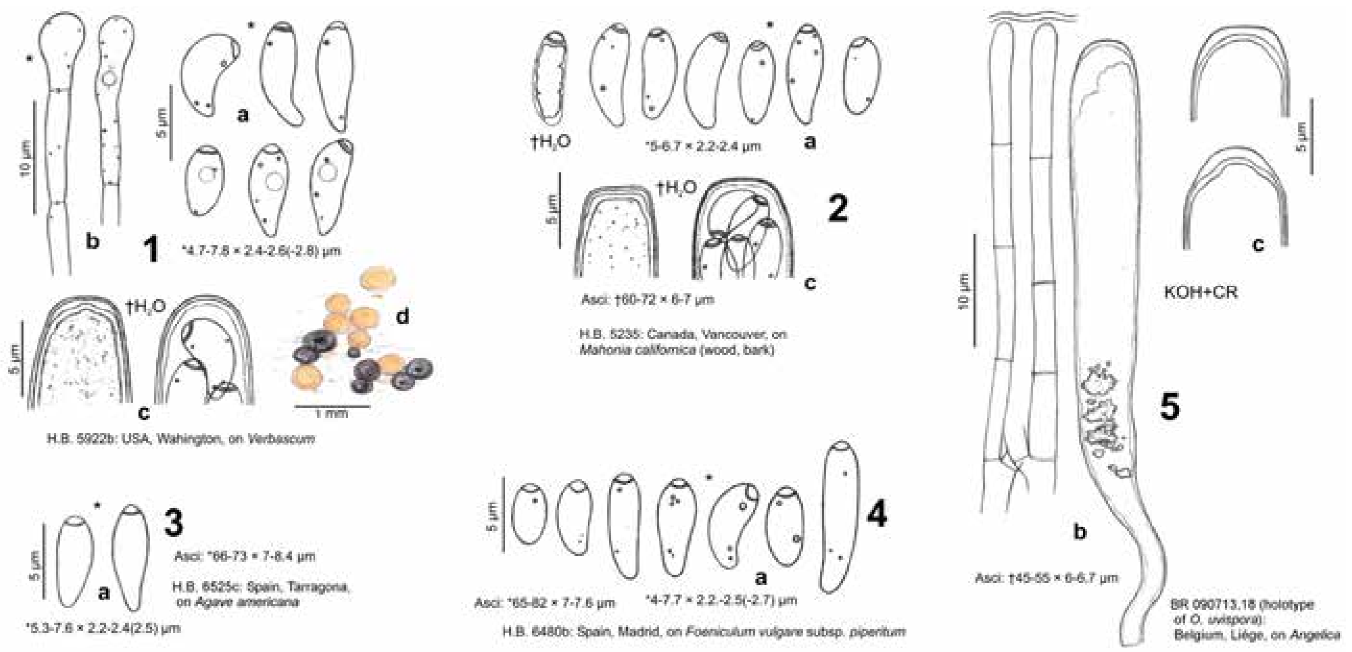


Plate 173. **1–4**: *Orbilia flavida*; **5**: *O.* cf. *flavida*. – **a**. ascospores; **b**. ascus (immature) and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia (**1d**. with ?*Phoma*).

belongs either in section *Lentiformes* or in sections *Hemiorbilia* or *Ovoideae*. The shape of the spores as drawn by Mouton might indicate that *O. uvispora* belongs in the neighbourhood of *O. vibrioides* (series *Vibrioides* of section *Hemiorbilia*). Regrettably, Mouton did not report spore bodies. In any case, the indicated spore size (6–7 × 2.5 µm) excludes the lignicolous *O. vibrioides* as well as the graminicolous *O. graminis* which both have smaller, more homopolar and more strongly curved spores, and also a much thicker apical ascus wall. Another member of section *Hemiorbilia*, *O. subcryptogena* (series *Hesperideae*), shows a similar spore shape and size but differs in 16-spored asci (*O. uvispora* is reported as 8-spored) and occurrence on woody substrate in North America. Within section *Ovoideae*, only extra-European taxa resemble *O. uvispora* to some extent.

Another possible relationship of *O. uvispora* points to series *Lentiformes*. Here the spores are often similarly curved and clavate as those reported for *O. uvispora*. Spore size as stated by Mouton, and also ascus apical thickening would fit *O. flavida*. A comparison of the size of here examined immature asci with the spore size as given by Mouton suggests that the asci contained more than 8 spores. If *O. uvispora* and *O. flavida* are in fact synonyms, then both Feltgen and Mouton neglected the lens-shaped spore bodies as well as ascus polyspory in their material. *O. uvispora* was described 4 years earlier, but its identity could not sufficiently be ascertained, therefore, we here adopt *O. flavida* as the oldest available name.

Anamorph. A few conidia were obtained in pure culture of one species (Pl. 172: 4), but only after flooding with water. They resemble *Trinacrium robustum* but have shorter arms. In a water agar plate of the same strain, mature apothecia developed in the presence of sterilized wood fragments after about 3 months, but here no conidia were seen.

Phylogeny. The single available sequence of *O. flavida* (Croatia, on *Euphorbia*, H.B. 6716, from pure culture, SSU+ITS+LSU) clustered in the *flavida-cucumispora* clade, though with a distance of 7–10.5 % in the ITS region to other species of this clade, with a minimum distance to *O. ocellata* (7 %, 0.5 % in LSU). Surprisingly, the similar *O. plurilentiformis* shows a 10 % ITS distance to *O. flavida* (1 % in LSU), though clustering also in the *flavida-cucumispora* clade.

Ecology. *O. flavida* preferably grows on rotten, xeric herbaceous stems, but also occurs on rotten wood and bark of xeric branches of different angiosperm trees and shrubs. To the present knowledge, the area of distribution includes supra- to mesotemperate (rarely orotemperate, Auvergne) humid or mesosub- to thermomediterranean semihumid, oceanic to subcontinental zones of Europe. The species also occurs in the thermomediterranean semihumid Canary pine forest (*Sideritido solutae-Pinetum canariensis cistetosum monspeliensis*), and in the mild-maritime humid lower pacific coastal region south of the Coast Mountains in the northwest of North America. *O. flavida* is not uncommon in central and southern Europe, yet no records from more northern and eastern areas came to our attention. The species appears to prefer thermophilous, sun-exposed sites in which the substrate rapidly dries out. In central Europe and North America these were usually sun-exposed, more or less ruderal places like quarries or railway tracks.

Specimens included. **LUXEMBOURG**: **L'Oesling**, **Diekirch**, 4.5 km SW of Diekirch, W of Ettelbruck, railway station, 196 m, branch of *Salix*, 6.VII.2002, G. Marson (ø). – ibid., stem of *Melilotus* (ø). – **Vianden**, ~5 km NNW of Diekirch, Brandenbourg, ?400 m, stem of *Seseli libanotis*, 7.VIII.1902, J. Feltgen (LUX 42552, **holotype** of *O. flavida*, H.B. 5358 ø). – **Clervaux**, 7.5 km NNW of Clervaux, Troisvierges, railway station, 422 m, stem of *Verbascum densiflorum*, 23.VII.1999, G. Marson (H.B. 6439a). – ibid., branch of *Cytisus scoparius*, on wood, 23.VII.1999, G. Marson (H.B. 6438). – **Gutland**, **Mersch**, 4.5 km S of Larochette, 1 km N of Koedange, Folkend, 293 m, on petioles of *Arecales* (deposited there since maybe a year), 23.VI.2005, G. Marson (H.B. 7820 ø). – **Grevenmacher**, 17 km NE of Luxembourg, 2.9 km NNE of Junglinster, Appelescht, 310 m, stem of *Sambucus ebulus*, 27.VIII.2004, G. Marson (ø). – **Capellen**, 6.5 km NW of Luxembourg, 3 km SW of Kopstal, Juckelsbusch, 340 m, stem of *Knautia arvensis*, 27.VIII.1900, V. Noppeney, vid. J. Feltgen (LUX 42439, as '*O.* aff. *rosella*', H.B. 7305 ø). – **Luxembourg**, 2 km SSW of Luxembourg, 0.5 km S of Hollerich, railway station, stem of *Echinops sphaerocephalus*, 280 m, 24.IX.1998, G. Marson (ø). – 2.5 km S of Luxembourg, SW of Bonnevoie, Zwickau, railway depot, 285 m, stem of *Heracleum sphondylium*, 17.IX.1998, G. Marson (H.B. 6253). – ibid., stem of ?*Rumex*, 29.VII.2002, G. Marson (H.B. 7185). – ibid., stem of *Rubus fruticosus* (on bark) and branch of *Salix* (on wood), 29.VII.2002, G. Marson (ø). – ibid., stem of *Heracleum sphondylium*, 4.VIII.2005, G. Marson (H.B. 7869g). – ibid., stem of *H. mantegazzianum*, 11.IX.2010, G. Marson (ø). – 3.5 km S of

Plate 174. **1–9**: *Orbilia flavida*. – **1a**. railway track, dead stems of *Urtica* and *Heracleum* lying on dry gravel; **2a**. dry stem of *Heracleum sphondylium*; **2b–c**, **3**, **4a–c**, **5a**, **6**, **7**. apothecia rehydrated, except for **4b**; **4d**. apothecium in median section; **1b**, **5b–c**, **8**. mature asci; **9**. ascospores. – Living state, except asci in **5c** (in H_2O) and **8** (in CRB); phot. **8**: J.P. Priou. — **1a–b**. H.B. 9209d: Luxembourg, Dudelange, on *Urtica*; **2a–c**. 14.X.2009: ibid., on *Heracleum*; **3**. H.B. 5110a: ibid., on *Melilotus*; **4a–d**. H.B. 7558: Luxembourg, Howald, on ?*Echium*; **5a–c**. H.B. 7869g: Luxembourg, Bonnevoie, on *Heracleum*; **6**. H.B. 7909: Germany, Tübingen, on *Melilotus*; **7**. H.B. 7231: France, Drôme, on *Ficus*; **8**. J.P.P. 28188: France, Vendée, on *Yucca*; **9**. 11.IX.2010: Luxembourg, Bonnevoie, on *Heracleum*.

Luxembourg, 0.7 km SW of Howald, 285 m, stem of indet. *Apiaceae*, 31.V.1999, G. Marson. – ibid., stem of ?*Echium vulgare*, 22.VII.2004, G. Marson (H.B. 7558). – 5.5 km SSE of Luxembourg, 1.2 km SSW of Hesperange, Fentange, Wéineguecht, 272 m, stem of *Echinops sphaerocephalus*, 20.III.1994, G. Marson (H.B. 5039). – ibid., stem of *E. sphaerocephalus*, 28.IV.1994, G. Marson & H.O. Baral (H.B. 5070a). – 6 km SSE of Luxembourg, 0.8 km SE of Fentange, Wénkel, 265 m, stem of *Tanacetum vulgare*, 29.V.2002, G. Marson (ø). – stem of *Melilotus*, 29.VII.2002, G. Marson (ø). – stem of *Echium vulgare*, 7.VIII.2004, G. Marson (ø). – **Esch-sur-Alzette**, 7 km S of Luxembourg, 1 km NE of Bivange, Lëschebann 266 m, stem of *Echinops sphaerocephalus*, 17.II.1994, G. Marson (G.M. 5196). – 3 km SE of Differdange, 1.3 km SW of Belvaux, Metzerbierg, 393 m, stem of *Melilotus albus*, 24.IV.2005, G. Marson (ø). – 2.5 km NE of Dudelange, 1.5 km SSW of Bettembourg, railway station, 275 m, branch of *Salix* ?*caprea*, on bark & wood, 15.VI.1994, G. Marson (H.B. 5119b, G.M. 5197). – ibid., stem of ?*Tanacetum vulgare*, 15.VI.1994, G. Marson (ex H.B. 5108a, M-0206385, in holotype of *Helicogonium cyathiculae*). – ibid., stem of *Epilobium* ?*angustifolium*, 15.VI.1994, G. Marson (H.B. 5110c). – ibid., stem of *Melilotus*, 15.VI.1994, G. Marson (H.B. 5110a). – ibid., stem of *Urtica dioica*, 19.VII.2009, G. Marson (H.B. 9209d ø). – ibid., stem of ?*Echium vulgare*, 9.VII.2002, G. Marson (H.B. 7167b). – ibid., stem of *Heracleum sphondylium*, 14.X.2009, G. Marson (ø). – ibid., stem of *Melilotus*, 27.V.2007, G. Marson (ø). – 3 km W of Esch-sur-Alzette, Belval Usines, 310 m, stem of *Sambucus ebulus*, 10.VI.1999, G. Marson (H.B. 6406d). — **GERMANY**: **Baden-Württemberg**, 5.5 km NE of Tübingen, Pfrondorf, Blaihofstraße, 430 m, on a rope, 24.XI.2009, H.O. Baral (H.B. 9226l ø). – 2 km WNW of Pfrondorf, Hägnach, 435 m, stem of *Melilotus albus*, 2.X.2005, H.O. Baral (H.B. 7909 ø). — **FRANCE**: **Bretagne**, **Morbihan**, 16 km SE of Quiberon, Île de Houat, 0.7 km E of Houat, Tréac'h er Gourèd, 2 m, stem of *Foeniculum vulgare*, 14.XI.2008, J.P. Priou (J.P.P. 28228, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 2 km NE of Piriac-sur-Mer, NNE of Port au Loup, Plage Pors Er Ster, 9 m, inflorescence stem of *Yucca gloriosa*, 13.XI.2016, J.P. Priou (J.P.P. 16314b, doc. vid.). – **Vendée**, 38 km SW of Nantes, 2.3 km SW of Bourgneuf-en-Retz, Port du Collet, Beauvoir-sur-Mer, 1 m, inflorescence stem of *Yucca*, 20.X.2008, J.P. Priou (J.P.P. 28188, doc. vid.). – **Aquitaine**, **Gironde**, 20 km SW of Royan, 6 km SSW of Soulac-sur-Mer, l'Amélie, Arrière dune, 12 m, on leaves of *Yucca*, 20.XI.2011, O. Priou (J.P.P. 11205, doc. vid.). – 8 km SW of Royan, 6 km NE of Soulac-sur-Mer, 8 m, on leaves of *Yucca*, 20.XI.2011, J.P. Priou (J.P.P. 11216, non vid.). – **Auvergne**, **Haute-Loire**, 18.5 km ENE of Brioude, NW of Cistrières, 1017 m, stem of *Verbascum lychnitis*, 23.V.2018, E. Stöckli (E.S. 2018-25, doc. vid.). – **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, W of Col du Pontias, 415 m, branch of *Ficus carica*, on wood, 11.X.2002, G. Marson (H.B. 7231c). — **SPAIN**: **Asturias**, 7.5 km WSW of Pola de Lena, 2.2 km S of Bárzana, E of Ronderos, 600 m, twig of *Clematis vitalba*, on bark, 11.VI.2013, M.A. Miranda, vid. E. Rubio (E.R.D. 5903). – **Navarra**, 3 km

Map 25. Known distribution of *O. flavida* in Europe and Macaronesia (yellow: types of *O. uvispora* and *O. paradoxa*).

NE of Pamplona, Burlada, twig of *Parthenocissus quinquefolia*, on wood, 18.II.2020, F.J. Balda (F.J.B. 18220). – **Madrid**, 3.5 km NE of Alcalá de Henares, University Campus, 610 m, stem of *Foeniculum vulgare*, 23.IX.1999, H.O. Baral & G. Marson (H.B. 6480b). – **Com. Valenciana**, **Castellón**, 13.5 km NNW of Castellón, 3.2 km WSW of Vilafamés, along road Camí de Costur, 400 m, stem of *F. vulgare*, 27.IX.1999, H.O. Baral & G. Marson (H.B. 6509e). – **Cataluña**, **Tarragona**, 3.7 km E of Tarragona, 7 km WSW of Altafulla, Cala Romana, 12 m, on inflorescence stem of *Agave americana*, 28.IX.1999, G. Marson & H.O. Baral (ø). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 8.5 km W of Korčula, Pupnat, 340 m, stem of *Euphorbia wulfenii*, 11.VI.2000, H.O. Baral (ex H.B. 6716, M-0291761, **epitype** of *O. flavida*, anam. cult., CBS 140807; sq.: KT215228). — **TURKEY**: **Marmara**, **Balıkesir**, 9 km W of Balıkesir, 2.1 km ENE of Çağdaskent, Edremit Yolu, 262 m, wood of *Salix*, 22.IX.02, T. Askun (T.A. 16, doc. vid.). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Vilaflor, 2.5 km SE of Vilaflor, 1195 m, branch of *Aeonium arboreum*, on wood, 19.IV.2012, L. & C. Quijada (TFC Mic. 23640, doc. vid.). — **CANADA**: **British Columbia**, 10 km W of Vancouver, University of British Columbia, west side of Walter Gage building, 90 m, branch of *Mahonia dictyota*, on wood & bark, 16.VIII.1994, G. Marson (H.B. 5235, D.H.P.). — **USA**: **Washington**, 14 km S of Acme, 5 km S of Whatcom, near rail track, 82 m, stem of *Verbascum*, 15.VIII.1997, G. Marson (H.B. 5922b).

Not included. **BELGIUM**: **Wallonie**, **Liège**, ~10 km SO of Liège, Beaufays, ~280 m, stem of *Angelica sylvestris*, undated, collector unknown (BR 090713-18, **holotype** of *O. uvispora*, H.B. 7643 ø). — **GERMANY**: **Baden-Württemberg**, ~6 km NNW of Tauberbischofsheim, ~2.5 km SE of Gamburg, Apfelberg towards Tauber valley, ~250 m, bracts of flower heads of *Cichorium intybus*, 27.IX.1923, A. Ade (**type** of *O. paradoxa*, not located).

Orbilia plurilentiformis Baral & G. Marson, **sp. nov.**, MB 813489 — Pls 175–176, Map 26

Etymology: named after the 32-spored asci and the lens-shaped spore bodies.

Typification: USA, Utah, Moab, branch of *Artemisia filifolia*, 18.VI.2000, G. Marson (ex H.B. 6740c, M-0276565, holotype; ex-type culture: CBS 140805; sq.: KT215230, MH878180).

Latin diagnosis: *Similis* Orbiliae flavidae *sed asci et ascosporae latiores, habitat ad lignum et corticem ramulorum siccorum fruticum in locis temperatis semiaridis ad borealis humidis Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.16–)0.22–0.55(–0.65) mm diam., 0.17–0.2 mm high, (light to) bright yellowish-) orange(-rose), round to slightly elliptical, scattered to subgregarious; disc flat, margin distinct, 0–10 µm rising above disc, even; externally somewhat whitish-rough, sessile, slightly or distinctly erumpent through small slits in the wood; dry deep orange. **Asci** *(60–)70–105(–120) × (8.4–)9–11(–12) µm {5}, †(55–)65–85(–93) × (7.3–)8–9.5 µm {4}, 32-spored, spores ± 4-seriate, lower spores inversely oriented (mixed), pars sporifera *45–70 µm long; **apex** (†) slightly to medium (rarely strongly) truncate, hemispherical in profile view, dome †1–1.4 → 0.7–1 µm thick {3}, with a narrow or wide, low apical chamber; **base** with short, thick, ± flexuous stalk, L-, T- or Y-shaped. **Ascospores** *((5.8–))7–10.5(–11.3) × (2.8–)3–3.6(–4)((–4.5)) µm {6}, †7–10 × 2.8–3.3 µm {3}, ellipsoid-clavate, also cylindric to ellipsoid-fusoid, apex rounded to obtuse, base slightly to strongly tapered, sometimes tail-like, straight or often slightly to strongly curved in the basal part; **SBs** *0.5–1 × 1.1–1.5 µm {4}, lens- to slightly plug-shaped, apically broadly attached; **LBs** ± sparse, small. **Paraphyses** apically slightly (to medium) clavate-capitate (to moniliform or lageniform), rarely cylindrical, terminal cell *(4–)6–17(–22) × 2.2–4(–4.5) µm {4}, lower cells *8–20 × 1.6–2.5 µm {4} (sometimes up to 3–4 µm wide near base or below terminal cell); medium to very frequently di(-tri) chotomously branched near apex {5}. **Medullary excipulum** hyaline, 40–70 µm thick, upper part of dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a 10–20 µm thick layer of t. porrecta. **Ectal excipulum** pale rose-orange, 25–40 µm thick near base, of thin-walled († slightly gelatinized), horizontal or vertical t. angularis(-prismatica), cells *7–12(–18) × 7–10 µm {1}; 15–30 µm thick at flanks and margin, at margin of t. angularis or t. prismatica-porrecta oriented at a 0–40° angle, marginal cortical cells *6–14 × 3.5–5 µm {2}. **Anchoring hyphae** sparse to abundant, *3–4 µm wide, †1.5–2.5 µm, walls 0.2 or 0.5–0.7 µm thick {2}, often extending up to margin as a 15–20 µm thick hyaline layer of ± gelatinized t. intricata-porrecta. **SCBs** globose, low-refractive, in paraphyses 1.2–2.5 µm diam.; in marginal excipular cells 1.5–2.8 µm. **Exudate** over paraphyses and margin 0.2–0.5(–1.5) µm thick, continuous or granular, loosely attached, hyaline. — **ANAMORPH**: unknown (no conidia developed in culture).

Habitat: collected 0.1–1 m above the ground, corticated to decorticated, 4–14 mm thick branches of *Artemisia filifolia* {2}, *A. tridentata* {1}, *Baccharis salicifolia* {1}, *Ericameria nauseosa* {1}, *Krascheninnikovia lanata* {2}, on 0.2 mm deep (medium to) strongly decayed wood {4} and bark {2}, medium to strongly greyed, with a few or many green algae. **Associated**: (?)*Coniochaeta* sp. {1}, *Orbilia bicknellensis* {2/1}, *O. delphinus* {1}, *O. dixiensis* {1}, *O. lentiformis* {2}, *O. macrodelphinus* {1}, *O. mesaverdiana* {2}, *O. multigambelii* {1}, *O. multimaeandrina* {3}, *O. multiphanosoma* {2}, *O. multitrapezoidea* {1}, *O. myriophanosoma* {1}, *O. ocellata* {4}, *O. serpentina* {1/1}, *O. subsiculispora* {1}, *Patellaria* ?*atrata* {1}, *Schizoxylon* sp. {1}, *Symbiotaphrina desertorum* {2}, *Teichospora* sp. {2}, *Teichosporella dura* {1}. **Desiccation tolerance**: fully viable for at least 6 months, after 24 months still some submature asci alive. **Altitude**: 1427–2450 m a.s.l. **Geology**: Triassic-Jurassic-Cretaceous (red) sand- and mudstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia plurilentiformis* is characterized by 32-spored asci and medium-sized, ellipsoid-clavate ascospores. The similar *O. flavida* is sharply delimited by distinctly narrower and slightly shorter asci and spores, and in a temperate to mediterranean distribution. The mediterranean *O. myriolentiformis* differs in larger, 64-spored asci and larger apothecia.

Variation. Little variation was noted among the collections, which mainly concerns spore width and shape.

Phylogeny. The single sequence of *O. plurilentiformis* (Utah, on *Artemisia*, from pure culture, SSU+ITS+LSU) clustered unexpectedly in vicinity of *O.* aff. *lentiformis* (H.B. 8002c) and *O. cucumispora*, with an ITS distance of 6.3 and 7% (LSU 0.5%), respectively, whereas the distance to *O. flavida* lies at 10% (LSU 1%).

Ecology. *O. plurilentiformis* inhabits rotten wood and bark of xeric branches of various angiosperm shrubs under a very diverse climate: in warm-temperate to boreal, mainly semiarid but also subhumid to humid sagebrush and winterfat desert scrubs and pinyon-juniper woodlands of the Colorado Plateau in the southwest of Northern America.

Specimens included. **USA**: **Utah**, Utah Mts., Dixie Forest, 15 km SSE of Torrey, 5.5 km S of Grover, Lion Mt., 2450 m, on wood of *Artemisia tridentata*,

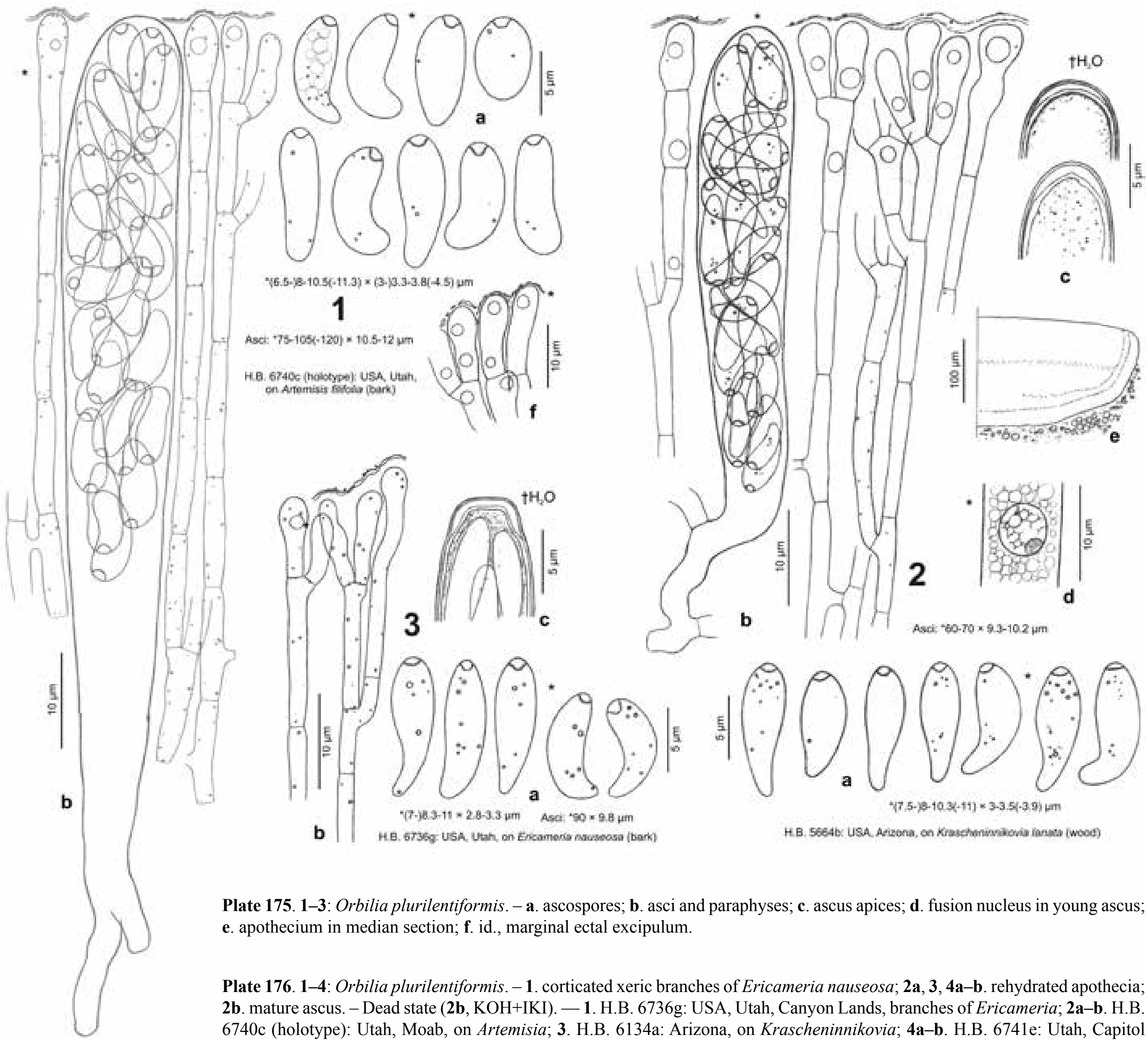
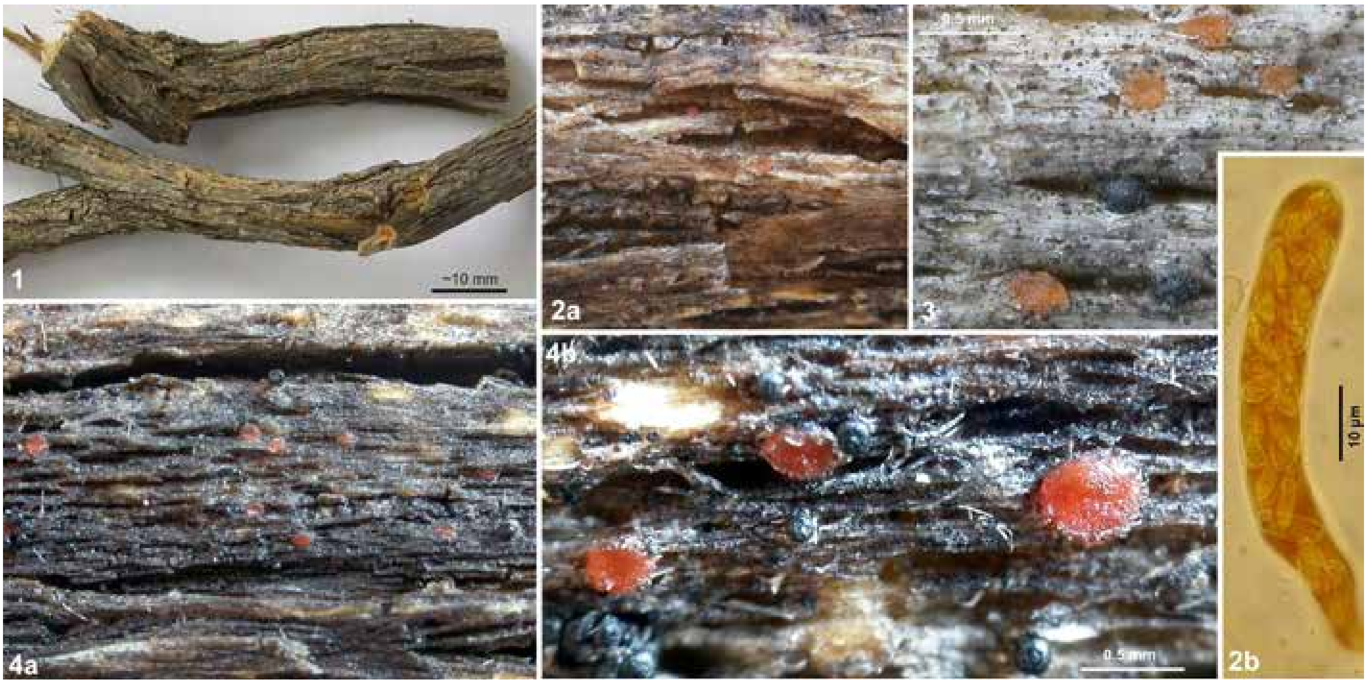


Plate 175. **1–3**: *Orbilia plurilentiformis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. fusion nucleus in young ascus; **e**. apothecium in median section; **f**. id., marginal ectal excipulum.

Plate 176. **1–4**: *Orbilia plurilentiformis*. – **1**. corticated xeric branches of *Ericameria nauseosa*; **2a**, **3**, **4a–b**. rehydrated apothecia; **2b**. mature ascus. – Dead state (**2b**, KOH+IKI). — **1**. H.B. 6736g: USA, Utah, Canyon Lands, branches of *Ericameria*; **2a–b**. H.B. 6740c (holotype): Utah, Moab, on *Artemisia*; **3**. H.B. 6134a: Arizona, on *Krascheninnikovia*; **4a–b**. H.B. 6741e: Utah, Capitol Reef, on *Baccharis*.



Map 26. Known distribution of *O. plurilentiformis* in North America.

15.V.1995, G. Marson (ø). – Canyonlands, Capitol Reef, 40 km WSW of Hanksville, 23 km E of Torrey, 1557 m, branch of *Baccharis salicifolia*, on wood, 19.VI.2000, G. Marson (H.B. 6741e). – Arches, 20 km NNW of Moab, Salt Valley Wash, 1427 m, branch of *Artemisia filifolia*, on bark, 18.VI.2000, G. Marson (ex H.B. 6740c, M-0276565, **holotype**, CBS 140805; sq.: KT215230, MH878180). – Canyonlands, 36 km S of Moab, 5 km WNW of Hatch Rock, 1813 m, branch of *Ericameria nauseosa*, on bark, 16.VI.2000, G. Marson (H.B. 6736g ø). – **Colorado**, Navajo, ~15.5 km SSE of Cortez, Mesa Verde, ~5 km NNW of Spruce Tree House, 2290 m, branch of *A. filifolia*, 31.V.1996, G. Marson (H.B. 6276d ø). – **Arizona**, Navajo, Petrified Forest, 12.5 km SW of Chambers, Navajo Travel Center, NE of North Entrance, 1730 m, branch of *Krascheninnikovia lanata*, on wood, 29.V.1996, G. Marson (H.B. 5664b). – ibid., 27 km ESE of Holbrook, S of South Entrance, 1645 m, branches of *K. lanata*, on wood, 29.V.1996, G. Marson (H.B. 6134a).

Orbilia myriolentiformis Baral & G. Marson, **sp. nov.**, MB 813490 — Pls 177–178

Etymology: named after the 64-spored asci and the lens-shaped spore bodies.
Typification: France, Drôme, Nyons, branch of *Cercis siliquastrum*, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (ex H.B. 9151g, M-0276530, holotype).

Latin diagnosis: *Similis* Orbiliae plurilentiformi *sed asci 64-spori, majores. Habitat ad corticem* Cercidis *in loco mesosubmediterraneo semihumido Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1 mm diam., 0.27–0.29 mm high, bright dirty orange, round, scattered, sometimes in groups of two; disc flat, finally slightly convex, margin indistinct to distinct, not rising above disc, even or finely rough to denticulate, broadly sessile, superficial, sometimes immersed in clefts of bark; dry somewhat contracted, deep dirty orange-red. **Asci** *120–138 × 10.7–12.5(–13) µm, †100–118 × 10–11(–12.5) µm, 64-spored (58 counted), spores ± 4-seriate, lower spores inversely oriented (strongly mixed), pars sporifera *85–95 µm long; **apex** (†) slightly to strongly truncate, hemispherical in profile view, dome †1–1.5 → 0.3–1.5 µm thick (KOH up to 1.7 µm), with indistinct apical chamber; **base** with short to medium long, thick, ± flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(7–)8–11(–12) × (2.8–)3–3.5(–3.7) µm, †7.5–10.5 × 2.8–3.4 µm, ellipsoid-clavate, apex obtuse, base medium to strongly attenuated, with or without a thick tail, straight or basal part often slightly to strongly curved or geniculate; **SBs** *0.9–1.1 × 1.3–1.5 µm, lens- to slightly plug-shaped, apically broadly attached; **LBs** ± sparse, small. **Paraphyses** apically uninflated to medium (also strongly) clavate, sometimes lageniform, terminal cell *5–16 × (2.5–)3–4.5(–5.5) µm, lower cells *10–18 × 1.7–2.6 µm (up to 2.5–3.8 µm wide below terminal cell); unbranched or frequently dichotomously branched near apex. **Medullary excipulum** hyaline, 70–80 µm thick, of dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a 5–7 µm thick layer of t. porrecta. **Ectal excipulum** hyaline, 35–55 µm thick near base, of (†) ± distinctly gelatinized, indistinctly oriented t. globulosa-angularis, cells *8–25 × (5–)7–13 µm; 40 µm thick at mid flanks, of t. prismatica-angularis oriented at a 40–50° angle, 20–30 µm thick at margin, of t. porrecta oriented at 10–30°, marginal cortical cells *7–12 × 2.5–3 µm; covered by a ~10 µm thick hyaline layer of slightly gelatinized t. intricata-porrecta. **Anchoring hyphae** abundant, *2–2.5 µm wide (2.5–3.5 µm at insertion), walls 0.2 µm thick, sometimes forming a gelatinized, dense, up to 70 µm thick t. intricata. **SCBs** globose, in paraphyses 1.8–3 µm diam., in marginal excipular cells 1.7–2 µm. **Exudate** over paraphyses and margin 0.2–2(–3) µm thick, continuous to granular or cloddy, loosely attached, hyaline. **— ANAMORPH**: unknown.

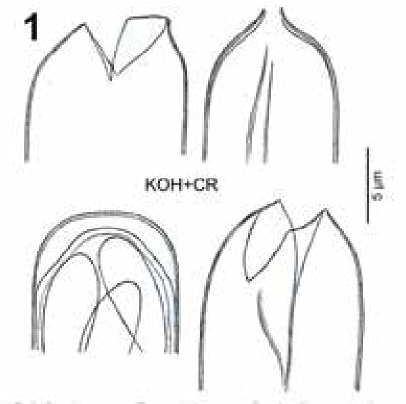


Plate 177. **1**: *Orbilia myriolentiformis* H.B. 9151g. – Ascus apices (3 emptied asci with a large split-like pore).

Habitat: collected ~1.5 m above the ground, corticated, 12 mm thick branch of *Cercis siliquastrum*, on medium decayed bark (bast), in cracks or holes of periderm, strongly greyed, with a few green algae. **Associated**: *Claussenomyces* sp., *Lecophagus vermicola*, *Nitschkia broomeana*, *Orbilia cercidicola*, *O. flagellispora*, *O. gambelii*, *O. myriosphaera*, *O. ocellata*, *O. subaristata*, *O. subclavuliformis*, *O. trapeziformis*. **Desiccation tolerance**: fully viable for at least 6 weeks. **Altitude**: 460 m a.s.l. **Geology**: Miocene sandstone near Cretaceous calcareous clay. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia myriolentiformis* is characterized by very large, 64-spored asci and medium-sized, ellipsoid-clavate ascospores. The similar *O. plurilentiformis* and *O. flavida* consistently differ in smaller, 32-spored asci and smaller apothecia, *O. flavida* also in smaller spores.

Ecology. *O. myriolentiformis* is only known from a single sparse collection (four apothecia) on rotten bark of a xeric branch of *Cercis* in a mesosubmediterranean semihumid maquis at the foothills of the Southern French Alps in southern Europe.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1 km N of Nyons, Col du Pontias, 460 m, branch of *Cercis siliquastrum*, on bark, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (ex H.B. 9151g, M-0276530, **holotype**).

Orbilia cucumispora Baral & G. Marson, **sp. nov.**, MB 813492 — Pls 179–180, Map 27

Etymology: referring to the shape of the spores resembling a cucumber.
Typification: USA, Arizona, Tusayan, branch of *Juniperus osteosperma*, 28.VIII.1994, G. Marson (ex H.B. 5178a, M-0276465, holotype).

Latin diagnosis: *Apothecia in statu rehydratata rosea, 0.25–0.5 mm diam. Asci 8-spori, apice in statu emortuo rotundati, modice crassitunicati. Ascosporae *11–22 × 4–5.7 µm, plus minusve curvatae, forma cucumeris, in statu vivo prope apicem corpusculum refringens obturamentiformem vel cylindricum continentes. Paraphyses ad apicem leniter clavatae, exsudato tenui hyalino tectae. Habitat ad*

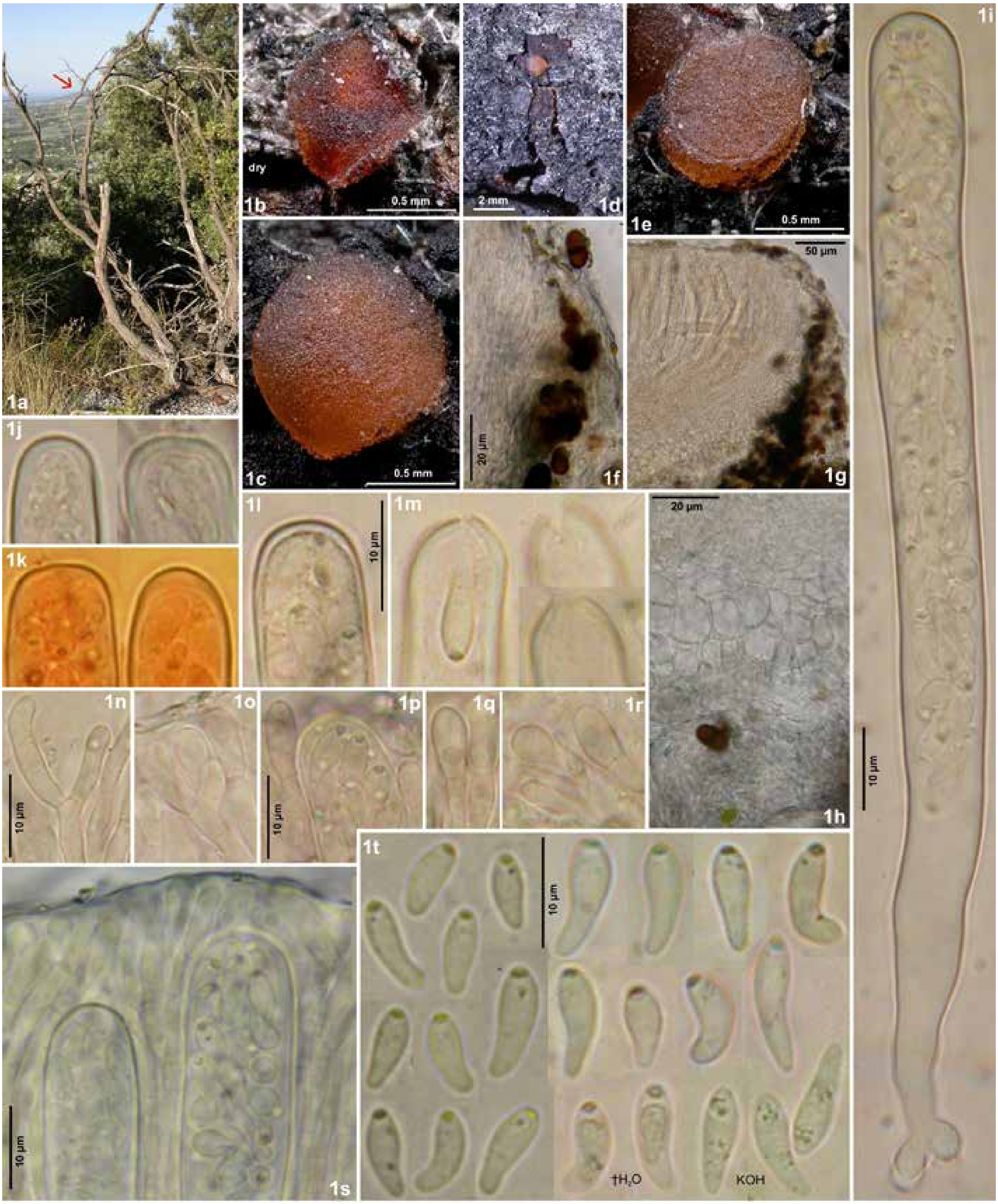
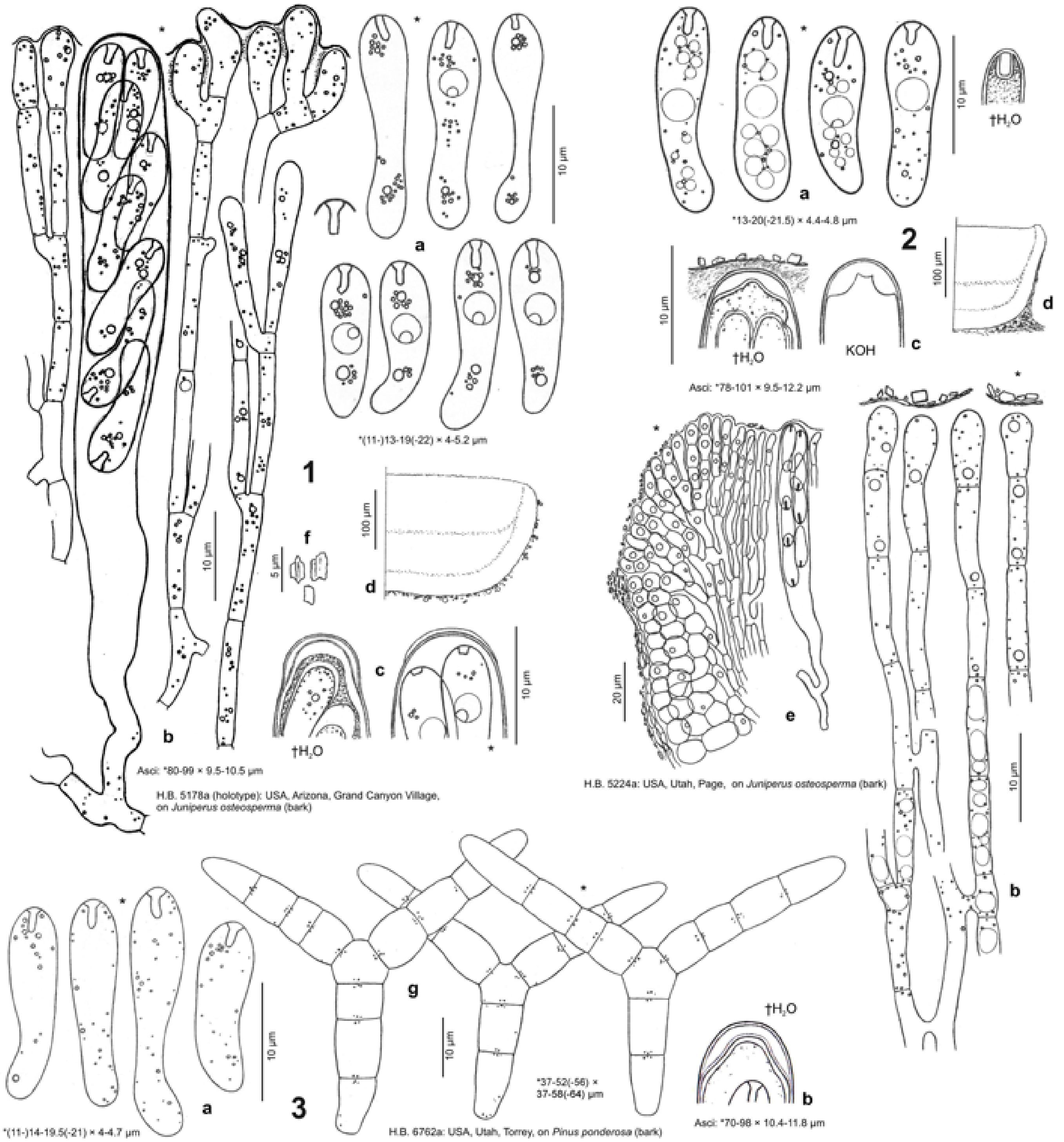


Plate 178. **1**: *Orbilia myriolentiformis*. – **1a**. mediterranean maquis with dead tree of *Cercis*, **1b**. dry apothecium, **1c–e**. rehydrated apothecia (**1b–c** closeup of **1d**); **1g**. apothecium in median section; **1f**. id., marginal ectal excipulum (with dark cells of hyphomycete); **1h**. id., basal excipulum, with subiculum below (t. intricata); **1i**. mature ascus; **1j–m**. ascus apices (**1m** emptied); **1n–r**. paraphyses; **1s**. tips of asci and paraphyses; **1t**. ascospores (SBs in dead spores remaining refractive in water but not in KOH). – Living state, except for asci in **1j**, **l–m** (in water), **1k** (in KOH+CR), **1t** (lower 5 spores). — **1a–t**. H.B. 9151g (holotype): France, Nyons, on *Cercis*.

corticem putridum, raro lignum, ramorum siccorum coniferarum in zona (oro) temperata (sub)humida Americae septentrionalis.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.4(–0.5) mm diam., 0.18–0.2 mm high, pale to bright pure rose(-violaceous) to pink-red(-orange), round, very scattered to moderately gregarious in small groups; disc slightly concave to flat, margin even, protruding 0–10 µm, exterior slightly rough; broadly sessile, erumpent through slits in outer layers of bark, sometimes superficial; dry deep pink-red, elliptical. **Asci** *70–101 × 9.5–11.5(–12.2) µm {4}, †65–100 × 7.5–10(–11.5) µm {2}, 8-spored, pars sporifera *42–68 µm long, 1–4(–5–6) lower spores inversely oriented {4}, **apex** (†) hemispherical to slightly truncate, dome



H.B. 5178a (holotype): USA, Arizona, Grand Canyon Village, on *Juniperus osteosperma* (bark)

H.B. 5224a: USA, Utah, Page, on *Juniperus osteosperma* (bark)

H.B. 6762a: USA, Utah, Torrey, on *Pinus ponderosa* (bark)

Plate 179. **1–3**: *Orbilia cucumispora*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., ectal excipulum at margin and mid flanks, part of hymenium; **f**. crystals on surface of exudate; **g**. conidia from culture.

†1.3–1.9 → 0.8–1.5 µm thick, with ± wide apical chamber; **base** with short to ± long, flexuous stalk with always T-shaped base. **Ascospores** *(11–)13–19(–22) × 4–5.2(–5.7) µm {5}, †13–19 × 4–4.7 µm {1}, slightly or medium clavate, rarely cylindrical, often slightly (to strongly) dumbbell-shaped, both ends rounded, straight to slightly (rarely strongly) curved near base; **SBs** *(1.5–)2–3(–3.5) × 0.6–1 µm {3}, plug- to rod-shaped, apically usually abruptly widened to 1–1.6 µm {3} (resembling a rivet), apically broadly attached; with several minute and sometimes a few large (0.8–1.5 µm) **LBs** grouped or scattered in each half. **Paraphyses** apically uninflated or usually slightly (to medium) clavate, terminal cell *(5–)8–17 × (2.3–)2.8–3.7(–4.2) µm {4}, †1.5–2.7 µm wide {2}, lower cells 9–18 × 1.7–2.6 µm {4}, †1.5–1.8 µm wide, at apex often di- or trichotomously branched {2} or always unbranched {1}. **Medullary excipulum** 40–70 µm thick, of ± dense textura intricata with rather few hyphae and many inflated cells suggesting a t. angularis, medium sharply delimited. **Ectal excipulum** of slightly gelatinous, vertically oriented t. angularis(-prismatica) from base to mid flanks, 35–40 µm thick at base, cells *7–16 × 6–11(–13) µm {2}; 25–30 µm thick at lower flanks, 15–30 µm at mid flanks, cells *9–16 × 7–14 µm, 15–25 µm thick at margin, of t. prismatica-angularis oriented at ~45–80°, cortical cells *7–10(–16) × 4–5 µm. **Anchoring hyphae** abundant, *2.5–4 µm wide, wall 0.2–0.8 µm thick {2}, covering the exterior up to mid flanks by a 5–15 µm thick dense layer. **SCBs** globose, low-refractive, in paraphyses 0.8–1.3 µm diam. {1}, partially absent {3}; in cortical cells of margin (and mid flanks) 1.5–2.8 µm. {2}.

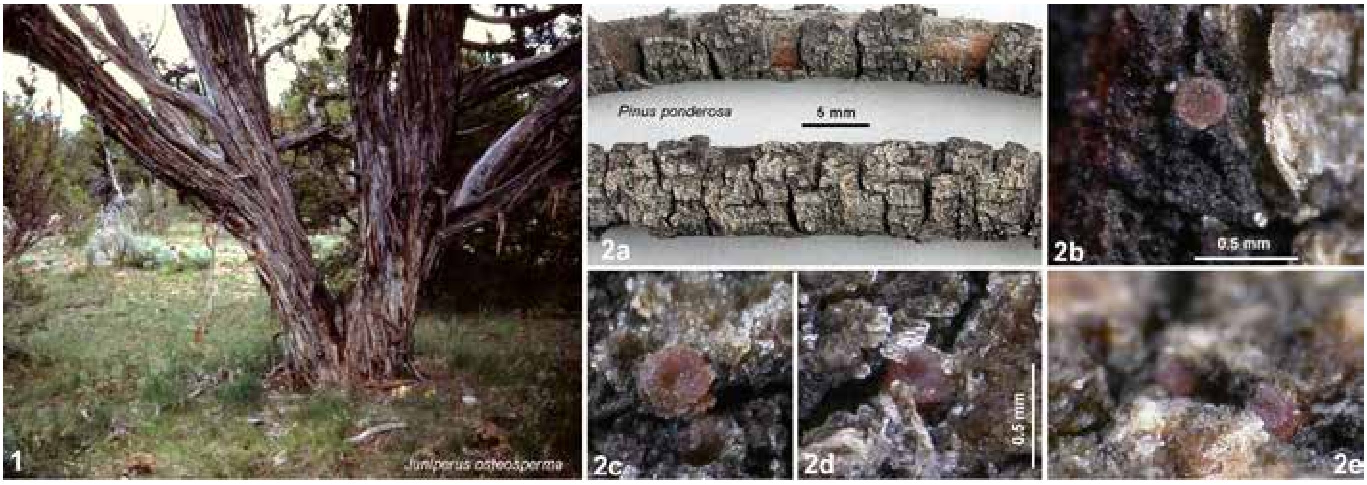


Plate 180. **1–2**: *Orbilia cucumispora*. – **1**. pinyon-juniper woodland in the Coconino Plateau, with *Juniperus osteosperma*, detached hanging bark; **2a**. corticated branches; **2b–e**. apothecia rehydrated after 6 years. — **1**. H.B. 5178a (holotype): USA, Arizona, Grand Canyon Village, on *Juniperus*; **2a–e**. H.B. 6762a: USA, Utah, Torrey, on *Pinus*.

Exudate over paraphyses and margin forming a continuous, thin, ± refractive line 0.2–1(–2) µm thick, loosely attached, hyaline; externally smooth {2} or covered by refractive, ± abundant crystals ~0.3–4 µm diam. (over paraphyses and/or excipulum) {3}, unstained in CRB. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1}). **Conidiophores** not observed. **Conidia** Y-shaped, total size *37–52(–56) × 37–58(–64) µm {1}, stipe *22–28 × (6–)6.5–8.5 µm, 2–3(–4)-septate, arms cylindrical to slightly tapering, with obtuse ends, *(23–)26–35(–38) × (6–)6.5–8(–8.5) µm, (2–)3–4-septate; a single phragmoconidium seen: *56 × 6.3 µm, 5-septate.

Habitat: collected 1–2 m above the ground, still-attached, corticated or partially, rarely entirely decorticated, 4–15 mm thick, dead branches of *Juniperus osteosperma* {3}, *Pinus ponderosa* {1}, indet. gymnosperm {1}, on (slightly to) medium decayed bark (bast and periderm) {4} or wood {1}, often in cracks, bark partially somewhat detached, nearly no green algae, distinctly greyed. **Associated**: closely associated with black pycnidia {2}, also with *Carestiella schizoxyloides* {1/2}, *Holmiella sabina* {1}, *Orbilia ?maeandrina* {1}, *O. multidelphinus* {1}, *O. multihamulata* {2}, *O. octosporoides* {1}, *O. ophiosoma* {1}, *O. osteospermae* {1}, *O. pisciculus* {1}. **Desiccation tolerance**: fully tolerant for at least 5 months, dead after 14 months (including ascospores). **Altitude**: 1225–2440 m a.s.l. **Geology**: Permian-Triassic-Jurassic-Cretaceous sand- & limestone. **Phenology**: long-lived.

Taxonomic remarks. The large, oblong, cucumber-like to dumbbell-shaped ascospores that contain broadly attached SBs with a remarkable inner prolongation (T-shaped) easily distinguish *O. cucumispora* from related taxa. The species is also characterized by a more or less striking pink colour. The inconsistent presence of CRB-unstainable small crystals over the exudate seems to be an exceptional feature within *Orbilia*. The broad attachment of the SBs to the spore apex suggests placement of *O. cucumispora* in series *Lentiformes*, which is supported by molecular data. *O. cercidicola* resembles *O. cucumispora* in spore size and shape, but has a very different type of SB which is narrowly attached to the spore apex by a ± thin filum, also it possesses striking orange crystalloid SCBs, for which reason it is placed in a series of its own.

Map 27. Known distribution of *O. cucumispora* in North America.

Variation. *O. cucumispora* varied somewhat in apothecial colour, also in the thickness of the apical dome, the apical branching of paraphyses, and in the presence of crystals on the exudate surface. Also the apical extension of SBs is not always well pronounced (Pl. 179: 1a).

Anamorph. *O. cucumispora* produces conidia that resemble *Trinacrium robustum* but differ in being larger-sized and with only slightly tapering arms. Conidia were obtained in abundance in culture, but only after flooding with water.

Phylogeny. Despite the deviating spore body type, our sequence of *O. cucumispora* (H.B. 6762a, from pure culture, SSU+ITS+LSU) clustered in the *flavida-cucumispora* clade, partially weakly supported with *O. plurilentiformis* (Phyls 8, S9, S11), with a 4.5 and 7 % ITS distance, respectively.

Ecology. *O. cucumispora* was found on slightly decayed bark (rarely wood) of dead xeric branches of different gymnosperm trees and shrubs in (warm- to) cold-temperate (to boreal), (semiarid to) subhumid (to humid) pinyon-juniper woodlands but also Douglas fir and Engelmann spruce forests in ravines, valleys, slopes or high plateaus of the Colorado Plateau of western North America.

Specimens included. **USA**: **Utah**, Utah Mts., Dixie Forest, 1.5 km ESE of Cedar City, 1815 m, branch of *Juniperus osteosperma*, on bark, 24.VIII.1994, G. Marson (ø). – 15 km SSE of Torrey, 5.5 km S of Grover, Lion Mt., 2440 m, branches of *Pinus ponderosa*, on bark, 19.VI.2000, G. Marson (H.B. 6762a, BBA 69342, anam. cult.; sq.: KT215231). – Bryce Canyon, Fairview Point, 2440 m, branch of indet. gymnosperm, on wood, 16.V.1995, G. Marson (ø). – **Arizona**, Canyonlands, ~35 km WNW of Page, Paria Canyon, ~1225 m, branch of *J. osteosperma*, on bark, 27.VIII.1994, G. Marson (H.B. 5224a). – Grand Canyon, Coconino Plateau, 3 km N of Tusayan, 2068 m, branch of *J. osteosperma*, on bark, 28.VIII.1994, G. Marson (M-0276465, **holotype**; **isotype** in H.B. 5178a).

Series *Ovales*

Orbilia subgenus ***Hemiorbilia*** section ***Lentiformes*** series ***Ovales*** Baral & E. Weber, **ser. nov.**, MB 815000 – Type species: *Orbilia ovalis* Baral & G. Marson

Latin diagnosis: *Apothecia rosea vel aurantiaca, margine laevi. Asci apice in statu emortuo valde truncato, tenuitunicato. Ascosporae ellipsoideo-ovoideae ad subglobosae, corpuscula refringentia bacilli-, pyri- vel ampulliformia. Paraphyses ad apicem leniter ad valde clavato-capitatae. Excipulum ectale textura globulosa-angulari, marginem versus cellulis vivis corpuscula globosa continentibus, absque processis vitreis.*

Recognized species: *O. ovalis*.

Orbilia ovalis Baral & G. Marson, **sp. nov.**, MB 813494 — Pls 181–182, Map 28

Etymology: named after the frequently ovoid spore shape, also referring to the substrate of the type, *Amelanchier ovalis*.

Typification: Spain, Cuenca, Guadalaviar, branches of *Amelanchier ovalis*, 26.IX.1999, G. Marson (ex H.B. 6486b, M-0276546, holotype; ex-type culture: CBS 140883; sq.: KT215235).

Latin diagnosis: *Apothecia rosea vel aurantiaca, sessilia, superficialia, 0.2–1.3 mm diam. in statu rehydratata, disco plano, margine laevi. Asci 8-spori, apice in statu emortuo valde truncato, tenuitunicato. Ascosporae in statu vivo *(3–)3.7–7.5 × 2.2–3.3 µm, ellipsoideo-ovoideae ad fusoideo-clavatae vel subglobosae, prope apicem corpusculum refringens bacilli-, pyri- vel ampulliformem*, ad apicem *anguste* affixum continentes. *Paraphyses ad apicem leniter ad valde clavato-capitatae. Excipulum ectale textura globulosa-angulari, marginem versus cellulis vivis corpuscula globosa continentibus. Habitat ad corticem, raro lignum putridum ramorum siccorum* Aceris, Amelanchieris, Rosae, Pruni *vel* Juniperi *in zona orotemperata ad mediterranea Europae et Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–0.9(–1.3) mm diam., 0.1–0.21 mm high, light to bright rose-pink or rose-orange to apricot, round to slightly undulating, scattered to subgregarious; disc slightly concave to flat, margin thin, 0–10 µm protruding, very slightly inrolled, smooth; broadly sessile, also with an obconical stipe up to 150 × 350 µm, ± superficial, also erumpent through holes in periderm. **Asci** *(43–)50–65(–70) × (4.2–)4.7–5.7 µm {4}, †38–63 × (3.5–)4–4.7(–5) µm {4}, 8-spored, spores obliquely 1–2-seriate, (1–)2–4(–5) lower spores inverted {5} (sometimes mixed, very rarely upper spores inverted), pars sporifera *(24–)28–34 µm long; **apex** (†) medium to strongly truncate (not or very slightly indented, laterally not or slightly inflated), hemispherical in profile view, thin-walled; **base** with short to long, thick or thin, flexuous stalk, T- or h-shaped. **Ascospores** *3–3.7 {1} or (3.7–)4.3–6.5(–7.5) {6} × (2.2–)2.4–2.8(–3.3) µm {8}, †4–5.8 × 2–2.7 µm {1}, subglobose to ellipsoid-obovoid to fusoid-clavate, apex rounded to obtuse, sometimes subacute, rarely with a short tail-like base, straight to inequilateral or basally slightly curved; **SBs** *(1–)1.4–2.1(–2.4) × (0.4–)0.5–0.8(–0.9) µm {7}, rod-shaped, ampulliform, or tear- to narrowly pear-shaped, lower part mostly distinctly swollen, apically narrowed to a ± wide, more rarely to a small point, predominantly straight, sometimes slightly to very strongly geniculate. **Paraphyses** apically slightly to strongly clavate-capitate (rarely uninflated), terminal cell *(10–)13–28 × 2.5–5.8 µm {4}, lower cells *6–16 × 1.6–2.7 µm {3}; unbranched near apex, hymenium very pale orange-rose. **Medullary excipulum** pale rose, 25–60(–120) µm thick, of ± loose or dense textura intricata with many inflated cells (also of t. globulosa), usually sharply delimited. **Ectal excipulum** pale to light rose, of thin-walled, (†) slightly to medium gelatinized, (indistinctly) vertically oriented t. globulosa-angularis(-prismatica) from base to margin or mid flanks, 30–60(–100) µm thick near base, cells *8–23(–26) × 7–17(–20) µm {4}, common walls †0.5–1(–2) µm; 20–30 µm thick near margin, of t. globulosa to t. prismatica oriented at a 30–90° angle to the surface, marginal cortical cells *6–18 × 3–6(–8) µm {2}, †7–13 × 2.5–4.5 µm {2}, slightly thick-walled (†0.2–0.4 µm), sometimes with internal low-refractive wall thickening (1–2 µm) {1}. **Anchoring hyphae** mostly very abundant, *2–4 µm wide, walls */†0.2–0.7(–1.2) µm thick {4}, forming a dense hyaline t. intricata 20–60 µm thick, at flanks a 10 µm thick t. porrecta. **SCBs** in paraphyses and cortical cells globose (in the latter partially absent) {4}, glassy processes absent {4}. **Exudate** over paraphyses 0.1–0.3 µm thick, continuous to granular, firmly attached; over margin and mid flanks 1–8 µm thick, continuous, granular-cloddy, or cap-like, ± layered, partially firmly attached, pale yellow. **— ANAMORPH**: dicranidion-like (presumed, from natural substrate {6, 2 of them without associated apothecia}). **Conidiophores** not observed. **Conidia** tuning fork shaped, total size *30–48 × 10–13.5(–20) {4} or 51–67 × 13–14(–17.5) µm {*Juniperus*}, stipe *5–7(–9) × (2.3–)2.7–3.5(–4.2) µm, 1-celled, arms usually parallel, apically often slightly converging, rarely diverging (nearly Y-shaped), *21.5–41 or 42–55 × 4.5–6.8 µm, 5–10 {4} or 9–13-septate {*Juniperus*}.

Habitat: collected 0.2–2.5 m above the ground, ± corticated, 3–35 mm thick twigs and branches of *Acer* sp. {1}, *Amelanchier ovalis* {2}, *Betula* sp. {1}, *Fraxinus* sp. {1}, *Juniperus communis* {1}, *Prunus* sp. {1}, *P. domestica* {1}, *Rosa* sp. {1}, on medium to strongly decayed bast {8} (periderm rolled aside or removed, also on inner surface of detached bark), more rarely wood {3}, slightly greyed, sometimes blackened, green algae sparsely present. **Associated**: *Baggea* sp. {1}, *Caloplaca* sp. {1}, *Hysteropatella prostii* {1}, *Lachnella* sp. {1}, *Melanelia exasperata* {1}, *Mellitiosporiella pulchella* {1}, *Orbilia delphinus* {1}, *O. flexisoma* {1}, *O. gambelii* {2}, *O. pleioalbidorosea* {1}, *O. pleiogambelii* {1}, *O. subaristata* {1}, *O. subtrapeziformis* {3}, *O. trapeziformis* {1}, *Ostropa barbara* {1}, *Parmelia* sp. {1}, *Perrotia flammea* {1}, *Physcia stellaris* {1}, *Propolis farinosa* {1}, ?*Schizoxylon* sp. {1}, various crustose lichens. **Desiccation tolerance**: fully tolerant for at least 14 months, ascospores and inflated cells of medullary excipulum still viable after 33 months, conidia partially viable after 3 years. **Altitude**: 340–1605 m a.s.l. **Geology**: Europe: Lower Jurassic & Cretaceous limestone & dolomite; Canada: alluvial deposits from Proterozoic & Cambrian-Ordovician sedimentary rock. **Phenology**: II–III, VIII–XI (but long-lived).

Taxonomic remarks. *Orbilia ovalis* is characterized by rather small, ellipsoid-ovoid ascospores, and rod-shaped to ampulliform spore bodies that are attached by a ± wide point. *O. caudata*, a species here assigned to series *Piliferae* of section *Aurantiorubrae*, closely resembles *O. ovalis*. It differs in narrower spores with a mostly distinct tail, a presumed trinacrium-like anamorph, and a (sub)tropical distribution. Spores and SBs of *O. ovalis* match also those of *O. macroasca* (series *Phanosomates*), a species differing in polysporous asci, paraphyses with more equally long cells and non-capitate apices, and in distinctly thick-walled ascus apices.

Except for its spore body, *O. ovalis* strongly resembles *O. eucalypti* (series and subgenus *Orbilia*) in various features, including the presumed dicranidion-like anamorph. *O. ovalis* actually recalls series *Orbilia* with its thin-walled, truncate (shouldered) ascus apices and capitate paraphyses with the terminal cells usually distinctly longer than the lower cells. *O. ovalis* differs from that series in ± ampulliform to rod-shaped SBs which resemble those of *O. macroasca* or *O. myriophanosoma* in series *Phanosomates*.

O. ovalis is placed in section *Lentiformes* here based on rDNA data. Since the species seriously deviates from all the remaining members of this section, we place it in a series of its own, which stands somewhat isolated and with unclear affinities.

Variation. The Canadian collection on *Acer* fits well the European specimens, including the holotype. Two of the three collections from southern France (on *Prunus*, Pl. 181: 5; on *Betula*, IVV: 13.IX.2015) differ from the remaining ones on angiosperm hosts in somewhat shorter spores. That on *Prunus* shows also more tear-shaped SBs,

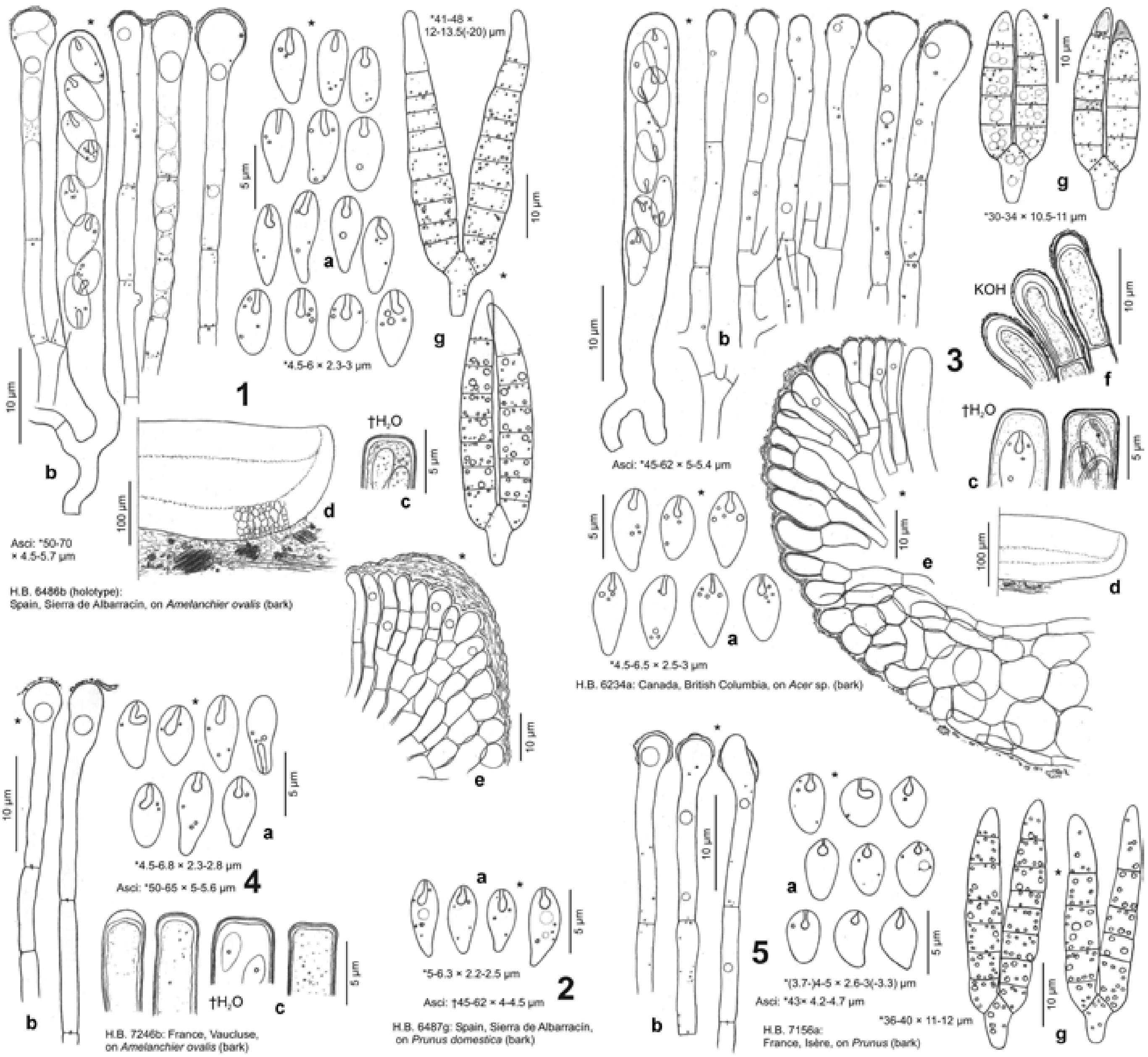


Plate 181. **1–5**: *Orbilia ovalis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. ectal excipulum (margin and mid flanks, median section); **f**. marginal cortical cells with internal wall thickening; **g**. conidia from substrate.

but the associated anamorph well concurs with that of the more typical collections. This specimen and the Austrian *Juniperus* sample, which shows extraordinarily short spores of *3–3.7 × 2.3–2.7 µm, somewhat resemble *O. dalmatica* (series *Orbilia*), a species that also grows on *Juniperus* but differs in smaller spores with much shorter SBs (0.8–1 µm) and in having glassy processes at the margin. Although the *Juniperus* sample of *O. ovalis* would fit *O. dalmatica* in spore size, its spore bodies are much more elongated (1.5–2.3 µm) and the asci distinctly wider (*5.5 µm, length not measured, Pl. 182: 3). In the collection from Canada, the dead marginal cortical cells show internal wall thickenings, which were not noticed in the European material.

Anamorph: In four of the seven records of teleomorphs of *O. ovalis*, dicranidion-like conidia were observed on the natural substrate. In two records (H.B. 6486b, 7246b) we obtained a pure culture in which, however, no conidia were formed. The presumed anamorph is similar in size to *Dicranidion parapalmicola*, from which it differs in more tapering arms. A dicranidion-like anamorph is so far extraordinary within section *Lentiformes*. The conidia in the *Juniperus* sample are distinctly longer than in those on angiosperm hosts, the arms having more septa.

Phylogeny. Sequences of four samples of *O. ovalis* were available: two from pure culture (France and Spain, on *Amelanchier*; both SSU+ITS+LSU), and two from apothecia (Austria, on *Juniperus*; France, on *Betula*; both ITS+LSU). The S1506 intron is absent in all of them. The two French samples differ by only 2 nt in the ITS and 1 nt in the LSU (D1–D2, pos. 631). The two on *Amelanchier* differ from each other by 3.9 % in the ITS (1.3 % in LSU), while that on *Juniperus* shows to the samples on angiosperms a distance of 2.9/0.3 % (Spain) and 3.8/0.8–0.9 % (France). It seems remarkable that in the D1–D2 domain the four sequences show deviations at 8 nucleotide positions, whereby the Austrian sample concurs with that from Spain at 5 positions

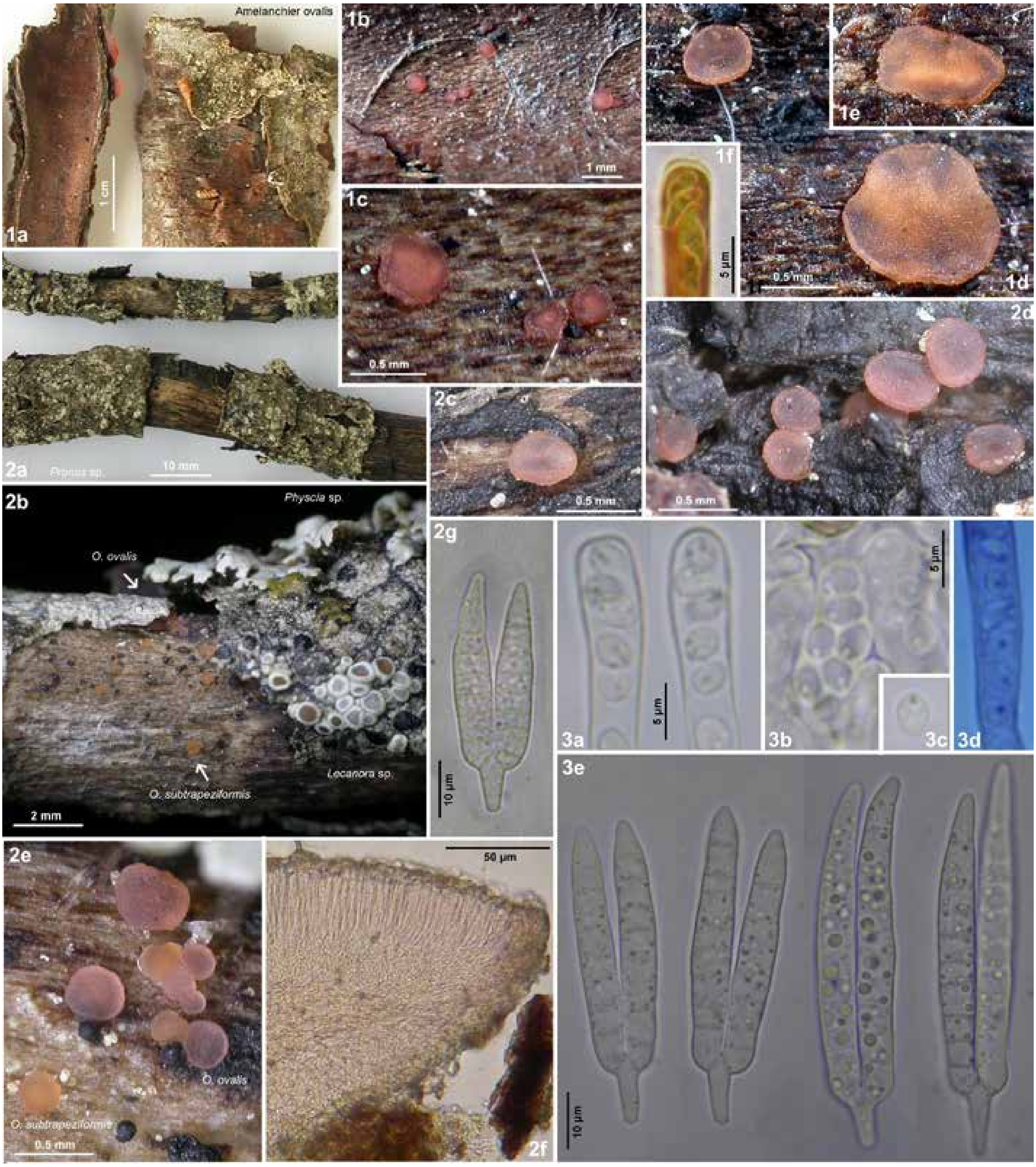


Plate 182. **1–3**: *Orbilia ovalis*. – **1a**. detached xeric bark of *Amelanchier ovalis*; **2a**. xeric branches of *Prunus*; **1b–e**, **2b–e**. rehydrated apothecia (**2b**, **e**. associated with orange *O. subtrapeziformis*); **1f**, **3a**. ascus apices; **2f**. apothecium in median section; **3a–d**. ascospores (**3a–b**, **d**. in asci); **2g**, **3e**. conidia from substrate. – Living state (**3d** in CRB), except for **1f** (KOH+IKI), asci in **3a–b**, **d**. — **1a–e**. H.B. 6486b (holotype): Spain, Sierra Albarracín, on *Amelanchier*; **2a–g**. H.B. 7156a: France, Isère, on *Prunus*; **3a–e**. G.F. 20160009: Austria, Steiermark, on *Juniperus*.

and with those from France at 2 positions, but there is no position where it deviates from both. Based on these findings and because of the similar morphology of the four samples, we consider them as conspecific.

In phylogenetic analyses of SSU+ITS+LSU (Baral et al. 2017b, Phyls 7–8), *O. ovalis* clustered strongly supported in section *Lentiformes*, though with a distance of ~20–25% in the ITS region to other members (3.5–7.5% in the LSU). In the 5.8S the distance is 0–2 nt (0–1.3%), with a full match with *O. patellarioides*. To members of series *Orbilia* the distance ranges at over 25% in the ITS (2–3.5% in the 5.8S) and 7.5–12.5% in the LSU.

Specific nucleotide positions. *O. ovalis* deviates from all other members of section *Lentiformes* in the SSU V8–V9 at pos. 60 and 252 (both A vs. G) and 269–270 (TT vs. CA), and in the LSU D1–D2 at pos. 138 (T vs. C), 432 (C vs. T), 446 (A vs. G or T), and 482/539/581 (T vs. C/A/G).

Ecology. *O. ovalis* was found on ± rotten bark but also wood of xeric twigs and branches of trees and shrubs of angiosperms (*Betulaceae*, *Rosaceae*, *Sapindaceae*), rarely gymnosperms (*Cupressaceae*). Collections are from mixed conifer forests of orotemperate and orosubmediterranean humid to suprasubmediterranean semihumid regions of southern Europe (Sistema Ibérico, Southern French Alps), from an orotemperate (altimontane) *Pinus-Picea*(-*Fagus*) forest with *Cypripedium* in the subcontinental humid eastern Austrian Alps, and from a boreal humid forest with *Populus tremuloides* and *Acer* adjacent to conifer forests in a valley of the Canadian Rocky Mountains. The sample without apothecia was from (?)supramediterranean semihumid western Anatolia. The soil at most collection sites was more or less strongly calcareous.

Specimens included. **AUSTRIA**: **Steiermark**, 20 km NNW of Bruck an der Mur, 3 km NNW of St. Ilgen, Karlschütt, 890 m, twig of *Juniperus communis*, on bark, 20.II.2016, G. Friebes (G.F. 20160009, doc. vid., anam. substr.; sq.: KY419190). — **FRANCE**: **Rhône-Alpes**, **Isère**, Préalpes du Dauphiné, 10 km W of Grenoble, 5 km NE of Autrans, la Molière, 1605 m, branch of *Prunus*, on bark & wood, 12.VIII.2001, G. Marson (H.B. 7156a, anam. substr.). – 24 km SE of Grenoble, 1.3 km WSW of La Paute, 1093 m, twig of *Betula*, on wood & bark, 3.IX.2015, G. Marson (G.M. 2015-09-13.1; sq.: MK473407). – **Provence-Alpes-Côte d'Azur**, **Vaucluse**, Préalpes du Dauphiné, 14 km SE of Carpentras, 4 km E of Venasque, D4, Aire de Pic-Nique de Venasque, 485 m, branch of *Amelanchier ovalis*, on bark, 9.X.2002, G. Marson (H.B. 7246b, BBA 69397; sq.: KT215236). — **SPAIN**: **Castilla-La Mancha**, **Cuenca**, Sierra de Albarracín, 43 km NE of Cuenca, 8 km SW of Guadalaviar, S of Mt. Mogorrit, 1600 m, branches of *Amelanchier ovalis*, on bark, 26.IX.1999, G. Marson (ex H.B. 6486b, M-0276546, **holotype**, CBS 140883, anam. substr.; sq.: KT215235). – ibid., branch of *Prunus domestica*, on bark, 26.IX.1999, H.O. Baral & G. Marson (H.B. 6487g). – 21 km WSW of Montalbán, SW of Pancrudo, 1220 m, twig of *Rosa*, on wood, 31.III.2013, R. Tena (R.T.L. 13033101 ø, anam. only, 1 conidium only, doc. vid.). — **TURKEY**: **Marmara**, **Balıkesir**, 50 km WSW of Balıkesir, 17.5 km SW of Ivrindi, 1 km SE of Büyükılıca, Korucu Forest, 340 m, branch of *Fraxinus*, on bark, 1.XI.2002, T. Askun (T.A. 37b, anam. only, doc. vid.). — **CANADA**: **British Columbia**, Canadian Rocky Mountains, 61 km SE of Golden, 1 km SE of Spillimacheen, road 95, 830 m, branch of *Acer*, on bark, 20.VIII.1997, G. Marson (H.B. 6234a, anam. substr.).

Series *Cercidicola*

Orbilia subgenus *Hemiorbilia* section *Lentiformes* series *Cercidicola* Baral, **ser. nov.**, MB 815001 – Type species: *Orbilia cercidicola* Baral, G. Marson & E.S. Popov

Latin diagnosis: *Apothecia aurantiaca, margine laevi. Asci apice in statu emortuo subtruncati, plerumque tenuitunicati. Ascosporae forma cucumeris, corpuscula refringentia bacilliformia, filo brevi ad apicem affixa. Paraphyses ad apicem leniter vel modice clavato-capitatae. Excipulum ectale textura angulari, cellulis vivis corpuscula aurantiaca crystalloidea continentibus, ad marginem textura porrecta.*

Recognized species: *O. cercidicola*.

Orbilia cercidicola Baral, G. Marson & E.S. Popov, **sp. nov.**, MB 813497 — Pls 183–185

Etymology: named according to the substrate in the holotype, *Cercis siliquastrum*.

Typification: France, Drôme, Nyons, branch of *Cercis siliquastrum*, 11.X.2002, G. Marson (ex H.B. 7272a, M-0276452, holotype).

Latin diagnosis: *Apothecia aurantiaca, subsessilia, erumpentia, 0.3–1.1 mm diam. in statu rehydratata, disco leniter concavo, margine laevi. Asci 8-spori, apice in statu emortuo subtruncati, plerumque tenuitunicati. Ascosporae in statu vino 11–18.7 × 3.5–5 µm, forma cucumeris, ad basim plus minusve curvatae, in statu vivo prope apicem corpusculum refringens bacilliformem, filo brevi ad apicem affixum continentes. Paraphyses ad apicem leniter vel modice clavato-capitatae. Excipulum ectale textura angulari, cellulis vivis corpuscula magna aurantiaca crystalloidea continentibus, ad marginem t. porrecta. Habitat ad corticem putridum in ramis* Cercidis *et* Ulmi *in aere prominentibus, in zona submediterranea semihumida et continentale subhumida Europae meridionalis et orientalis.*

Map 28. Known distribution of *O. ovalis* in Europe and eastern Asia (Turkey).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1.1 mm diam., 0.2–0.3 mm high (receptacle 0.18–0.2 mm), light to bright orange(-red) or brick-red, round or ellipsoid-compressed, scattered to gregarious, sometimes 1–4 apothecia fasciculate; disc slightly concave to flat, margin rather thick, 0–20 µm protruding, smooth or finely rough; subsessile or with a thick and short, hidden stipe, erumpent from small holes in periderm or by lifting fragments of periderm. **Asci** *90–121 × 8.2–9.8 µm {4}, †84–108 × 7–8.7 µm {2}, 8-spored, spores *2-seriate, ((1–))(2–)4(–6) lower spores inverted (sometimes mixed) {4}, pars sporifera *47–65(–73) µm long; **apex** (†) slightly (to medium) truncate (laterally not or slightly inflated), rarely hemispherical, thin-walled (apical wall †0.3–0.4 µm thick) {3}, in a few immature asci with †1–1.3 µm thick dome {1} with slight apical chamber; **base** with short to long, ± thin, flexuous stalk, L- to Y-shaped. **Ascospores** *(11–)12.5–17(–18.7) × (3.5–)3.8–4.5(–5) µm {4}, †13–16 × 3.7–4.5 µm {1}, cylindrical to somewhat clavate, slightly, sometimes medium dumbbell-shaped, both ends rounded, apical part mostly a bit broader, slightly or mostly medium (to strongly) curved, especially near base; **SBs** *(2.5–)3.5–4.7(–5.5) × 0.8–1.1 µm {4}, broadly rod-shaped, often ± geniculate, with a short (0.6–1.2 µm), apically attached, ± thin filum; consistently with 2 groups of **LBs** up to 0.7–1.5 µm diam.; overmature spores 1-septate, partially with larger LBs. **Paraphyses** apically uninflated to mostly slightly to medium clavate-capitate (exceptionally spathulate), terminal cell *6–22 × (2–)2.5–4(–4.5) µm {3}, straight or partially flexuous, lower cells *9–22 × 1.4–2.5(–3.4) µm {3}; rarely branched at apical septum {2} or quite frequently so {1}, hymenium hyaline to pale orange. **Medullary excipulum** ± hyaline, 50–80 µm thick, of ± dense textura intricata with many inflated cells, very sharply delimited from ectal excipulum by a parallel 10 µm thick layer of t. porrecta {3}. **Ectal excipulum** hyaline, light orange near margin, of (†) slightly gelatinized, vertically oriented t. angularis-prismatica from base to mid flanks, 30–100 µm thick near base, cells *9–25 × 7–16 µm {2}; 30–50 µm thick at lower flanks, cells *9–18(–24) × 6–12.5 µm, at flanks often covered by a 15–20 µm thick, very sharply delimited layer of hyaline, ± gelatinized hyphae, margin 30–40(–50) µm thick, inner part of t. angularis(-prismatica) oriented at a 40–80° angle, outer part of t. porrecta oriented at 10–40°, not or slightly gelatinized, densely agglutinated but separable on pressure, marginal cortical cells */†7–18 × 2.5–4 µm {3}. **Anchoring hyphae** abundant, *2.5–4.5(–5.3) µm wide {2} (†2–3.5 µm {1}), wall *0.2–0.5 µm thick (†0.2–0.8 µm), containing scattered LBs 1.5–2.8 µm diam. (these also in basal cells of stipe), forming a loose t. intricata near stipe, intergrading at flanks with the covering layer. **SCBs** in paraphyses small, angular to rod-shaped, hyaline to very pale orange, rarely globose; in ectal excipulum inside angular cells of flanks and margin forming large elongate bodies of partially zigzag-like outline, (3–)5–9(–11) × (2–)3–5.5 µm {2}, in top view ring- to horseshoe-shaped, 3–5.8 × (2–)2.5–4.3 µm {2}, pale to light orange, near base subhyaline. **Exudate** over paraphyses 0.2–1.5 µm thick, cloddy, hyaline, loosely attached; over margin and flanks 0.5–2 µm thick, cloddy-continuous. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {2}). **Conidiophores** not

Plate 183. **1–2**: *Orbilia cercidicola*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum (cells containing orange SCBs); **f**. id., at lower flanks; **g**. SCBs in ± top view; **h**. anchoring hypha at insertion to excipulum; **i**. conidia (from substrate).

observed. **Conidia** *17–21 × 3.8–4 µm, C-shaped, 2–3-septate (only 3 conidia seen).

Habitat: collected 1–3 m above the ground, corticated, 8–13 mm thick branches of dead trees of *Cercis siliquastrum* {3}, *Ulmus minor* {2}, *U. pumila* {1}, on medium to strongly decayed bark (on bast, often in small cracks of periderm) {6}, greyed, with some to many green algae. **Associated**: *Baggea* sp. {1}, *Claussenomyces* sp. {1}, *Diplodia* sp. {1}, *Durella ?compressa* {1}, *Nitschkia broomeana* {2/1}, *Orbilia aurantiorubra* {1}, *O. carpoboloides* {2}, *O. flagellispora* {1}, *O. gambelii* {1}, *O. myriolentiformis* {1}, *O. myriosphaera* {3}, *O. pleiogambelii* {1}, *O. polyspora* {2}, *O. subaristata* {3}, *O. subclavuliformis* {2}, *O. subocellata* {1}, *O. trapeziformis* {2}, *Patellaria atrata* {2}, *Phragmiticola* sp. {1}. **Desiccation tolerance**: ascospores, submature asci, excipular cells and paraphyses still viable after 17 months. **Altitude**: -17–460 m a.s.l. **Geology**: France: Miocene sandstone near Cretaceous clayey limestone; Russia: Pleistocene sediments. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia cercidicola* is characterized by large, cucumber-like ascospores and rather large, bright orange apothecia. The species resembles *O. cucumispora* (series *Lentiformes*) in size and shape of spores and paraphyses. It sharply differs in shape and attachment of SBs (in *O. cucumispora* very broadly attached, in *O. cercidicola* ± narrowly attached), furthermore in having very large, orange, crystalloid SCBs in the living excipular cells (resulting in a bright orange apothecial colour), in lacking an apical endoascal thickening in most asci, and in a textura porrecta at the margin.

A similarity in SB shape between *O. cercidicola* and species such as *O. macroasca* and *O. phanosoma* appears to indicate a relationship to series *Phanosomates*. However, the presence of prominent crystalloid SCBs in *O. cercidicola* is so far unique within the entire section *Lentiformes*, in which otherwise

Plate 184. **1–2**: *Orbilia cercidicola*. – **2a**. mediterranean maquis with dead *Cercis*; **2b**. dead corticated xeric branch; **1a–c**, **2c–h**. rehydrated apothecia; **1d**, **2i–j**. apothecia in median section; **2k**. id., marginal region; **1e**, **2l**. SCBs in excipular cells of margin and lower flanks; **2m–n**. asci; **2o**. ascospores; **2p**. conidium (from substrate). – Living state. — **1a–e**. H.B. 7272a (holotype): France, Nyons, on *Cercis*; **2a–p**. H.B. 9151e: ibid.

Plate 185. **1**: *Orbilia cercidicola*. – **1a**. apothecia on bark (rehydrated); **1b**. median section of lower flanks, showing medullary (hyaline) and ectal (orange) excipulum, and hyaline anchoring hyphae with brown stray fungal cells below; **1c**., ascospores; **1d–e**. SCBs in excipular cells at mid flanks; **1f**. upper part of paraphyses and ascus (squash mount). – Living state, except for ascus in **1f**; phot. E.S. Popov (**1c** right, **d–f** DIC). — **1a–f**. LE 247090, 247091: Russia, Volgograd, Astrakhan, Baskunchak, on *Ulmus*.

exclusively globose SCBs were observed. Therefore, *O. cercidicola* is placed in a series of its own. Before molecular data was available, we were reluctant about the correct placement of this species, because similarities exist also with *O. cryptogena* of series *Hesperideae* of section *Hemiorbilia*.

Variation. In the holotype the paraphyses were frequently flexuous and branched near their tip, but in the two other collections on *Cercis* the tips were instead straight and unbranched. The specimens on *Ulmus* did not noticeably differ in any respect from those from France, with the paraphyses partially showing apical branching.

Type studies. The description of *Orbilia ulicis* (Chenant.) Trotter by Chenantais (1918, as *Hyalinia ulicis*) resembles the present species in its micromorphology, but the smaller spores and strongly lacerate apothecial margin rather suggest identity with *O. carpoboloides*. No type material appears to have survived, therefore, the identity of this taxon could not be settled (see p. 1033).

Anamorph. Only a few vermispora-like conidia were seen on the natural substrate (Pls.. 183: 1i; 184: 2p) which resemble those observed in some taxa of series *Lentiformes* and *Microspermae*.

Phylogeny. Molecular data gained from a pure culture of a topotype (SSU, ITS, LSU) place *O. cercidicola* in the core clade of section *Lentiformes*. When analysing SSU+ITS+LSU (Phyl. 8) or ITS (S9) it clustered weakly to medium supported with *O. myriosphaera* (series *Phanosomates*), but unresolved when analysing LSU (S11). Its distance in the ITS region is rather high, the minimum being 12.5% to *O. myriosphaera* and 14% to *O. ocellata*, but in the LSU the minimum is 2.5% to species around *O. ocellata*, while 3.5% to *O. myriosphaera*. The occurrence of crystalloid SCBs in *O. cercidicola*, being unique within section *Lentiformes*, remains unexplained in the present phylogenetic analyses, since a polyphyletic origin of these cell organelles is most unlikely.

Specific nucleotide positions. Series *Cercidicola* is unique within section *Lentiformes* in the ITS1 at pos. 1 having ATCATTA**T** instead of ATCATTA**C** (series *Microspermae*) or ATCATTA**A** (remaining taxa).

Ecology. *O. cercidicola* is so far only known from two very disjunct areas, where it occurred on medium rotten bark of dead xeric branches of two rather unrelated angiosperms (*Cercis* and *Ulmus*). At the type locality at the foothills of the Southern French Alps in southern Europe the species was collected three times on *Cercis siliquastrum* in a mesosubmediterranean semihumid maquis. Three collections were on *Ulmus* spp. from the warm-continental subhumid steppic zone of the Caspian lowland in southwestern Russia (easternmost part of Europe), either in the Volga floodplain forests with *Populus nigra*, *Fraxinus excelsior*, *Ulmus laevis*, *U. minor*, *Morus* sp., or nearby in the semidesert of the Bogdo-Baskunchak Reserve in the shelterbelt with *Ulmus pumila*.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1 km N of Nyons, Col du Pontias, Forêt Domaniale de Vaux, 460 m, branch of *Cercis siliquastrum*, on bark, 18.VIII.2001, G. Marson (H.B. 7077h, anam. substr.). – ibid., branch of *C. siliquastrum*, on bark, 11.X.2002, G. Marson (ex H.B. 7272a, M-0276452, **holotype**). – ibid., branch of *C. siliquastrum*, on bark, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9151e, anam. substr.; sq.: KT222416). — **RUSSIA (West)**: **Volgograd**, **Svetloyarskiy**, 33 km SE of Volgograd, 9 km NE of Svetly Yar, Volga-Akhtuba floodplain, E of Sotovo lake, -7 m, branch of *U. minor*, on bark, 21.IX.2012, E.S. Popov (LE 248353, non vid.). – **Astrakhan**, **Akhtubinsk**, 160 km SE of Volgograd, 2.3 km SW of Bolkhuny, Volga river valley, left bank of Akhtuba river, -17 m, branch of *Ulmus minor*, on bark, 24.IX.2012, E.S. Popov (LE 248354, 248355, doc. vid.). – 189 km ESE of Volgograd, 35 km ENE of Bolkhuny, S of Baskunchak salt lake, WNW of Zeleny Sad, 2 m, branches of *U. pumila*, on bark, 27.IV.2009, E.S. Popov (LE 247090, 247091, doc. vid.).

Series *Phanosomates*

Orbilia subgenus ***Hemiorbilia*** section ***Lentiformes*** series ***Phanosomates*** Baral & E. Weber, **ser. nov.**, MB 815002 – Type species: *Orbilia phanosoma* Baral & G. Marson

Etymology: named after the spore body resembling a lantern.

Latin diagnosis: *Seriei* Lentiformium *similis, sed corpusculum refringens ascosporarum globosum ad lacrimiforme, bacilliforme vel angulare, filo tenui ad apicem affixum.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–0.5(–1.1) mm diam., pale to bright orange(-rose), sessile, ± smooth. **Asci** *(48–)60–120(–140) × (7–)8–14(–15.3) µm, 8- up to 128-spored, (0–)1/3–2/3 of lower spores inversely oriented or oriented in all directions; **apex** (†) hemispherical or slightly to medium, sometimes strongly truncate, never indented, rarely laterally slightly inflated, thin-walled or often with an (immature) †1–1.5(–2) µm thick dome with ± distinct apical chamber; **base** L-, T-, Y-, h-, never H-shaped. **Ascospores** *(3.7–)4.5–15(–17.3) × (2.4–)2.8–4.8(–6) µm, subglobose to obovoid, ellipsoid, clavate, or subcylindrical, straight or partially slightly curved near base; **SBs** *(1.5–)2–4(–5.5) × (0.2–)0.5–1.3(–1.5) µm, divided into a ± abruptly swollen, variously-shaped lower part and a fine filum of varying length, also rod-shaped with subapical constriction, apically narrowed to a small, rarely wide point. **Paraphyses** uninflated or slightly, sometimes strongly clavate(-capitate) at the apex, terminal cells (0.5–)0.7–1.5(–2)× longer than lower cells, sometimes branched near apex. **SCBs** always globose. **Exudate** 0.1–1.5(–3) µm thick, continuous to granular, smooth or ± rough, hyaline (to pale yellow), loosely attached. — **ANAMORPH**: trinacrium-like. **Conidiophores** short (~10 µm). **Conidia** Y/T-shaped, *15.5–35 × 14–31 µm, arms slightly to strongly bent downwards.

Habitat: on wood and bark of both gymno- and angiosperms, cold-temperate to subtropical, humid to semiarid, always desiccation-tolerant.

Recognized species: 11, plus 2 species with provisional name.

Taxonomic remarks. Members of series *Phanosomates* resemble those of series *Lentiformes* in many respects, but sharply differ in their peculiar type of spore bodies, which are divided into a thickened lower part and a very thin filiform upper part by which they are narrowly attached at the spore apex, thereby more or less resembling a lantern. Remarkable in some of the species is the stomach-shaped lower part of the SBs, after which some species are named, though this feature is apparently not consistent at the species level.

Variation in the ascus apex between hemispherical/thick-walled and truncate/thin-walled was noted in *O. magnifica*, *O. pleiostomachia*, *O. pluristomachia*, *O. phanosoma*, and *O. myriosphaera*. Species with rather strongly inflated paraphysis apices in combination with truncate, partially thin-walled and rarely shouldered asci (especially *O. myriosphaera*) resemble *O. ovalis* (series *Ovales*, asci often with shoulders), but also members of section *Ovoideae* (subgenus *Orbilia*, asci rarely with shoulders). *O. macroasca* and its 32-spored variant differ from the remaining species of series *Phanosomates* in their SBs having a short and rather wide upper part which is attached by a more or less wide point, similar as in *O. ovalis*.

Species delimitation. The limits between several of the included species are rather vague; moreover, only one or a few collections of some of them were available, their intraspecific variation being unexplored. For instance, *O. magnifica* is only tentatively separated from *O. lanternae*, and this in turn is only gradually different from *O. tremuloidis*, which again appears to be merely a long-spored variant of *O. phanosoma*, in which spore size and shape vary considerably. Sharp limits are also lacking between *O. multiphanosoma* and *O. pluristomachia*, in which spores and SBs also vary to some extent. The three collections included in *O. myriophanosoma* show rather different spore and SB shapes, nevertheless we assume that they belong to one species.

Anamorph. In only three of the twelve recognized species an anamorph was observed. In *O. pluristomachia* and *O. myriosphaera* trinacrium-like conidia were obtained in pure culture, while in *O. macroasca* only one such conidium was observed on the natural substrate. In all of them the conidial arms are bent downwards, either slightly or strongly. Conidia of *O. pluristomachia* closely resemble those of *O. lentiformis* (Pl. 159: 3), *O. ocellata* (Pl. 164: 7) and *O. foliicola* (Pl. 168: 1), which underlines the affiliation of this species in our phylogenetic analysis.

Phylogeny. The two sequences available at present (*O. pluristomachia*, *O. myriosphaera*) do not support a

Key to species of series *Phanosomates*

1. Inflated part of SBs rod-shaped, apically narrowed to a short and thick connecting part (~ 1/3–1/6 × the length and 1/4–3/4 × the width of the inflated part); spores *6.2–12.8 × 3.2–5.3 µm; on *Pinus*, temperate western North America 2
1. Inflated part of SBs rod- to tear-shaped or globose, apically abruptly narrowed to a long and thin connecting part ('filum', ~ 1/2–2 × the length and 1/10–1/20 × the width of the inflated part) 3

2. Asci 64-spored; bark of *Pinus edulis*, subhumid to semiarid .... ***O. macroasca***, p. 507
2. Asci 32-spored; ?bark of *Pinus ponderosa*, humid .... ***O. multimacroasca*** nom. prov. (mentioned under *O. macroasca*), p. 509

3. Asci 64- to 128–spored; spores *(2.5–)2.7–3.5(–4) µm wide 4
3. Asci 32-spored 7
3. Asci 8–16-spored 8

4. Inflated part of SBs globose, often laterally positioned, filum of equal length or often longer (sometimes almost invisible); asci *80–128 µm long, 64–128-spored; (sub)mediterranean Europe 5
4. Inflated part of SBs broadly tear-shaped to elongated, ± central, filum of equal length or shorter, exceptionally longer; asci *73–108 µm long, 64-spored; subhumid to arid North America and Australia 6

5. Asci 128-spored, *108–128 × 13.3–15 µm; spores *(6–)6.5–8(–8.5) µm long, clavate (pear-shaped); bark of *Berberis* .... ***O. pleistosphaera***, p. 526
5. Asci 64-spored, *80–105(–115) × (8.7–)9.5–10.5(–12) µm; spores *(3.8–)4.2–6(–6.8) µm long, ellipsoid-obovoid; wood and bark of *Cercis*, *Olea*, *Punica*, *Quercus* .... ***O. myriosphaera***, p. 523

6. Spores *4–4.6 × 2.9–3.4 µm, ovoid-subglobose; inflated part of SBs tear- to stomach-shaped, filum shorter than inflated part; asci †8.2–10 µm wide; wood of *Atriplex nummularia*, subtropical central Australia .... ***O. myriostomachia*** (mentioned under *O. pluristomachia*), p. 523
6. Spores *(4.5–)5.5–7.3(–8) × (2.5–)2.7–3.6(–4) µm, cylindric-ovoid; inflated part of SBs ovoid to filiform-allantoid, filum of equal length or shorter; asci †9.5–12 µm wide; bark of gymno- and angiosperms, temperate, subhumid to semiarid western North America .... ***O. myriophanosoma***, p. 517

7. Spores *(3.7–)4–6(–7.2) × (2.4–)2.8–3.5(–4) µm, ellipsoid-ovoid; SBs pyriform to stomach-shaped; wood & bark of angiosperms, semihumid to arid, mostly subtropical western North America, southern Africa, western & central Australia ***O. pluristomachia***, p. 520
7. Spores *(5.5–)6–8.5(–10) × (2.8–)3–4.2(–4.5) µm, ellipsoid-ovoid to cylindric-ellipsoid; SBs pyriform to ovoid-amygdaliform; bark of angiosperms, boreal to warm-temperate, humid to arid western North America .... ***O. multiphanosoma***, p. 515
8. Asci 16-spored; spores ovoid, *6.5–8.5 × 3.8–4.5 µm; wood of *Acacia*, tropical semiarid central Australia .... ***O. pleiostomachia***, p. 519
8. Asci 8-spored 9

9. SBs 1–2.2(–2.8) µm long, inflated part globose .... see ***O. clavipisca*** (p. 1283) **&** ***O. lilacina*** (p. 1265, **section *Ovoideae***)
9. SBs 2–5 µm long, inflated part only exceptionally globose 10

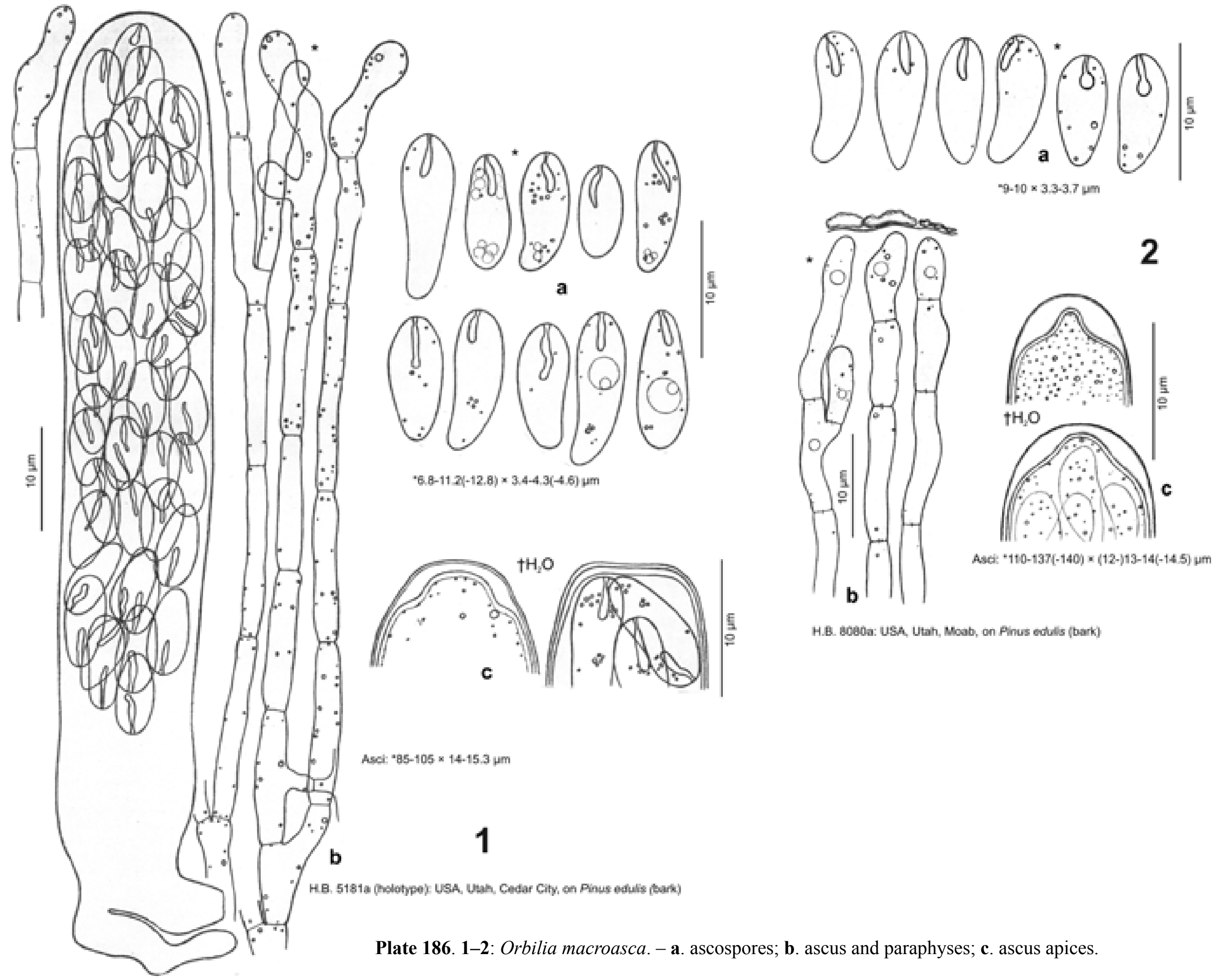
10. Spores cylindric-ellipsoid to obovoid or subglobose, mostly ± homopolar, *(6–)7–9(–11) × (3.2–)3.6–4.8(–5.2) µm, filum about as long as inflated part; wood and bark of gymno- and angiosperms, temperate to tropical, humid to arid western North America, central Asia, central Australia .... ***O. phanosoma***, p. 514
10. Spores ± clavate, slightly to strongly heteropolar, min. *(7.5–)8.5–12 µm long 11

11. Spores predominantly abruptly narrowed below in a thick tail, *(9–)12–15(–16) × (3.2–)3.4–4.2(–4.5) µm; SBs 2–3.8 × 0.8–1 µm, filum and globose to tear-shaped inflated part of ± equal length; bark of *Abies*, *Picea*, *Pseudotsuga*, boreal humid western North America .... ***O. magnifica***, p. 509
11. Spores slightly to moderately narrowed below but ± without tail-like base 12

12. SBs 3.8–5.2 × 1.3–1.5 µm, inflated part angular, ± isodiametric, filum often longer than inflated part; spores *11–17.3 × 3.6–3.8(–4.5) µm; immature asci with †1–1.3 µm thick apical thickening; wood of *Atriplex*, tropical arid central Australia .... ***O. lanternae***, p. 511
12. SBs 2.3–2.8 × 0.6–1 µm, inflated part elongate, not angular, filum shorter than inflated part; spores *(7.5–)8.5–12(–14.5) × 3.3–4 µm; immature dead asci without apical thickening; wood of *Populus tremuloides*, temperate humid western North America .... ***O. tremuloidis***, p. 512

monophyletic series *Phanosomates*, but are found within the series *Lentiformes* core clade in SSU+ITS+LSU analyses (Phyls 7–8, Baral et al. 2017b) or analyses restricted to either SSU or ITS (S8, S9). In the ITS analysis *O. myriosphaera* clustered with *O. cercidicola* and *O. pluristomachia* with *O. lentiformis* in 2 ± medium supported clades. Only when analysing LSU (D1–D2) *O. myriosphaera* formed a weakly supported clade with *O. pluristomachia*. A close molecular relationship between *O. pluristomachia* and *O. lentiformis* is also seen when analysing SSU or 5.8S alone (S8, S10).

Ecology. All 13 known species of series *Phanosomates* were exclusively recorded on ligneous substrate. Three of them were so far exclusively found on gymnosperm hosts (*O. magnifica*, *O. macroasca*, *O. multimacroasca* nom. prov.), though the latter two were only rarely collected. *O. phanosoma* and *O. myriophanosoma* occurred on both gymno- and angiosperm hosts. *O. myriosphaera* and *O. pleistosphaera* were exclusively found in Europe and here only in the (sub) mediterranean belt. Eight species were found in North America in the boreal humid to subtropical arid, ± continental Rocky Mountains, Colorado Plateau, and deserts in the south. Two of them (*O. phanosoma*, *O. pluristomachia*) were also collected in subtropical semihumid to arid Australia, the former also in cold-continental semiarid Asia and the latter in subtropical arid Africa. *O. lanternae* and *O. pleiostomachia* are only known from tropical arid Australia.



H.B. 5181a (holotype): USA, Utah, Cedar City, on *Pinus edulis* (bark)

H.B. 8080a: USA, Utah, Moab, on *Pinus edulis* (bark)

Plate 186. **1–2**: *Orbilia macroasca*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices.

Orbilia macroasca Baral & G. Marson, **sp. nov.**, MB 813498 — Pls 186–187

Etymology: referring to the extraordinarily large size of the asci.

Typification: USA, Utah, Cedar City, branch of *Pinus edulis*, 24.VIII.1994, G. Marson (ex H.B. 5181a, M-0276502, holotype).

Latin diagnosis: Apothecia *in statu* rehydratata 0.3–0.7 mm diam. Asci 64-spori. Ascosporae *6.8–12.8 × 3.2–4.6 µm, ellipsoideo-clavatae, *in statu vivo* corpusculum refringens bacilliformem *absque filo* continentes. Paraphyses ad apicem non vel leniter inflatae. *Habitat ad corticem putridum ramorum siccorum* Pini edulis*, in zona temperata subhumida ad semiarida montana America septentrionali.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.7 mm diam., 0.2–0.24 mm high, light to bright orange, round, rarely somewhat lobate, scattered to ± gregarious in small groups; disc slightly concave to flat; margin distinct, thin, whitish-powdered, somewhat crenulate to hairy, protruding 10–30 µm, half to entirely immersed; dry rather closed and retracted. **Asci** *85–140 × (12–)13–15.3 µm {2}, †80–135 × (9–)11–12(–13) µm {2}, 64-spored (50–54 counted), spores multiseriate, partially inversely oriented (especially the lower spores), pars sporifera *65–80 µm long; **apex** (†) slightly to medium (to strongly) truncate, hemispherical in profile view, dome †1.5–2 → 0.3–1.5 µm thick {2}, with distinct, finally broad and low apical chamber; **base** with or without short to medium long stalk, L- to h-shaped. **Ascospores** *(6.8–)8–11(–12.8) × 3.2–4(–4.6) µm {2}, †5.5–10.3 × 3–3.7 µm {2}, (cylindric-)ellipsoid to clavate, apex rounded, straight to slightly curved towards base; **SBs** *2.5–3.5(–4.7) × (0.5–)0.6–0.8(–1) µm {2}, rod-shaped, base sometimes tapered, also inflated (ampulliform), apically narrowed to a ± wide, rarely small point, subapically partially distinctly constricted, straight or ± flexuous; **LBs** sparse, minute. **Paraphyses** apically uninflated, also slightly clavate or sublageniform, terminal cell *(5–)7–17(–23) × (2–)2.5–3.5(–3.8) µm {2}, lower cells *(8–)11–18(–21) × 1.8–2.8 µm {2} (near base or apex 3–3.8 µm); very rarely or quite frequently branched near apex. **Medullary excipulum** hyaline, 50–60 µm thick, of dense textura intricata with some inflated cells, sharply delimited. **Ectal excipulum** hyaline, pale orange at flanks and margin, of thin-walled († slightly to medium gelatinized), irregularly or vertically oriented t. angularis from base to submargin, 30–40 µm thick at base and flanks, cells */†8–15 × 7–10(–12) µm {2}; 20–30 µm thick near margin, of t. porrecta oriented at a 0–10° angle to the surface, forming paraphysis-like, somewhat free hairs with rough surface, terminal cells *12–15 × 3–4 µm {1}. **Anchoring hyphae** sparse to rather abundant, †1.7–3.3 µm wide, walls 0.2–0.3(–0.8) µm thick {1}, forming at flanks and margin a hyaline t. porrecta-intricata that projects beyond the hymenium. **SCBs** in paraphyses absent or present, globose, small, scarcely visible. **Exudate** over paraphyses visible as a 0.2 µm thick refractive line, lying over thick gel, partially also 1–2(–3) µm thick, cloddy, pale yellow(-orange), loosely attached. **— ANAMORPH**: trinacrium-like (presumed, from natural substrate {1}). **Conidiophores** unknown. **Conidia**: T-shaped, 2-armed, total size *32 × 31 µm, stipe *25 × 6 µm, 2-septate, arms tapering, somewhat bent downwards, *13–14.5 × 5–5.3 µm, 1-septate (only 1 conidium seen).

Habitat: collected 0.5–2 m above the ground, on corticated (upper side partially somewhat decorticated), 8–16 mm thick branches

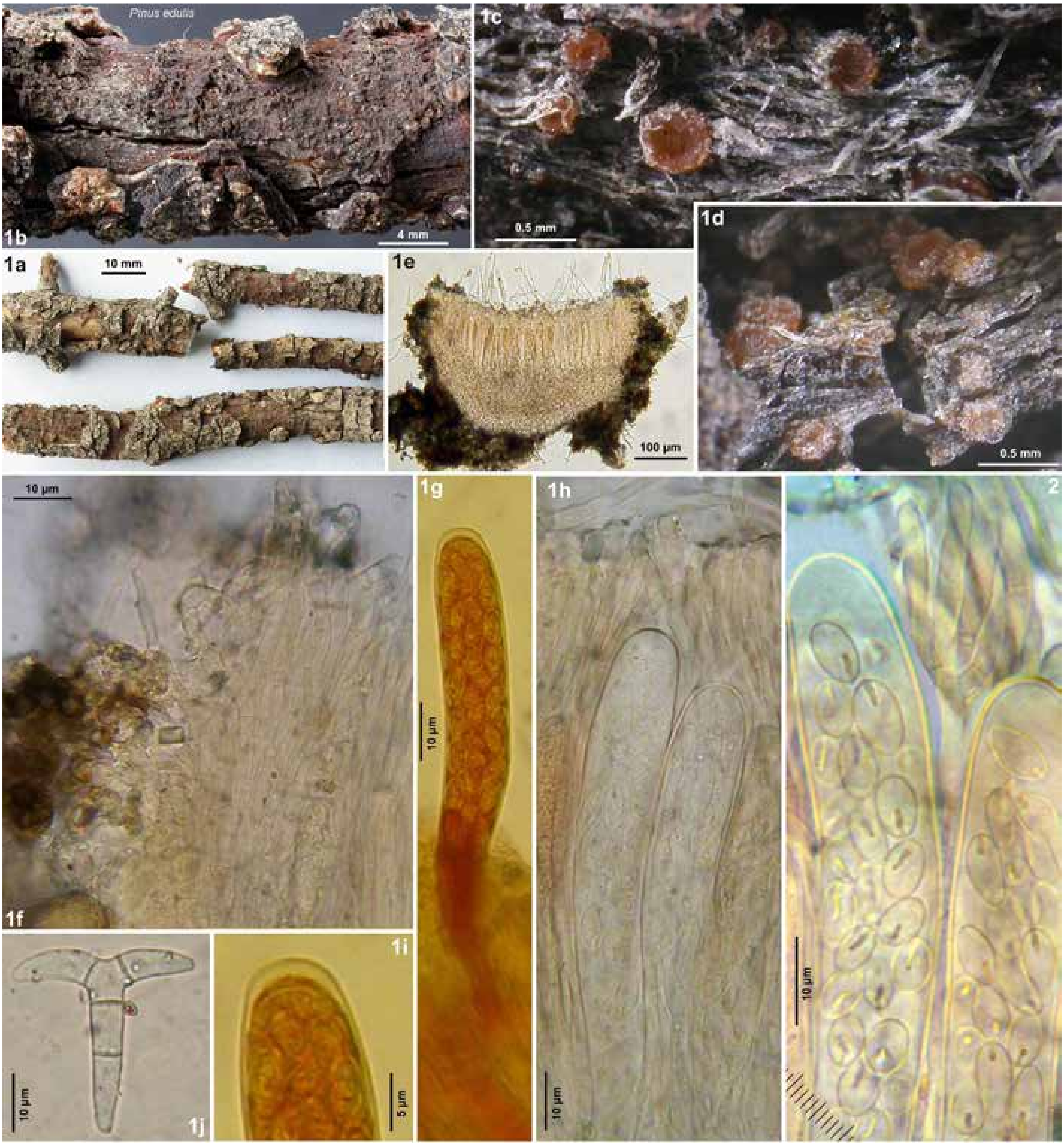


Plate 187. **1**: *Orbilia macroasca*; **2**: *O. multimacroasca* nom. prov. – **1a–b**. branches of *Pinus edulis*; **1c–d**. rehydrated apothecia; 1e. apothecium in median section; **1f**. marginal ectal excipulum in median section; **1g–h**, **2**. asci and paraphyses; **1i**. ascus apex; 1j. conidium from substrate. – Living state, except for **1g**, **i** (in KOH+IKI). — **1a–j**. H.B. 8080a: USA, Utah, on *Pinus edulis*; **2**. 17.VI.2003: USA, Arizona, on *Pinus ponderosa*.

of *Pinus edulis* {2}, in small cross-cracks or larger periderm-free areas on medium to strongly decayed bark (bast) {2}, with scattered resin, greyed and with some green algae. **Associated**: *Acremonium limoniforme* (parasitic in *O. macroasca*) {1}, *Amphosoma macrosporum* {1}, *Dothideales* {1}, *Encoelioideae* {1}, crustose lichen. **Desiccation tolerance**: fully viable for at least 33 months. **Altitude**: 1815–1920 m a.s.l. **Geology**: Triassic & Upper Cretaceous (calcareous) sandstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia macroasca* is characterized by 64-spored asci and ellipsoid-clavate ascospores with ± rod-shaped SBs. The species differs from the similar *O. myriophanosoma* in longer and wider spores, thicker asci, larger apothecia, and especially in the SBs that lack a fine filum but are, instead, more broadly inserted to the apical spore wall by a distinctly thicker, very short connecting part. Due to the absence of a filum the species might instead belong to section *Hemiorbilia*, but the SBs resemble those occasionally seen in *O. magnifica* (Pl. 188: 2a upper row).

Not included collection. A sparse, unpreserved sample on *Pinus ponderosa* differs mainly in 32-spored asci and was not studied in detail. Only a microphoto exists (Pl. 187: 2): asci *13.2–13.7 µm wide, pars sporifera *42 µm long; ascospores

*6.2–8.3(–9) × 3.5–4.7(–5.3) µm, SBs 2.7–4 × 0.6–0.8 µm; paraphyses apically uninflated, terminal cell *18.5–21 × 2.6–3.1 µm (all data evaluated from photo). This might well represent a different species due to the deviating spore number, and is provisionally called ***O*. *multimacroasca*** G. Marson & Baral nom. prov.

Anamorph. Only one conidium was found on the substrate which resembles those trinacrium-like conidia of some other members of section *Lentiformes*.

Ecology. *O. macroasca* is so far only known from two records from pinyon-juniper woodlands in western North America: on rotten bark of dead xeric branches of *Pinus edulis* from a warm-continental semiarid high plateau in the Canyonlands section of the Colorado Plateau (paratype) and from a cold-temperate subhumid dry riverbed in the Utah Mountains (holotype). The 32-spored population (*O. multimacroasca*) occurred in a cold-temperate humid pure ponderosa pine forest at higher altitude in the Mogollon Rim in association with *Orbilia spermoides*.

Specimens included. **USA**: **Utah**, Utah Mts. adjacent to Great Basin, 1.5 km ESE of Cedar City, Dixie Forest, 1815 m, branch of *Pinus edulis*, on bark, 24.VIII.1994, G. Marson (ex H.B. 5181a, M-0276502, **holotype**). – Canyonlands, 35 km SSW of Moab, 1.3 km E of Needles Overlook, Hatch Point, 1920 m, branch of *Pinus edulis*, on bark, 7.VI.2003, G. Marson (H.B. 8080a, anam. substr.).

O*. *multimacroasca nom. prov.: **USA**: **Arizona**, Mogollon Rim, 16 km NW of Flagstaff, San Francisco Peaks, 6 km WSW of Humphreys Peak, 2550 m, branch of *Pinus ponderosa*, 17.VI.2003, G. Marson (ø).

Orbilia magnifica Baral & G. Marson, **sp**. **nov**., MB 813499 — Pls 188–189, Map 29

Etymology: at first named '*magnificae*' after the type host, originally misidentified as *Abies magnifica*, then changed to *magnifica* (= magnificent).

Typification: USA, Arizona, Jacob Lake, branches of (?)*Pseudotsuga menziesii*, 17.V.1995, G. Marson (ex H.B. 5404b, M-0276507, holotype).

Latin diagnosis: *Differt ab* Orbilia phanosomate *et* O. lanternae *ascosporis ad basim valde attenuatis et caudatis. Habitat ad corticem putridum ramorum siccorum arborum coniferarum in zona boreali ad temperata humida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.5(–0.7) mm diam., 0.16–0.23 mm high (receptacle 0.15 mm), pale to bright (rose-)orange(-ochraceous), round, gregarious in ± small groups; disc slightly concave (to flat), margin ± thick, even, protruding 0–10 µm; sessile or with a hidden stipe 0.05 × 0.2 mm, ± erumpent (partially hidden in cracks); dry bright orange-red. **Asci** *(53–)65–86(–92) × 7–8 {2} or 8.5–9.3(–10) µm {3}, †(50–)60–85(–94) × (6–)6.5–8(–9.5) µm {5}, 8-spored, spores *2–3-seriate, 0–4(–6) lower spores inversely oriented {4} (not or sometimes mixed), pars sporifera *33–43 → 26 µm long; **apex** (†) hemispherical or slightly to medium truncate, dome present {5}, †1–1.3 → 0.3–0.8 µm thick {4}, with ± distinct apical chamber; also partially absent (immature, wall †0.3–0.5 µm thick) {2}; **base** with short to long, ± thin or thick, flexuous stalk, T- to L- or Y-shaped. **Ascospores** *(9–)12–15(–16) × (3.2–)3.4–4.2(–4.5)((–5)) µm {4}, † (8–)9–11(–11.5) {1} or (10–)12–15(–16.7)((–18.5)) {2} × (3–)3.2–3.8(–4) µm {3}, (slightly to) strongly clavate or mostly ± ellipsoid, with a thick tail *(2–)3–5(–7) × 1.3–2(–2.4) µm, apex rounded, tail sometimes with inflated base, straight to slightly (or medium) curved in lower part; **SBs** *(1.5–)2–3.8(–4.5) × 0.8–1(–1.2) µm, divided into a very abruptly swollen, tear- to pear- or rod-shaped or ellipsoid to globose lower part and a fine filum of ± equal or shorter length, filum either thin up to the apex {3}, or distinctly widened at point

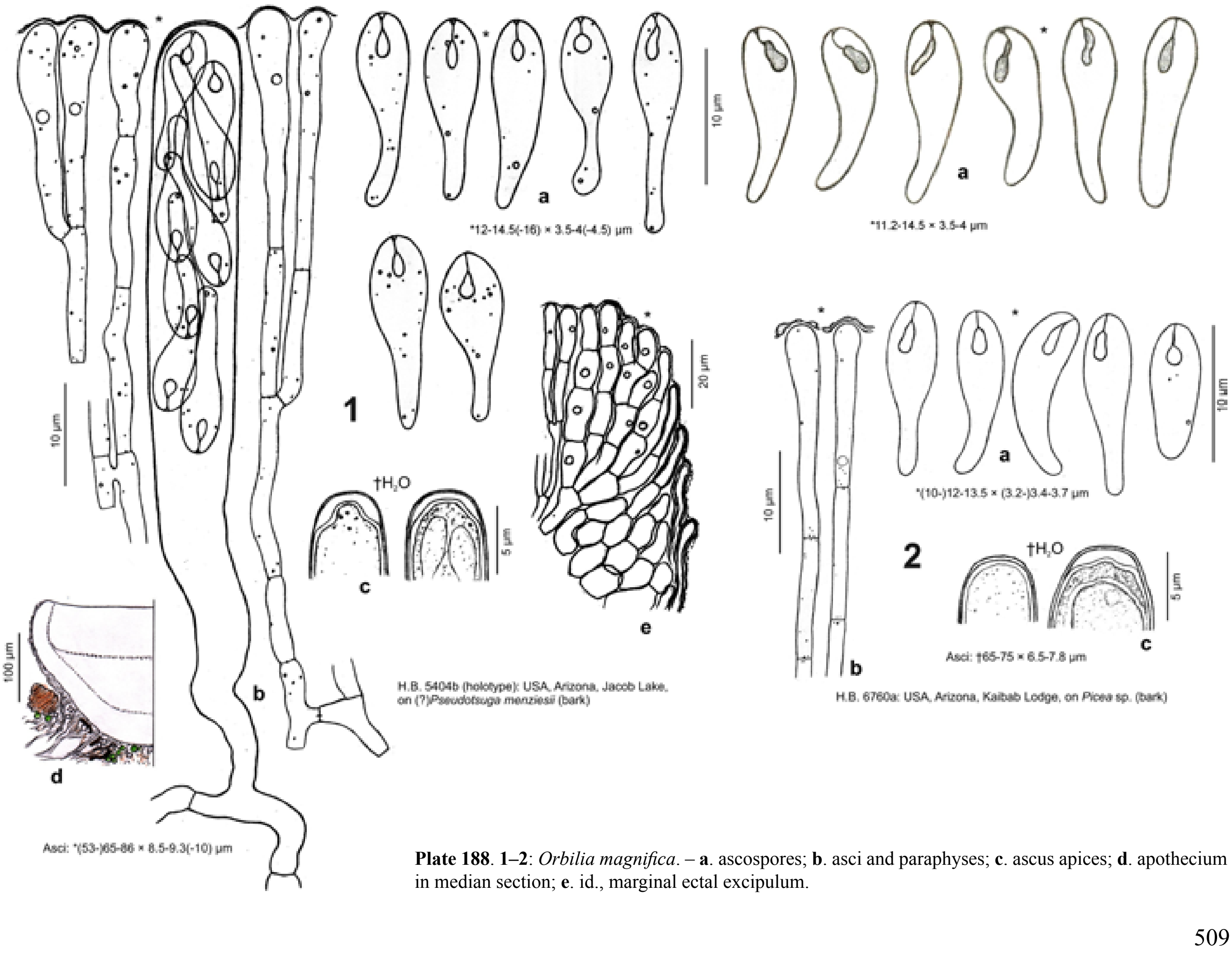


Plate 188. **1–2**: *Orbilia magnifica*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

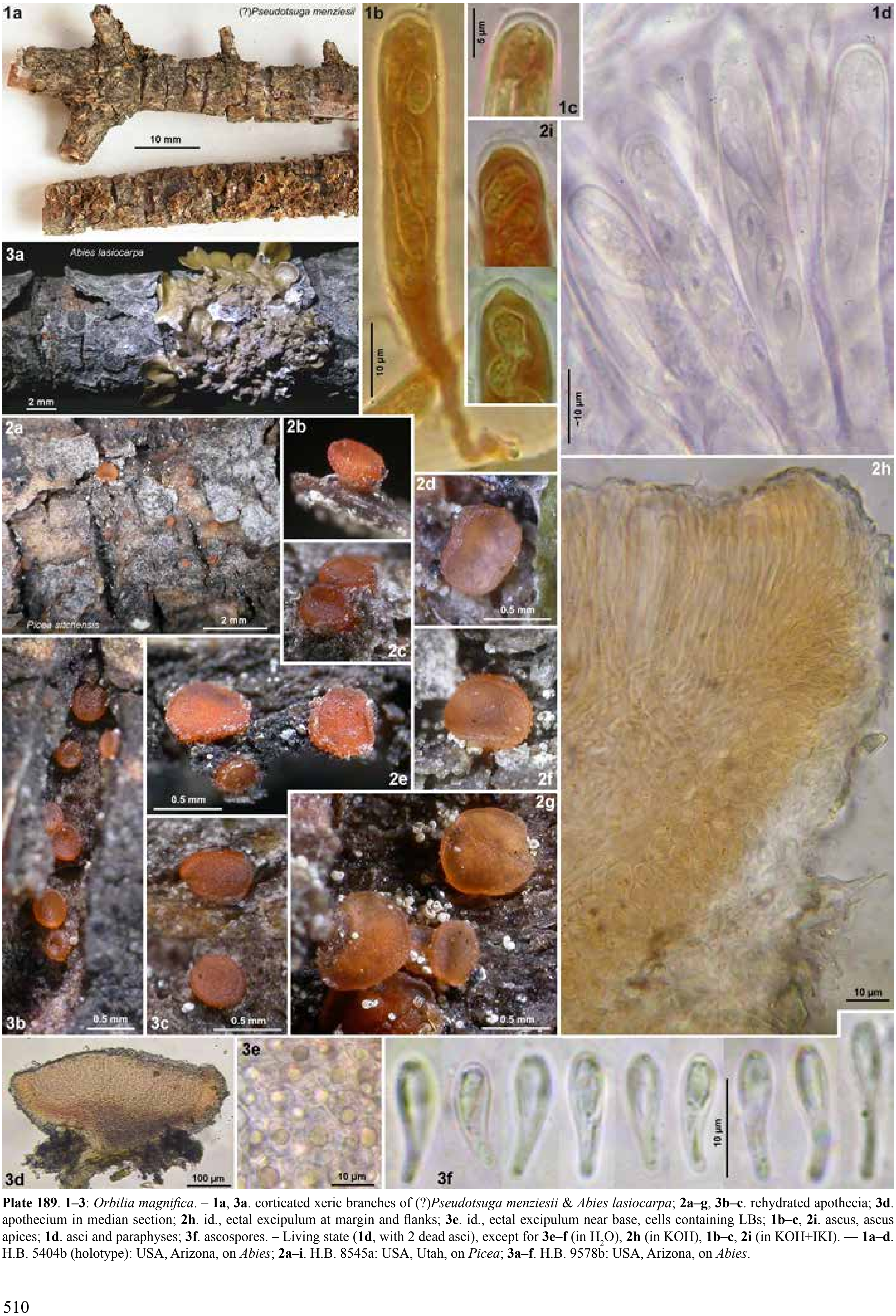


Plate 189. **1–3**: *Orbilia magnifica*. – **1a**, **3a**. corticated xeric branches of (?)*Pseudotsuga menziesii* & *Abies lasiocarpa*; **2a–g**, **3b–c**. rehydrated apothecia; **3d**. apothecium in median section; **2h**. id., ectal excipulum at margin and flanks; **3e**. id., ectal excipulum near base, cells containing LBs; **1b–c**, **2i**. ascus, ascus apices; **1d**. asci and paraphyses; **3f**. ascospores. – Living state (**1d**, with 2 dead asci), except for **3e–f** (in H_2O), **2h** (in KOH), **1b–c**, **2i** (in KOH+IKI). — **1a–d**. H.B. 5404b (holotype): USA, Arizona, on *Abies*; **2a–i**. H.B. 8545a: USA, Utah, on *Picea*; **3a–f**. H.B. 9578b: USA, Arizona, on *Abies*.

of attachment {T}, straight, rarely curved or bent. **Paraphyses** apically slightly to medium (sometimes strongly) clavate(-capitate), terminal cell *(8–)13–21(–26) × 2–4.7 µm {2}, †2.5–5 µm wide {1}, lower cells *9–18 × 1.7–2.3 µm {1}; sometimes branched near apex. **Medullary excipulum** pale rose, 40–70 µm thick, of ± dense textura intricata with a few or many inflated cells, sharply delimited. **Ectal excipulum** pale rose, from base to mid flanks of (†) thick-walled (common cells 1–2 µm {1}), vertically oriented t. angularis(-prismatica), 30–60 µm thick near base, cells */†8–21 × 7–14(–18) µm {2}; 15–25 µm thick at flanks, cells *6–12 × 5–8 µm, 15–20 µm thick at margin, of t. angularis(-prismatica) oriented at 80° at submargin, at margin of t. porrecta oriented at 0–45°, cortical cells elongate, *7–14 × 2–3.5 µm {1}. **Anchoring hyphae** abundant, */†2–3.5 µm wide, walls 0.2–0.4(–0.8) µm thick {2}, forming thin, long hyphal strands, covering flanks and submargin by a 3–15 µm thick ± gelatinized layer. **SCBs** globose, in terminal cells of paraphyses 1–1.3 µm diam., 1 per cell, very slightly refractive, partially absent; in cortical cells 1.3–1.5 µm diam. **LBs** in basal ectal excipulum small and sparse {1} or large {1}. **Exudate** over paraphyses 0.1–1.5 µm thick {2}, continuous, ± rough; over margin and flanks 0.5–1 µm thick. — **ANAMORPH**: unknown (but 1 vermispora-like conidium seen emerging from hymenium).

Habitat: collected 1.2–3 m above the ground, corticated, 4–14 mm thick branches of ?*Abies* sp. {1}, *A. lasiocarpa* {1}, *Picea* sp. {1}, *P. sitchensis* {1}, *Pseudotsuga menziesii* {1/1}, on loosely attached, medium decayed bark {5} (bast, often in cracks of periderm) or wood {1}, greyed, slightly covered by green algae. **Associated**: *Helicogonium orbiliarum* (parasitic in *O. magnifica*) {1}, *Lachnellula* sp. {1}, *Lecanora caesiorubella* {1}, *Melanohalea subolivacea* {2}, *Orbilia aristata* {1}, *O.* ?*carpoboloides* {1}, *O. coniferarum* {1}, *O. lentiformis* {2}, *O. macrodelphinus* {1}, *O. maeandrina* {2}, ?*Physcia* sp. {1}, *Stictis* sp. {1}, *Teichospora* sp. {1}, *Xanthoria* sp. {1}. **Desiccation tolerance**: fully viable for at least 1 year, a few spores and many paraphyses still viable after 5 ⅓ years. **Altitude**: 2000–2800 m a.s.l. **Geology**: Mississippian-Permian, Triassic-Jurassic and Cretaceous sand- and limestone; basalt breccia with andesite & rhyolite. **Phenology**: long-lived.

Taxonomic remarks. *O. magnifica* is characterized by clavate ascospores with often distinct thick tails, also by rather large apothecia. Despite a strong heteropolarity in spore shape, inversely oriented spores are entirely lacking in some of the asci. In spore shape *O. magnifica* resembles *O. patellarioides*, a species differing in lens-shaped SBs and black apothecia, but also *O. clavuliformis* in which the SBs have no filum. *O. magnifica* is obviously closely related to *O. lanternae* (see p. 512).

Variation. Although *O. magnifica* appears to be a rather constant species, some variation was noted among the collections. From the other three samples that were studied in the living state, the holotype differed in the SB filum being apically often abruptly widened (funnel-shaped). In the two collections on *Picea* the ascus apical thickening was sometimes or often absent, whereas in the those on *Abies* and (?)*Pseudotsuga* examined for this feature it was always present.

Phylogeny: A sequence taken in Feb. 2020 from apothecia on *Pseudotsuga* clustered in our ITS+LSU ML analysis (not shown) supported sister to the *flavida-cucumispora* clade. The minimum ITS distance was 10.5% to *O.* aff. *lentiformis* (H.B. 8002c) and 11.5% to *O. cucumispora*.

Ecology. *O. magnifica* was collected on rotten bark of dead xeric branches of *Abies* and *Picea* in a cold-temperate humid ponderosa pine forest (holotype) and in cold-temperate to boreal humid Douglas fir and Engelmann spruce forests of the Middle Rocky Mountains and Colorado Plateau (Utah Mountains, Kaibab Plateau, Mogollon Rim) in western North America.

Map 29. Known distribution of *O. magnifica* in North America.

Specimens included. **USA**: **Wyoming**, Middle Rocky Mountains, Grand Teton, N of Jackson, ~2000 m, on branch of ?*Abies*, 6.VI.1996, G. Marson (ø). – **Utah**, Utah Mts., Dixie Forest, 22 km SSE of Torrey, 13 km S of Grover, 1 km N of Pleasant Creek Campground, 2650 m, branches of *Picea sitchensis*, on bark & wood, 19.VI.2000, G. Marson (H.B. 8545a). – ibid., NW of Pleasant Creek Campground, 2664 m, branches of *Pseudotsuga menziesii*, on bark, 11.VI.2003, G. Marson (G.M. 2003-06-03.1, sq.: MT356589). – **Arizona**, Grand Canyon, Kaibab Plateau, 37 km SE of Fredonia, S of Jacob Lake, 2415 m, branches of (?)*Pseudotsuga menziesii*, on bark, 17.V.1995, G. Marson (M-0276507, **holotype**; **isotypes** in M & H.B. 5404b). – 3 km N of Kaibab Lodge, 2680 m, branch of *Picea*, on bark, 17.V.1995, G. Marson (H.B. 6760a). – Mogollon Rim, 83 km SSE of Vernon, 9.5 km SSW of Hannagan Meadow, Rte. 191 (Coronado Trail), 2800 m, branches of *Abies lasiocarpa*, on bark, 2.VI.2003, G. Marson (H.B. 9578b).

Orbilia lanternae Baral & G. Marson, **sp. nov.**, MB 813500 — Pl. 190

Etymology: named after the spore body resembling a lantern.

Typification: Australia, Northern Territories, Wilora, branch of *Atriplex*, 8.X.1998, G. Marson (ex H.B. 6262f, MEL 2389197, holotype).

Latin diagnosis: *Differt ab* Orbilia magnifica *ascosporis ad basim minus attenuatis neque caudatis*, *corpusculis refringentibus angularibus*; O. lentiformis *differt ab* O. lanternae *corpusculis refringentibus lentiformibus. Habitat ad lignum putridum ramorum siccorum* Atriplicis *in zona tropica arida Australiae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.5 mm diam., 0.14 mm high, light (dirty) orange-rose, ± round, scattered to gregarious; disc slightly concave, margin thin, scarcely protruding, smooth; sessile, slightly erumpent between fibres. **Asci** *70–80 × 9.5–10.5 µm, 8-spored, spores *2–3-seriate, 3–5 lower spores inverted (slightly mixed), pars sporifera *44 µm long; **apex** (†) hemispherical to slightly truncate, dome immature †1–1.3 µm thick, with slight apical chamber; **base** with short, thick, flexuous stalk, L-shaped. **Ascospores** *11–17.3 × 3.6–3.8(–4.5) µm, (ellipsoid-)clavate, apex rounded, base medium to strongly attenuated, sometimes thick and tail-like, straight to slightly inequilateral or curved at base; **SBs** *3.8–5.2 × 1.3–1.5 µm, divided into an abruptly swollen, angular or sometimes tear-shaped lower part and a filum of equal or often double length. **Paraphyses** apically uninflated to very slightly clavate, terminal cell *5–14 × 2.5–3.7 µm, lower cells *9–16 × 1.8–2.5(–2.8) µm; sometimes branched at upper septum. **Medullary excipulum** pale rose, 20 µm thick, of dense textura globulosa(-intricata), horizontally oriented, ± sharply delimited. **Ectal excipulum** of thin-walled, irregularly oriented t. angularis(-prismatica) from base to mid flanks, 40 µm thick near base, cells *10–

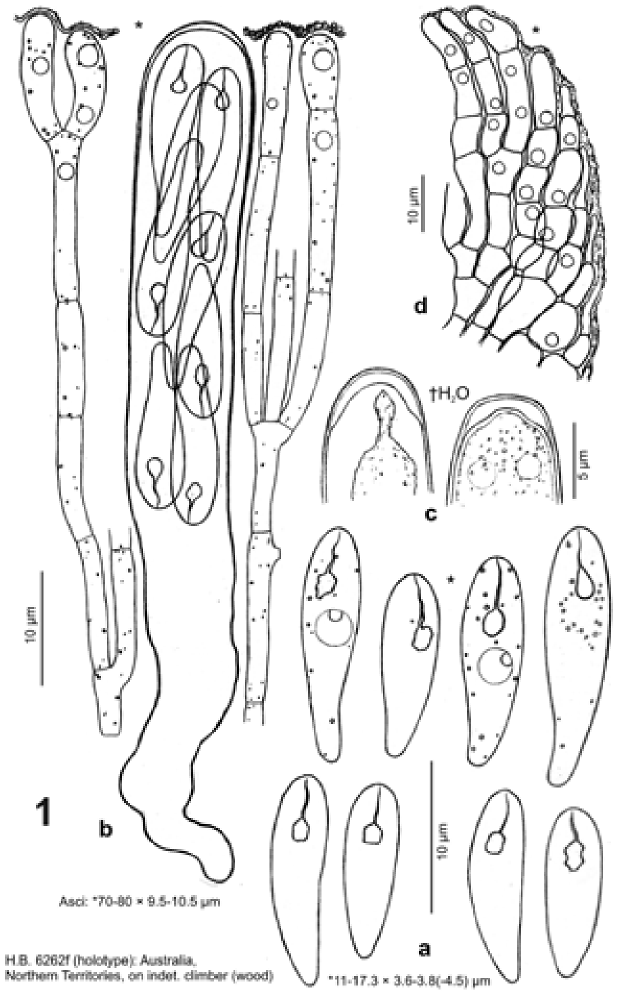


Plate 190. **1**: *Orbilia lanternae*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum (median section).

15 × 7–10 µm; 20 µm thick near margin, of t. prismatica oriented at a 10–20° angle to the surface, marginal cortical cells *(6–)9–11 × 4–5 µm. **Anchoring hyphae** not examined. **SCBs** globose, in paraphyses 1.3–2 µm diam., in ectal excipulum (near margin) 2–2.5 µm. **Exudate** over paraphyses and margin 0.5–2 µm thick, granular-continuous, loosely attached. **— ANAMORPH**: unknown.

Habitat: collected 0.2–2 m above the ground, decorticated, 9–10 mm thick branches of *Atriplex* sp., on 0.2 mm deep very decayed wood, strongly greyed, no algae. **Associated**: *Dothideales*, *Orbilia barrowensis*, *O. livistonae*, *O. multiaustrocylindrica*, *O. multigambelii*, *O. octocercocarpi*, *O. pleioaustraliensis*. **Altitude**: 480 m a.s.l. **Desiccation tolerance**: fully tolerant for at least 3 weeks. **Geology**: Cenozoic regolith. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia lanternae* differs from the conifericolous North American *O. magnifica* in slightly to medium tapered spore bases without distinct tails, also in mostly angular inflated parts of the SBs. Moreover, the paraphyses have shorter terminal cells and the marginal cortical cells of the excipulum are wider. *O. lanternae* closely resembles *O. lentiformis* (series *Lentiformes*) in spore shape. However, the two species can easily be distinguished by the very different type of spore body. The lens-shaped SBs in *O. lentiformis* can even be seen in dead spores whereas those in species of series *Phanosomates* become invisible.

Ecology. *O. lanternae* is only known from a single sparse collection which is now without apothecia. The species grew on rotten wood of dead xeric twigs of *Atriplex* sp. climbing up trees of *Acacia* sp. in an acacia open shrubland north of MacDonnell Ranges in tropical arid central Australia.

Specimens included. **AUSTRALIA**: **Northern Territories**, Burt Plain, 31 km SW of Barrow-Creek Hotel, 3.7 km WSW of Wilora, Stuart Hwy, 480 m, branch of *Atriplex*, on wood, 8.X.1998, G. Marson (ex H.B. 6262f, MEL 2389197, **holotype**).

Orbilia tremuloidis Baral & E. Weber, **sp. nov.**,

MB 813501 — Pl. 191

Etymology: named after the substrate of the type, *Populus tremuloides*.

Typification: USA, Arizona, Flagstaff, branch of *Populus tremuloides*, 12.VI.2000, G. Marson (ex H.B. 7086d, M-0276603, holotype).

Latin diagnosis: *Differt ab* Orbilia phanosomate *ascosporis longioribus*, *ad basim magis attenuatis*, *corpusculis refringentibus filis multo brevioribus. Habitat ad lignum putridum ramorum siccorum* Populi tremuloidis *in zona temperata humida altimontana Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.3 mm diam., 0.15 mm high, light orange(-rose), hardly translucent, round to elliptical, subgregarious in a small group; disc slightly concave, margin thin, not protruding, smooth; broadly sessile, superficial to erumpent. **Asci** †60–80 × 7–8.5 µm, 8-spored, spores (†) obliquely biseriate, 1–4 lower spores inverted (partially strongly mixed); **apex** (†) hemispherical to very slightly truncate, rarely conico-truncate, thin-walled (†0.2–0.3 µm thick); **base** with short to medium long,

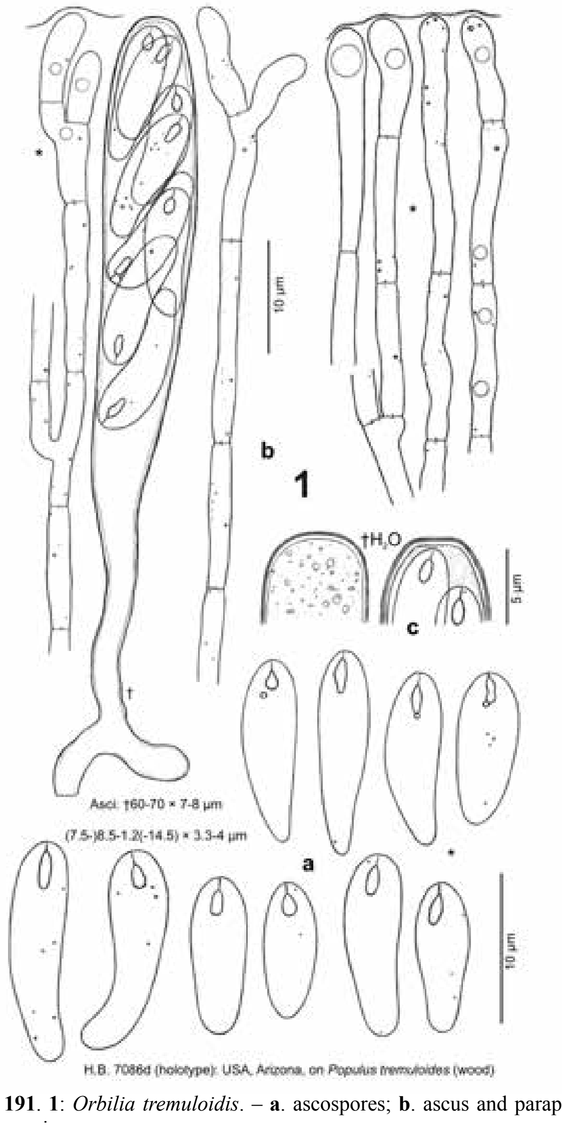
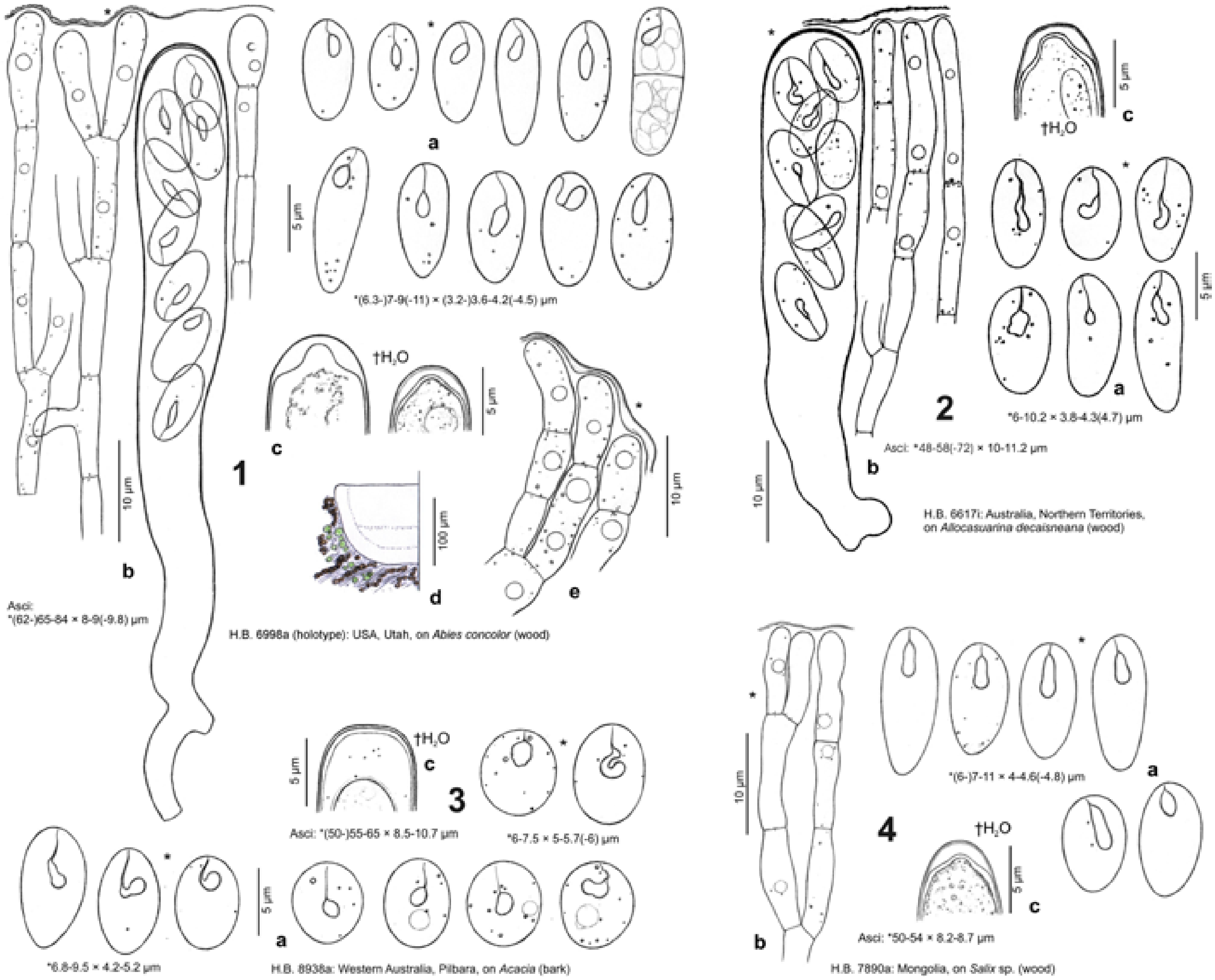


Plate 191. **1**: *Orbilia tremuloidis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices.



H.B. 6998a (holotype): USA, Utah, on *Abies concolor* (wood)

H.B. 6617i: Australia, Northern Territories, on *Allocasuarina decaisneana* (wood)

H.B. 8938a: Western Australia, Pilbara, on *Acacia* (bark)

H.B. 7890a: Mongolia, on *Salix* sp. (wood)

Plate 192. **1–4**: *Orbilia phanosoma*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

thick, flexuous stalk, Y- to L-shaped. **Ascospores** *(7.5–)8.5–12(–14.5) × 3.3–4 µm, †9–12.5 × 3.3–3.7 µm, subcylindric-ellipsoid to ellipsoid-clavate, apex rounded, towards base slightly or strongly attenuated and straight to slightly (to medium) curved; **SBs** *(2–)2.3–2.8(–3.2) × 0.6–1 µm, lower part cylindrical to ellipsoid-fusoid or pyriform, rarely constricted, apically narrowed to a short filum (½ to ¼ of length of inflated part), ± straight. **Paraphyses** apically uninflated or slightly (to medium) clavate, terminal cell *8–23 × 2–3(–4) µm, lower cells *9.5–18 × 1.8–2.5(–3.3) µm; sometimes branched at upper septum. **Medullary excipulum** hyaline, 50 µm thick, of ± dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** pale orange, of ± thin-walled, irregularly (to horizontally) oriented t. angularis(-prismatica) from base to mid flanks, 20 µm thick near base, cells †6–11 × 5–8 µm; 15–20 µm thick near margin, of t. prismatica oriented at a 0–10° angle to the surface, marginal cortical cells †9–15 × 3–4 µm. **Anchoring hyphae** medium abundant, †1.5–3 µm wide, walls 0.2–0.3 µm thick, extending to the margin as a thin layer. **SCBs** in paraphyses globose, 1.2–2.7 µm diam. **Exudate** over paraphyses 0.1 µm thick, continuous, smooth, loosely attached, over margin and flanks 0.2–0.3 µm thick. — **ANAMORPH**: unknown.

Habitat: collected 3 m above the ground, partially to entirely decorticated, 18–24 mm thick branches of *Populus tremuloides*, on 1 mm deep very decayed wood, slightly to strongly greyed, a few to many green algae. **Associated**: *Hysterium* spp. {2}, *Hysteropatella* sp., *Mellitiosporiella pulchella*, *Odontotrema oregonensis*, *Orbilia delphinus*, *O. gambelii*, *O. microsoma*, *O. navajoana*, *Phragmiticola* sp. **Desiccation tolerance**: paraphyses and spores still viable after 1.5 years. **Altitude**: 2450 m a.s.l. **Geology**: basaltic lava and cinders with andesite, dacite & rhyolite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia tremuloidis* is tentatively segregated from *O. phanosoma* based on its longer, more clavate ascospores and by spore bodies with a shorter filum. *O. tremuloidis* resembles *O. lanternae* in spore shape, but the latter species differs in the SBs having a much longer filum and broader, angular inflated parts. *O. tremuloidis* differs from both species in the absence of an apical thickening of the asci. However, also in *O. phanosoma* thin-walled asci rarely occur, and *O. tremuloidis* might vary in a similar way if more collections will be available for study.

Ecology. *O. tremuloidis* is only known from a single collection on rotten wood of dead xeric branches of *Populus tremuloides* from the cold-temperate humid ponderosa pine forest on a high plateau at the northwest-end of the Mogollon Rim in the southwest of Northern America.

Specimens included. **USA**: **Arizona**, Mogollon Rim, 23 km NW of Flagstaff, 10.5 km WNW of Humphreys Peak, Rte. 180, 2450 m, branch of *Populus tremuloides*, on wood, 12.VI.2000, G. Marson (ex H.B. 7086d, M-0276603, **holotype**).

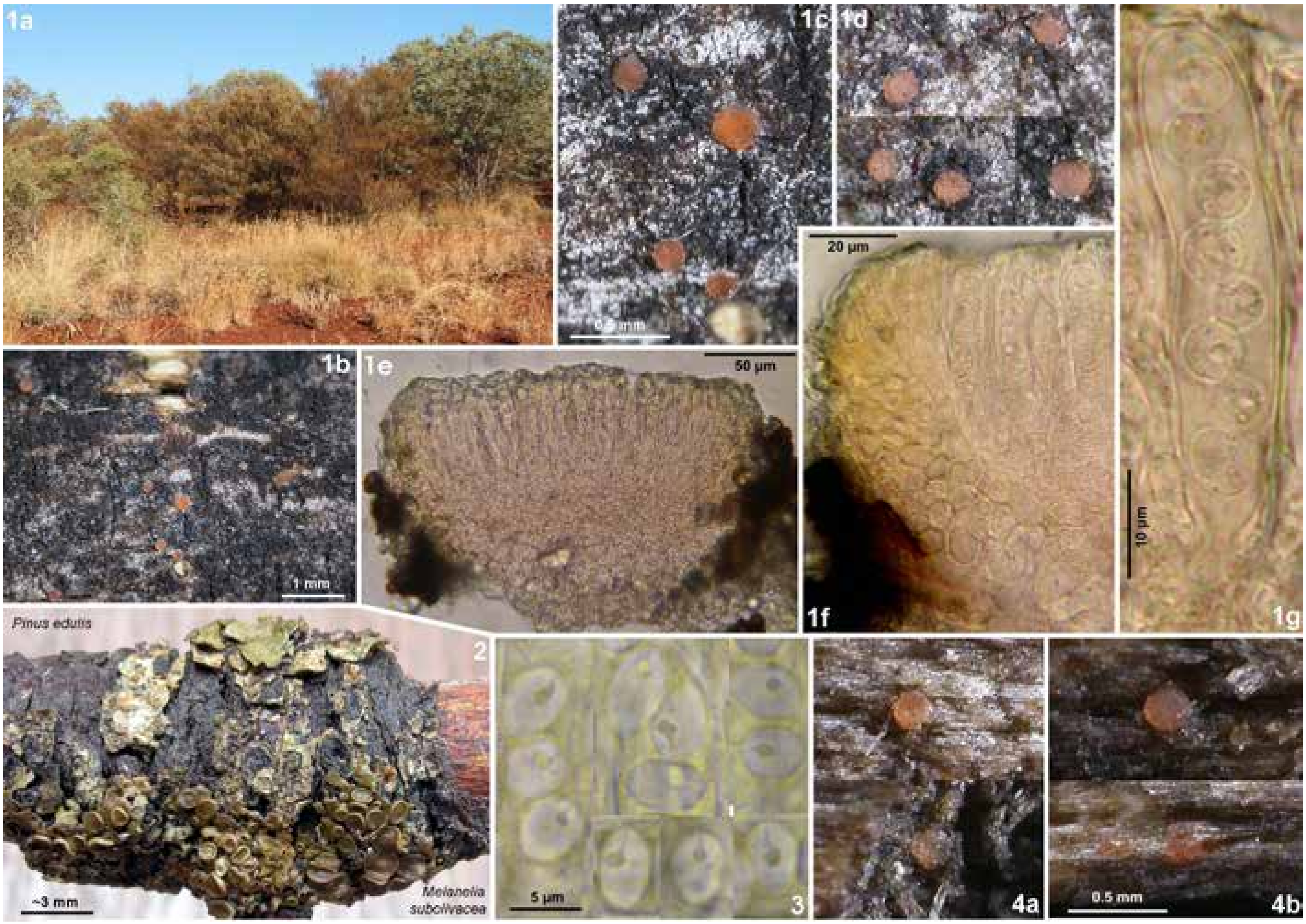


Plate 193. **1–4**: *Orbilia phanosoma*. – **1a**. arid acacia shrubland and hummock grassland; **2**. branch of *Pinus edulis* with *Melanohalea subolivacea*; **1b–d**, **4a–b**. rehydrated apothecia; **1e**. apothecium in median section; **1f**. id., marginal region; **1g**. mature ascus; **3**. ascospores inside asci. – Living state, except for asci in **3**. — **1a–g**. H.B. 8938a: Western Australia, Pilbara, on *Acacia*; **2**. H.B. 5227b: USA, Arizona; **3**. H.B. 8879d: Western Australia, Pilbara, on *Acacia*; **4a–b**. H.B. 6998a (holotype): USA, Utah, on *Abies*.

Orbilia phanosoma Baral & Marson, **sp. nov.**, MB 813502 — Pls 192–193

Etymology: named after the shape of the spore body resembling a lantern.

Typification: USA, Utah, Panguitch, branch of *Abies concolor*, 20.VI.2000, G. Marson (ex H.B. 6998a, M-0276553, holotype).

Latin diagnosis: *Apothecia* in statu *rehydratata 0.2–0.6 mm diam. Asci 8-spori. Ascosporae *6–11 × 3.2–5.2 µm, ellipsoideae, interdum subclavatae, in statu vivo corpusculum refringens ellipsoideum ad pyriformem, partim curvatum, continentes*, *filo longo et tenui ad apicem affixum. Paraphyses ad apicem non vel leniter inflatae. Habitat ad lignum vel corticem putridum ramorum siccorum arborum coniferarum vel angiospermarum*, *in zona temperata ad tropica humida ad arida Americae septentrionalis, Asiae et Australiae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.5(–0.6) mm diam., (0.09–)0.12–0.15(–0.2) mm high, light to bright orange(-rose), round, scattered to subgregarious; disc slightly concave to flat, margin medium thick, even, protruding 0–10 µm; broadly sessile, slightly to strongly erumpent. **Asci** *(48–)55–72(–82) × 8–10(–11.2) {4} µm, †43–70 × 7.5–9(–10.5) µm {4}, 8-spored, spores (1–)2(–3)-seriate, (2–)3–5 lower spores inversely oriented (often mixed) {6}, pars sporifera *30–44 µm long; **apex** (†) hemispherical to slightly or medium truncate, dome absent {1}or †1–1.4 → 0.5–1 µm thick {3}, with ± distinct apical chamber; **base** with short to medium long stalk, L- to h-shaped. **Ascospores** *(6–)7–9(–11)((–12)) × (3.2–)3.6–4.8(–5.2) µm {5}, (cylindric-)ellipsoid(-obovoid), sometimes slightly clavate, rarely subglobose, *6–7.5 × 5–5.7(–6) µm {1}, ends rounded, straight, rarely slightly inequilateral; **SBs** *(2.5–)3–5(–5.5) × 0.8–1.3(–1.5) µm {5}, divided into an abruptly swollen, ellipsoid, tear-shaped or cylindric-pyriform to angular, often stomach-shaped lower part and a fine filum of about ½–2 × the length of the lower part, straight to strongly flexuous; germinating spores 1-septate. **Paraphyses** apically uninflated to slightly clavate or sublageniform, terminal cell *5–16.5 × (2–)2.3–3.3(–3.7) µm {4}, lower cells *(5.5–)7.5–15(–17) × 2–3 µm {4}; rarely to frequently branched near apex. **Medullary excipulum** 20–70 µm thick, of dense textura intricata with many inflated cells (resembling t. angularis), indistinctly delimited, towards margin more sharply. **Ectal excipulum** from base to mid flanks of (†) thin-walled to medium gelatinized, irregularly oriented t. (globulosa-)angularis(-prismatica), near base 20–50 µm thick, cells *7–16(–20) × 6–12(–16) µm {2}, common walls (†) up to 1 µm thick, gel hyaline to pale yellowish-amber, near margin of 20–30 µm thick t. angularis-prismatica-porrecta oriented at 10–45°, marginal cortical cells *6–13 × 3.3–4.5(–5) µm {2}, †7–11 × 2–4 µm {2}, embedded in some gel, no glassy caps. **Anchoring hyphae** sparse to medium abundant, hyphae †1.8–3.5 µm wide, walls 0.2–0.8 µm thick {2}. **SCBs** globose {4}, in paraphyses 1–1.5 µm diam., in marginal excipulum 1.5–3.3 µm. **Exudate** continuous to granular, over paraphyses 0.2–1.8 µm thick, loosely attached, over excipulum 0.2–1.3(–3) µm thick. — **ANAMORPH**: unknown.

Habitat: collected 1–4 m above the ground, decorticated, 7–22 mm thick branches of *Abies concolor* {1}, *Acacia aneura* {1}, *Acacia* sp. {3}, *Allocasuarina decaisneana* {1}, *Pinus edulis* {2}, *Salix* sp. {1}, on 0.1–0.5 mm deep (medium to) strongly decayed wood {4} and bark (periderm & bast) {4}, sometimes in old beetle galleries, strongly greyed, with a few or quite many green algae. **Associated**: *Amandinea* sp. {1}, *Claussenomyces* sp. {1}, *Durella atrocyanea* {1}, *Lachnellula* sp. {1}, *Melanohalea subolivacea* {1}, *Orbilia concoloris* {1}, *O. macrotrapeziformis* {1}, *O. ?multitrapezoidea* {1}, *O. multivinosa* {1}, *O. myrioaustraliensis* {1}, *O. myriomuscula* {2}, *O. phragmotricha* {1}, *O. pileosoma* {1}, *O. pleiolentiformis* {1}, *O. pleioobtusispora* {1}, *O. pleioserpens* {2}, *O. pleiovitalbae* {1}, *O.*

pluristomachia {2}, *O. serpentina* {2}, *O. spermoides* {1}, *Parmelia* sp. {1}, *Patinella abietina* {1}, *Propolis farinosa* {1}, *Sclerococcum* sp. {1}, *Symbiotaphrina desertorum* {1}, *Teichosporella dura* {1}, *Usnea* sp. {1}. **Desiccation tolerance**: desiccation-tolerant for at least 20 months, some spores, excipular cells and paraphyses still viable after 3.5 years. **Altitude**: 2033–2778 m a.s.l. (USA, Mongolia), 500–690 m (Australia). **Geology**: USA: Permian and Upper Cretaceous sand- & limestone; Australia: Archean to Paleoproterozoic sedimentary rock, Cenozoic regolith (red-brown sand & gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia phanosoma* is characterized by 8-spored asci and ± (cylindric-)ellipsoid ascospores. From *O. pleiostomachia* and *O. multiphanosoma* it differs mainly in spore number. The 8-spored *O. lanternae* and *O. tremuloidis* are also very similar, but their spores are longer and more or less clearly clavate (for further differences see under these species).

Variation. Usually, the lower parts of SBs are partially or predominantly curved (stomach-shaped). However, in two collections (on *Abies* and *Salix*) the lower parts were apparently always straight. The SBs in the *Salix* sample had an exceptionally short filum (Pl. 192: 4), and the Australian one on *Allocasuarina* (Pl. 192: 2) differs from the remaining in rather wide asci. In one of the specimens on *Acacia* the spores were consistently subglobose in some of the apothecia, i. e., shorter and wider than typical, but ellipsoid-ovoid in others (3a). In this collection the ascus apices were unexpectedly medium truncate and thin-walled, irrespective of the spore type which the asci contained. For the time being all these differences are thought to lie within the scope of variation of a single species.

Ecology. *O. phanosoma* grew on rotten wood and bark of xeric branches of different gymno- and angiosperms. The few known records indicate that the species shows a worldwide distribution. It was found in western North America in a cold-temperate subhumid pinyon-juniper woodland and boreal humid Douglas fir mixed forest in the Colorado Plateau (Utah Mountains and Grand Canyon), in a continental, orotemperate (sub)humid (winter-dry), subalpine steppe of central Asia (western Mongolia), and in (sub)tropical arid acacia open wood- and shrublands (mulga) in western and central Australia (Pilbara and Ayers Rock area).

Specimens included. **USA**: **Utah**, Utah Mts., Dixie Forest, Bryce Canyon, 42 km SSE of Panguitch, Rainbow Point, 2778 m, branch of *Abies concolor*, on wood, 20.VI.2000, G. Marson (M-0276553, **holotype**; **isotype** in H.B. 6998a). – **Arizona**, Grand Canyon, Coconino Plateau, 3 km N of Tusayan, 2068 m, branch of *Pinus edulis*, on bark, 28.VIII.1994, G. Marson (H.B. 5227b ø). – 3 km S of Tusayan, 2033 m, twig of *P. edulis*, 28.VIII.1994, G. Marson (ø). — **MONGOLIA**: **Bayan Ölgii**, Sagsai, Altay Mts., Tavan Bogd, 25 km SSE of Dayan lake, Songino Gol, 2400 m, branch of *Salix*, on wood, 15.VIII.2005, P. Karasch (H.B. 7890a ø). — **AUSTRALIA**: **Western Australia**, centre of Pilbara, 49 km NW of Newman, Great Northern Hwy, northern border of Ophthalmia Range, 690 m, branch of *Acacia*, on bark, 28.X.2007, G. Marson (H.B. 8938a). – ibid., branch of *Acacia*, on bark, 28.X.2007, G. Marson (H.B. 8940c ø). – ibid., branch of *Acacia*, on bark, 28.X.2007, G. Marson (H.B. 8879d ø). – **Northern Territories**, Great Sandy Desert, 12 km SE of Yulara, 0.7 km N of Ayers Rock (Uluru), 515 m, branch of *Acacia aneura*, on wood, 11.X.1998, G. Marson (H.B. 7129b). – 11.5 km ENE of Yulara, 14 km NNE of Ayers Rock, Lasseter Hwy, 500 m, branch of *Allocasuarina decaisneana*, on wood, 12.X.1998, G. Marson (H.B. 6617i ø).

Orbilia multiphanosoma Baral & G. Marson, **sp. nov.**, MB 813503 — Pls 194–195, Map 30

Etymology: named according to the 32-spored asci and lantern-like spore bodies.
Typification: USA, Arizona, Tusayan, branch of *Quercus gambelii*, 28.VIII.1994, G. Marson (ex H.B. 5287a, M-0276524, holotype).

Latin diagnosis: *Differt ab* Orbilia phanosomate *ascis 32-sporis*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.35(–0.5) mm diam., 0.11–0.23 mm high, light (to bright) orange(-rose), non-translucent, round, scattered to subgregarious; disc flat, margin distinct, 0–5 µm protruding, finely rough; broadly sessile, superficial or ± immersed among fibres or detritus. **Asci** *(60–)70–96(–105) × 9.2–11.8(–12.5) µm {4}, †(53–)60–80(–90) × 7–10.5 µm {3}, 32-spored (28–32 spores counted), spores *3–5-seriate, partially inverted (strongly mixed, some spores ± horizontal), pars sporifera *44–52 µm long; **apex** (†) slightly to medium (or strongly) truncate, hemispherical in profile view, dome †0.5–1.5 → 0.3–1 µm thick {4}, often with ± distinct, broad apical chamber; **base** with or without short, thick, flexuous stalk, L- to Y- or h-shaped. **Ascospores** *(5.5–)6–8.5(–10)((–11)) × (2.8–)3–4.2(–4.5) µm {9}, †5–7(–8.5) × (2.5–)3–3.5(–4) µm {2}, cylindric-ellipsoid to obovoid(-clavate), apex rounded, base sometimes slightly to medium (to strongly) tapered, ± straight, sometimes slightly curved, rarely medium geniculate at base; **SBs** *(2.3–)2.7–3.8(–4.5)((–5)) × (0.6–)0.8–1.1 µm {5}, divided into an abruptly swollen, tear-shaped to pyriform, also ellipsoid to ovoid, rarely rod-shaped lower part and a fine filum of varying length, both parts ± straight, rarely slightly curved. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cell *5.5–19(–23) × 2.3–3.7(–4.4) µm {5}, lower cells *(7–)9–15(–20) × 1.7–3 µm {4}; rarely or often branched at upper septum. **Medullary excipulum** 30–70 µm thick, of loose to dense textura intricata with some or many inflated cells, sharply delimited from ectal excipulum at flanks by a parallel 10 µm thick layer of t. porrecta. **Ectal excipulum** pale rose-orange (with yellow-orange LBs), of thin-walled, (†) distinctly gelatinized, vertically or horizontally oriented t. angularis(-globulosa) from base to mid flanks or margin, 15–40 µm thick near base, cells *7–20 × 6–16 µm {2}, †8–10 × 5–7 µm {1}; 15–25 µm thick near margin, of t. angularis or t. prismatica-porrecta oriented at a 30–60° angle to the surface, marginal cortical cells *6–11 × 3–5.5 µm, uppermost cells *9–14 × 3 µm {1}. **Anchoring hyphae** medium abundant, †2.2–3.5(–4) µm wide, walls 0.2–0.7 µm thick {1}, partially extending to the margin as a 5–15 µm thick layer. **SCBs** in paraphyses and ectal excipulum (near margin) globose {5}, 1–2.2 µm diam. **Exudate** over paraphyses and excipulum 0.2–0.5(–0.8) µm thick, granular to continuous, loosely attached, sometimes as thin caps being firmly attached to the paraphysis tips. — **ANAMORPH**: unknown.

Habitat: collected ~0.2–1.5 m above the ground, corticated to somewhat decorticated, 8–15 mm thick, sometimes still-living branches of *Artemisia tridentata* {2}, *Ericameria nauseosa* {3}, *Quercus gambelii* {1}, *Salix ?bebbiana* {1}, indet. angiosperm {1}, on (medium to) strongly decayed bark (bast) {5}, more rarely wood {2}, not or often strongly greyed or blackened, no or a few green algae. **Associated**: *Carestiella schizoxyloides* {1/1}, *Corticiaceae* {1}, *Dothideales* {1}, *Hysteropatella* sp. {1}, *Melanohalea subolivacea* {1}, *Mellitiosporiella* sp. {1}, *Orbilia bicknellensis* {1}, *O. delphinus* {3}, *O. dixiensis* {1}, *O. flexisoma* {1}, *O. gambelii* {1} *O. lentiformis* {2}, *O. macroserpens* {1}, *O. mesaverdiana* {1}, *O. multimaeandrina* {2}, *O. multitrapezoidea* {2}, *O. myriophanosoma* {1}, *O. ocellata* {4}, *O. pleiolentiformis* {1}, *O. plurilentiformis* {2}, *O. serpentina* {1/1}, *O. subtrapeziformis* {1}, *Perrotia flammea* {1}, *Stictis* sp. {1}, *Teichospora* sp. {1}. **Desiccation tolerance**: fully viable for at least 9 months, immature asci still viable after 14 months. **Altitude**: 1315–2600 m a.s.l. **Geology**: Proterozoic-Cambrian & Eocene sedimentary rock, Pennsylvanian-Permian to Triassic-Jurassic red carbonate sandstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia multiphanosoma* differs from the very similar *O. pluristomachia* in longer and also wider ascospores, and in never strongly curved (stomach-shaped) SBs. *O. multiphanosoma* appears to be a close relative of the 8-spored *O. phanosoma* and the 64-spored *O. myriophanosoma*. The latter was two times found in association with *O. multiphanosoma*.

Variation. *O. multiphanosoma* varies somewhat in shape and size of spores and SBs, even within a collection. The holotype (on *Quercus*, Pl. 194: 5) deviates in consistently obovoid spores from those on desert shrubs, but also from

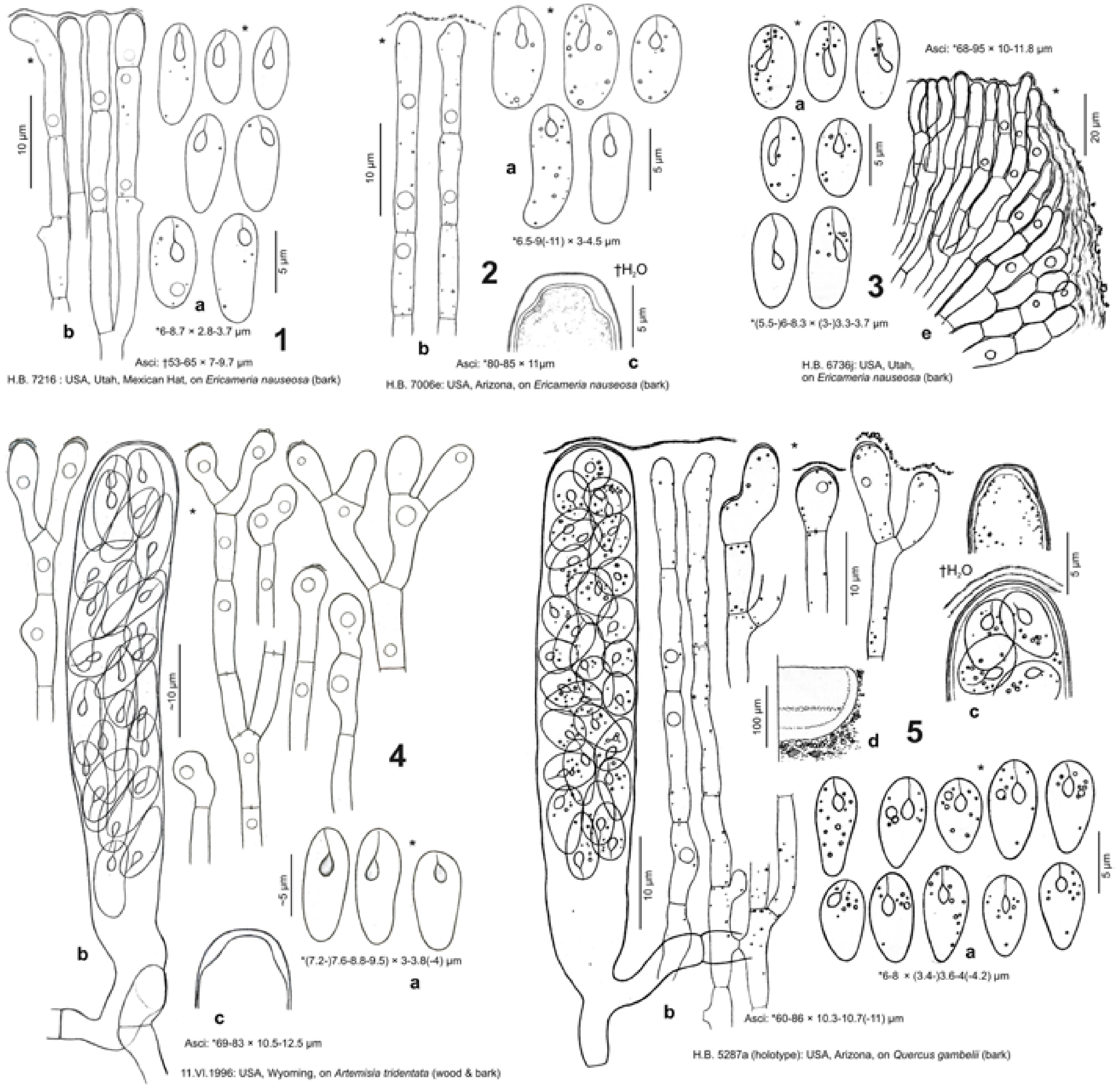


Plate 194. **1–5**: *Orbilia multiphanosoma*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

one on *Salix* (IVV: 15.V.1995), in all of which the spores are (sub)cylindrical. In some of these finds, however, the spore shape varies from cylindrical to clavate. In some collections, including the holotype, the inflated part of SBs is rather regularly short and ellipsoid-ovoid, whereas in others it varies from ellipsoid-ovoid to pyriform (exceptionally reniform). Those spores in the holotype, being distinctly over 7 µm long were probably formed in asci with a reduced spore number, while in the other samples spores of ~8–9 µm length were apparently formed in 32-spored asci.

Ecology. *O. multiphanosoma* was recorded on rotten bark (rarely wood) of xeric branches of desert shrubs such as *Artemisia* and *Ericameria*, but also on angiosperm trees. It is known from boreal to cold-temperate, humid to subhumid Douglas fir forests (with *Salix*) and pinyon-juniper woodlands, and from cold- to warm-temperate subhumid to arid sagebrush and saltbush desert scrubs in the Wyoming Basin (south of Wind River Range), Colorado Plateau, and Mojave Desert in western North America.

Specimens included. **USA**: **Wyoming**, Wyoming Basin, 24 km SE of Pinedale, 7 km S of Boulder, 2140 m, branch of *Artemisia tridentata*, on bark & wood, 11.VI.1996, G. Marson (ø). – **Utah**, Utah Mts., Dixie Forest, 15 km SSE of Torrey, 5.5 km S of Grover, Lion Mt., 2450 m, branch of *A. tridentata*, 15.V.1995, G. Marson (ø). – 14 km S of Grover, N of Pleasant Creek Campground, 2600 m, branch of *Salix ?bebbiana*, 15.V.1995, G. Marson (ø). – Canyonlands, near Valley of the Gods, 25 km NNW of Mexican Hat, 10 km N of Mokee Dugway, Cedar Mesa, 1990 m, branch of *Ericameria nauseosa*, on bark, 14.VI.2000, G. Marson (H.B. 7216). – Canyonlands, 36 km S of Moab, 5 km WNW of Hatch Rock, 1813 m, branch of *E. nauseosa*, on bark, 16.VI.2000, G. Marson (H.B. 6736j). – **Arizona**, Navajo, 85 km SW of Mexican Hat, 27 km SW of Kayenta, Klethla Valley, 2015 m, branch of *E. nauseosa*, on bark, 13.VI.2000, G. Marson (H.B. 7006e ø). – Grand Canyon, Coconino Plateau, 3 km N of Tusayan, 2068 m, branch of *Quercus gambelii*, on bark, 28.VIII.1994, G. Marson (ex H.B. 5287a, M-0276524, **holotype**). – **California** (border to Nevada), Mojave Desert, 20 km SW of Beatty, 16 km SW of Rhyolite, Daylight Pass E of Death Valley, 1315 m, branch of indet. angiosperm, on wood, 2.V.1995, G. Marson (H.B. 8528a).

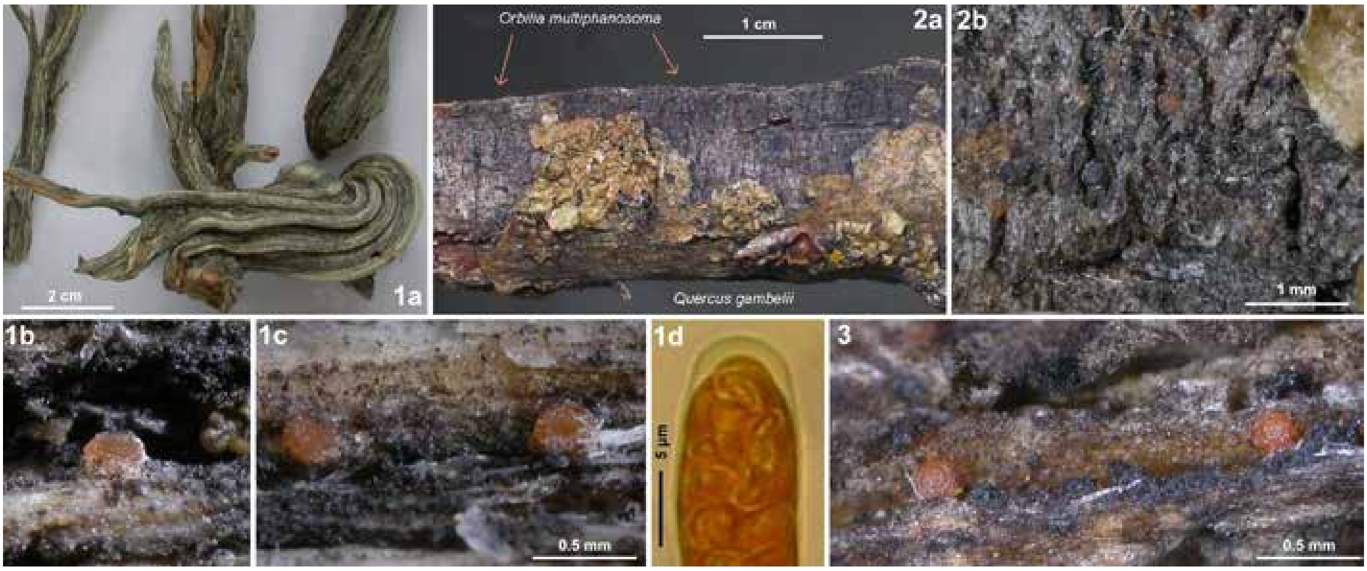


Plate 195. **1–3**: *Orbilia multiphanosoma*. – **1a**, **2a**. inhabited dead xeric branches; **1b–c**, **2b**, **3**. rehydrated apothecia; **1d**. ascus apex (dead state, in IKI). — **1a–d**. H.B. 8528a: USA, California, on indet. angiosperm; **2a–b**. H.B. 5287a (holotype): USA, Arizona, on *Quercus*; **3**. H.B. 7216: USA, Utah, on *Ericameria*.

Orbilia myriophanosoma Baral & G. Marson, **sp. nov.**, MB 813504 — Pls 196–197, Map 31

Etymology: referring to the 64-spored asci and the spore body resembling a stomach.

Typification: USA, Utah, Hatch Rock, branch of *Ericameria nauseosa*, 16.VI.2000, G. Marson (ex H.B. 6736f, M-0276532, holotype).

Latin diagnosis: *Differt ab* Orbilia multiphanosomate *ascis 64-sporis*, *ab* O. myriosphaera *ascosporis cylindricis vel ellipsoideo-ovoideo-clavatis*, *corpusculis refringentibus lacrimi- vel bacilliformibus. Habitat ad corticem putridum*, *raro lignum*, *ramorum siccorum arborum vel fruticum in zona temperata subhumida ad semiarida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.35 mm diam., 0.12–0.2 mm high, pale to light greyish-orange-ochraceous, round, ± scattered to gregarious in small groups; disc slightly concave to flat, margin ± distinct, scarcely protruding, smooth or finely rough; sessile, slightly erumpent. **Asci** *73–108 × (11–)11.3–12.5(–13.4) µm {2}, †(58–)63–96(–118) × (9.5–)10–11.5(–12) µm {3}, 64-spored (55–62 spores counted), spores ± 4–6-seriate, lower spores inversely oriented (strongly mixed), pars sporifera *47–68 µm long; **apex** (†) hemispherical or slightly, rarely strongly truncate, dome †1–1.7 → 0.5–1.2 µm thick {3}, some with broad apical chamber; **base** unstalked or with short to long, thick stalk, T-, L-, Y- to h-shaped. **Ascospores** *(4.5–)5.5–7.3(–8) × (2.5–)2.7–3.6(–4) µm {3}, †(4.5–)6–7(–9) × 2.8–3.5 µm {2}, subcylindrical to ellipsoid or often obovoid to ± clavate, apex rounded, straight to slightly curved; **SBs** *(2–)2.6–3.7(–4.5) × 0.2–0.7 or 0.8–1 µm {2}, divided into an ovoid to tear-shaped or narrowly pyriform, also rod-shaped to vermiform lower part (1–)1.3–2.5(–3.5) µm long, and a filum of varying length, straight to strongly curved or geniculate. **Paraphyses** apically uninflated to medium clavate-capitate, terminal cell *6–18(–23) × 2–3–4.5 µm {2}, lower cells *10–18 × 1.7–2 µm {1}; sometimes branched near apex. **Medullary excipulum** hyaline, 20–50 µm thick, of dense textura intricata-angularis, sharply delimited. **Ectal excipulum** very pale (cream-)rose, of (†) thin-walled to slightly gelatinized, vertically oriented t. angularis(-prismatica) from base to submargin, 20–30 µm thick near base, cells †5–9 × 3.5–6 µm {2}; 15–20 µm near margin, oriented at a 30–40° angle to the surface, submarginal cortical cells †5–7 × 3–4 µm {1}, at uppermost margin of t. porrecta, cells 8–14 × 2.5–3 µm. **Anchoring hyphae** sparse to medium abundant, †(1.8–)2.5–3.5 µm wide, walls 0.2–0.5(–1) µm thick {2}, sometimes also covering flanks and margin. **SCBs** in paraphyses globose, 1–2 µm diam. **Exudate** over paraphyses ~0.2–0.6 µm thick, continuous, ± rough, loosely attached. **— ANAMORPH**: unknown.

Map 30. Known distribution of *O. multiphanosoma* in North America.

Habitat: collected 0.1–0.5 m above the ground, corticated to decorticated, 6–20 mm thick branches of *Ericameria nauseosa* {1}, *Pinus* sp. {1}, *Quercus gambelii* {2}, on medium to strongly decayed bark {4} (periderm & bast), strongly greyed, no algae, on *Pinus* sometimes near resinous patches. **Associated**: *Orbilia delphinus* {2}, *O. dixiensis* {1}, *O. lentiformis* {1}, *O. mesaverdiana* {1}, *O. multimaeandrina* {1}, *O. multiphanosoma* {1}, *O. multitrapezoidea* {1}, *O. ocellata* {1}, *O. plurilentiformis* {1}, ?*Teichospora* sp. {1}. **Desiccation tolerance**: fully viable for at least 17 months. **Altitude**: 1813–2500 m a.s.l. **Geology**: Triassic-Jurassic-Cretaceous and Oligo- & Miocene calcareous sandstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia myriophanosoma* is characterized by 64-spored asci and ± ellipsoid-clavate ascospores. It differs from European *O. myriosphaera* in longer spores and in elongate inflated parts of SBs, also in wider asci. *O. multiphanosoma* differs mainly in 32-spored asci. In the holotype collection (on *Ericameria*) both species occur on the same branches: 17 out of roughly 60 apothecia have been examined and found to have 64-spored asci, but only three with 32-spored asci were detected (Pl. 194: 3). Also on *Quercus gambelii* both species occur as a mixture. A single apothecium in an Australian collection on *Atriplex* (Pl. 200: 7) differs from

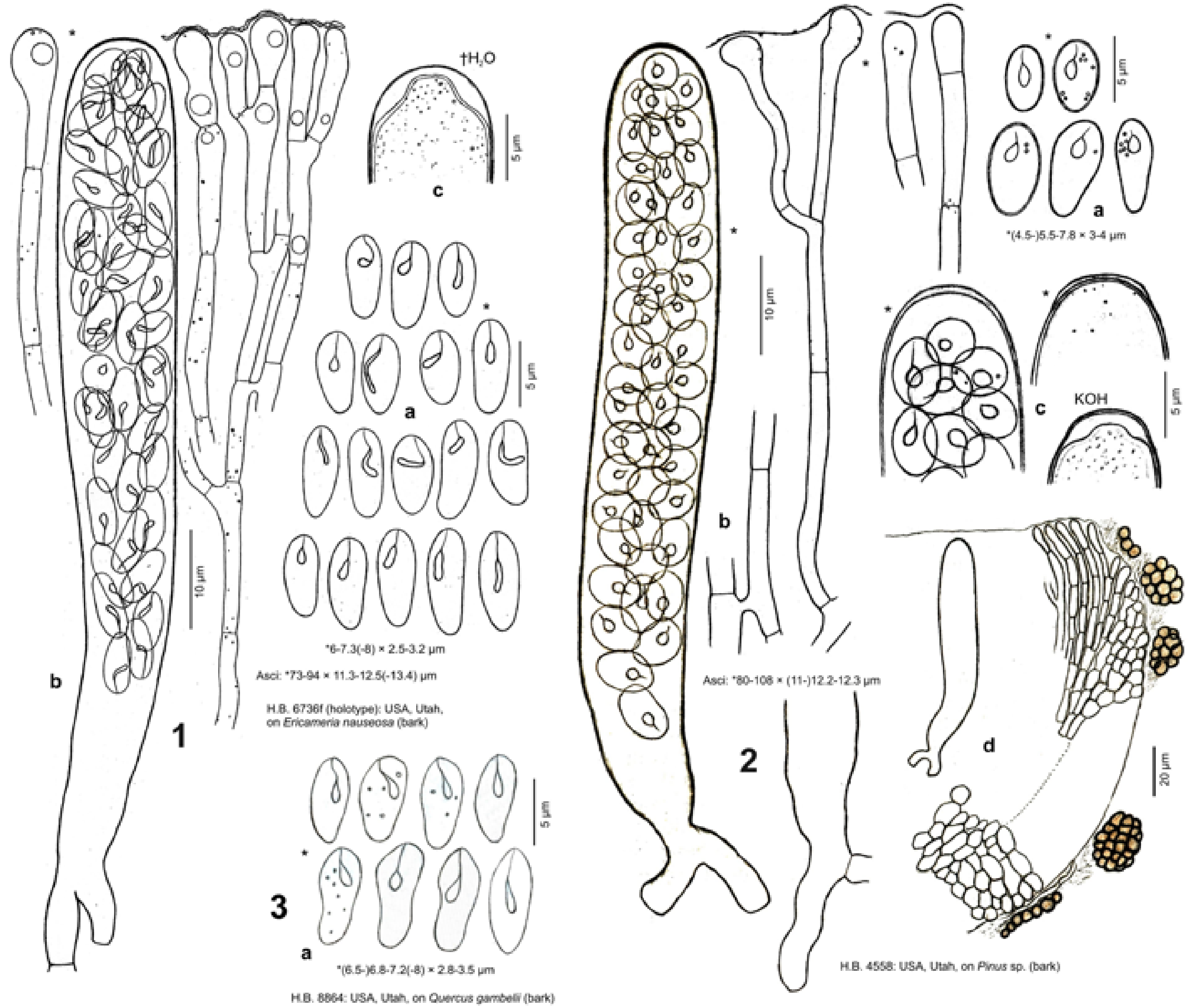


Plate 196. **1–3**: *Orbilia myriophanosoma*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium near margin in median section.

O. myriophanosoma in shorter spores with a somewhat different spore body shape. It might be a 64-spored derivative of *O. pluristomachia* with which it grew in association.

Variation. The holotype of *O. myriophanosoma* has rather narrow, often cylindrical spores with quite variable SBs (mostly ± rod-shaped, often curved). In the collection on *Pinus* the spores are more ellipsoid-clavate and the inflated parts of the SBs consistently ovoid. Those shorter, broadly ellipsoid spores observed here concur very well with the typical spores of *O. pluristomachia*, a species to which this collection actually might belong instead. The one on *Quercus* is somewhat intermediate, with a spore shape similar as in the *Pinus* collection but with the lower parts of SBs sometimes cylindrical and slightly curved.

Ecology. The few records of *O. myriophanosoma* were from rotten bark (rarely wood) of dead xeric branches of different coniferous and angiosperm trees and shrubs. The species was found in a cold-temperate subhumid pinyon-juniper woodland and ponderosa pine forest and in a boreal humid Douglas fir mixed forest in the Utah Mts., also in a warm-continental semiarid sagebrush desert scrub in the Canyonlands section of the Colorado Plateau in the southwest of Northern America.

Specimens included. **USA**: **Utah**, Utah Mts., Dixie Forest, 1.5 km ESE of Cedar City, 1815 m, branch of *Quercus gambelii*, on bark, 24.VIII.1994, G. Marson (H.B. 8865a). – Bryce Canyon, 30 km SE of Panguitch, 7.5 km WNW of Tropic, near Visitor Center, 2410 m, branch of *Pinus*, on bark, 25.IX.1991, G. Marson (H.B. 4558). – 32 m SE of Panguitch, 13 km WSW of Tropic, near Trough

Map 31. Known distribution of *O. myriophanosoma* in North America.

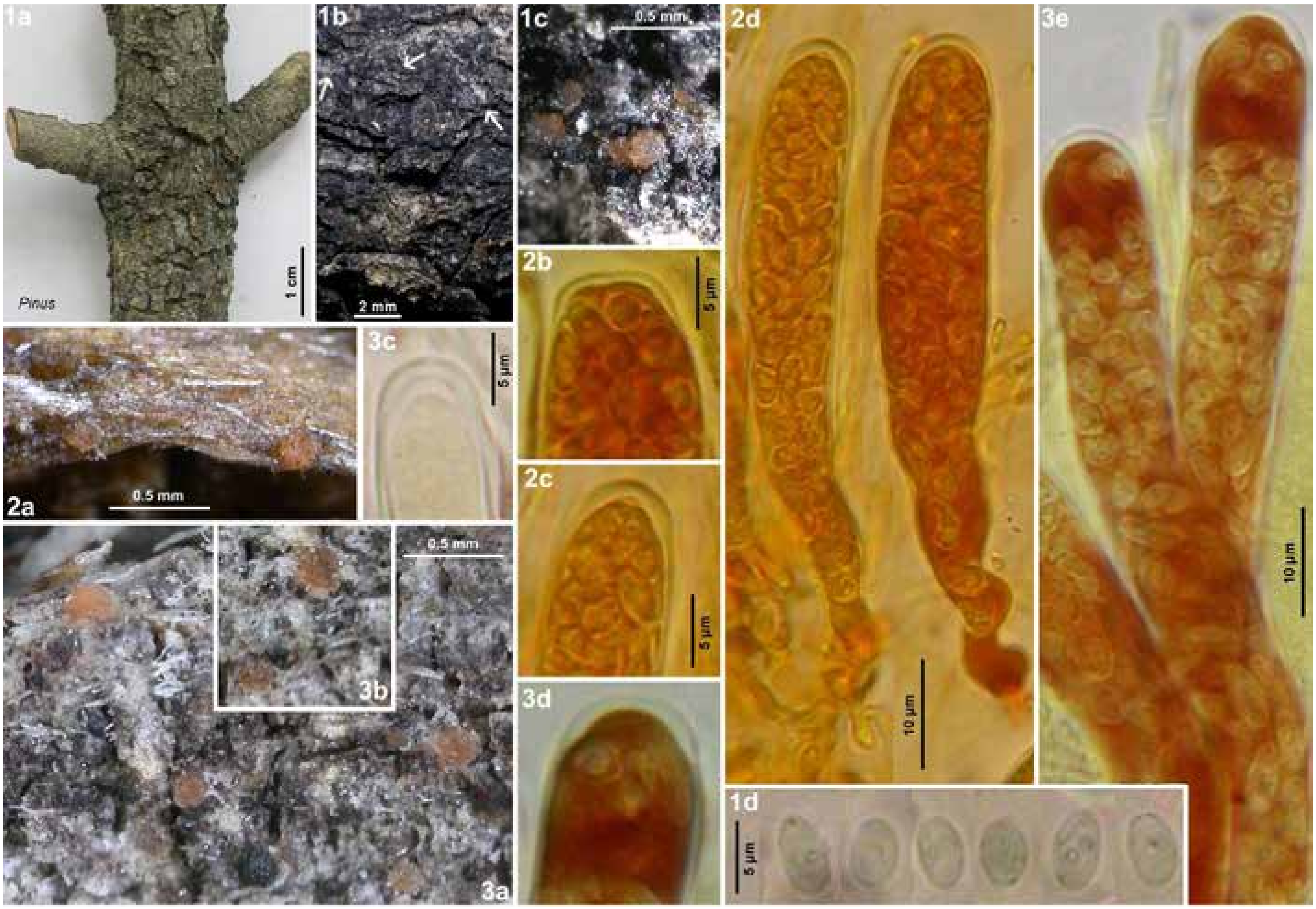


Plate 197. **1–3**: *Orbilia myriophanosoma*. – **1a**. dead corticated branch of *Pinus*; **1b**. bark surface; **1c**, **2a**, **3a–b**. rehydrated apothecia; **2b–c**, **3c–d**. ascus apices; **2d**, **3e**. mature asci; **1d**. ascospores. – **2b–d**, **3c–e** in KOH+IKI, **1d** in KOH. — **1a–d**. H.B. 4558: USA, Utah, on *Pinus*; **2a–d**. H.B. 6736f (holotype): USA, Utah, on *Ericameria*; **3a–e**. H.B. 8865: USA, Utah, on *Quercus*.

Spring, 2500 m, branch of *Quercus gambelii*, on bark, 24.VIII.1994, G. Marson (H.B. 8864 ø). – Canyonlands, 36 km S of Moab, 5 km WNW of Hatch Rock, 1813 m, branch of *Ericameria nauseosa*, on bark, 16.VI.2000, G. Marson (M-0276532, **holotype**; **isotype** in H.B. 6736f).

Orbilia pleiostomachia Baral, **sp. nov.**,

MB 813505 **—** Pls 198–199

Etymology: referring to spore number and shape of spore body resembling a stomach.

Typification: Australia, Northern Territories, Wilora, branch of *Acacia*, 8.X.1998, G. Marson (ex H.B. 6260f, MEL 2389194, holotype).

Latin diagnosis: *Differt ab* Orbilia pluristomachia *ascis 16-sporis*, *ascosporis corpusculis refringentibus partim curvatis. Habitat ad lignum putridum rami sicci* Acaciae *in zona tropica arida Australiae centralis*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.22 mm diam., 0.12 µm thick, light orange, round, subgregarious; disc slightly concave to flat, margin ± distinct, 10 µm protruding, smooth; sessile, half immersed. **Asci** *80–90 × 10.4–11(–11.5) µm, †65–78 × 9–10 µm, 16-spored, spores 3–4-seriate, 6–12 lower spores inversely oriented (often mixed), pars sporifera *40–55 µm long; **apex** (†) slightly to medium truncate (hemispherical in profile view), with or without distinct dome †1.8–2 → 0.6–1 µm thick, with indistinct apical chamber; **base** with short to medium long, thick, flexuous stalk, L-(to Y-)shaped. **Ascospores** *6.5–8.5 × 3.8–4.5 µm, obovoid(-clavate), apex rounded, straight; **SBs** *3.3–4 × 1–1.2 µm, divided into a ± abruptly swollen, tear- to stomach-shaped lower part and a filum of ± equal length, mostly strongly geniculate; with some minute **LBs**. **Paraphyses** apically uninflated (to slightly clavate), terminal cell *7–12 × 2.8–3 µm, lower cells *12–20 × 2.2–3.5 µm; branched only near base. **Medullary excipulum** hyaline, 20 µm thick, medium sharply delimited. **Ectal excipulum** pale orange, of non- to slightly gelatinized, indistinctly horizontally oriented textura angularis from base to mid flanks, 20–25 µm thick near base, cells *9–12 × 8–10 µm, 20 µm thick at margin, of t. prismatica oriented at a 10° angle, marginal cortical cells †8–11 × 3–5 µm, firm-walled. **Anchoring hyphae** medium abundant, †1.8–2.5(–3) µm wide, walls 0.2–0.4 µm thick. **SCBs** absent. **Exudate** scattered, 0.1–0.3 µ thick, granular, lying over abundant gel, over margin more abundant, 0.2–1 µm thick, pale yellowish. **— ANAMORPH**: unknown.

Habitat: collected on the ground, decorticated, 20 mm thick branch of *Acacia* sp., on ¼ mm deep strongly decayed and greyed wood, no algae. **Associated**: closely intermingled with a dothidealean pyrenomycete, also with *Acanthostigma ellisii*, *Capronia* sp., *Orbilia barrowensis*, *O. maeandrina*, *O. pleioungulata*, *O. pluristomachia*. **Desiccation tolerance**: fully viable for at least 3 weeks. **Altitude**: 480 m a.s.l. **Geology**: Cenozoic regolith. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleiostomachia* is characterized by 16-spored asci and obovoid ascospores. In its stomach-shaped SBs it resembles *O. pluristomachia* which differs in 32-spored asci and distinctly smaller spores. The two taxa grew on the same branch in separate but closely associated populations, each consisting of about 10 apothecia.

Variation. The dead ascus apices were thin-walled in that apothecium, on which the drawing of the living elements was based (Pl. 198: 1c below), whereas in another apothecium examined 10 years later, the likewise 16-spored asci possessed distinct apical domes (Pl. 198: 1c, the two above).

Ecology. *O. pleiostomachia* is only known from a single sparse collection on rotten wood of a dead xeric branch of

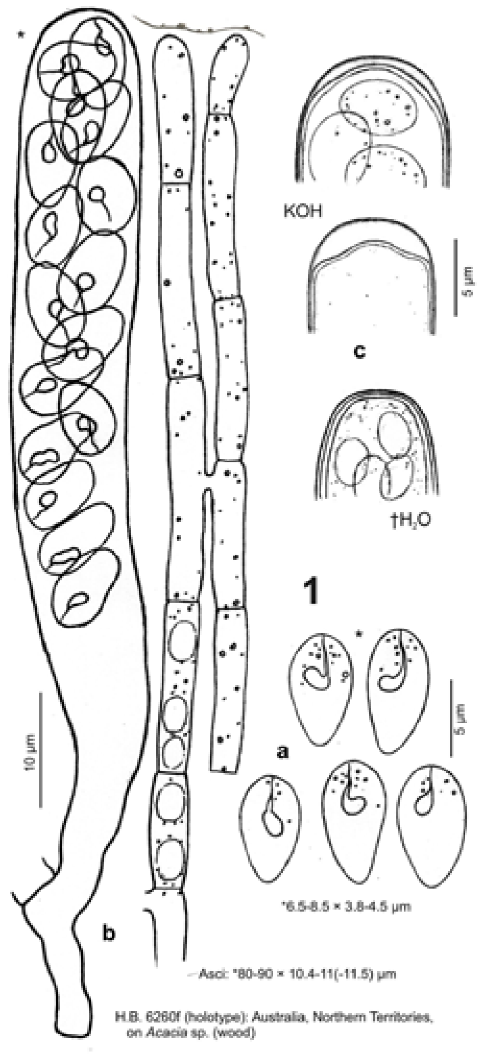


Plate 198. **1**: *Orbilia pleiostomachia*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices (mature, immature, and half mature).

Acacia in an acacia open shrubland at the north of MacDonnell Range in tropical arid central Australia.

Specimens included. **AUSTRALIA**: **Northern Territories**, Burt Plain, 31 km SW of Barrow-Creek Hotel, 3.7 km WSW of Wilora, Stuart Hwy, 480 m, branch of *Acacia*, on wood, 8.X.1998, G. Marson (ex H.B. 6260f, MEL 2389194, **holotype**).

Orbilia pluristomachia Baral & G. Marson, **sp. nov.**, MB 813506 — Pls 200–201, Map 32

Etymology: referring to the 32-spored asci and the spore body resembling a stomach.

Typification: Western Australia, Yulara, branch of *Allocasuarina decaisneana*, 12.X.1998, G. Marson (ex H.B. 6617a, MEL 2389212, holotype; ex-type culture: CBS 116235; sq.: KT215232).

Latin diagnosis: *Differt ab* Orbilia multiphanosomate *ascosporis brevioribus, corpusculis refringentibus partim valde curvatis. Habitat ad lignum vel corticem putridum ramorum siccorum arborum vel fruticum in zona subtropica semihumida ad arida Americae septentrionalis, Africae et Australiae.*

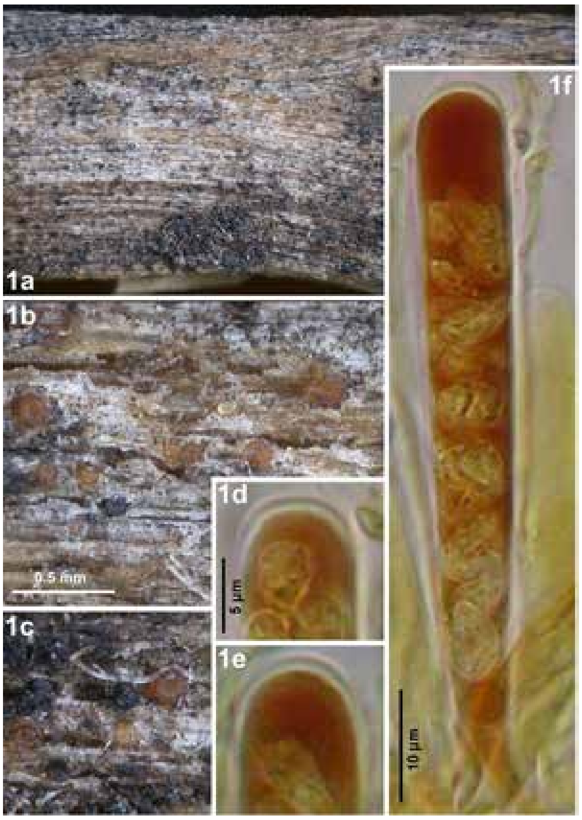


Plate 199. **1**: *Orbilia pleiostomachia*. – **1a**. xeric branch of *Acacia*; **1b–c**. rehydrated apothecia; **1d–e**. ascus apices; **1f**. ascus. – Dead state (in KOH+IKI). — **1a–f**. H.B. 6260f (holotype): Australia, Northern Territories, Wilora, on *Acacia*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.32 mm diam., 0.095–0.13 mm high, light to bright orange(-rose), round, scattered to ± gregarious; disc flat, margin thin or thick, also indistinct, 0–15 µm protruding, smooth or rough; broadly sessile, nearly superficial to almost completely immersed between fibres. **Asci** *(50–)60–80(–89) {7} × 8.3–8.8 {2} or 9–10.5 {6} µm, †(45–)54–70(–75) {5} × 6.8–7.5 {1} or 7.5–9.5 µm {4}, 32-spored, spores 3–4-seriate, lower spores indistinctly inversely oriented (strongly mixed), pars sporifera */†38–54 µm long; **apex** (†) slightly to medium truncate, hemispherical in profile view, dome †1–1.2 → 0.4–1 µm thick {5}, with ± broad apical chamber, rarely absent in some apothecia {1}; **base** with ± short, thick stalk, L- to Y-shaped. **Ascospores** *(3.7–)4–6(–7.2) × (2.4–)2.8–3.5(–4) µm {10}, †(3.8–)4.5–5.5(–6) × 3–3.3(–3.5) µm {2}, ellipsoid to ovoid or obovoid, sometimes subglobose, apex rounded or obtuse, straight, rarely very slightly curved; **SBs** *(2–)2.5–3(–3.6) × (0.4–)0.7–1.1 µm {8}, divided into an abruptly swollen, tear- to pear- or often stomach-shaped lower part and a filum of ± equal (or shorter) length, thickened part straight to often ± strongly curved (geniculate). **Paraphyses** apically uninflated to slightly (or medium) clavate-capitate, terminal cell *6.5–20 × (2–)2.3–4.3(–5) µm {7}, lower cells *(6.5–)9–17 × 1.7–3(–4.5) µm {6}, near base sometimes 4.5–7.5 µm wide; sometimes branched near apex, hymenium pale orange-rose. **Medullary excipulum** pale rose-orange, 15–30 µm thick, of dense textura intricata with many inflated cells, very indistinctly to medium sharply delimited. **Ectal excipulum** subhyaline to pale rose, of thin-walled to medium gelatinized, ± horizontally oriented t. angularis-globulosa from base to flanks, 15–25 µm thick near base, cells */†7–15(–20) × 6–10(–13) µm {3}; 10–30 µm thick near margin, of t. prismatica-porrecta oriented at a 0–40° angle to the surface, marginal cortical cells with †0.5–1 µm thick glassy walls, *(5.5–)7–13 × 4–7 µm {3}, towards hymenium up to 20 × 3 µm; **SCBs** globose, in paraphyses 1–2.5 µm diam., in marginal excipulum 1.5–3 µm. **Exudate** over paraphyses and margin 0.3–0.5(–1.2) µm thick, continuous, smooth or granular, loosely attached. **Anchoring hyphae** ± sparse, †1.6–3 µm wide, walls 0.2–0.5 µm thick {3}. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** *~10 × 4 µm. **Conidia** Y/T-shaped, 2-armed, total size *24–30(–35) × 14–20(–25) µm {1}, stipe *19–22 × 5.5–6.3 µm, 2–3(–5)-septate, arms tapering, somewhat bent downwards, *7–12 × 4–4.5(–5) µm, 1(–2)-septate.

Habitat: collected 0–4 m above the ground, partially to entirely decorticated, 4–30 mm thick branches of *Atriplex nummularia* {1}, *Acacia* sp. {2}, *A. aneura* {1}, *Allocasuarina decaisneana* {1}, *Fraxinus velutina* {1}, ?*Glossopetalon spinescens* {1}, *Larrea tridentata* {3},

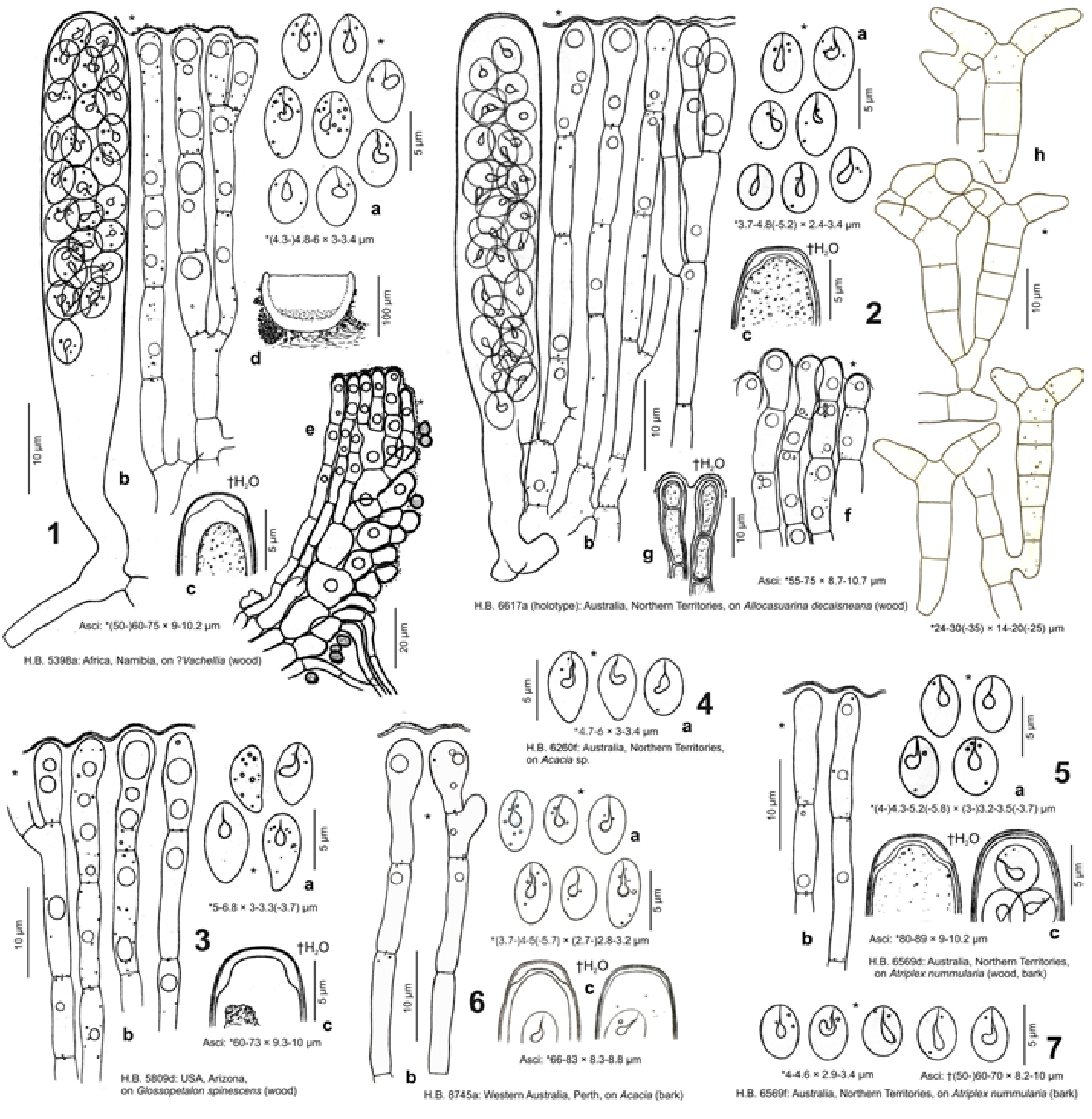


Plate 200. **1–6**: *Orbilia pluristomachia*; **7**. *O. myriostomachia* nom. prov. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. marginal ectal excipulum in median section; **f–g**. id., external view; **h**. conidia from culture.

Parkinsonia microphylla {1}, *Vachellia* {1}, indet. angiosperm {1}, on 0.1–1 mm deep (medium to) strongly decayed wood {8} and bark (bast) {2}, sometimes in old beetle galleries or along clefts, (slightly to) strongly greyed, no or a few green algae. **Associated**: *Acanthostigma ellisii* {1}, *Baggea* sp. {1}, *Capronia* sp. {1}, *Carestiella* ?*schizoxyloides* {1}, *Coniochaeta* sp. {1}, *Hypoxylon* sp. {1}, *Hysterobrevium mori* {1}, ?*Hysteropatella* sp. {1}, ?*Muellerella* sp. {1}, *M. lichenicola* {1}, *Orbilia atriplicis* {1}, *O. barrowensis* {1}, *O. bicknellensis* {1}, *O. breviclava* {1}, *O. commarosa* {1}, *O. cryptogena* {3}, *O. lentiformis* {2}, *O. macrotrapeziformis* {2}, *O. maeandrina* {3}, *O. microserpens* {1}, *O. multicercocarpi* {1}, *O.* ?*multitrapezoidea* {1}, *O. multiurosperma* {3}, *O. multivinosa* {1}, *O. myrioflexa* {1}, *O. myriofusiclava* {1}, *O. myriostomachia* {1}, *O. myriourosperma* {1}, *O. namibica* {1}, *O.* ?*navajoana* {1}, *O. phanosoma* {2}, *O. pleiolentiformis* {1}, *O. pleionavajoana* {1}, *O. pleioobtusispora* {1}, *O. pleioquaestiformis* {1}, *O. pleiostomachia* {1}, *O. pleioungulata* {1}, *O. pleiourosperma* {1}, *O. pleiovitalbae* {1}, *O. sedonensis* {1}, *O. serpentina* {2/1}, *O. sonorensis* {1}, *O. wannerooensis* {1}, *Patellaria atrata* {1}, ?*Peniophora* sp. {1}, *Schizoxylon* sp. {2}, *Symbiotaphrina desertorum* {1}, *S. larreae* {1}, *Teichospora* ?*obducens* {1}, *Teichosporella dura* {2}, 3 different indet. coelomycetes. **Desiccation tolerance**: fully viable for at least 17 months, some mature asci and spores still viable after 3.5 years. **Altitude**: 500–1700 m a.s.l. (USA), 1560 m (Africa), 40–586 m (Australia). **Geology**: Neoproterozoic to Ordovician sedimentary rock, Triassic-Jurassic-Cretaceous or Cenozoic (whitish or red-brown) sand-, lime- and mudstone; granite, felsic volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pluristomachia* is characterized by 32-spored asci and ± ellipsoid ascospores. The very similar *O. multiphanosoma* differs in longer, partially more cylindrical

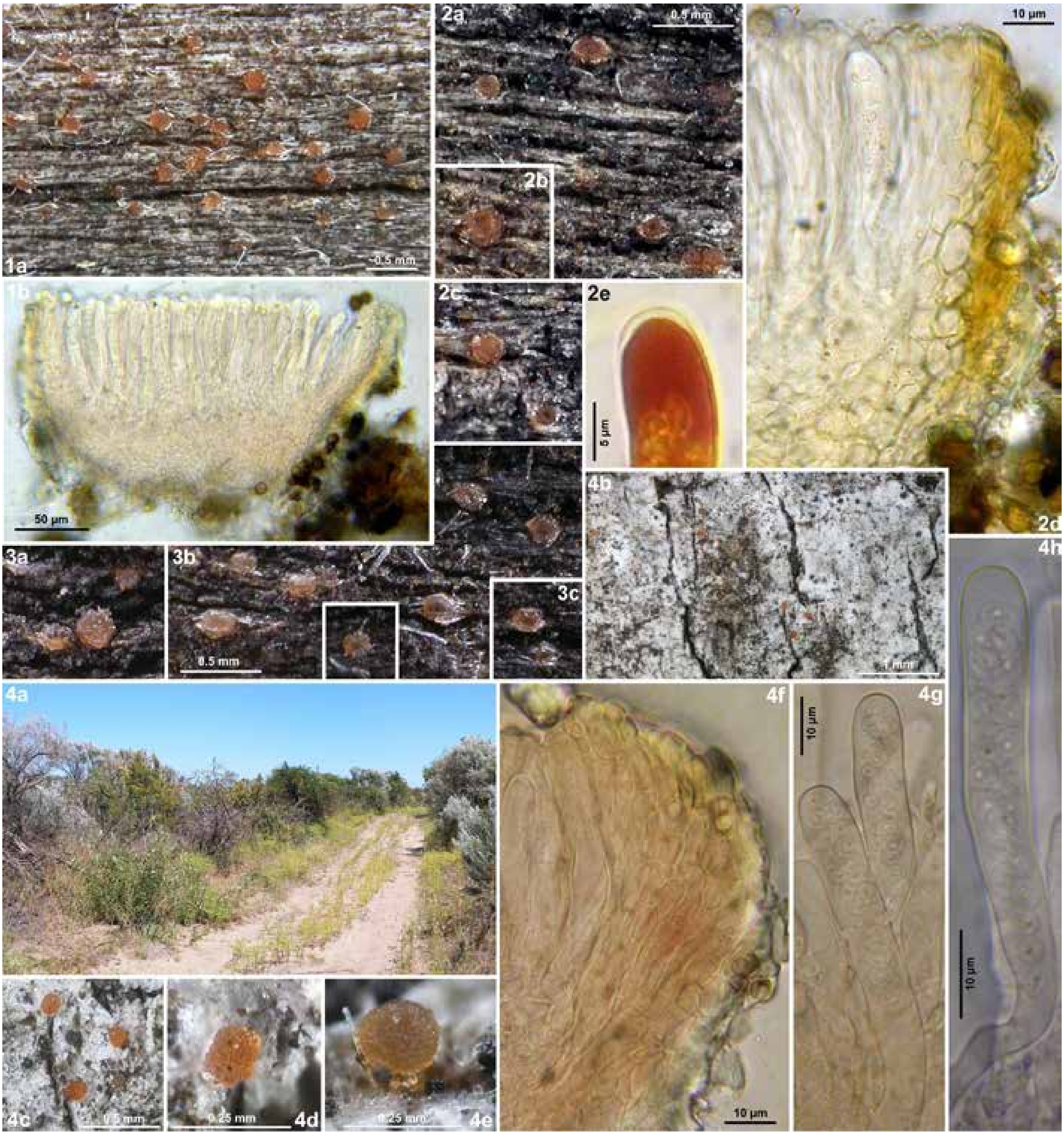


Plate 201. **1–4**: *Orbilia pluristomachia*. – **4a**. semihumid sandy acacia shrubland NNW of Perth; **1a**, **2a–c**, **3a–c**, **4b–e**. rehydrated apothecia; **1b**. apothecium in median section; **2d**, **4f**. id., marginal ectal excipulum; **2e**. ascus apex; **4g–h**. asci. – Living state, except for **2e** (in IKI). — **1a–b**. H.B. 7397d: USA, Arizona, on *Larrea*; **2a–e**. H.B. 6617a (holotype): Australia, Ayers Rock, on *Allocasuarina*; **3a–c**. H.B. 7129a: ibid., on *Acacia*; **4a–h**. H.B. 8745a: Western Australia, Perth, on *Acacia*.

spores and a less pronounced tendency to curved SBs, but is not sharply delimited. *O. myriophanosoma* differs in 64-spored asci and distinctly longer spores. In two of the examined collections of *O. pluristomachia* (Pl. 200: 4–5) very similar taxa with deviating spore numbers were detected. In one on *Acacia* the similar *O. pleiostomachia* occurred, which has 16-spored asci and distinctly larger spores.

Variation. Typically, the ascospores are ellipsoid to almost subglobose and 4–5(–6) µm long. Ovoid spores were seen in four collections (Pl. 200: 1, 3–4). In two of them (Pl. 200: 3; IVV: H.B. 5658f, *5.6–7.2 × 3–3.4 µm) some of the spores exceeded 6 µm in length, and thus formed a transition to *O. multiphanosoma*. In a collection on *Parkinsonia* (IVV: 7.V.1995) the spores were partially medium curved, for which reason we excluded it from the description.

Not included collection. In the collection from Northern Territories on *Atriplex* only two apothecia of series *Phanosomates* were found, besides apothecia of four *Orbilia* spp. from other series: one apothecium was *O. pluristomachia*, while the other deviated in 64-spored asci and slightly smaller spores with narrower SBs (Pl. 200: 7). This appears to represent a taxon of its own which differs from European *O. myriosphaera* in SB

Map 32. Known distribution of *O. pluristomachia* in North America and Australia.

shape and from *O. myriophanosoma* in much shorter spores. It is provisionally called ***O. myriostomachia*** Baral nom. prov., but not described due to the sparse microscopic data.

Anamorph. The anamorph of *O. pluristomachia* (Pl. 200: 2h) resembles *Trinacrium incurvum*; however, the arms are only slightly bent by pointing upwards or laterally, whereas in *T. incurvum* they are more strongly curved and consistently point downwards.

Phylogeny. A sequence gained from the ex-type culture of *O. pluristomachia* (SSU+ITS+LSU, S1506 intron absent) clustered weakly to strongly supported with *O. lentiformis* in a clade in the combined analyses in Baral et al. (2017b) and Phyl. 7, or in our ITS analysis (S9). However, it clustered unresolved in the combined analysis of Phyl. 8, and when analysing LSU (S11) it formed a weakly supported clade with the morphologically similar *O. myriosphaera*, to which it shows a 12% distance in the ITS region (4% in LSU, D1–D2).

Ecology. *O. pluristomachia* grew on dead xeric branches of very different woody substrates of angiosperm trees and shrubs, predominantly on decorticated rotten wood. The known records indicate that the species shows a worldwide distribution in desert regions. It was so far recorded in the southwest of Northern America in subtropical semiarid (to arid) paloverde-mixed cacti or creosotebush-bursage desert scrubs of the Sonoran Desert and a warm-continental subhumid manzanita chaparral scrubland in the Chihuahuan Desert, in southwestern Africa in the hot, subtropical arid (winter-dry) Kalahari highland thornbush savannah about 150 km away from the Namib Desert, and within Australia in subtropical arid acacia open shrublands in central Australia and in a subtropical semihumid acacia mixed shrubland in southwestern Australia. *O. myriostomachia* on wood of *Atriplex* was from subtropical arid central Australia on Neoproterozoic sedimentary rock.

Specimens included. **NAMIBIA**: **Khomas**, 60 km S of Windhoek, 25 km N of Rehoboth, Central Plateau, Auas Mts., 1560 m, branch of ?*Vachellia*, on wood, 25.VIII.1995, R. Reuter (H.B. 5398a). — **USA**: **Arizona**, Sonoran Desert, 200 km NW of Phoenix, Wikieup, ~600 m, branch of *Larrea tridentata*, on wood, 3.V.1995, G. Marson (H.B. 9573a). – 82 km NW of Phoenix, ~1.5 km SE of Wickenburg, 615 m, branch of *L. tridentata*, on wood, 4.V.1995, G. Marson (H.B. 5658f ø). – ibid., branch of indet. angiosperm, 4.V.1995, G. Marson (H.B. 8579d ø). – 32 km NNW of Phoenix, 13 km SW of New River, 500 m, branch of *L. tridentata*, on wood, 19.VI.2003, G. Marson (H.B. 7397d). – 17.5 km NNE of Lukeville, Ajo Mountain Trail, 700 m, branch of ?*Glossopetalon spinescens*, on wood, 5.V.1995, G. Marson (H.B. 5809d). – 40 km NNE of Tucson, 11 km NE of Catalina, Casa del Oro, Biosphere, Rte. 89, 1165 m, of *Parkinsonia microphylla*, 7.V.1995, G. Marson (ø). – Chihuahuan Desert, 150 km ESE of Tucson, northwest-end of Chiricahua Mts., ~1700 m, on *Fraxinus velutina*, 26.V.1996, G. Marson (ø). — **AUSTRALIA**: **Western Australia**, Swan Coastal Plain, 30 km NNW of Perth, 1 km NW of Kinross, Tamala Park, 40 m, branches of *Acacia*, on bark, 23.X.2007, G. Marson (H.B. 8745a). – **Northern Territories**, northeast of MacDonnell Ranges, 15 km WNW of Alice Springs, N of Honey Moon Gap, Larapinta Drive, 586 m, twig of *Atriplex nummularia*, on bark, 9.X.1998, G. Marson (H.B. 6569d ø). – 12 km SE of Yulara, N of Ayers Rock, 515 m, branches of *Acacia aneura*, on wood, 11.X.1998, G. Marson (H.B. 7129a). – 11.5 km ENE of Yulara, 500 m, branch of *Allocasuarina decaisneana*, on wood, 12.X.1998, G. Marson (ex H.B. 6617a, MEL.2389212, **holotype**, **isotype** in MEL 2389214B; CBS 116235, anam. substr., anam. cult.; sq.: KT215232). – Burt Plain, 31 km SW of Barrow-Creek Hotel, 3.7 km WSW of Wilora, 480 m, branch of *Acacia*, on wood, 8.X.1998, G. Marson (ex H.B. 6260g, in holotype of *O. pleiostomachia*, MEL 2389194).

O. myriostomachia nom. prov.: **AUSTRALIA**: **Northern Territories**, northeast of MacDonnell Ranges, 15 km WNW of Alice Springs, N of Honey Moon Gap, Larapinta Drive, 586 m, twig of *Atriplex nummularia*, on wood, 9.X.1998, G. Marson (H.B. 6569f ø).

Orbilia myriosphaera Baral & E. Weber, **sp. nov.**, MB 813507 — Pls 202–203, Map 33

Etymology: named after the 64-spored asci and the globose spore bodies.

Typification: Croatia, Korčula island, branch of *Olea europaea*, 4.VI.2000, H.O. Baral (ex H.B. 6679a, M-0276533, holotype; ex-type culture: CBS 140830; sq.: KT215233, MH878190).

Latin diagnosis: *Apothecia in statu rehydratata 0.2–0.5 mm, aurantiaca. Asci 64-spori, apice in statu emortuo rotundati vel valde truncati, leniter crassitunicati. Ascosporae *3.8–6.8 × 2.7–3.7 µm, ellipsoideae vel ovoideae, corpusculo globoso vel lacrimiforme, filo tenui ad apicem affixo. Paraphyses ad apicem leniter vel fortiter inflatae. Habitat ad lignum vel corticem putridum ramorum in aere prominentium arborum angiospermarum in zona mediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.5(–0.6) mm diam., 0.14–0.26 mm high, pale to bright (cream-)orange(-rose) to dirty brick-orange, round, scattered to densely gregarious; disc flat, margin thin or thick, 0–10 µm protruding, ± smooth; broadly sessile, superficial or ± deeply immersed in detritus. **Asci** *80–105(–115) × (8.7–)9.5–10.5(–12) µm {7}, †(70–)84–100(–105) × 7–9.2 µm {3}, 64-spored (57–63 spores counted), spores ± 4-seriate, orientation irregular, pars sporifera *61–74(–85) µm long; **apex** (†) slightly to medium, sometimes strongly truncate, hemispherical in profile view, with a †0.8–1.3((–2.7)) µm thick dome {4}, some with slight apical chamber, a part of the asci ± thin-walled; **base** with short, thick, flexuous stalk, L- or Y-shaped. **Ascospores** *(3.8–)4.2–6(–6.8) × (2.5–)2.7–3.3(–3.7) µm {7}, ellipsoid-obovoid (to broadly clavate), apex rounded to obtuse, straight (to slightly inequilateral); **SBs** *(1.4–)2–3(–3.5) × 0.8–1.3 µm {7}, divided into a very abruptly swollen, globose (rarely broadly tear-shaped) lower part and a very fine, 0.9–2.5(–3) µm long filum, ± straight, globose part often laterally positioned. **Paraphyses** apically slightly to strongly clavate-capitate,

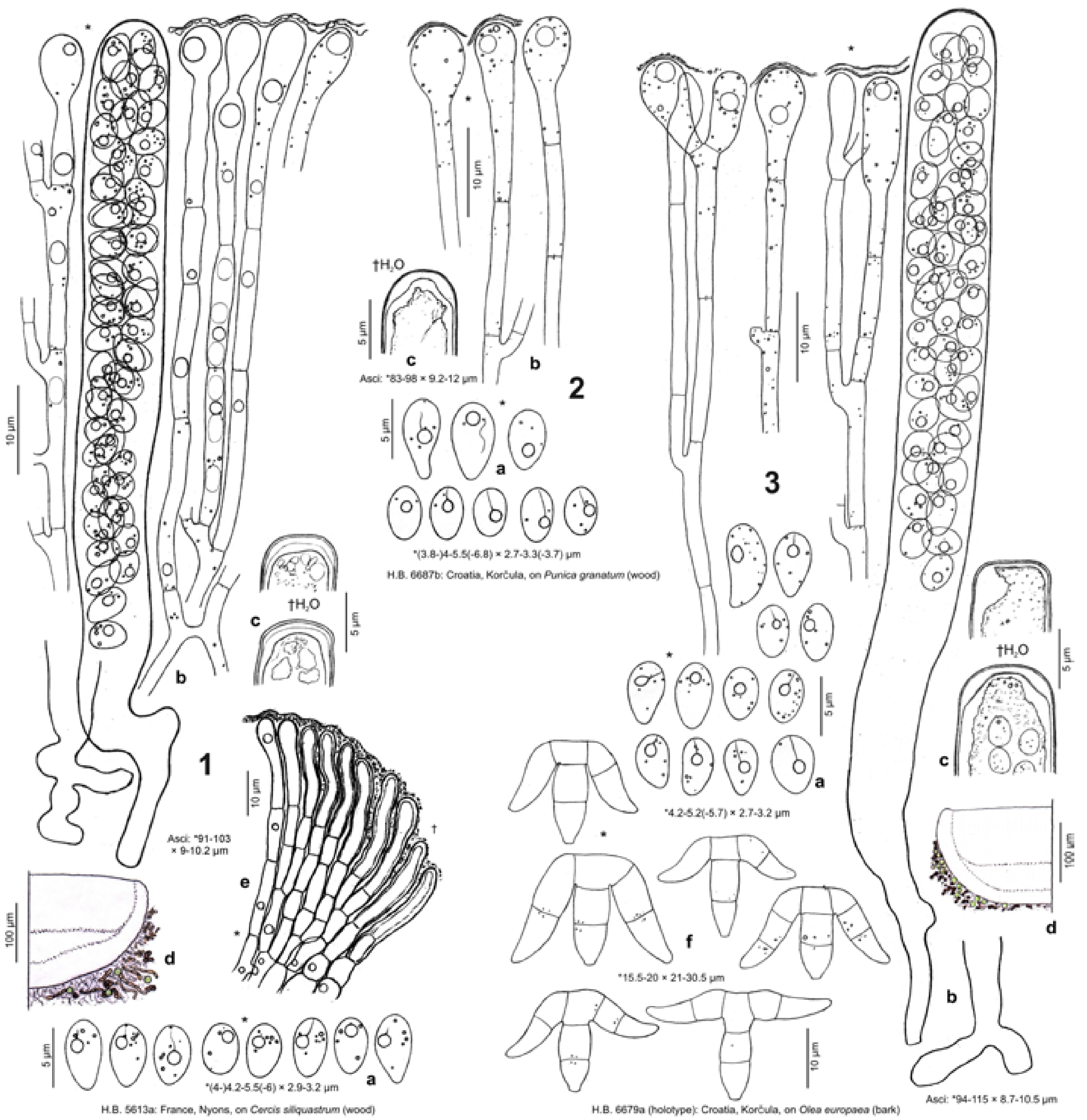


Plate 202. **1–3**: *Orbilia myriosphaera*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. conidia from culture.

rarely spathulate, partially moniliform, terminal cell *(9–)11–28(–35) × (2.5–)3.5–5(–6.3) µm {4}, lower cells *(5–)10–25 × 1.5–2.5(–3) µm {4}; not or sometimes branched near apex; hymenium very pale rose. **Medullary excipulum** very pale rose, 30–60 µm thick, of ± dense textura intricata-porrecta with many inflated cells, sharply delimited. **Ectal excipulum** very pale rose, of (†) slightly gelatinized, vertically or irregularly oriented t. angularis-prismatica from base to mid flanks (rarely up to margin), 20–50 µm thick near base, cells *(6–)9–18(–25) × (5–)7–11(–15) µm {4}; 20–30 µm thick at flanks, 10–50 µm near margin, of firmly agglutinated t. porrecta oriented at a 10–45° angle to the surface, marginal cortical cells */†8–25 × 2.2–4.3 µm {5}, lateral wall †(0.3–)0.5–1(–1.5) µm thick {4}, sometimes somewhat flexuous and hair-like. **Anchoring hyphae** (medium) abundant from base to mid flanks, *2–3 µm wide, walls *0.2–0.4 µm thick {1}, †0.2–0.8 µm {2}. **SCBs** globose, in paraphyses 1.5–3 µm diam., in cortical cells 1–1.5 µm diam. {5}. **Exudate** over paraphyses 0.5–1(–2) µm thick, ± continuous, slightly rough, loosely attached; over margin 1–2 µm thick, granular. **— ANAMORPH**: trinacrium-like (from ascospore isolate {1}). **Conidiophores** not observed. **Conidia** T-shaped, total size *15.5–18 × 21–30.5 µm {1}, stipe *11–14 × 4.5–6 µm, 2-septate, arms tapering, slightly to strongly pointing downwards at their base, consistently slightly curved outwards, *11–20.5 × 3.5–5.5 µm, (1–)2–3-septate.

Habitat: collected 0.3–3 m above the ground, corticated to ± decorticated, 3–15 mm thick branches of *Cercis siliquastrum* {6}, *Olea europaea* {1}, *Punica granatum* {1}, *Quercus coccifera* {1}, *Q. ilex* {1}, on 0.2–0.5 mm deep medium to strongly decayed wood {7} and bark {7} (bast {4} or periderm {1}), sometimes in old beetle galleries,

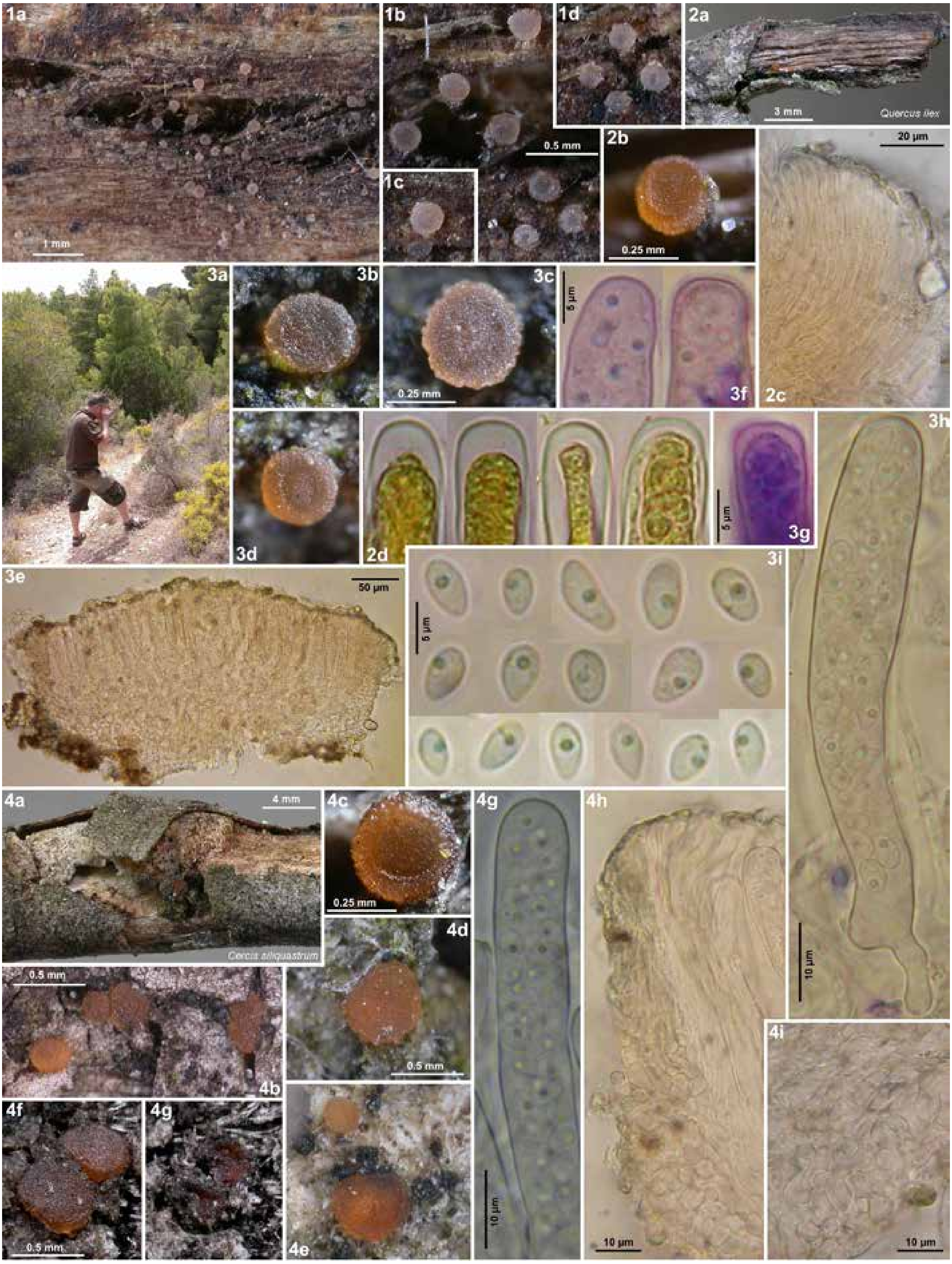


Plate 203. **1–4**: *Orbilia myriosphaera*. – **3a**. mediterranean maquis near Isthmia; **2a**, **4a**. partially decorticated xeric branches of *Quercus ilex*, *Cercis siliquastrum*; **1a–d**, **2a–b**, **3b–d**, **4b–f**. rehydrated apothecia (mainly on bast, **2**: on wood, **4**: partly on boring dust; **1**: phot. after 3.5 years); **3e**. apothecium in median section; **2c**, **4h**. id., marginal ectal excipulum; **4i**. id., lower flanks; **3h**, **4g**. asci; **2d**, **3f–g**. ascus apices; **3i**. ascospores. – Living state, except for asci in **2d** (in IKI), **3f–g** (in CRB). – **3a**: phot. J. Helleman-Fransen. — **1a–d**. H.B. 7272e: France, Nyons, on *Cercis*; **2a–d**. H.B. 9097: Greece, Peloponnes, on *Quercus ilex*; **3a–i**. H.B. 9096: ibid., on *Q. coccifera*; **4a–i**. H.B. 9151b: France, Nyons, on *Cercis*.

sometimes on boring dust of a bark beetle, greyed or not, green algae sparse to abundant. **Associated**: *Baggea* sp. {1}, *Claussenomyces* sp. {1}, *Dothideales* {1}, *Durella ?compressa* {1}, *Hysterobrevium mori* {1}, *Mellitiosporiella pulchella* {1}, *Nitschkia broomeana* {2/1}, *Orbilia carpoboloides* {1}, *O. cercidicola* {3}, *O. flagellispora* {1}, *O. gambelii* {2}, *O. hesperidea* {2}, *O. myriolentiformis* {1}, *O. obtusispora* {1}, *O. pleiogambelii* {2}, *O. polyspora* {4}, *O. subaristata* {4}, *O. subclavuliformis* {3}, *O. subocellata* {1}, *O. trapeziformis* {2}, *O. vinosa* {1}, *O. xanthoguttulata* {1}, *Patellaria atrata* {3}, *Patellariopsis dennisii* {1}, *Phragmiticola* sp. {1}, *Propolis ?farinosa* {1}, *P. viridis* {1}. **Desiccation tolerance**: fully viable for at least 5 months. **Altitude**: 1–855 m a.s.l. **Geology**: Cretaceous limestone, Miocene sandstone. **Phenology**: VI–IX (but long-lived).

Taxonomic remarks. *Orbilia myriosphaera* is easily recognized by its 64-spored asci and ellipsoid-obovoid ascospores containing a globose spore body attached apically by a rather long, hardly visible filum. The globose part of the SB is often positioned close to the lateral wall. *O. myriostomachia* from Australia (Pl. 200: 7) differs hereof in more consistently subglobose spores with pear- to stomach-shaped SBs. The North American *O. myriophanosoma* is very similar to *O. myriosphaera*: especially the collection on *Pinus* differ only in slightly larger spores and more ovoid SBs (Pl. 196: 2).

Taxa with lower spore numbers that resemble *O. myriosphaera* in the globose SBs could so far not be found. However, a striking similarity with the 8-spored *O. clavipisca* is obvious, which is tentatively placed in section *Ovoideae* but could as well belong to section *Lentiformes*. Even the hyphoid marginal cortical cells of *O. myriosphaera*, being thick-walled in the dead state, resemble those of typical representatives of section *Ovoideae*. Nevertheless, in our phylogenetic analysis section *Ovoideae* is very distant from section *Lentiformes* in which *O. myriosphaera* clusters.

Variation. The apical dome of dead asci varies in thickness within a population, being usually thick-walled with a slight apical chamber, but in some asci rather thin-walled and the ascus apex then often more truncate.

Anamorph. The conidia of *O. myriosphaera* differ from *Trinacrium incurvum* in the arms pointing much more downwards at their base, and particularly in being slightly curved up- instead of downwards (Pl. 202: 3f). The observed conidia developed only when the culture was flooded by water.

Phylogeny. Sequences of two samples were gained, one from pure culture of the holotype on *Olea*, the other (not shown in phylograms) from a sample on *Cercis* (G.M. 2018-09-12.10a), comprising SSU (with S1506 intron), ITS, and LSU. They differ in the ITS by 3 nt, in the intron by 3 nt, and in the LSU D1–D3 by 1 nt (D1), while the SSU V8–V9 fully concurs. A further sequence from another group of apothecia of the *Cercis* sample (G.M. 2018-09-12.10b) lacks the intron and further differs by 2–4 nt in the ITS and 2–3 nt in the LSU (D1–D2).

The species clustered unresolved in the strongly supported core clade of section *Lentiformes* (Phyl. 8). Surprisingly, it clustered in a weakly to medium supported clade with *O. cercidicola* (Phyls 8, S9), though with a distance of 12.5%, while the distance to the morphologically much closer *O. pluristomachia* lies also at 12%. Likewise, in the LSU region it shows a 4% distance to *O. pluristomachia*, with which it formed a weakly supported clade (Phyl. S11), and a similar distance (3–5%) to members of section *Lentiformes*. The intron is so far rather exceptional in the whole section *Lentiformes*, being otherwise only observed in series *Microspermae*.

Map 33. Known distribution of *O. myriosphaera* in southern Europe.

Ecology. *O. myriosphaera* is known from a few collection sites in Provence, Dalmatia, and Peloponnese, but is expected to occur throughout the mediterranean belt. It grew on rotten wood and bark of dead xeric branches of *Cercis*, *Olea*, *Punica* and *Quercus* in the suprasub- to thermomediterranean but mainly mesosubmediterranean semihumid maquis.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1 km N of Nyons, Col du Pontias, 460 m, branches of *Cercis siliquastrum*, on wood, 22.VIII.1996, G. Marson (H.B. 5613a). – ibid., on wood & bark, 18.VIII.2001, G. Marson (H.B. 7077a). – ibid., 11.X.2002, (H.B. 7272e). – ibid., 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9151b). – ibid., on bark, 12.IX.2018, G. Marson (G.M. 2018-09-12.10; sq.: MK473392, MK473424). – 10 km ENE of Nyons, 1 km N of Curnier, 383 m, branch of *C. siliquastrum*, on bark, 12.VIII.2009, G. Marson (H.B. 9182c ø). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 11.5 km W of Korčula, 2 km W of Račišće, below Samograd cave, 40 m, branch of *Olea europaea*, on bark, 4.VI.2000, H.O. Baral (ex H.B. 6679a, M-0276533, **holotype**, anam. cult., CBS 140830; sq.: KT215233, MH878190). – ibid., Samograd bay, 2 m, twig of *Punica granatum*, on wood, 4.VI.2000, H.O. Baral & N. Matočec (H.B. 6687b ø). — **GREECE**: **Peloponnese**, 25 km E of Sparta, 4 km SW of Kosmas, chapel between Geraki and Kosmas, 855 m, twig of *Quercus ilex*, on wood, 8.VI.2009, S. Helleman (H.B. 9097). – 8.5 km SE of Korinthos, 2 km SSE of Isthmia, Kalamaki beach, 1 m, twig of *Quercus coccifera*, on bark, 1.VI.2009, S. Helleman (H.B. 9096).

Orbilia pleistosphaera S. Tello & Baral, **sp. nov.**, MB 825629 — Pl. 204

Etymology: named after the 128-spored asci and the globose spore bodies.
Typification: Spain, Andalucía, Jaén, twig of *Berberis hispanica*, 13.VIII.2017, S. Tello (ex S.T. 13081701, AH 48635, holotype).

Latin diagnosis: *Similis* Orbiliae myriosphaerae *sed asci 128-spori, longiores et latiores, ascosporae longiores, clavatae. Habitat ad corticem putridum ramuli in aere prominentis* Berberidis hispanicae *in zona supramediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.35 mm diam., pale greyish-orange, round, scattered; disc flat, margin distinct, ~10–15 µm protruding, ± uneven; broadly sessile, superficial. **Asci** *108–128 × 13.3–15 µm, †~95 × 11.5–12.8 µm, 128-spored (min. 74 spores counted on photo), spores ± 4-seriate, orientation irregular, pars sporifera *92–103 µm long; **apex** (†) slightly truncate, hemispherical in profile view, with †~0.5–1 µm thick dome; **base** unstalked or with short, thick, Y-shaped. **Ascospores** *(6–)6.5–8(–8.5) × (2.8–)3–3.3(–3.5) µm, broadly clavate (pyriform), apex rounded to obtuse, base always medium to strongly attenuated, straight to slightly inequilateral; **SBs** *3–3.7 × 0.9–1.1 µm, divided into a very abruptly swollen, globose lower part and a very fine, 2–3 µm long filum, ± straight, globose part often laterally positioned. **Paraphyses** apically slightly to strongly clavate-capitate, terminal cell *16–37 × (3–)4–5.5 µm, lower cells *12–17 × 1.7–2.3(–3) µm; sometimes branched near apex. **Medullary**

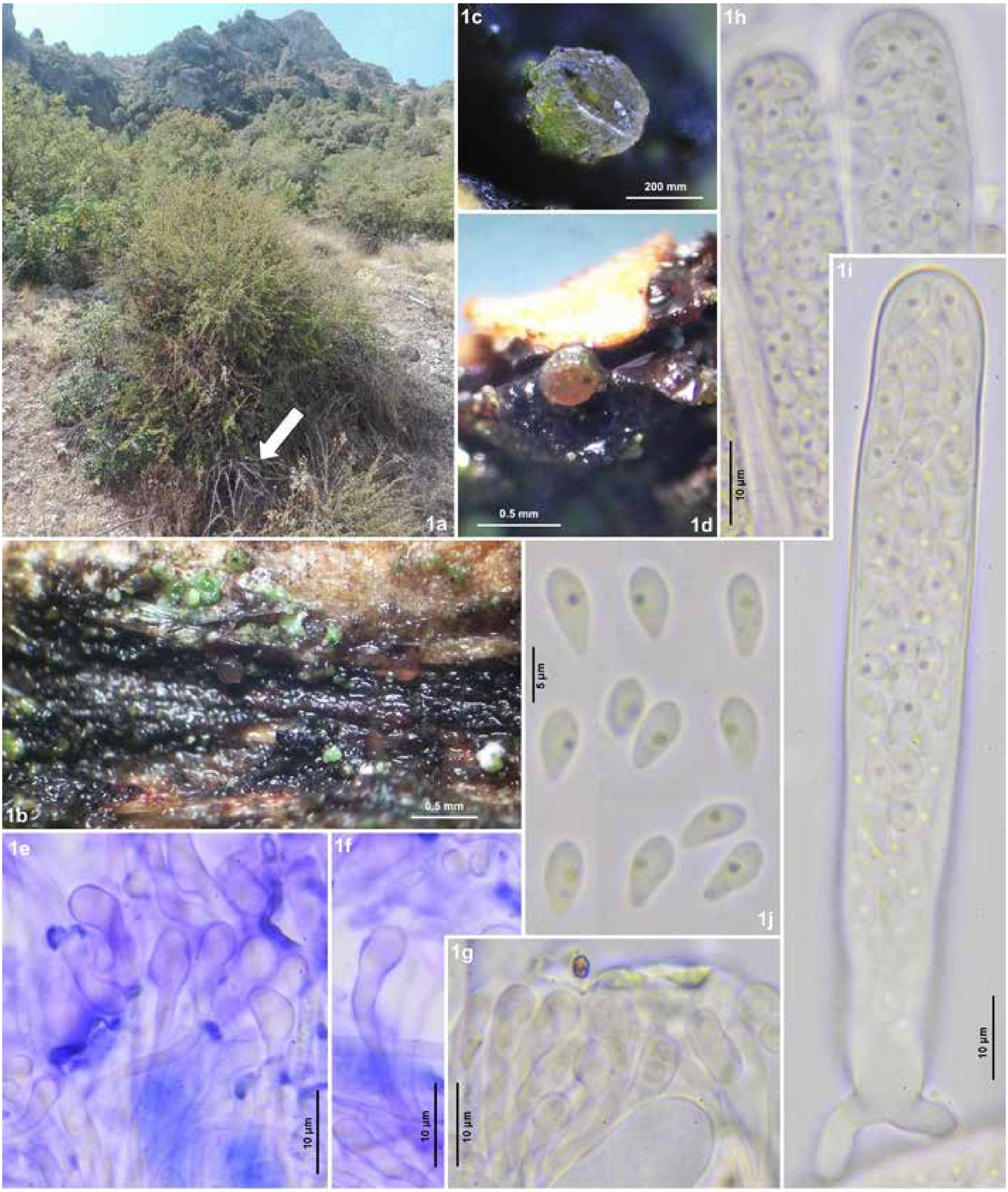


Plate 204. **1**: *Orbilia pleistosphaera*. – **1a**. open supramediterranean shrubland on a north-exposed scree slope in the Sierra de Ventisqueros of Andalucía; **1b**. twig of *Berberis hispanica*; **1b–d**. rehydrated apothecia; **1e–g**. paraphyses (**1e–f** in CRB); **1h–i**. asci; **1j**. ascospores. – Living state, except for left ascus in **1h**. — **1a–j**: phot. S. Tello; AH 48635: Spain, Valdepeñas de Jaén, on *Berberis*.

excipulum not studied. **Ectal excipulum** of t. angularis(-prismatica) from base to mid flanks, cells at flanks *6–12 × 4–7 µm, at margin of firmly agglutinated t. porrecta, marginal cortical cells *~13–15 × 3–4 µm, sometimes somewhat flexuous. **Anchoring hyphae** not studied. **SCBs** globose, in paraphyses 1.7–2.7 µm diam., in marginal cortical cells 1.7–2 µm. **Exudate** over paraphyses 0.5–1.7 µm thick, continuous to cloddy, loosely attached. — **ANAMORPH**: unknown.

Habitat: collected 0.4 m above the ground, 5 mm thick, dead corticated twig of *Berberis hispanica*, on very decayed bark (bast). **Associated**: *Thyronectria lamyi*. **Desiccation tolerance**: fully viable for at least 2 months. **Altitude**: 1200 m a.s.l. **Geology**: Cretaceous marly limestone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleistosphaera* differs from *O. myriosphaera* in larger asci which contain many more spores than 64, and in clavate, pear-shaped, basally usually strongly narrowed ascospores (Pl. 204). The protologue is entirely based on the description and photos of the finder, S. Tello (pers. comm.).

Ecology. *O. pleistosphaera* is only known from the single sparse holotype collection. It grew on rotten bark of a dead xeric twig of *Berberis* in a supramediterranean semihumid open shrubland in a north-exposed scree slope in the Sierra de Ventisqueros of Andalucía. The vegetation includes *Quercus rotundifolia*, *Crataegus monogyna*, *Pistacia terebinthus*, *Juniperus oxycedrus*, *Acer monspessulanum*, *Pinus nigra*, and *Prunus mahaleb*.

Specimens included. **SPAIN**: **Andalucía**, **Jaén**, Sierra de Ventisqueros, 18.5 km SSE of Jaén, 7 km ENE of Valdepeñas de Jaén, 2 km S of El Parrizoso, 1200 m, twig of *Berberis hispanica*, on bark, 13.VIII.2017, S. Tello (ex S.T. 13081701, AH 48635, **holotype**).

Series *Microspermae*

Orbilia subgenus ***Hemiorbilia*** section ***Lentiformes*** series ***Microspermae*** Baral & E. Weber, **ser. nov.**, MB 815003 – Type species: *Orbilia euonymi* Velen.

Etymology: named after the minute ascospores.

Latin diagnosis*: Asci 16- ad 128-spori, apice in statu emortuo hemisphaerico, crassitunicato. Ascosporae *2.2–5.5 × 1.5–2.8 µm, subglobosae, ovoideae, cylindrico-ellipsoideae vel fusoideo-clavatae, apice rotundatae vel obtusae, in statu vivo corpusculum refringens minutum lacrimiformem, filo breve ad apicem affixum continentes.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.08–)0.12–0.6(–0.9) mm diam., pale to bright yellowish-orange(-rose), margin smooth, sessile. **Asci** *(26–)30–70(–86) × (6–)7–9(–10) µm, 16- up to 128-spored, orientation in all directions; **apex** (†) hemispherical (to slightly truncate), dome immature 1.2–2(–2.5) µm thick, with apical chamber; **base** L-, T-, Y- or h-, but never H-shaped. **Ascospores** *(2.2–)2.5–4(–5.5) × 1.5–2.5(–3) µm, subglobose, ovoid, ellipsoid, subcylindrical, or fusoid-clavate, apex rounded to obtuse, straight or slightly (rarely medium) curved; **SBs** *(0.8–)1–1.8(–2) × 0.2–0.6(–0.8) µm, divided into a ± abruptly swollen, tear-shaped (also pear-shaped or subglobose) lower part and a filum of ± equal length. **Paraphyses** uninflated or only slightly clavate at the apex, terminal cells (0.5–)0.8–1.5(–2)× longer than lower cells, sometimes branched near apex. **SCBs** always globose. **Exudate** 0.5–2(–4) µm thick, continuous to cloddy, ± rough, loosely attached, hyaline or pale yellowish. **— ANAMORPH**: vermispora-like. **Conidiophores** short (10–35 µm), unbranched, simple or with swollen cells. **Conidiogenous cells** monoblastic or sympodial, with denticles. **Conidia** *(12–)20–62 × 2.8–5.5 µm (in situ and actual length), (1–)3–10(–12)-septate, slightly to strongly curved.

Habitat: wood and bark of gymno- and angiosperms (sometimes resinicolous), rarely on petioles of a palm, temperate to subtropical, humid to semiarid, always desiccation-tolerant.

Recognized species: *O. euonymi*, *O. myrioeuonymi*, *O. pleioeuonymi*, *O. pleistoeuonymi*.

Taxonomic remarks. Members of series *Microspermae* form a small homogeneous group. They resemble series *Phanosomates* in shape of ascospores and SBs, the latter being divided into a tear-shaped lower and a short filiform upper part. Series *Microspermae* differs in distinctly smaller spores and SBs, and consequently in smaller asci when comparing taxa with corresponding spore numbers, with always thick-walled apices which are never truncate.

Species delimitation. The four taxa included in this series are very similar. They mainly differ in spore number, therefore, they might as well be recognized as varieties of a single species. However, some differences are noted in the associated anamorphs, and molecular data support distinction at the species level.

Spore size and shape is hardly different among the included taxa, except for *O. pleioeuonymi* which has wider, more subglobose spores. In addition, these features show a certain variation within each species, therefore, the spores alone cannot be used for identification of species with a spore number higher than 16. Size and shape of the SBs are quite similar in the four species.

Anamorph. The conidia of series *Microspermae* are phragmosporous, mostly slightly curved (like in *Vermispora*), formed on denticles on short conidiophores. None of the observed anamorphs could by identified with a described species. The conidia of *O. euonymi* and *O. myrioeuonymi* were only found on the natural substrate, but in *O. pleioeuonymi* and *O. pleistoeuonymi* we obtained them in pure culture. The conidiophores of *O. pleistoeuonymi* are remarkable by their swollen conidiogenous cells with abundant prominent denticles. In this respect the anamorph somewhat resembles *Sigmoidea aurantiaca* Descals which, however, differs in distinctly longer conidia. Similar conidiogenous cells were observed in pure culture of *O. carpoboloides* (subgen. *Habrostictis*, Pl. 568: 3j).

Conidial morphology as observed within series *Microspermae* is rather similar, differing between *O. euonymi* and *O. pleistoeuonymi* mainly in size and number of septa. The conidia of *O. pleioeuonymi* are distinctly narrower than in the other three species, while those of *O. pleistoeuonymi* are comparatively short and with fewer septa (Pl. 205: 4).

Phylogeny. Sequences were available for three species, which formed a strongly supported clade of their own within the rather strongly supported monophyletic clade of section *Lentiformes* (Baral 2017b, Phyl. 7). Irrespective of whether analysing ITS, LSU, or combinations with SSU, *O. pleistoeuonymi* consistently clustered sister to the other two taxa of the series. Which spore number was the ancestral character state within series *Microspermae* is unclear since spore numbers appear to have frequently changed within a series, which is obvious from our phylogenetic analyses of series *Lentiformes* and *Phanosomates*.

Despite its morphological similarity to series *Phanosomates*, series *Microspermae* is genetically not closely associated herewith. The distance in the ITS region to other series of section *Lentiformes* is very high (18.5–25 %). Also in the SSU (V8–V9, 362 nt) a distance of 4–6 % is observed, which is extraordinary within section *Lentiformes*, compared to merely 3.3–4 % to members of section *Hemiorbilia*. In the LSU D1–D2 domain the distance to the other series of section *Lentiformes* is 4–8 %, compared to 6–11 % to section *Hemiorbilia*. In the 5.8S region series *Microspermae* fully concurs with series *Phanosomates* and most species of series *Lentiformes*, but differs from section *Hemiorbilia* by 2–5 nt.

Contrary to the other series of section *Lentiformes*, species of series *Microsomates* possess the S1506 intron, with so far two exceptions: the single sequence of *O. myriosphaera* also has this intron, and one out of five sequences of *O. euonymi* appeared to lack it.

Specific nucleotide positions. Series *Microsomates* deviates from all other members of section *Lentiformes* in the ITS1 at pos. 1 by ATCATTA**C** vs. ATCATTA**A** (or ATCATTA**T** in *O.*

Table 65. Comparison of ascus, ascospore, and conidial data among the four species of series *Microspermae*.

Spore number	*Asci [µm]	†Asci [µm]	*Spores [µm]	*Conidia [µm]	Conidial septa
16 (*pleioeuonymi*)	(26–)30–40(–45) × 6–7.5(–8)	25–38 × (5–)5.5–6(–6.5)	(2.5–)2.8–3.5(–3.8) × (2–)2.2–2.8(–3)	(38–)42–54(–62) × 2.8–3.6	(4–)5–6(–8)
32 (*euonymi*)	(30–)34–55(–68) × 6.3–8.5(–9)	(29–)31–50(–54) × (5–)5.5–7(–7.5)	(2.2–)2.6–4.3(–5.5) × (1.5–)1.6–2.1(–2.3)	(21–)28–49(–58.5) × (3.5–)4–5(–5.5)	(1–)5–9(–12)
64 (*myrioeuonymi*)	37–48 × 7.5–10	29–46(–67) × (5–)6–7.5(–8.5)	(2.8–)3–4.3(–4.8) × 1.5–1.8(–2)	~52 × 4	8
128 (*pleistoeuonymi*)	(45–)55–75(–86) × (8.5–)9–10	(38–)45–70(–80) × (7–)7.5–9(–10)	(2.2–)2.5–3.5(–4.5) × (1.5–)1.7–2.2(–2.4)	(12–)18–31(–34) × (3.5–)4–4.5(–5)	(1–)3–5(–6)

cercidicola), in the ITS2 at pos. 9 by C vs. A, and in the middle of ITS2 by GC**T**GGTGA vs. GC**G**GGTGA, besides some other characteristic motifs. It also deviates in the LSU D1–D2 at pos. 176 by **A**TAG or **A**TGG vs. **C**CGG or **C**TGG, at 189 by TTC**T**TT vs. TTC**C**TT, at 205 by GTC**A** vs. GTC**G**, at 235 & 238 by A**T**GG**T** vs. G**C**GG**C** or A**C**GG**C**, and at 600–601 by **AA**GCTAGG vs. **TT**GCTAGG or **TC**GCTAGG. Some further positions in the D1–D2 (142, 162, 228, 252, 254, 442, 560) are only unique for this series when excluding *O. pleistoeuonymi* which shows the character of the remaining section *Lentiformes*.

Ecology. Among the four recognized taxa, *O. euonymi* is by far the most frequently encountered species, which seems to occur ubiquitous throughout Europe from cold-temperate humid to subtropical semihumid regions, except for the northern, (hemi)boreal parts. *O. pleioeuonymi* is much less frequent, and the other two were only rarely encountered. The four species have almost never been observed to grow in association on the same branch. The 64-spored species is so far geographically restricted to southeastern Asia and Australia, whereas the other three were mainly recorded in Europe. *O. euonymi* also occurs in the humid Rocky Mountains of North America, the dry summit broom scrubs in Macaronesia, and in semiarid cold-continental central Asia. The four species inhabit exclusively ligneous substrate, with a single exception of a palm petiole.

Orbilia pleioeuonymi Baral, G. Marson & Priou, **sp. nov.**, MB 813508 — Pls 205–206, Map 34

Etymology: named after the 16-spored asci and the close relation to *O. euonymi*. **Typification**: Luxembourg, Dudelange, branch of *Robinia pseudoacacia*, 29.X.1993, G. Marson (ex H.B. 4984a, M-0276557, holotype).

Latin diagnosis: *Differt ab* Orbilia euonymi *ascis 16-sporis, ascosporis subglobosis vel late ellipsoideo-ovatis. Habitat ad lignum vel corticem putridum ramorum in aere prominentium arboris vel fruticis variis, in silvis supra- ad mesotemperatis humidis, plerumque thermophilis Europae centralis et occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.08–0.25(–0.3) mm diam., 0.08–0.11 mm high (receptacle 0.06–0.07 mm), subhyaline or pale to light yellowish-amber-orange, translucent, round, very scattered to medium gregarious; disc flat, sometimes slightly convex, margin thin, not protruding, smooth; sessile or with distinct stipe 0.02–0.05 × 0.06–0.1 mm, superficial to slightly immersed; dry pale yellowish-cream or light orange. **Asci** *(26–)30–40(–45) × 6–7.5(–8) µm {5}, †25–38 × (5–)5.5–6(–6.5) µm {3}, 16-spored, spores *± 4-seriate, orientation irregular, pars sporifera *13–15(–19.5) µm long; **apex** (†) hemispherical to slightly truncate, with dome †1.2–1.6 → 1 µm thick {2}, with apical chamber; **base** with or without short to long, flexuous stalk, L- or Y-shaped. **Ascospores** *(2.5–)2.8–3.5(–3.8) × (2–)2.2–2.8(–3) µm {11}, subglobose to broadly ellipsoid-ovoid or -obovoid, also broadly fusoid, ends rounded (to obtuse); **SBs** *(1–)1.2–1.8 × 0.3–0.8 µm {5}, divided into a ± abruptly swollen, tear-shaped to subglobose lower part and a filum of ± equal length, straight or slightly curved. **Paraphyses** apically uninflated to slightly clavate-capitate, rarely sublageniform, straight or ± flexuous, terminal cell *(4–)5–12(–14) × (1.3–)1.7–2.5(–3.2) µm {5}, lower cells *3.5–9 × (1.6–)1.8–2.4(–3.2) µm {5}; frequently branched in middle and basal part, never at upper septum. **Medullary excipulum** 20–40 µm thick, of ± loose to dense textura intricata-angularis with many inflated cells, sharply delimited. **Ectal excipulum** of thin-walled, ± vertically oriented t. angularis from base to lower flanks, 15–50 µm thick near base, cells *5–13 × 5–11 µm {2}; at flanks of t. prismatica oriented at a 30–40° angle to the surface, at margin at 10–30°, marginal cortical cells *(4–)5–8(–12) × (1.6–)2–3(–3.7) µm {2}. **Anchoring hyphae** sparse, */†1.8–2.7 µm wide, walls 0.2(–0.3) µm thick {3}. **SCBs** in paraphyses and ectal excipulum (near margin) globose to ellipsoid, low-refractive, (1–)1.5–2.3 µm diam. **Exudate** over paraphyses, margin and flanks (0.2–)0.5–1.5(–2) µm thick, cloddy, hyaline to pale amber-coloured, loosely attached. **— ANAMORPH**: vermispora-like (from ascospore isolate {1}). **Conidiophores** *~11–30 × 3.2–4 µm, unbranched, irregularly bent and ± moniliform. **Conidiogenous cells** monoblastic, partially with a short, *1.6–1.8 µm wide apical denticle. **Conidia** unbranched, narrowly cylindric-fusoid, tapered towards both ends, ± straight but slightly to medium curved near each end, *(38–)42–54(–62) × 2.8–3.6 µm, (4–)5–6(–8)-septate {1}, containing a few minute LBs in each cell.

Habitat: collected 0.1–2.2 m above the ground, corticated to ± decorticated, 7–26 mm thick branches (rarely cones) of *Acer campestre* {1}, *Clematis vitalba* {3}, *Fagus sylvatica* {2}, *Ilex aquifolium* {1},

Key to species of series *Microspermae*

1. Asci 16-spored; spores *(2–)2.2–2.8(–3) µm wide, subglobose to ovoid (length/width ratio 1.1–1.6); conidia *38–62 × 2.8–3.6 µm; wood and bark of gymno- and angiosperms, cold- to warm-temperate humid Europe .... ***O. pleioeuonymi***, p. 529
1. Asci 32–128-spored; spores *(1.5–)1.7–2.1(–2.4) µm wide, mostly cylindric-ellipsoid, distinctly longer than wide (length/width ratio 1.3–3); conidia *21–58.5 × 3.5–5.5 µm 2

2. Asci 32-spored, *6.3–9 µm wide (†5–7.5 µm); conidia mainly 5–9-septate; wood and bark of gymno- and angiosperms, boreal to subtropical, humid to semi- or subhumid Europe, Macaronesia, central Asia, west & south of Northern America .... ***O. euonymi***, p. 532
2. Asci 64–128-spored, *7.5–10 µm wide (†6–9 µm)..3

3. Asci 64-spored; conidia (presumed) *~52 µm long, 8-septate; wood of *Melaleuca*, *Jacksonia* etc., petioles of *Livistona*, subtropical semi- to (sub)humid eastern & western Australia and eastern Asia .... ***O. myrioeuonymi***, p. 538
3. Asci (?64–)128-spored; conidia *12–34 µm long, mostly 3–5-septate; wood of *Quercus*, *Carpinus*, *Robinia*, cold-temperate humid and (sub)mediterranean semihumid Europe .... ***O. pleistoeuonymi***, p. 539

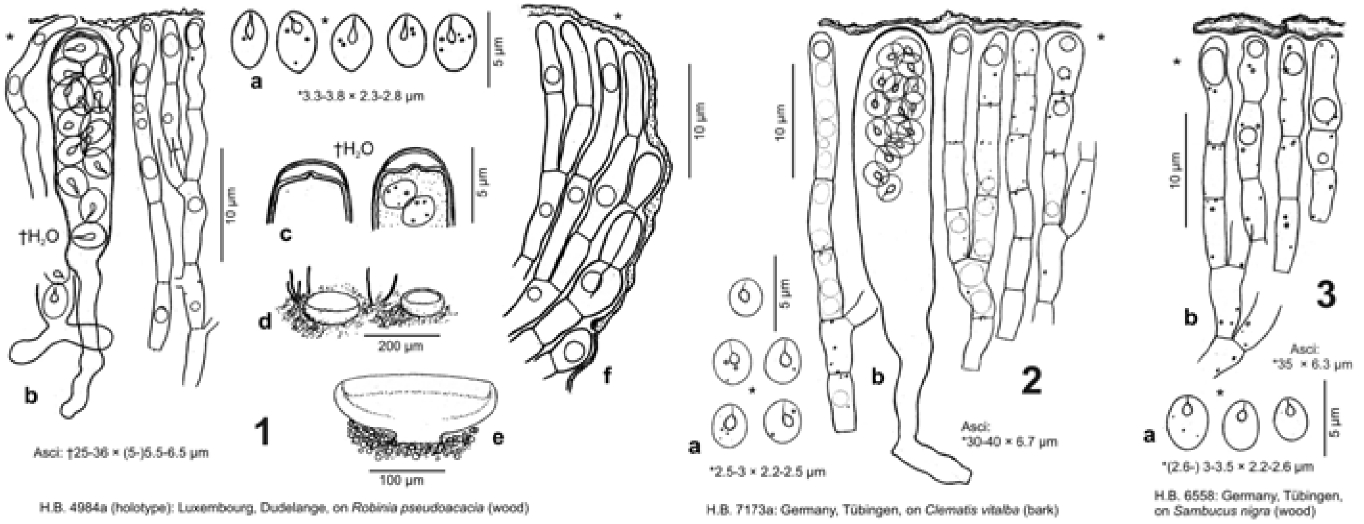


Plate 205. **1–3**: *Orbilia pleioeuonymi*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. marginal ectal excipulum (median section).

Larix sp. {1}, *Ligustrum vulgare* {1}, *Picea abies* {1}, *Robinia pseudoacacia* {1}, *Sambucus nigra* {2/1}, *Ulex europaeus* {2}, on 0.2–2 mm deep strongly decayed wood {11} and bark {4} (bast and periderm), rarely cones, greyed, ± strongly covered by green algae. **Associated**: *Bulbillomyces* sp. {1}, *Corticiaceae* {1}, *Durella connivens* {1}, '*Helotium*' *uvidulum* {2}, *Hyalorbilia latispora* {1}, *H. subfusispora* {2}, *Karstenia idaei* {1}, *K. rhopaloides* {1}, *Lecophagus ellipsoideus* {2}, ?*Marchandiomyces* sp. {1}, *Mollisia* ?*fusca* {1}, *Orbilia* ?*cejpii* {1/1}, *O. montigena* {1}, *O. obtusispora* {1}, *O. trapeziformis* {1}, *O. vitalbae* {1}, *Physcia* sp. {2}, *Pseudospiropes simplex* {1}, *Sporidesmium* sp. {1}, *Unguiculariopsis* sp. {1}, *Xanthoria parietina* {1}, crustose lichens. **Desiccation tolerance**: paraphyses and excipular cells survive for min. 1 month. **Altitude**: 38–720 m a.s.l. **Geology**: Cambrian, Ordovician & Carboniferous shale, siltstone & calcareous or quartzitic greywacke, mica schist, Keuper (marl- & sandstone), Lower & Middle Jurassic shale, sand- & limestone, Pleistocene loess & till. **Phenology**: I–II, IV, VII–XII (throughout the year, long-lived).

Taxonomic remarks. *Orbilia pleioeuonymi* differs from the other taxa of series *Microspermae* in (max.) 16-spored asci, also in distinctly wider, more ovoid-subglobose ascospores, and in longer and particularly narrower conidia. In at least one of the collections, the similar 32-spored *O. euonymi* grew in association, the two species being macroscopically hardly distinguishable. Based on micromorphological and molecular data we separate *O. pleioeuonymi* from *O. euonymi* at the species level.

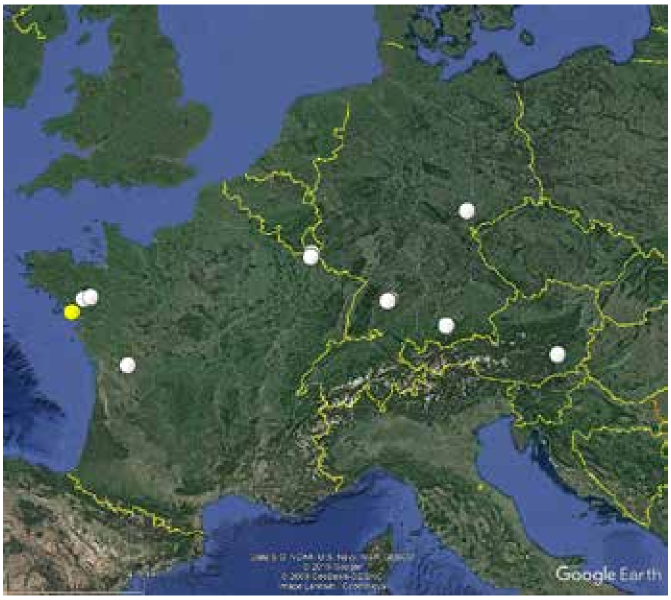
Variation. We sometimes observed in *O. pleioeuonymi* a few asci with reduced spore numbers, e.g., 13–14-spored, which contained some oversized spores measuring *4–4.7 × 3.5–4 µm among the normal ones. However, the asci never contained more than 16 spores in all apothecia which we have examined. Likewise, some collections of *O. euonymi* showed a few asci with reduced spore numbers of 16–22, with some or all of the spores corresponding very well in size and shape to those of *O. pleioeuonymi*. However, G. Friebes (pers. comm.) observed in the sparse Austrian sample besides 16-spored asci also more spores in several asci, but the spores were always subglobose (IVV: 9.XII.2017). Slight variation was noted in spore length, and in width and curvature of the terminal cells of paraphyses.

Not included collection. An unpreserved sample from Bretagne (one apothecium on *Ulex*) differs in extraordinarily long asci (†45–60 × 7–7.5 µm) and a spore size at the upper end of the range (*3.5–4 × 3 µm, IVV: J.P.P. 28219).

Anamorph. The conidia of *O. pleioeuonymi* were obtained in pure culture of a single collection (Pl. 206: 6). They resemble those of the other species of series *Microspermae* except for being longer and especially narrower. The conidiophores are unbranched and the conidiogenesis is always terminal, in contrast to *O. pleistoeuonymi* in which often many denticles were found on a single conidiophore.

Phylogeny. A sequence comprising S1506 intron, ITS, and LSU was taken from a pure culture of *O. pleioeuonymi* from Luxembourg (16.XI.2013, on *Clematis*). In the ITS region the distance to *O. euonymi* is 6.3–6.5% and to *O. pleistoeuonymi* 15%, in the intron it lies at 7.5–8.5% and 18.5%, and in the LSU at 2.2% and 5.2% (overlapping 633 nt), respectively. These distances confirm the values of spore numbers and that *O. pleioeuonymi* is a species of its own. For its phylogeny see under *O. euonymi*, p. 535.

Ecology. *O. pleioeuonymi* occurs on a wide range of substrates: rotten wood and bark of dead xeric branches of angiosperm trees, shrubs and climbers, two times also on conifers (*Picea* wood, *Larix* cone). The first record of



Map 34. Known distribution of *O. pleioeuonymi* in Europe (yellow = not included collection).

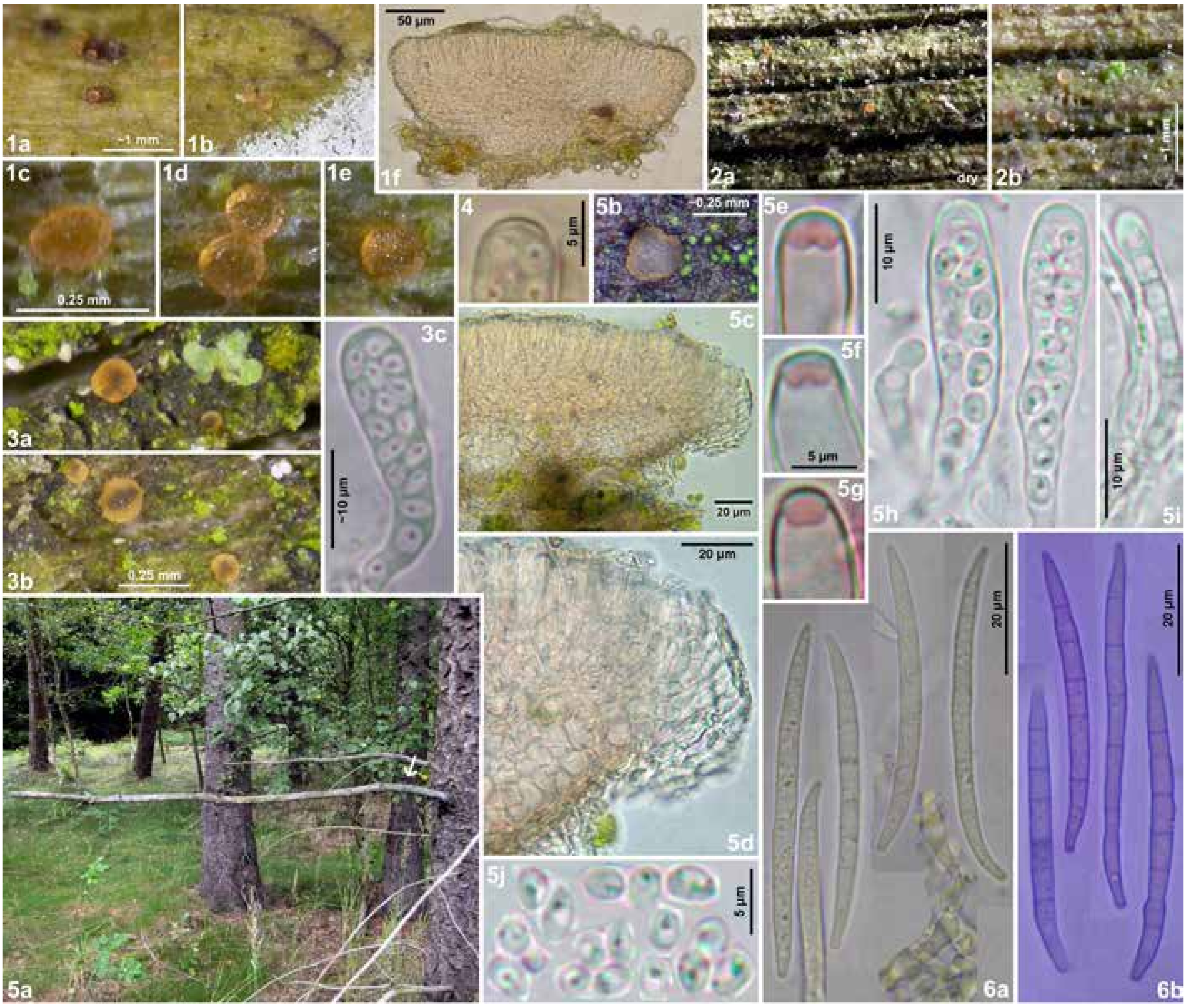


Plate 206. **1–6**: *Orbilia pleioeuonymi*. – **5a**. Clearing in moist, acidic *Picea-Betula* forest; **1a–e**, **2b**, **3a–b**, **5b**. rehydrated apothecia; **2a**. dry apothecia; **1f**, **5c**. apothecia in median section; **5d**. id., marginal ectal excipulum; **3c**, **5h**. asci; **5i**. paraphysis; **4**, **5e–g**. ascus apices; **5j**. ascospores; **6a–b**. conidia and conidiophore (from culture). – Living state (**6b** in CRB) except for asci in **3c**, **5e–g** (in $\mathrm{CR}_{\mathrm{SDS}}$), **4**, **5h**. – **3a–c**: phot. J.P. Priou, **5a–j**: phot. M. Bemmann. — **1a–f**. H.B. 8815: France, Melle, on *Ligustrum*; **2a–b**. H.B. 7446: Germany, Tübingen, on *Clematis*; **3a–c**. J.P.P. 29023: France, La Gacilly, on *Ilex*; **4**. H.B. 7933b: Germany, Tutzing, on *Fagus*; **5a–j**. 29.VIII.2010: Germany, Gera, on *Picea*; **6a–b**. 16.XI.2013. Luxembourg, Dudelange, on *Clematis*.

this species was rather abundant, but later collections often contained only a few apothecia. The species is mainly known from supratemperate humid, rarely mesotemperate and mesomediterranean humid or almost semihumid atlantic western and subcontinental central Europe. It occurs in ± thermophilous, usually deciduous forests on both alkaline and acidic soils, often at sun-exposed borders of forests or on free-standing trees and shrubs, also in old vineyards and gardens.

Specimens included. **LUXEMBOURG**: **Gutland**, **Esch-sur-Alzette**, 4.5 km S of Luxembourg, 1 km W of Hesperange, Biersak, 300 m, ?*Sambucus nigra*, on wood, 20.XII.1997, G. Marson (ø). – 4.2 km S of Bettembourg, 1.7 km E of Dudelange, 2.6 km NW of Zoufftgen, along railway, 290 m, twig of *Clematis vitalba*, on wood, 16.XI.2013, G. Marson (G.M. 2013-11-16.1, anam. cult.; sq.: KT380070). – 2.3 km SE of Dudelange, Daereboesch, 272 m, branch of *Robinia pseudoacacia*, on wood, 29.X.1993, G. Marson (ex H.B. 4984a, M-0276557, **holotype**; G.M. 5057 **isotype**). — **GERMANY**: **Thüringen**, 18 km SSW of Gera, 9.5 km N of Zeulenroda, NW of Staitz, 400 m, branch of *Picea abies*, on wood, 29.VIII.2010, M. Bemmann (ø, doc. vid.). – **Baden-Württemberg**, 5.5 km ENE of Tübingen, Pfrondorf, Blaihofstraße, 430 m, branch of *Sambucus nigra*, on wood, 21.I.2000, H.O. Baral (H.B. 6558 ø). – 0.7 km WSW of Tübingen, Schloss Hohentübingen, 360 m, branch of *Sambucus nigra*, on wood, 20.X.2002, E. Weber (ø). – 2.5 km SW of Tübingen, Spitzberg, Ödenburg, 405 m, branch of *Acer campestre*, on wood, 1.XII.2002, H.O. Baral (ø). – ibid., N of Ödenburg, 420 m, branch of *Clematis vitalba*, on bark, 21.XII.2003, H.O. Baral (H.B. 7446). – ibid., Sonnenhalde, 370 m, branch of *C. vitalba*, on bark, 28.VII.2002, V. Baral (H.B. 7173a). – **Bayern**, **Oberbayern**, Fünfseenland, 8 km NW of Tutzing, 3.5 km S of Andechs, Goaslweide, 720 m, branch of *Fagus sylvatica*, on wood, 15.X.2005, H.O. Baral (H.B. 7933b, ø, anam. substr.). – **AUSTRIA**: **Steiermark**, 3.8 km NNW of Gratwein, 3.3 km WSW of Unterfriesach, E of Hörgasgraben, NW hospital Enzenbach, 560 m, branch of *Fagus sylvatica*, on wood, 9.XII.2017, G. Friebes (ø, doc. vid.). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 5.3 km NE of Pipriac, 0.7 km NE of Courbouton, 38 m, branch of *Ulex europaeus*, on wood, 27.XI.2007, J.P. Priou (J.P.P. 27131 ø, doc. vid.). – **Morbihan**, 1.5 km W of La Gacilly, Croix de Jacquary, 40 m, branch of *Ilex aquifolium*, on bark, 26.II.2009, J.P. Priou (J.P.P. 29023 ø, doc. vid.). – **Poitou-Charentes**, **Deux-Sèvres**, 13 km N of Melle, 1.8 km S of Fonfreroux, Forêt de L'Hermitain, 180 m, cones of *Larix*, 27.IV.2006, H.O. Baral (ø). – ibid., 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 90 m, branch of *Ligustrum vulgare*, on wood, 17.IV.2008, H.O. Baral (H.B. 8815).

Not included. **FRANCE**: **Pays-de-la-Loire**, **Loire-Atlantique**, 2.4 km NE of Piriac-sur-Mer, SW of Kerdrien, Pors er Ster, 15 m, branch of *Ulex europaeus*, on bark, 12.XI.2008, J.P. Priou (J.P.P. 28219 ø, doc. vid.).

Orbilia euonymi Velen., Monogr. Discom. Bohem.: 95, pl. 11 fig. 14 (1934) (as '*evonymi*', ICN Art. 60.5) — Pls 207–208, Map 35

Etymology: referring to the host plant in the type material, *Euonymus europaeus*. **Typification**: Czechia, Central Bohemia, Mnichovice, twig of *Euonymus europaeus*, 18.III.1928, J. Velenovský (PRM 152459, holotype); Luxembourg, Waldhaff, Gréngewald, twigs of *Pseudotsuga menziesii*, 20.VIII.2009, G. Marson (ex H.B. 9152, M-0291775, epitype, designated here, MBT385112; sq.: KT222444).

Misinterpretation of *O. euonymi*: Hawksworth & Sivanesan (1975: 109), Ellis & Ellis (1985: 12), (?)= *Hyalorbilia erythrostigma*; Liu (2006: 78), = *Helicogonium orbiliarum* (intrahymenial parasite of *O. luteorubella*).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.09–)0.13–0.4(–0.6)((–0.9)) mm diam., 0.08–0.16 mm high (receptacle 0.075–0.11 mm), pale to light (rose-)orange(-ochraceous), rarely bright apricot, sometimes whitish, cream, or pale to light amber-yellowish, ± translucent, round, very scattered or often gregarious; disc flat, sometimes slightly (rarely strongly) convex, margin even, indistinct, protruding 0–8 µm, exterior ± smooth, sessile or subsessile with an ill-defined stipe 0.02 × 0.09–0.12 mm, ± superficial; dry pale rose-orange-ochraceous. **Asci** *(30–)34–55(–68) × 6.3–8.5(–9)((–10)) µm {32}, †(29–)31–50(–54) × (5–)5.5–7(–7.5) µm {17}, 32-spored (28–32 spores counted), spores multiseriate in a cluster, orientation irregular or lower spores with a tendency to be inverted, pars sporifera *(16–)21–28(–31) → 15–16.5 µm; **apex** (†) hemispherical, dome 1.2–2(–2.8) {10} → 0.7–1.3 {9} or 1.3–2.5 {1} µm, with distinct small apical chamber, endotunica bright red in $\mathrm{CR_{SDS}}$; **base** with a very short to long, ± thin or thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(2.2–)2.6–4.3(–5.5) × (1.5–)1.6–2.1(–2.3) µm {52}, †2.5–4.5(–5.2) × (1.4–)1.5–2(–2.3) µm {4}, ellipsoid to subcylindrical or sometimes fusoid-clavate, sometimes subglobose, with rounded to obtuse ends, base slightly or exceptionally strongly attenuated, straight or sometimes slightly (to medium) curved; **SBs** *(1.2–)1.3–1.8(–2) × (0.2–)0.3–0.6(–0.8) µm {22}, divided into a ± abruptly inflated, tear- to rarely pear-shaped lower part and a filum of equal or slightly shorter length, straight or slightly curved. **Paraphyses** apically uninflated, sometimes slightly clavate-capitate or sublageniform, also moniliform or flexuous, terminal cell *4–10(–19) × 1.8–3.2 µm {7}, †5–10 {T} × (1.5–)1.7–3(–3.2) µm {3}, lower cells *5–9.5(–11.5) {3} × (1.5–)2–2.7(–3.5) µm {6}, †(4–)5.5–12 {T} × (1.5–)1.8–2.5(–3) µm {2}; sometimes branched at upper septum, sometimes ± flexuous. **Medullary excipulum** hyaline, 15–45 µm thick, of dense textura intricata with many inflated cells, indistinctly to sharply delimited. **Ectal excipulum** hyaline, of thin-walled to slightly gelatinized, irregularly vertically oriented t. (prismatica-)angularis(-globulosa) from base to mid flanks, 10–30(–60) µm thick at base, cells *(5–)9–15(–20) × (4–)5–13 µm {8}; 15–25 µm thick at lower flanks, cells *6–11 × 4–8.5 µm {2}, 7–15 µm thick at mid flanks, oriented at a 30–70° angle to the surface, 7–15 µm thick at margin, of t. globulosa-prismatica to t. prismatica-porrecta oriented at 0–40°, marginal cortical cells *5–11 × 2–3(–3.5) µm {5}, †6–10 × 4–5 µm {1}. **Anchoring hyphae** sparse, *(1.6–)2–3 µm wide, wall *0.2–0.3 µm thick {4}. **SCBs** in paraphyses globose (to ellipsoid), 1.2–2 µm diam.; in excipular cells at flanks and margin globose, 1.5–4 µm. **Exudate** over paraphyses 0.5–2.5(–3.5) µm thick, cloddy, hyaline or pale yellowish; over margin and flanks 1.5–4 µm thick, with abundant crevices forming small to minute clods in surface view. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {13}). **Conidiophores** ?15 × 3 µm, conidia formed on terminal denticles, sympodial. **Conidia** unbranched, slightly to medium, sometimes strongly curved, especially near upper end, often also near base, *(21–)28–49(–58.5) × (3.5–)4–5(–5.5) µm, (1–)5–9(–12)-septate {12}, containing some minute LBs.

Habitat: collected (0–)0.5–6(–17) m above the ground, ± corticated or partially to entirely decorticated, (1–)2–25(–30) mm thick branches, rarely ~15 cm thick trunks, or timber, of *Abies balsamea* {1}, *Acer campestre* {1}, *A. glabrum* {1}, *A. platanoides* {2}, *A. pseudoplatanus* {2}, *Adenocarpus viscosus* {1}, *Aesculus hippocastanum* {1}, *Berberis vulgaris* {1/1}, *Buxus sempervirens* {3}, *Carpinus betulus* {2}, *Cercocarpus ledifolius* {1}, *Clematis vitalba* {5}, *Cornus mas* {1}, *C. sanguinea* {1}, *Corylus cornuta* {1}, ?*Crataegus* sp. {1}, *Cryptomeria japonica* {1}, *Cytisus alpinus* {1}, *C. scoparius* {1}, *C. subranubius* {1}, *Euonymus europaeus* {1}, *Fagus sylvatica* {1}, *Fraxinus excelsior* {1}, *Genista scorpius* {2}, *Ginkgo biloba* {1}, *Hedera helix* {1}, *Ilex aquifolium* {1}, *Juglans regia* {1}, *Juniperus* sp. {1}, *J. ?chinensis* {1}, *J. communis* {1}, *J. thurifera* {1}, *Larix decidua* {1/1}, *Lonicera* sp. {1}, *L. xylosteum* {1/1}, *L. altaica* {1}, *Picea abies* {17}, *Pinus* sp. {2}, *P. brutia* {4}, *P. pinaster* {1}, *P. radiata* {1}, *P. strobus* {1}, *P. sylvestris* {4/1}, *Pseudotsuga menziesii* {7}, *Purshia tridentata* {1}, *Quercus* sp. {2}, *Q. robur* {1}, *Q. ?rubra* {1}, *Ribes cereum* {1}, *Robinia pseudoacacia* {5}, *Rosa* sp. {1}, *Rubus fruticosus* {1}, *Salix* sp. {2}, *S. alba* {1}, *S. ?bebbiana* {1}, *S. caprea* {2/1}, *Sambucus nigra* {3}, *S. racemosa* {2}, *Sequoiadendron giganteum* {1}, *Syringa vulgaris* {1/1}, *Taxodium distichum* {1}, *Taxus baccata* {1}, *Thuja occidentalis* {1}, *T. plicata* {1}, *Tsuga canadensis* {1}, *Ulex europaeus* {1}, outer 0.1–2 mm mostly strongly (rarely slightly or medium) decayed, often ± eroded, white- or brown-rotten, on wood {109}, more rarely bark {16} (bast, rarely periderm), sometimes in clefts in wood, often in old beetle galleries, rarely in or close to resinous wounds or cankers {3}, exceptionally on old basidiocarps of *Peniophora* sp. {1} or *Vuilleminia comedens* {1}, slightly to medium greyed, slightly to usually strongly covered by green algae. **Associated**: *Amandinea punctata* {1}, *Bulbillomyces farinosus* {2}, *Capronia* sp. {1}, *Ciliolarina laricina* {1}, ?*Ciliolarina* sp. {1}, *Claussenomyces* sp. {1}, *Coniochaeta velutina* {1}, *Corticiaceae* {2}, *Cryptodiscus foveolaris* {1}, *Cyathicula* aff. *nigrofusca* {1}, *Dacrymyces* sp. {4}, *Durella atrocyanea* {4}, *D. connivens* {5}, *Glyphium corrugatum* {1}, *Helicogonium orbiliarum* (parasitic in *O. euonymi*) {2}, '*Helotium*' *uvidulum* {3}, *Hyalorbilia juliae* {1}, *H. subfusispora* {2} *Hylocomium splendens* {1}, *Hyphodiscus theiodeus* {1}, *Hyphodontia sambuci* {2}, *Hysterographium fraxini* {1}, *Karstenia* sp. {1}, *K. rhopaloides* {1}, *Lachnellula* (?)*calycina* {1}, *L. occidentalis* {1}, *L. pseudofarinacea* {1}, *Laetinaevia* sp. {1}, *Lecanora conizaeoides* {1}, *Merismodes* sp. {1}, *Mollisia ligni* {1}, *Orbilia alpigena* {4}, *O. aprilis* {6}, *O. aristata* {2}, *O. arizonensis* {1}, *O. cejpii* {1}, *O. concoloris* {1}, *O. cylindrospora* {3}, *O. delphinus* {2}, *O. filiformis* {1}, *O. flexisoma* {1}, *O. gambelii* {1/1}, *O. maeandrina* {1}, *O. obtusispora* {1/1}, *O. patellarioides* {2}, *O. pleiomicrosoma* {1}, *O. purshiae* {1}, *O. quaestiformis* {1}, *O. subaristata* {1}, *O. subovoidea* {3}, *O. subvinosa* {1}, *O. ?trapeziformis* {1}, *O. vibrioides* {2}, *O. vinosa* {9}, *O. vitalbae* {1}, *Parmelia sulcata* {2}, *Peniophora ?lycii* {1}, ?*Perrotia* sp. {1}, *Perzia triseptata* {1}, ?*Phoma* sp. {1}, *Phragmiticola* sp. {2}, ?*Physcia* sp. {2}, *Polydesmia pruinosa* {1}, *Propolis farinosa* {2}, *P. hillmanniana* {1}, *Pseudolachnea ?hispidula* {1}, *Resinomyces kirschsteinianus* {1}, *Sarea difformis* {1}, *Sclerococcum* sp. {2}, *Stictis friabilis* {1}, *Strossmayeria basitricha* {1}, *Symbiotaphrina microtheca* {1}, *Trichonectria* sp. {1}, *T. hirta* {1}, *Tubeufia cerea* {1}, *Unguiculariopsis ?thallophila* {1}, *Usnea* sp. {1}, *Xanthoria parietina* {1}. **Desiccation tolerance**: fully viable for at least 2 months, immature asci, paraphyses and ascospores survived for up to 11 months, conidia for at least 23 days. **Altitude**: 2–1590 m a.s.l. (central and western Europe), 320–1725 m (southern Europe), 2100 m (Mongolia), ~150–2825 m (USA). **Geology**: Ordovician, Devonian, Carboniferous & Permian sand-, silt-, mud- & limestone or greywacke, Buntsandstein, Muschelkalk, Keuper (sand- and marlstone), Lower to Upper Jurassic shale, sand- & limestone, Minette, dolomite, Cretaceous & Miocene clayey lime- & marlstone, flysch, Tertiary molasse, Pleistocene till, loess; basalt, quartz diorite, mica schist, gneiss, biotite-amphibole. **Phenology**: throughout the year (long-lived).

Phenology of *O. euonymi*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
5	6	14	3	22	16	8	15	13	7	7	6

Taxonomic remarks. *Orbilia euonymi* is characterized by 32-spored asci and small, cylindric-ellipsoid to clavate ascospores with small, ± tear-shaped SBs with a short filum.

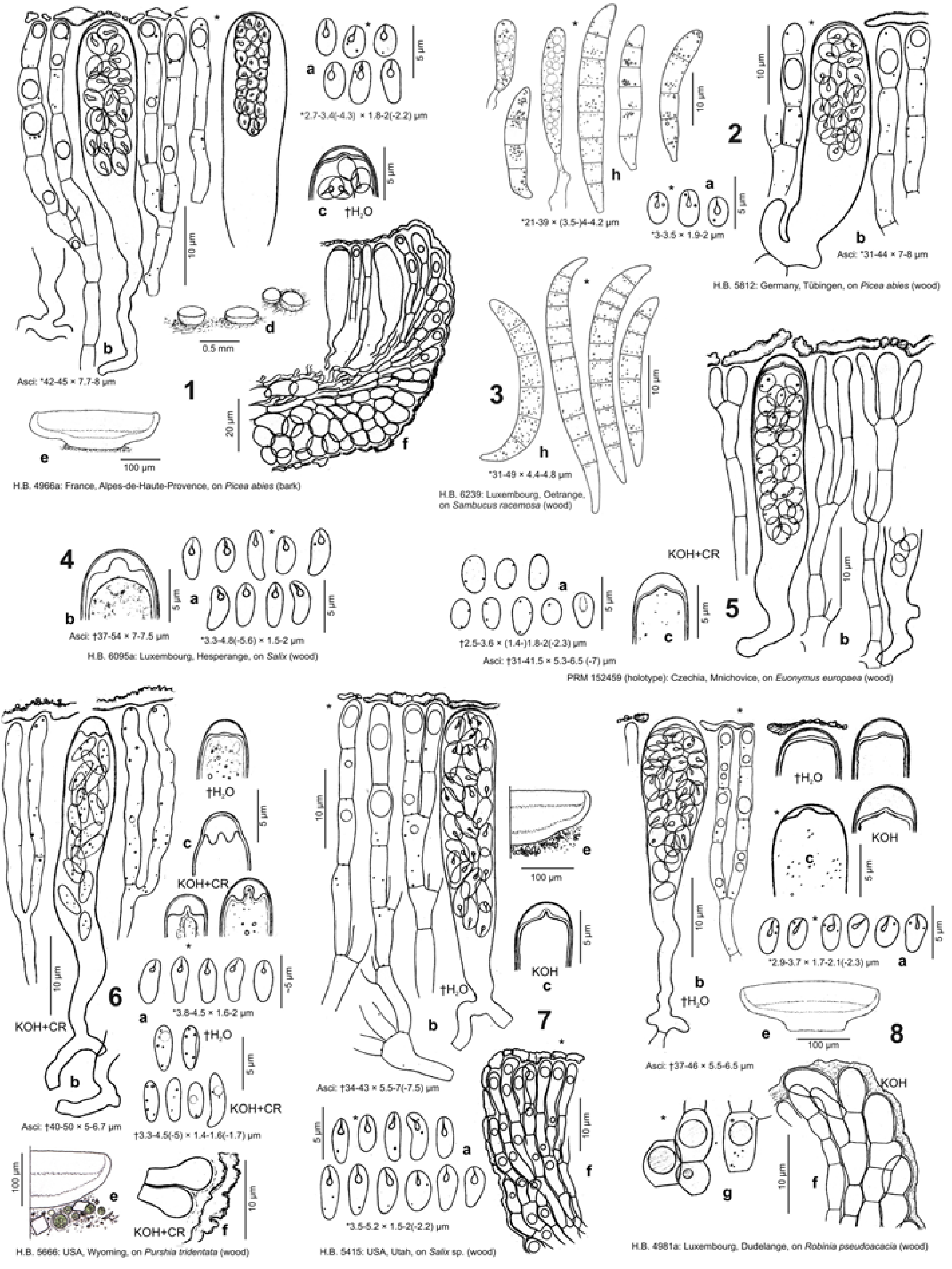


Plate 207. **1–8**: *Orbilia euonymi*. – **a**. ascospores; **b**. asci and paraphyses (**1b** right ascus fully turgescent); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., ectal excipulum at margin and flanks; **g**. marginal excipular cells in external view; **h**. conidia and conidiophore tips (from substrate).

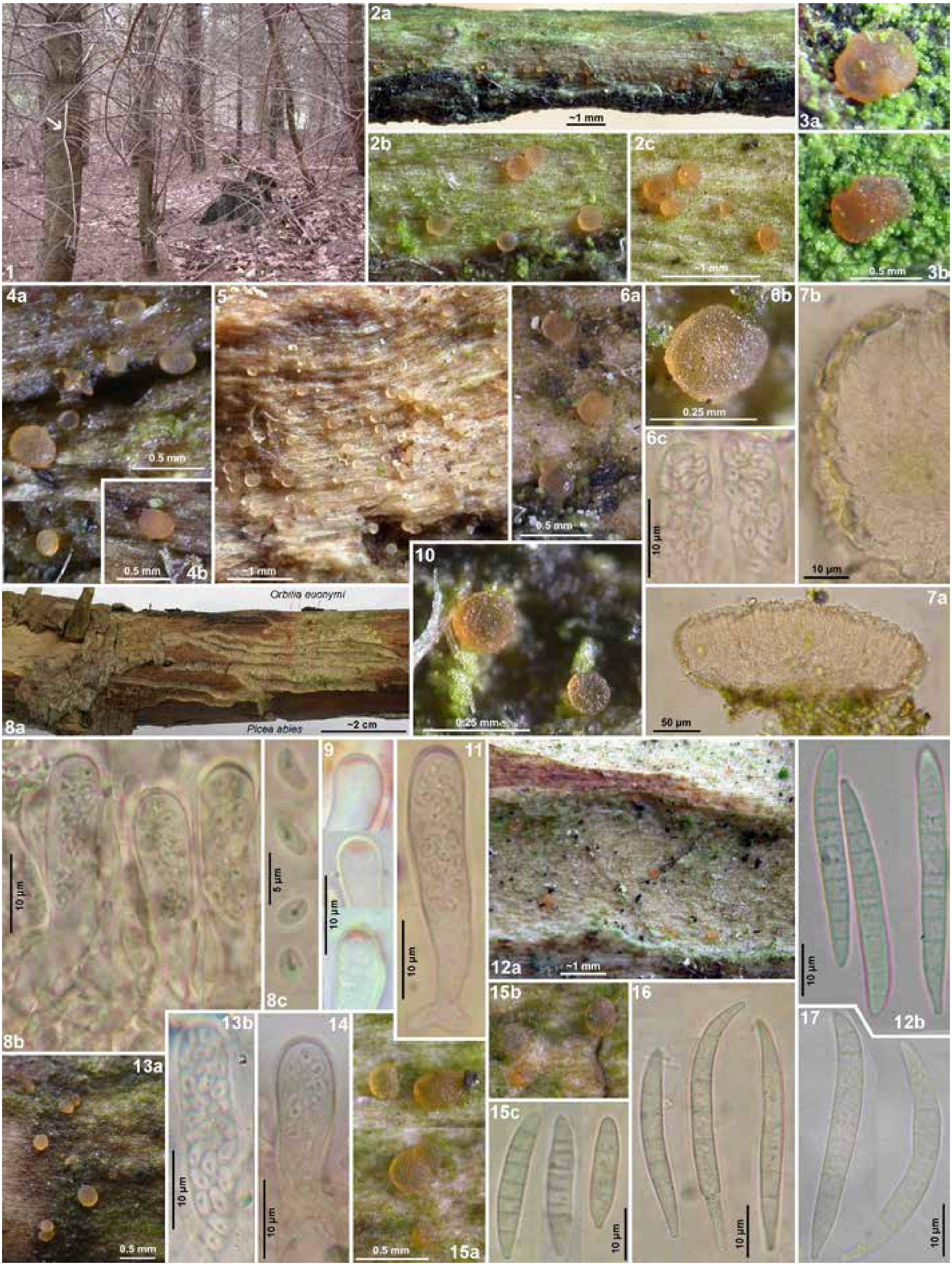


Plate 208. **1–17**: *Orbilia euonymi*. – **1**. *Pseudotsuga* plantation; **2a**, **8a**. dead xeric branches; **2b–c**, **3a–b**, **4a–b**, **5**, **6a–b**, **10**, **12a**, **13a**, **15a–b**. rehydrated apothecia; **7a**. apothecium in median section; **7b**. id., marginal ectal excipulum; **6c**, **8b**, **11**, **13b**, **14**. mature asci; **9**. ascus apices with apical dome (stained red); **8c**. ascospores; **12b**, **15c**, **16**, **17**. conidia from substrate. – Living state (**11** in Bailenger) except for asci in **6c**, **9** (in CR) and **13b**. – **9**: phot. I. Wagner, **13a–b**: phot. P. Perz. — **1**. 17.VII.2004: Luxembourg, Echternach, on *Pseudotsuga*; **2a–c**. H.B. 7553: Luxembourg, Wiltz, on *Pseudotsuga*; **3a–b**. H.B. 7554: Luxembourg, Limpertsberg, on *Sequoiadendron*; **4a–b**. H.B. 7887d: Mongolia, on *Lonicera*; **5**. H.B. 7407: Germany, Tübingen, on *Aesculus*; **6a–c**. H.B. 9195: France,

O. myrioeuonymi and *O. pleistoeuonymi* differ in higher spore numbers and larger asci, whereas spore size and SBs are more or less the same. Confusion with 8-spored taxa around *O. eucalypti* (subgen. *Orbilia*) seems possible due to a similar spore size and shape, especially when studying dead herbarium material in which polyspory is easily overlooked and the characteristic SBs are invisible. Yet, the much wider asci of *O. euonymi* and their hemispherical, thick-walled apices are very different from those of section *Orbilia*.

Variation. Spore number in some of the asci was rarely reduced to (8–)16–22 spores (H.B. 5174, 6001; also in two collections from Poland, P. Perz pers. comm.). In asci with spore numbers between 16 and 32, some of the spores are wider than the others. This variation illustrates the difficulty to separate the closely related 16-spored *O. pleioeuonymi* (see p. 530). Oversized spores from asci with a reduced spore number measured *3.2–4.2 × 2.3–2.7(–3) μm {2} and their SBs ~2–2.2 × 0.5–0.8 μm.

Pronounced variation in spore shape and length (but hardly in width) among the collections can be noted, ranging from rarely subglobose-ovoid (2.2–3 μm long) over mostly cylindric-ellipsoid (3–4 μm) to rarely elongate-cylindrical (4.5–5.5 μm). Longer spores appear to be correlated with longer asci and were mainly observed in mediterranean and semiarid areas of southern Europe and North America. Longer spores were sometimes found to be correlated with thicker apical domes, but in other cases no such correlation was noted. Collections on gymnosperms concurred in all respects with those on angiosperms. The observed variation in colour is probably due to the rate of insolation during growth: whitish apothecia occurred at more shady sites, whereas reddish ones at more open thermophilous places.

One of the North American collections (Pl. 207: 6) slightly deviates in asci with rather thick apical domes (KOH 2–2.8 → 1.3–2.5 μm) with deep apical chamber, and wider marginal cortical cells (†6–10 × 4–5 μm), also in rather long and narrow spores. Similar spores were observed in two samples from Tenerife (*3.5–)4.2–5.2 × 1.6–1.8 μm, see Quijada (2016: fig. 2).

Type studies. Both Svrček (1954: 14) and Hawksworth & Sivanesan (l.c.) could not find any apothecia on the small twig fragment in the holotype of *O. euonymi*. In the present study four pale cream-amber apothecia of 0.2–0.3 mm diam. were detected after rehydration. One was examined and the asci found to be polysporous (28 spores seen, Pl. 207: 5b), contrary to Velenovský's (1934) protologue and drawing which shows 8-spored asci. The ascospores were found to be ellipsoid-ovoid unlike Velenovský's report ('2–3 μm, globose, eguttulate'). However, the sketch in Velenovský's original manuscript (see Fig. 156) shows more distinctly subglobose spores which better match our observation. There is no doubt that the examined apothecium represents the taxon described by Velenovský, especially because ascus size and the uninflated paraphyses with their exudate fit well.

A specimen from Luxembourg (Waldhaff, on *Pseudotsuga*, IVV: H.B. 9152), from which a sequence was gained, is designated here as **epitype** of *O. euonymi*.

Misapplications. In the type collection of *O. euonymi*, Velenovský (1934) reported the spores as globose and overlooked polyspory of the asci (see below). Therefore, Hawksworth & Sivanesan (1975) referred a British collection with 8-spored asci and 'globose' spores to this taxon, after a suggestion by W.D. Graddon. Reexamination of this specimen (Pl. 126: 3) showed that it represents a *Hyalorbilia*, probably *H. erythrostigma*. An unpublished collection on *Euonymus europaeus* identified by Velenovský as '*O. evonymi*' (PRM 147968) was studied by Svrček (l.c.) and found to be *O. curvatispora* (= *O. auricolor*). This material was not examined in the present study.

A Chinese report under the name '*O. evonymi*' (HMAS 75874) was so named by Liu (2006) according to drawings of *O. euonymi* distributed on DVD (Baral & Marson 2005). This record concerns an intrahymenial parasite, *Helicogonium orbiliarum*, that produces ascoconidia in abundance from subglobose ascospores inside the asci. Two large (2 mm), sterile apothecia of *O. luteorubella* were infected by this parasite and grew in mixture with mature, uninfected apothecia of that *Orbilia*. Liu gave the spore number as 'up to 32', but on his photos about 40 ascoconidia can be seen, moreover, some of the 8 much larger ascospores are visible.

Anamorph. We observed the vermispora-like anamorph of *O. euonymi* only on the natural substrate. In one collection (on *Ginkgo*, Tübingen) the conidiophores emerged from the margin of a mature apothecium and were undoubtedly connected to the marginal excipular cells.

Phylogeny. Five sequences comprising ITS and LSU were taken from apothecia of *O. euonymi*: three on *Pseudotsuga* from Luxembourg, one on *Cedrus* from Turkey, and one on *Buxus* from southern France. All of them possess the S1506 intron, except for one from Luxembourg (Waldhaff, H.B. 9152) which appears to lack it (but the 3'-end of SSU was not unequivocally evaluated here). Therefore, the absence of the intron remains uncertain. This sequence and that from southern France include also SSU. In the LSU the five strains are identical in the overlapping 572–920 nt, whereas a difference of 2–4 nt (0.4–0.7%) and a few gaps is found in the ITS, mainly in the ITS1.

Although *O. pleistoeuonymi* is very similar in morphology, its molecular distance to *O. euonymi* is considerably high (in the ITS region 15.5–16%, in the LSU 5.8% in the overlapping 633 nt), whereas *O. pleioeuonymi* with its much broader spores is less distant from *O. euonymi* (6.3–6.5% and 2.2%, respectively).

The intron region is almost identical in the two *O. euonymi* sequences on *Pseudotsuga* (0.6% distance in overlapping 353 nt), whereas the *Cedrus* strain shows some more deviations to them (2.5–2.7%), and the one on *Buxus* 2% to *Cedrus* and 4.2–4.5% to *Pseudotsuga*. The distance to *O. pleioeuonymi* ranges at 7.5–8.5% and to *O. pleistoeuonymi* at 18.5%. The five strains clustered in a medium to strongly supported sister clade to *O. pleioeuonymi* (Phyls 8, S9, S11).

Ecology. *O. euonymi* belongs to the most frequently collected species within this study, although no material referable to it was found in the consulted herbaria, except for the holotype. The species has obviously been overlooked due to its minute apothecia and xeric habitat. At the present state of knowledge it is only known from the northern hemisphere. *O. euonymi* occurs on rotten wood (more rarely bark) of dead xeric twigs

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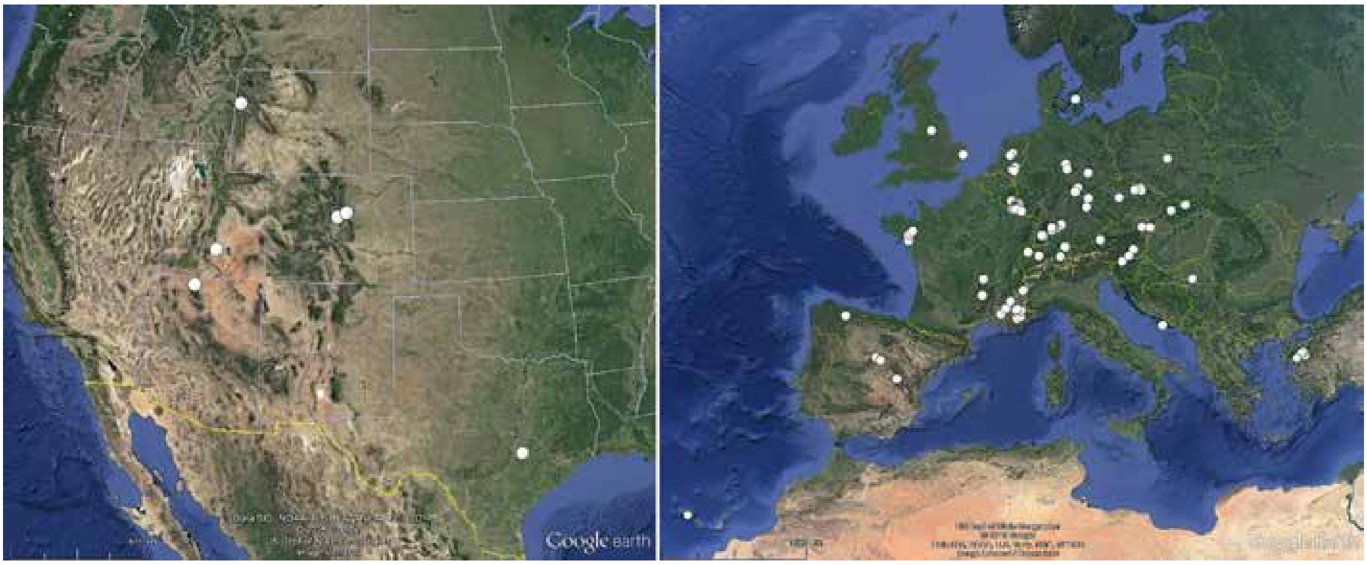
Alpes-de-Haute-Provence, on *Buxus*; **7a–b**. H.B. 9159: Germany, Saalfeld, on *Picea*; **8a–c**. H.B. 7874b: Germany, Villingen, on *Picea*; **9**. 11.II.2012: Germany, Sonneberg, on *Larix* (I. Wagner); **10**. H.B. 9234a: Poland, Kłodzko, on *Picea*; **11**. H.B. 9288b: France, Auvergne, on *Picea*; **12a–b**. H.B. 7529: Luxembourg, Waldhaff, on *Pseudotsuga*; **13a–b**. P.P. 20061228: Poland, Kłodzko, on *Pinus*; **14**. H.B. 8516a: Denmark, Sjælland, on *Fagus*; **15a–c**. H.B. 9319: Germany, Schwäbische Alb, on *Carpinus*; **16**. H.B. 7989a: Germany, Tübingen, on *Cornus*; **17**. T.A. 35b: Turkey, Balıkesir, on *Pinus*.

and branches of a broad range of gymno- and angiosperm trees and shrubs. Records from Europe include atlantic (see Priou 2005) to subcontinental, cold- to warm-temperate as well as orotemperate to orosubmediterranean humid, but also suprasub- to supramediterranean or rarely mesosub- to mesomediterranean semihumid regions, from planar to subalpine altitude and on mainly calcareous or neutral but also acidic soils. The species prefers thermophilous forests, particularly their sun-exposed borders, or free-standing trees and shrubs, but it occurs sometimes also in shady forests. It was repeatedly collected in the mediterranean maquis (*Juniperetum thuriferae*) of the Iberian Peninsula, and in submediterranean forests of western Anatolia it belongs to the most often detected species, according to an unpublished study by T. Askun (pers. comm.). In the European boreal zone it is so far not found.

Within Macaronesia *O. euonymi* was recorded in Tenerife around the Teide in the supramediterranean semihumid summit broom scrub (*Spartocytisetum supranubii*) near to vegetationless lava areas, or in the adjacent upper mesomediterranean *Erysimo scoparii-Pterocephaletum lasiospermi* near to the pine forest. Records were also made in the west of Northern America in cold-temperate to boreal (sub)humid pinyon-juniper woodland, ponderosa pine, Douglas fir, and Engelmann spruce forests of Middle and Southern Rocky Mountains and Colorado Plateau, and in the south in a subtropical subhumid broad-leaved woodland of Texas. In central Asia it occurred in continental, orotemperate (sub)humid (winter-dry) western Mongolia (*Larix-Picea* taiga with *Betula rotundifolia*). The species can be expected to occur also in (hemi)boreal regions of Europe, but it appears to avoid warm-temperate to subtropical (semi)arid regions because it was never found in our many collections from the North American semideserts.

Specimens included. **GREAT BRITAIN**: **Yorkshire**, **South Yorkshire**, 4 km SW of Barnsley, 0.2 km W of Wentworth Castle, Stainborough Park, 185 m, branch of *Ilex aquifolium*, on wood, 14.V.2011, H.O. Baral (H.B. 9508b, J.H.P. 11.100). – **East England**, **Suffolk**, 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Ulex europaeus*, on wood, 20.IX.2004, E. Batten (ø). — **DENMARK**: **Sjælland**, 8 km NNW of Ringsted, 1 km S of Allindelille, Fredskov, 65 m, branch of *Fagus sylvatica*, on wood and *Peniophora*, 26.V.2007, H.O. Baral (H.B. 8516a ø). — **NETHERLANDS**: **Flevoland**, 17 km SE of Lelystad, 5 km N of Harderwijk, Broekbos, 2 m, branch of *Sambucus nigra*, on wood, 20.III.2005, H.O. Baral (ø). – 6 km SW of Kampen, 9 km E of Dronten, Reve Abbert, Revebos, 9 m, branch of *Fraxinus excelsior*, on bark, 20.III.2005, H.O. Baral (ø). – **Noord-Brabant**, 10 km WSW of Boxmeer, 3.3 km WSW of Oploo, St. Anthonisbos 30 m, branches of *Thuja occidentalis*, on wood, 19. III.2011, S. Helleman (ø, doc. vid.). – ibid., branch of *Pinus strobus*, on wood, 19.III.2011, S. Helleman (ø, non vid.). – ibid., twig of *Abies balsamea*, on wood, 19.III.2011, S. Helleman (ø, non vid.). – **Limburg**, 38 km ENE of Eindhoven, 2.7 km NE of Venray, 22 m, branch of *Juniperus communis*, on wood, 13.V.2012, S. Helleman (ø, non vid.). — **LUXEMBOURG**: **L'Oesling**, **Wiltz**, 11 km WSW of Wiltz, NE of Harlange, 440 m, twig of *Pseudotsuga menziesii*, on bark & wood, 19.VI.2004, G. Marson (H.B. 7553). – **Gutland**, **Mersch**, 8 km NW of Mersch, 1.6 km E of Schrondweiler, Bakes, 305 m, branch of *Robinia pseudoacacia*, on wood, 6.XI.1993, G. Marson (ø). – 14 km N of Luxembourg, 4 km SE of Mersch, Schoos, 417 m, twigs of *P. menziesii*, on wood, 4.V.2014, G. Marson (G.M. 2014-05-04.2; sq.: KT222390). – **Echternach**, 2.5 km SSW of Echternach, Haard (north-part), 355 m, twigs of *P. menziesii*, on wood & bark, 17.VII.2004, G. Marson (ø). – **Grevenmacher**, 4.5 km W of Grevenmacher, 1 km SW of Potaschberg, Buchholzerwiss, 270 m, twig of *P. menziesii*, 10.VI.2008, G. Marson (ø). – 3.5 km NNE of Grevenmacher, 1.5 km ENE of Manternach, WNW of Fielsmillen, 185 m, branches of *R. pseudoacacia*, on wood, 16. XI.1993, G. Marson (H.B. 5006). – **Remich**, 7.5 km SW of Remich, SE of Mondorf-les-Bains, 210 m, branches of *Cryptomeria japonica*, on wood, 4. II.2004, G. Marson (ø). – **Capellen**, 4.5 km NW of Luxembourg, S of Bridel, 370 m, twigs of *P. menziesii*, on wood, 4.V.2014, G. Marson (G.M. 2014-05-04.1; sq.: KT380071). – **Luxembourg**, 6 km NE of Luxembourg, SE of Waldhaff (Waldhof), Gréngewald (Grünewald), Arboretum, 410 m, twigs of *P. menziesii*, on wood, 20.VIII.2009, G. Marson (ex H.B. 9152, M-0291775, **epitype**; sq.: KT222444). – 2 km NW of Luxembourg, Limpertsberg, Park Neumann, 320 m, twigs of *Sequoiadendron giganteum*, on bark & wood, 3.VII.2004, G. Marson (H.B. 7554). – 1 km N of Waldhaff, Schetzelklaus, 410 m, branches of *P. menziesii*, on wood, 23.V.2004, G. Marson (H.B. 7529, anam. substr.). – 11 km ESE of Luxembourg, 2 km E of Oetrange, Draf, 268 m, branch of *Sambucus racemosa*, on wood, 4.IX.1998, G. Marson (H.B. 6239, anam. substr.). – 5 km SSW of Luxembourg, 0.7 km N of Kockelscheier, Weier, 300 m, branch of *Picea abies*, on wood, 10.I.2000, G. Marson (ø, anam. substr.). – 4.5 km S of Luxembourg, 1 km W of Hesperange, Biersak/Géisselbierg, 290 m, branch of *Salix*, on wood, ?9.XII.1997, G. Marson (ø). – ibid., branch of *Sambucus nigra*, 22.V.2002, G. Marson (ø, anam. substr.). – ibid., branch of *Picea abies*, on wood, 3.I.2004, G. Marson (ø). – branch of *Salix ?caprea*, on wood, 23.XII.1997, G. Marson (H.B. 6095a). – 6 km SSE of Luxembourg, 0.8 km SE of Fentange, Wénkel, 265 m, branches of *Clematis vitalba*, on bark & wood, 20.III.1994, G. Marson (ø). – **Esch-sur-Alzette**, 0.9 km SE of Kockelscheier, Angelsbierg, 310 m, branch of *Carpinus betulus*, on wood, 17.VIII.2010, G. Marson (ø). – 6.7 km W of Esch-sur-Alzette, 1.5 km S of Obercorn, Ronnebierg, 410 m, branch of *Clematis vitalba*, 4.V.2009, G. Marson (ø, anam. substr.). – 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, branch of *C. vitalba*, on bark, 12.VI.1994, G. Marson (H.B. 6263). – 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 272 m, branches of *Robinia pseudoacacia*, on wood, 31.X.1993, G. Marson (H.B. 4981a). — **POLAND**: **Łódź**, 2.3 km E of Łódź, University, 230 m, branch of *Syringa vulgaris*, on wood, 6.XI.2011, P. Perz (P.P. 20111106-1, doc. vid.). – **Lower Silesia**, 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, branch of *Pinus*, on wood, 28.XII.2006, P. Perz (P.P. 20061228-1, doc. vid.). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, plank of *Picea abies*, on wood, 25.IX.2009, P. Perz (H.B. 9234a ø). — **CZECHIA**: **Central Bohemia**, 26 km SE of Praha, NNW of Mnichovice, above Zíttův mlýn mill, 360 m, twig of *Euonymus europaeus*, on wood, 18.III.1928, J. Velenovský (PRM 152459, **holotype**, H.B. 6128 ø). – **Hradec Králové**, 23 km ENE of Hradec Králové, 1.8 km SW of Dobruška, 300 m, branch of *Juglans regia*, on wood, 16.IX.2009, P. Perz (P.P. 20090916-1, doc. vid.). – **SLOVAKIA**: **Žilina**, 13 km SSE of Martin, 1.8 km SE of Folkušová, 880 m, branch of *Pinus sylvestris*, on wood, 30.III.2017, A. Polhorský (A.P. 18/51, doc. vid.). – **Bratislava**, 10.5 km WNW of Bratislava, 1 km N of Devín, Sandberg, 272 m, branch of *Quercus*, on wood, 15.VI. 2018, A. Polhorský (A.P. 18/57, doc. vid.). – **Prešov**, Carpathian Mts., Vysoké Tatry, 2 km S of Tatranská Lomnica, Stará Lesná, 803 m, branch of *Salix caprea*, on wood, 19.VIII.2019, A. Polhorský (A.P. 19/32b, doc. vid.). — **GERMANY**: **Niedersachsen**, Harz, 5 km E of Bad Lauterberg, 3.5 km NW of Bad Sachsa, Ravensberg, Sendeturm, 640 m, branch of *Acer platanoides*, on wood, 21.V.2012, S. Helleman (ø, non vid.). – 0.5 km S of Goslar, Königsberg, 290 m, branch of *Salix caprea*, on wood, 2.VI.2004, H.O. Baral (H.B. 7533a). – **Nordrhein-Westfalen**, 6 km SW of Kleve, Reichswald, 45 m, branch of *Tsuga canadensis*, on wood, 21.III.2009, S. Helleman (S.H. 603, non vid.). – **Saarland**, 6.5 km S of Merzig, 0.5 km NNW of Eimersdorf, N of Heiligenkopf, 337 m, branch of *Cornus mas*, on wood, 18.IV.2004, H.O. Baral (ø). – **Thüringen**, 8 km NW of Sonneberg, 1.2 km SW of Rabenäußig, Langeberg, 510 m, branch of *Picea abies*, on wood, 20.IX.2010, S. Helleman (S.H. 668 ø, doc. vid.). – 2.5 km WNW of Sonneberg, W of Bettelhecken, 388 m, branch of *Larix decidua*, on bark, 11. II.2012, I. Wagner (ø, doc. vid.). – 7.3 km SSW of Saalfeld, 0.8 km SE of Kleingeschwenda, 627 m, branch of *Sambucus racemosa*, on wood, 12. VIII.2009, S. Helleman (S.H. 562). – 3 km SSW of Saalfeld, 1.5 km NNE of Eyba, 552 m, branch of *Picea abies*, on wood, 10.VIII.2009, S. Helleman (H.B. 9159 ø). – **Sachsen**, 6 km NW of Leipzig, 1 km SW of Wahren, Burgaue, 100 m, branch of *Quercus robur*, on old *Vuilleminia comedens*, 27.III.2003, M. Unterseher (H.B. 7433). – **Baden-Württemberg**, Schönbuch, **Tübingen**, NE of main station, 323 m, branch of *Aesculus hippocastanum*, on wood, 30.VII.2003, H.O. Baral (H.B. 7407, anam. substr.). – Österberg, Wielandshöhe, 390 m, branch of *Ginkgo biloba*, on wood, 13.VII.2002, E. Weber & H.O. Baral (ø). – Wilhelmstraße, Old Botanical Garden, 330 m, twigs of *Thuja plicata*, on bark & wood, 22.VII.2004, H.O. Baral (ø). – 2 km NNW of Tübingen, Morgenstelle, 440 m, branch of *Taxodium distichum*, on wood, 24.V.2002, H.O. Baral (H.B. 7137). – 2.5 km SW of Tübingen, Spitzberg, 370 m, branch of *Juniperus ?chinensis*, on wood & bark, 28.VII.2002, H.O. Baral (H.B. 7174). – 5 km NE of Tübingen, Pfrondorf, Blaihofstraße, 430 m, branch of *Robinia pseudoacacia*, on wood, 3.VIII.2002, H.O. Baral (ø). – NE of Pfrondorf, Gähklinge, 410 m, branch of *Picea abies*, on wood, 25.VIII.2004, H.O. Baral (H.B. 7571). – S of Pfrondorf, Haldenbach, 385 m, branch of *P. abies*, on wood, 8.VI.1997, H.O. Baral (H.B. 5812 ø, anam. substr.). – ENE of Pfrondorf, Tiefenbach, 410 m, branch of *Quercus ?rubra*, on bark, 30.X.1994, H.O. Baral (H.B. 5174). – ibid., branch of *Quercus*, on wood, 26.IX.2004, H.O. Baral (ø). – 1 km SE of Pfrondorf, Höhberg, 395 m, branch of *Sambucus nigra*, on wood, 30.XII.1997, H.O. Baral (H.B. 6001). – 1.6 km SE of Pfrondorf, Neckar river, 320 m, branch of *Cornus sanguinea*, on wood, 30.X.2005, H.O. Baral (H.B. 7989a ø, anam. substr.). – **Schwarzwald**, 8.3 km WNW of Villingen, 1 km NW of Unterkirnach, E of



Map 35. Known distribution of *O. euonymi* in North America, Macaronesia, Europe, and eastern Asia (Turkey).

Behringerhof, 870 m, branch & branch of *Picea abies*, on wood, 19.VIII.2005, H.O. Baral (H.B. 7874b ø). – **Schwäbische Alb**, 3 km S of Donzdorf, 0.8 km W of Kuchalb, Hohenstein, 700 m, branch of *Carpinus betulus*, on wood, 15.V.2010, H.O. Baral (H.B. 9319 ø). – 5.3 km E of Reutlingen, 1.4 km E of Eningen, Geißberg, 700 m, branch of *Clematis vitalba*, on bark & wood, 30.X.2001, H.O. Baral (ø) – 3 km SE of Urach, 1 km W of Wittlingen, Gehöft Hohenwittlingen, 680 m, branch of ?*Syringa vulgaris*, on wood, 16.III.2003, G. Marson (ø). – 3.5 km SSW of Mössingen, 1.7 km NE of Beuren, Dreifürstenstein, 850 m, branch of *Acer campestre*, on wood, 23.VI.2002, H.O. Baral (H.B. 7153b ø). – **Bayern**, **Oberfranken**, 3.8 km E of Marktredwitz, S of Brand, Kleeschlag, 570 m, branch of *Acer pseudoplatanus*, on wood, 17.III.2019, M. Reul (M.R. 6763, anam. substr., doc. vid.). – **Oberpfalz**, 13 km NE of Amberg, W of Hirschau, Moosweiher, 415 m, trunk of *A. pseudoplatanus*, on bark, 28.XII.2004, H.O. Baral (H.B. 7639b, anam. substr.). – **Oberbayern**, 5.3 km NW of Bad Reichenhall, 2.8 km SW of Aufham, Steineralm, 1083 m, branch of *Picea abies*, on wood, 12.VIII.2018, H.O. Baral (H.B. 10170b ø). — **SWITZERLAND**: **Jura**, 12 km NW of Biel, 5 km ENE of Tramelan, NE of Orange, 880 m, branch of *Pinus sylvestris*, on wood, 16.VI.2018, H.O. Baral (H.B. 10157 ø). – **Luzern**, 24 km W of Luzern, Menzberg, 1022 m, branch of *Pinus*, on wood, 27.IX.2013, H. Aeberhard (ø, doc. vid.). – **Graubünden**, 6.3 km ENE of Landquart, NW of Grüsch, SE of Seewis, 860 m, branch of ?*Berberis vulgaris*, on wood, 20. VIII.2014, H.O. Baral (H.B. 9904a ø). — **AUSTRIA**: **Vorarlberg** (border to Bayern), 7.7 km SSE of Oberstaufen, E of Falken-Hütte, Eineguntkopf, 1590 m, branch of *Picea abies*, on wood, 2.VII.2011, H.O. Baral (H.B. 9566b ø). – **Wien**, 7.5 km NW of Wien, 2 km NW of Grinzing, 400 m, branch of *Acer platanoides*, on bark, 11.II.1995, W. Jaklitsch (H.B. 5231). – **Steiermark**, 6 km NNW of Graz, 2 km NW of Andritz, 500 m, branch of *Pinus sylvestris*, on wood, 1. IV.2013, G. Friebes (ø, doc. vid.). – Koralpe, 13.5 km ESE of Wolfsberg, 3.5 km WSW of Glashütten, NE of Grünangerhütte, 1550 m, branch of *Picea abies*, on wood, 6.V.2016, G. Friebes (G.F. 20160114, doc. vid.). – **Kärnten**, 12 km SE of Klagenfurt, NNE of St. Margareten im Rosental, 582 m, branch of *Lonicera xylosteum*, on wood, 9.I.1995, W. Jaklitsch (H.B. 5219). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 15 km W of Bruz, 1.8 km WSW of St.-Thurial, Barrage Chèze, 94 m, branch of *Pinus pinaster*, on wood, 12.III.2003, J.P. Priou (ø non vid.). – **Morbihan**, 1.7 km SSW of Guer, Pont de l'Oyon, 37 m, branch of *P. sylvestris*, on wood, 18.XII.2003, J.P. Priou (J.P.P. 23136, doc. vid.). – 1 km WNW of La Gacilly, rue de Picardie, 38 m, branches of *Lonicera*, on wood, 20.II.2009, J.P. Priou (J.P.P. 29027, doc. vid.). – 9.5 km SE of Malestroit, 2.7 km WNW of St.-Martin-sur-Oust, Beauvais, 8 m, twig of *Pinus radiata*, on wood, 14.I.2004, J.P. Priou (J.P.P. 24025, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 10 km ESE of La Roche-Bernard, W of Missillac, Chateau de la a Bretesche, 36 m, branch of *Taxus baccata*, on wood, 15.I.2010, J.P. Priou (J.P.P. 10002, non vid.). – **Auvergne**, **Haute-Loire**, Massif central, 15 km SSW of Le-Puy-en-Velay, 2.7 km WNW of Cayres, 1275 m, branch of *Picea abies*, on wood, 4.X.2002, G. Marson (ø). – **Rhône-Alpes**, **Loire**, 16 km WNW of Boën, 1.5 km S of St.-Jean-la-Vêtre, Ventuel, 880 m, branch of *P. abies*, on wood, 6.V.2010, P. Perz (H.B. 9288b ø). – **Savoie**, 40 km NNE of Briançon, 3.8 km SSW of Termignon, Le Châtel, 1270 m, branch of *Pinus* (?)*sylvestris*, on wood, 5.VIII.1995, G. Marson (H.B. 5321b). – **Isère**, 21 km NW of Gap, E of Les Coutières, Col du Festre, 1390 m, branch of *Larix* ?*decidua*, on wood, 23.VIII.2000, G. Marson (H.B. 6761b, anam. substr.). – **Drôme**, 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branch of *Clematis vitalba*, on wood, 23.VIII.1996, G. Marson (H.B. 5625). – **Provence-Alpes-Côte d'Azur**, **Vaucluse**, 14 km SE of Carpentras, 4 km SE of Venasque, 485 m, branch of *Lonicera* ?*xylosteum*, on wood, 9.X.2002, G. Marson (H.B. 7238b). – **Alpes-de-Haute-Provence**, 8 km SE of St.-Julien-du-Verdon, 3 km NW of Soleilhas, Vauplane, 1595 m, twigs & branches of *Buxus sempervirens*, on wood, 16.VII.1994, G. Marson (H.B. 5130). – 12.5 km NNE of Digne-les-Bains, N of Esclangon, 778 m, branch of *B. sempervirens*, on wood, 14.IX.2009, H.O. Baral (H.B. 9195 ø). – 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *Picea abies*, on wood & resin, 6.X.1993, G. Marson (H.B. 4966a). – 5 km WNW of Trigance, 3.5 km E of La Palud-sur-Verdon, 1025 m, branches of *Buxus sempervirens*, on wood, 10.IX.2016, G. Marson (G.M. 2016-09-10.1; sq.: MH221048). – **Alpes Maritimes**, 33 km ENE of Digne-les-Bains, SE of Colmars-les-Alpes, 1270 m, branch of *P. abies*, on wood, 6.VI.2010, J.P. Priou (J.P.P. 10120, non vid.). – 3.2 km ENE of Colmars-les-Alpes, 1.7 km SE of Haut-Clignon, 1725 m, on *Cytisus alpinus*, 8.VI.2010, J.P. Priou (J.P.P. 10135, non vid.). — **SPAIN**: **Asturias**, 3 km SSE of Pola de Somiedo, 1.3 km SSW of Coto de Buenamadre, Braña de Mumián, 1390 m, branch of *C. scoparius*, on wood, 2.VI.2013, H.O. Baral (ø). – **Castilla-La Mancha**, **Cuenca**, Sierra de Cuenca, 16 km ENE of Cuenca, 3 km E of Buenache de la Sierra, Vía del Saca, 1370 m, branches of *Berberis vulgaris*, on wood, 25.IX.1999, G. Marson & H.O. Baral (H.B. 6485). – **Guadalajara**, Sierra de Guadarrama, 43 km NNW of Guadalajara, 2 km NNW of Tamajón, Ermita de los Enebrales, 1040 m, branch of *Rosa*, on wood & bark, 14.V.1996, H.O. Baral (H.B. 5499). – ibid., branch of *Juniperus thurifera*, on wood, 14.V.1996, H.O. Baral (H.B. 5500c). – ibid., branches of *Genista scorpius*, on wood and bark, 14.V.1996, H.O. Baral (H.B. 5512a, 5517b). – 3.5 km NW of Tamajón, 1.5 km NW of Ermita de los Enebrales, 1015 m, branches of *Robinia pseudoacacia*, on wood, 14.V.1996, H.O. Baral (H.B. 5481a, AH). – **Madrid**, Sierra de Guadarrama, 48 km ENE of Segovia, N of Robregordo, 1310 m, branches of *Salix*, on wood, 26.V.1996, H.O. Baral (H.B. 5501, AH 7638). – ibid., branches of *Rubus fruticosus*, on wood, 26.V.1996, H.O. Baral (ø). — **SERBIA**: **Vojvodina**, Fruška Gora, WSW of WWII memorial, 452 m, branch of *Picea abies*, on wood, 4.IX.2019, D. Savić (doc. vid.). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 8 km W of Korčula, Pupnat, 320 m, branch of *Hedera helix*, on wood, 11.VI.2000, H.O. Baral (H.B. 6698 ø, CNF 2/4767). — **TURKEY**: **Marmara**, **Balıkesir**, 9.5 km W of Balıkesir, 1.8 km ENE of Çağdaskent, Edremit Yolu, 258 m, branch of *Salix alba*, on wood, 10. IX.2002, T. Askun (T.A. 1, anam. substr., doc. vid.). – 9 km NE of Balıkesir, 2.5 km SW of Ayvatlar, Değirmen Boğazı, 135 m, branches of *Pinus brutia*, on wood, 4.II.2003, T. Askun (T.A. 62, 63, non vid.). – ibid., branch of *Cedrus*, on wood, 4.II.2003 (T.A. 54, non vid.; sq.: KT380072). – 50 km WSW of Balıkesir, 16.5 km SW of Ivrindi, 2 km NW of Korucu, Sarıpınar Mevkii, 425 m, branch of *Juniperus*, on bark & wood, 1.XI.2002, T. Askun (T.A. 28, doc. vid.). – ibid., branch of *P. brutia*, on wood, 1.XI.2002, T. Askun (T.A. 35b, H.B. 7294b). – 1 km NW of Korucu, 460 m, branches of *P. brutia*, on wood, 1.XI.2002, T. Askun (T.A. 25, anam. substr., doc. vid.). – 27.5 km SE of Balıkesir, 8.5 km NNW of Bigadiç, N of Kadıköy, 270 m, branch of *P. brutia*, on wood, 14.XI.2013, S. Yurtseven (anam. substr., ø). — **MACARONESIA**: **Canary Islands**, **Tenerife**, La Orotava, 3 km SSW of Teide, Morros Pardos, 2456 m, branch of *Adenocarpus viscosus*, on wood, 25.IV.2014, A. Rodríguez-Romero, L. & C. Quijada (TFC Mic. 24156, doc. vid.). – Guía de Isora, 8 km NE of Guía de Isora, Morro los Cerrillos, 2014 m, branch of *Cytisus supranubius*, on wood 22.III.2014, R. Negrín, L. & C. Quijada (TFC Mic. 24549, 24556, doc. vid.). — **MONGOLIA**:

Bayan Ölgii, Sagsai, Altay Mts., Tavan Bogd, 25 km SE of Dayan lake, 8 km NE of Chinese border, Songino Gol river valley, 2100 m, branch of *Lonicera altaica*, on wood, 15. VIII.2005, P. Karasch (H.B. 7887d, P.K. 15082005-18). — **USA**: **Wyoming**, Middle Rocky Mountains, 18.5 km N of Jackson, Grand Teton, 1960 m, branch of *Purshia tridentata*, on wood, 6.VI.1996, G. Marson (H.B. 5666). – **Utah**, Utah Mts., Dixie Forest, 27 km SSE of Torrey, 18 km S of Grover, 2825 m, branch of *Salix ?bebbiana*, on wood, 15.V.1995, G. Marson (H.B. 5415). – **Colorado**, Southern Rocky Mountains, 25 km SW of Denver, 11.5 km NE of Conifer, around Tiny Town, 2100 m, branch of *Acer glabrum*, on wood, 14.VI.1996, G. Marson (H.B. 5667a). – ibid., branches of *Corylus cornuta*, on wood, 14.VI.1996, G. Marson (H.B. 6029a). – 65 km SW of Denver, 7.5 km WNW of Shawnee, Santa Maria, 2615 m, branch of *Ribes cereum*, on wood, 14.VI.1996, G. Marson (ø). – **Arizona**, Grand Canyon, Kaibab Plateau, 93 km SSE of Fredonia, S of North Rim, 2500 m, branch of *Cercocarpus ledifolius*, 17.V.1995, G. Marson (ø). – **Texas**, Oaks and Prairies, ~45 km E of Austin, ~35 km W of Giddings, ~150 m, branch of (?)*Crataegus*, on wood, 19.VI.1996, G. Marson (ø).

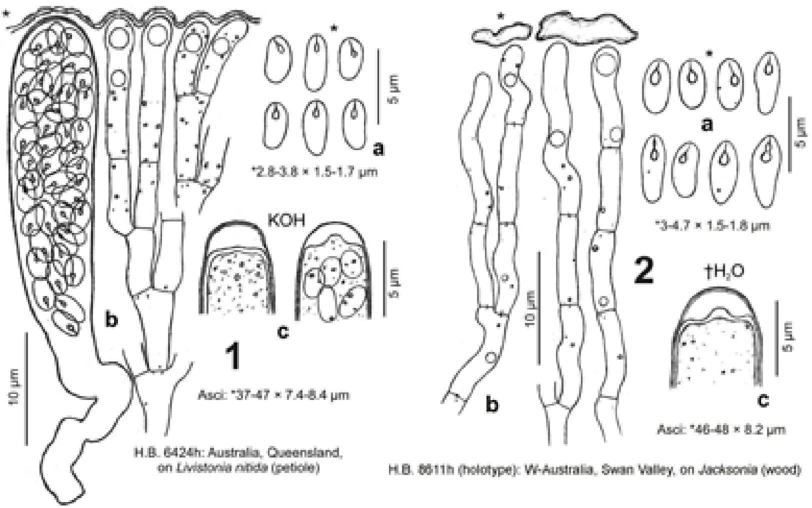


Plate 209. **1–2**: *Orbilia myrioeuonymi*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices.

Orbilia myrioeuonymi Baral & G. Marson, **sp. nov.**, MB 813509 — Pls 209–210

Etymology: named after the 64-spored asci and a close relationship to *O. euonymi*.

Typification: Western Australia, Upper Swan, branches of *Jacksonia*, 2.IX.2006, G. Marson (ex H.B. 8611h, MEL 2389244, holotype).

Latin diagnosis: *Differt ab* Orbilia euonymi *ascis 64-sporis. Habitat ad lignum putridum ramorum in aere prominentium arborum angiospermarum vel petiolos palmae, in zona temperata ad subtropica semihumida ad humida Australiae meridio-occidentalis vel -orientalis et Asiae orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.16–0.24 mm diam., 0.075–0.11 mm high, pale to light cream-reddish to orange, ± round, ± scattered; disc flat, margin indistinct or distinct, ~0–10 µm protruding, smooth; sessile to subsessile, superficial; dry bright orange. **Asci** *37–48 {3} × 7.4–8.4 {2} or 8.5–10 µm {1}, †29–46(–67) × (5–)6–7.5(–8.5) {3}, 64-spored (40–52 spores counted), spores multiseriate, pars sporifera *21–29 µm long; **apex** (†) hemispherical to slightly truncate, dome †1.5–2 → (0.7–)1–1.3(–1.7) µm thick {3}, some with very distinct apical chamber; **base** with short to medium long, thin or thick, flexuous stalk, L-shaped. **Ascospores** *(2.8–)3–4.3(–4.8) × 1.5–1.8(–2) µm {3}, †2.7–4(–4.8) × 1.5–1.7 µm {2}, cylindric-ellipsoid to slightly clavate, ends rounded to obtuse, straight (to slightly inequilateral); **SBs** *1.1–1.9 × 0.3–0.5(–0.6) µm {3}, divided into an abruptly swollen tear-shaped lower part and a filum of ± equal or shorter length. **Paraphyses** apically uninflated to slightly capitate, terminal cell *6–15 × (1.5–)2–2.5(–3) µm {2}, lower cells *5–11 × 1.5–2.7 µm {2}; rarely branched near apex. **Medullary excipulum** pale orange, 15–30 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** pale rose, of thin-walled, irregularly oriented t. angularis from base to mid flanks, 15–35 µm thick near base, cells *6–10 × 5–7(–8) µm {1}; 5–15 µm near margin, of t. porrecta oriented at a 10–30° angle to the surface, marginal cortical cells †5–10 × 2–2.5 µm. **Anchoring hyphae** medium abundant, *2–3 µm wide (†1.5–2 µm), walls 0.2 µm thick {1}, at lower flanks forming a gelatinized layer 20–30 µm thick, towards base sometimes with 3.5–5 µm wide angular cells near cortex of excipulum. **SCBs** in paraphyses globose to short elongate, 1.2–2 µm diam. **Exudate** over paraphyses 0.3–1 µm thick, ± continuous, or 1–2.5 µm thick, cloddy, slightly rough, loosely attached; over margin rough-cloddy, pale yellowish, 1–3 µm thick. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {1}). **Conidiophores** not observed. A single **conidium** seen, unbranched, slightly curved, *52 × 4 µm, 8-septate, with pointed ends.

Habitat: collected 0.2–2 m above the ground or on the moist ground, on 11–18 mm thick, ± decorticated branches of *Jacksonia* sp. {1}, *Melaleuca* sp. {1}, indet. angiosperm {2}, on 0.1 mm deep strongly decayed, partially eroded wood {3}, petiole of *Livistona nitida* {1}, greyed, green algae absent or scattered. **Associated**: *Claussenomyces* sp. {1}, *Gloniopsis* sp. {1}, *G. praelonga* {1}, *Mellitiosporiella* sp. {1}, *Orbilia acaciae* {1}, *O. australiensis* {1/1}, *O. ?commarosa* {1}, *O. coronohesperidea* {1}, *O. curvativitalbae* {1}, *O. ?dixiensis* {1}, *O. eucalypti* {1}, *O. livistonae* {1}, *O. multiserpens* {1}, *O. myriofusiclava* {1}, *O. myrioobliqua* {1}, *O. palmicola* {1}, *O. parviclava* {1}, *O. pleiohesperidea* {1}, *Patellaria atrata* {1}. **Desiccation tolerance**: fully viable for at least 9 months. **Altitude**: 76–875 m a.s.l. (Australia), 1890 m (southern China). **Geology**: Triassic and Jurassic sedimentary rock; granite. **Phenology**: VI (N-hemisphere), IX–X (southern hemisphere).

Taxonomic remarks. *Orbilia myrioeuonymi* deviates from *O. euonymi* and *O. pleistoeuonymi* merely in 64-spored asci, whereas ascospore size and shape is about the same. It could well be a rare molecular variant which was, however, so far not observed to grow in association with any other taxon of this series, and not even on the same continent. However, a European collection was first thought to be 64-spored, but differs in larger asci and might therefore belong to *O. pleistoeuonymi* (see Pl. 211: 3).

Variation. Ascus size but also spore length varies somewhat within *O. myrioeuonymi*. Asci were largest in the collection from China (but see below), while its spores fit quite well the Australian records.

Literature report. A Chinese report by Zhang et al. (2009b, as *O.* cf. *euonymi*) obviously refers to *O. myrioeuonymi* (Pl. 210: 2), although collected on the moist ground. The reported spore number of 64 was evaluated from the volume of the pars sporifera on the photographed living asci. Ascus and spore size were undoubtedly given too small by the authors. We assume that the scale in a previous version of the plate (Y. Zhang pers. comm.) was correct. According to that scale the here figured ascus has a size of 39 × 9 µm, whereas it has 30 × 6.8 µm in the published version. A comparable error of 130% affects the spore scale, therefore, we here reproduce all these images with a corrected scale. Apothecia where described as pale yellow to watery-whitish, 0.15–0.8 mm diam., but such large range in size is not confirmed by the illustrations: the sectioned apothecium has a diameter of 0.16 mm, and those on the macrophoto appear to lie in the range of 0.15–0.2 mm.

Ecology. The few Australian samples of *O. myrioeuonymi* have been collected on rotten wood of dead xeric branches of different angiosperm trees and on dead dry leaves of a palm in a subtropical semihumid eucalypt open woodland in southwestern

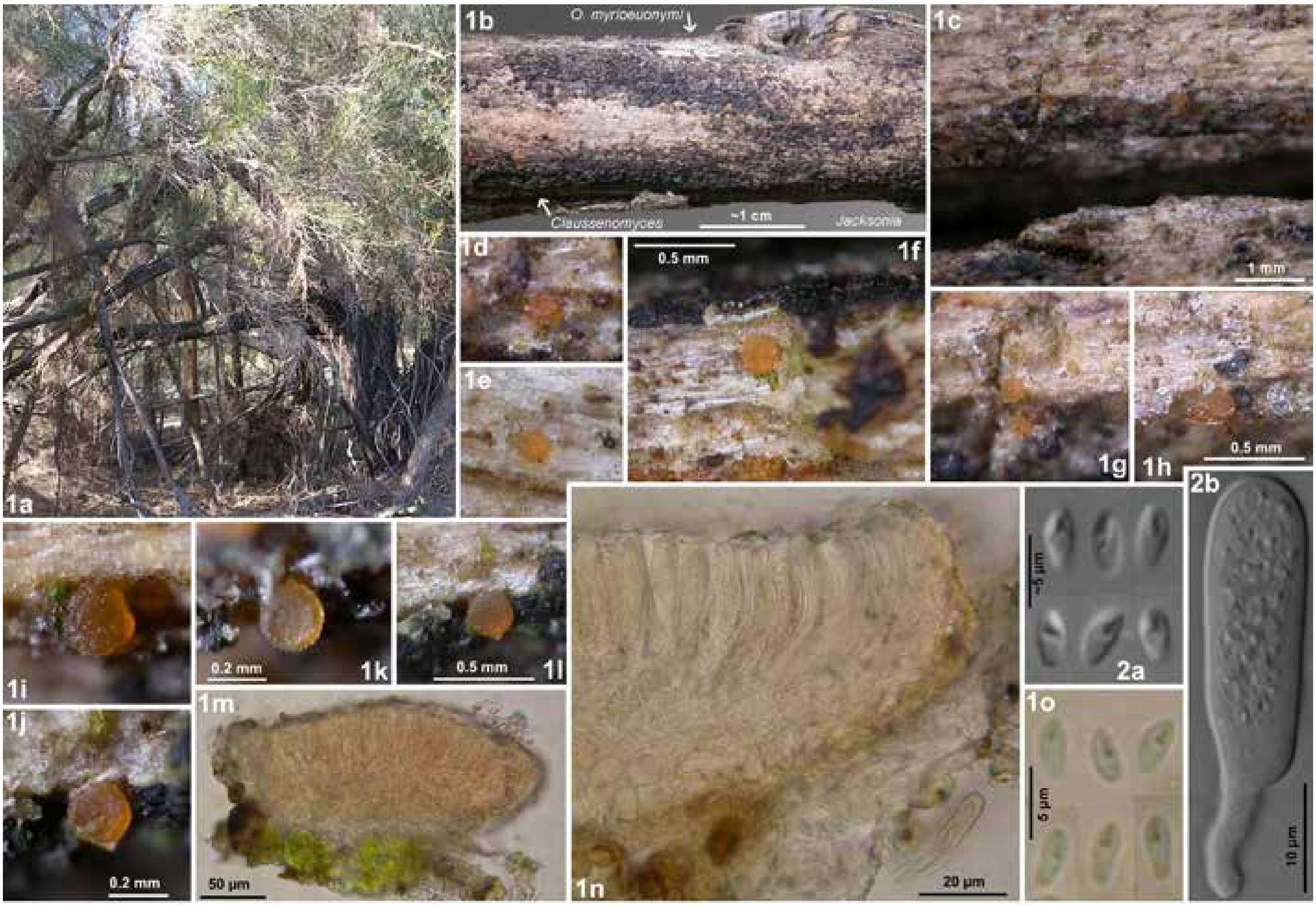


Plate 210. **1–2**: *Orbilia myrioeuonymi*. – **1a**. semihumid Eucalypt open forest with *Jacksonia*; **1b**. decorticated branch of *Jacksonia*; **1c–l**. rehydrated apothecia; **1m**. apothecium in median section; **1n**. ectal excipulum in median section (margin and flanks); **2b**. ascus; **1o**, **2a**. ascospores. – Living state. – **2a–b**: phot. Zhang et al. 2009b. — **1a–o**. H.B. 8611h (holotype): Western Australia, Swan Valley; **2a–b**. YMFT004: China, Yimen, on indet. angiosperm.

Australia and in subtropical subhumid to warm-temperate humid eucalypt woodland and open forest in eastern and southeastern Australia (eastern side of Great Dividing Range). The specimen from southern China was on hygric wood ('bark' in the description in Zhang et al. is probably erroneous) of an unidentified angiosperm in a subtropical humid (winterdry), monsoon-dominated evergreen forest. Only one apothecium was detected in the collection on *Livistona* and ~15 on *Jacksonia*; that on *Melaleuca* was more abundant but could only be studied in the dead state.

Specimens included. **AUSTRALIA**: **Western Australia**, Swan Coastal Plain, 30 km NE of Perth, 4 km NE of Upper Swan, 76 m, branches of *Jacksonia*, on wood, 2.IX.2006, G. Marson (ex H.B. 8611h, MEL 2389244, **holotype**). – **Queensland**, Brigalow Belt South, 69 km SSW of Theodore, 15 km N of Taroom, Palm-Tree Creek, Roy Staines Bridge, 200 m, petiole of *Livistona nitida*, 22.X.1998, G. Marson (H.B. 6424h). – **New South Wales**, Sydney Basin, 84 km W of Sydney, 2 km S of Katoomba, Blue Mountains, Echo Point, Spooner Outlook, 875 m, branch of *Melaleuca*, on wood, 26.X.1998, G. Marson (H.B. 6822, anam. substr.). — **CHINA**: **Yunnan**, **Yuxi**, Yimen, 75 km SW of Kunming, 53 km NW of Yuxi, Longkou Forest Park, 1890 m, on wood of indet. angiosperm, 27.VI.2006, Y. Zhang (YMFT004, doc. vid.).

Orbilia pleistoeuonymi Baral & P. Perz, **sp. nov.**, MB 814371 — Pls 211–212, Map 36

Etymology: referring to the 128-spored asci and the close relation to *O. euonymi*.
Typification: Spain, Cataluña, Cambrils, branch of *Robinia pseudoacacia*, 27.IX.1999, H.O. Baral & G. Marson (ex H.B. 6494a, M-0276564, holotype; ex-type culture: CBS 116274; sq.: KT215234).

Latin diagnosis: *Differt ab* Orbilia euonymi *ascis 128-sporis. Habitat ad lignum putridum ramorum in aere prominentium arborum deciduarum, plerumque* Quercus*, in zona supratemperata humida (sub)continentale ad thermomediterranea semihumida Europae centralis, orientalis et meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.12–)0.15–0.4(–0.5) mm diam., (0.08–)0.1–0.18(–0.23) mm high, light to bright (rose-)orange(-ochraceous), also pale yellow, round, scattered to often densely gregarious; disc flat, margin distinct, thin, 0–10 µm protruding, smooth; sessile or with a very short and thick, ill-defined stipe, superficial; dry bright orange. **Asci** *(45–)55–75(–86) × (8.5–)9–10(–10.7) µm {5}, †(38–)45–70(–80) × (6.8–)7.5–9(–10) µm {6}, 128-spored (min. 70–100 spores counted), spores multiseriate, irregularly oriented, pars sporifera *(27–)30–44 µm long, †(28–)33–44(–50) µm; **apex** (†) hemispherical, dome †1.5–2.2(–2.5) → 0.7–1.7 µm thick {3}, with apical chamber; **base** with short to long, thick, flexuous stalk, L-, T- or often Y-shaped with sometimes very long legs. **Ascospores** *(2.2–)2.5–3.5(–4.5) × (1.5–)1.6–2.2(–2.4) µm {5}, †(1.8–)2.2–3(–4) × 1.4–2(–2.2) {3} µm, cylindric-ellipsoid to somewhat clavate or obovoid, ends rounded, straight or rarely slightly to medium curved; **SBs** *(0.8–)1–1.5(–1.7) × (0.2–)0.3–0.4(–0.5) µm {5}, divided into an abruptly swollen, tear-shaped to subglobose, rarely fusoid lower part and a filum of ± equal length. **Paraphyses** apically uninflated or slightly clavate-capitate, terminal cell *6–12(–14) × (1.7–)2–3(–4) µm {3}, lower cells *(3.5–)5–9(–10) × 1.5–2.5(–3.3) µm {3}; rarely branched at upper septum. **Medullary excipulum** hyaline, 20–40 µm thick, of dense textura intricata-angularis, medium sharply delimited. **Ectal excipulum** pale rose, of (†) thin-walled (cortical part distinctly gelatinized), indistinctly oriented t. angularis(-prismatica) from base to mid flanks, 20–80 µm thick near base, cells *(5–)8–15(–20) × (3–)5–11(–13) µm {3}; 20–35 µm thick at lower flanks, 10–20 µm thick near margin, of t. prismatica-porrecta oriented at a 10–30° angle to the surface, marginal cortical cells */†(6–)7–9(–10) × 2.2–3(–4) µm {3}. **Anchoring hyphae** very sparse to medium abundant, hyphae †1.5–2.8

µm wide, wall 0.2(–0.3) µm thick {3}. **SCBs** globose, in paraphyses 0.9–1.5(–2.5) µm diam., in marginal excipulum 1.2–2 µm. **Exudate** over paraphyses (0.3–)0.5–2(–4) µm thick, ± continuous to cloddy, very rough, loosely attached, over margin (0.5–)1–3(–5) µm thick, hyaline to pale yellowish-chlorinaceous. **— ANAMORPH**: vermispora-like (from ascospore isolate {1} and natural substrate {3}). **Conidiophores** *~10–35 µm long {3}, 0–5-septate, often irregularly bent, sterile basal cells *2.5–3.8 µm wide. **Conidiogenous cells** often broader than basal cells, either simple with a single apical denticle, *6–12 × 2.2–4.4 µm, or mostly in a row, *4–8 × 2.8–5.5 µm, each with 1–4 cylindrical denticles *1–2.5(–3) × 0.9–1.3 µm. **Conidia** unbranched, slightly (rarely strongly) curved, *(12–)18–31(–34) × (3.5–)4–4.7(–5) µm {3}, (1–)3–5(–6)-septate {4}, containing some minute LBs.

Habitat: collected (0–)0.5–3 m above the ground, partially to entirely decorticated, 15–100 mm thick branches and logs of *Carpinus betulus* {1}, *Quercus* sp. {3}, *Q. pubescens* {1}, *Q. robur* {4}, *Robinia pseudoacacia* {1}, on 0.1–2 mm deep or entirely strongly decayed wood {10}, ± weathered and bleached, slightly to medium greyed, green algae absent or sparse to abundant. **Associated**: *Chaetosphaeria myriocarpa* {1}, *Durella atrocyanea* {1}, *D. connivens* {1}, *Hyalorbilia helicospora* {1}, *Mollisia ligni* {1}, *Orbilia aprilis* {4}, *O. bicknellensis* {1}, *O. montigena* {1}, *O. pleiomicrosoma* {1}, *O. tremulae* {1}, *O. ungulata* {1}, *O. vinosa* {1}, *Patellaria atrata* {1}, *Phellinus* (?) *contiguus* {1}. **Desiccation tolerance**: fully viable for at least 1 month, many ascospores and basal ectal excipular cells still viable after almost 5 years. **Altitude**: 15–445 m a.s.l. **Geology**: Keuper (Knollenmergel), Upper Cretaceous calcareous clay- & marlstone, Quaternary fluviatile sand & gravel; granite & granodiorite, gneiss & migmatite. **Phenology**: III–IV, VI, IX, XII (throughout the year, long-lived).

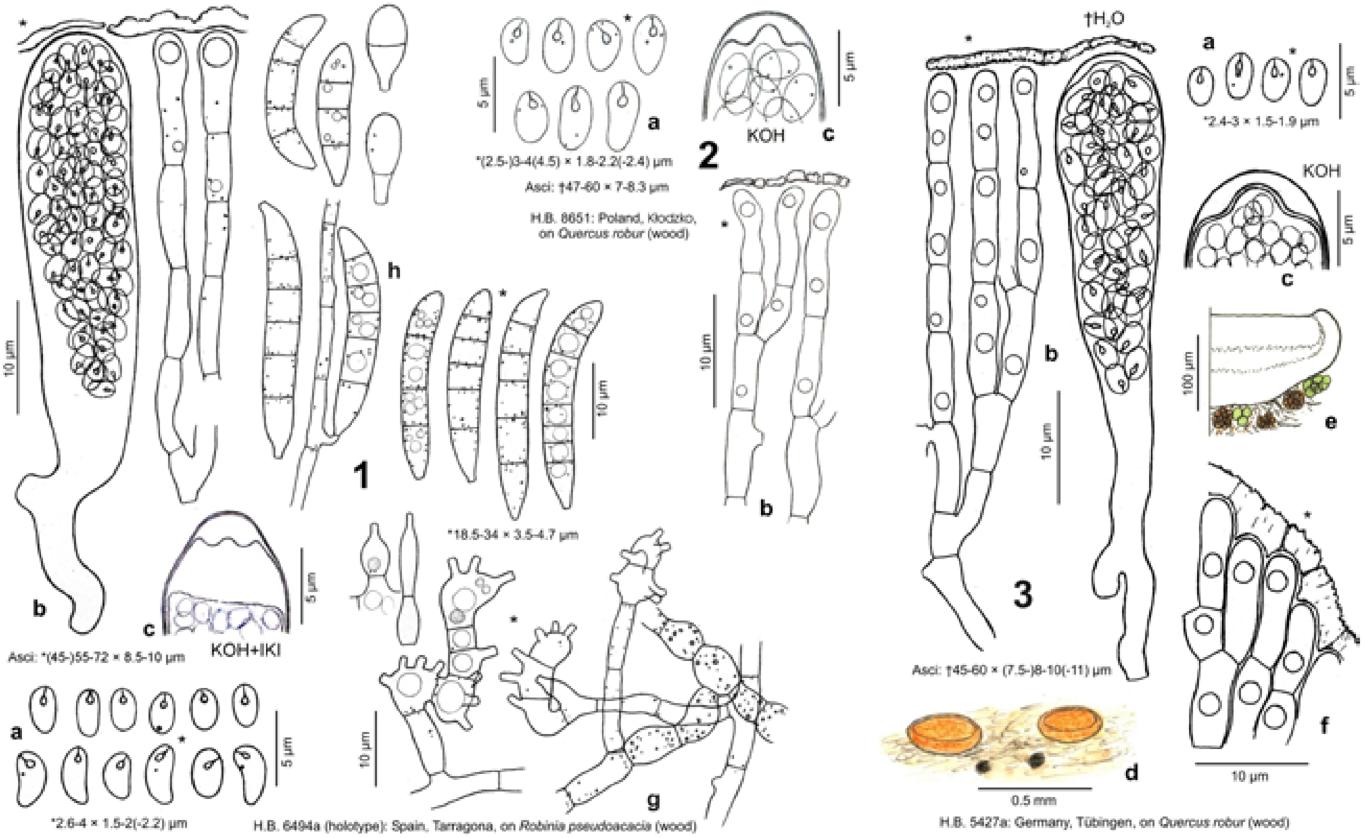
Taxonomic remarks. *Orbilia pleistoeuonymi* differs from *O. euonymi* and *O. myrioeuonymi* in larger, 128-spored asci. Although the number of such small ascospores is difficult to count, the asci were found to be at least 100-spored in most of the specimens examined. The spores are scarcely shorter than in *O. euonymi* and *O. myrioeuonymi*. Also spore width corresponds well and lies even slightly above that of *O. myrioeuonymi*. Due to the high spore number the asci of *O. pleistoeuonymi* tend to be distinctly larger than in the other three species of the series.

Variation. Spore size in *O. pleistoeuonymi* was quite variable, ranging among the collections from *2.4–2.8 to 3–4 µm in length and *1.5–1.8 to 2–2.3 µm in width. However, this variation was also noted among apothecia of a single sample (e. g., Pls 211: 1–2, 212: 4).

In a collection from Tübingen (Pl. 211: 3) the asci were originally thought to be 64-spored and to belong to *O. myrioeuonymi*. Over a third of the ~50 apothecia have been examined. In most of these apothecia the asci were found to contain many more spores than 32, and it is well possible that they contained more than 64 spores, especially because the ascus size fits better *O. pleistoeuonymi*. Its extraordinarily large ascus width in the dead state is perhaps due to artificial flattening. In the rather short spores this specimen fits the smaller spores illustrated in Pl. 211: 1a (upper row). Also in a specimen from Russia studied by E.S. Popov (pers. comm.) the spore number possibly exceeds 64, considering the rather large asci (†63–65 × 8–9 µm) and the short, 5-septate conidia.

Anamorph. The vermispora-like anamorph obtained in pure culture differs from that of *O. euonymi* in slightly smaller conidia. Whether the swollen conidiogenous cells with prominent denticles are typical of this species needs to be clarified from further cultures, particularly in comparison with *O. euonymi*.

Phylogeny. A sequence comprising SSU, ITS, and LSU was taken from pure culture of the holotype of *O. pleistoeuonymi*. The distance to *O. euonymi* is unexpectedly high (see p. 535).



H.B. 6494a (holotype): Spain, Tarragona, on *Robinia pseudoacacia* (wood)

H.B. 8651: Poland, Klodzko, on *Quercus robur* (wood)

H.B. 5427a: Germany, Tübingen, on *Quercus robur* (wood)

Plate 211. **1–3**: *Orbilia pleistoeuonymi*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. conidiophores; **h**. conidia (both from culture).

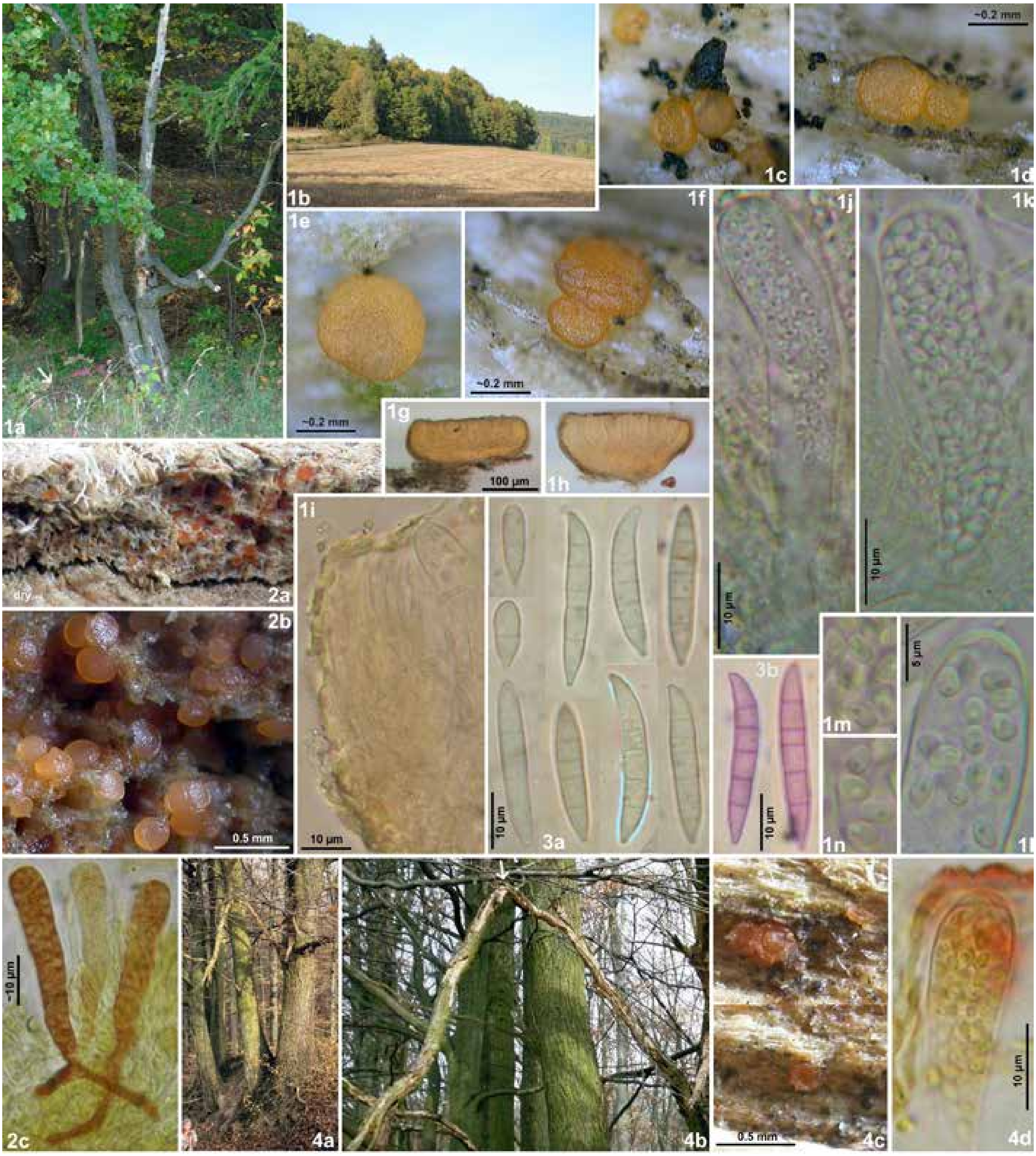


Plate 212. **1–4**: *Orbilia pleistoeuonymi*. – **1a–b**. south-exposed border of a mixed oak forest with dead *Quercus*; **4a–b**. *Querco-Carpinetum* near west-exposed border of forest, with attached decayed *Quercus* branch; **1c–f**, **2b**, **4c**. rehydrated apothecia; **2a**. dry apothecia; **1g–h**. apothecia in median section; **1i**. id., marginal ectal excipulum; **1j–k**, **2c**, **4d**. asci; **1l**. ascus apex; **1l–n**. ascospores; **3a–b**. conidia from substrate. – Living state (**3b** in CRB), except for asci in **1k–l**, asci and spores in **2c** (KOH+IKI), **4d** (KOH+CR+IKI). – **1a–h**, **j–n**: phot. P. Perz. — **1a–n**. H.B. 8651: Poland, Kłodzko, on *Quercus*; **2a–c**. H.B. 6494a (holotype): Spain, Tarragona, on *Robinia*; **3a–b**. H.B. 9237a: Poland, Domaszków, on *Quercus*; **4a–d**. H.B. 5427a: Germany, Tübingen, on *Quercus*.

The S1506 intron is here much larger (1555 vs. 444 nt in *O. euonymi*) than in most other species of *Orbiliomycetes* (see Tab. 24). When comparing the ~350 overlapping nucleotides, it shows 18.5% distance to *O. pleioeuonymi*, 20–20.5% to *O. euonymi*, and 18.5% to *O. myriosphaera*, the only further member of section *Lentiformes* in which we found this intron.

Ecology. The few records of *O. pleistoeuonymi* were on rotten wood of dead xeric branches of mainly *Quercus*, but also *Carpinus* and *Robinia*. In central Europe (Poland, Czechia, Slovakia, Germany) it was found in cold-temperate humid, ± thermophilous *Querco-Carpinetum* forests, especially near the border to open woodland and pastures or agriculture. In southern Europe it grew in a mesosubmediterranean semihumid *Quercetum pubescentis* (Drôme) and in the thermomediterranean coastal zone at a rivulet with *Phragmites* and planted *Robinia* (Tarragona, holotype). The collection from the Caspian lowland

Map 36. Known distribution of *O. pleistoeuonymi* in Europe.

(Astrakhan) was from a warm-continental steppic subhumid grassland area near a salt lake, with scattered *Quercus* and *Ulmus*.

Several collections of *O. pleistoeuonymi* were quite sparse (1–10 apothecia), whereas others, including the holotype, were abundant, comprising ca. 50–100 apothecia. The holotype, however, grew in close association with the holotype of *O. pleiomicrosoma*, sometimes even intermingled, and since these two species are macroscopically indistinguishable, their relative abundance in this collection remained unclear. In four other samples *O. aprilis* grew close to or sometimes intermingled with *O. pleistoeuonymi*.

Specimens included. **POLAND**: **Lower Silesia**, Kłodzko, 12 km SE of Kłodzko, 1.8 km S of Skrzynka, N of Trzebieszowice, 400 m, branch of *Quercus robur*, on wood, 19.IX.2007, P. Perz (P.P. 20070919-4, H.B. 8651). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, branch of *Q. robur*, on wood, 27.XII.2009, A. Perz (P.P. 20091227-2 ø, doc. vid., anam. substr.). — **CZECHIA**: **South Moravia**, 3.2 km WSW of Znojmo, 2.7 km SE of Mašovice, Podyjí National Park, 355 m, branch of *Carpinus betulus*, on wood, 17.IX.2008, S. Helleman (S.H. 562, doc. vid.). — **SLOVAKIA**: **Bratislava**, 10 km SE of Bratislava, 4.8 km S of Podunajské Biskupice, Topoľové hony, 130 m, log of *Quercus*, on wood, 1.VI.2019, A. Polhorský (ø, doc. vid.). – 5 km SW of Podunajské Biskupice, Kopáč, 133 m, branch of *Quercus*, on wood, 10.IX.2019, A. Polhorský (A.P. 19/34, anam. substr., doc. vid.). — **GERMANY**: **Sachsen**, 14.5 km NW of Bautzen, 0.6 km SW of Wartha, Guttauer Teiche, 162 m, branch of *Quercus*, on wood, 20.IX.2018, H.O. Baral (H.B. 10176a). – **Baden-Württemberg**, 6 km NE of Tübingen, ENE of Pfrondorf, Tiefenbach, 410 m, branch of *Q. robur*, on wood, 1.III.1996, H.O. Baral (H.B. 5427a). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 7.8 km NNE of Pierrelatte, 2.5 km E of Donzère, 120 m, branch of *Q. pubescens*, on wood, 20.IX.1999, H.O. Baral (ø). — **SPAIN**: **Cataluña**, **Tarragona**, 20 km WSW of Tarragona, 3 km W of Cambrils, Carrer Gotic, La Dorada, 15 m, branch of *Robinia pseudoacacia*, on wood, 27.IX.1999, H.O. Baral & G. Marson (ex H.B. 6494a, M-0276564, **holotype**, CBS 116274, anam. cult.; sq.: KT215234). — **RUSSIA (West)**: **Astrakhan**, **Akhtubinsk**, 189 km ESE of Volgograd, 35 km ENE of Bolkhuny, S of Baskunchak salt lake, NW of Zeleny Sad, 1 m, branches of *Q. robur*, on wood, 27.IV.2009, E.S. Popov (LE 248029, anam. substr., doc. vid.).

Section *Hemiorblia*

Orbilia subgenus ***Hemiorbilia*** section ***Hemiorbilia*** –
Type species: *Calloria occulta* Rehm [≡ *Orbilia occulta* (Rehm) Sacc.]

Description: — **TELEOMORPH**: **Apothecia** rehydrated ((0.07–)) (0.1–)0.15–1(–1.5) mm diam., pale to bright orange, ochraceous-orange, brick-red, or rose(-lilaceous), disc smooth or pruinose, margin smooth to rough, whitish pubescent to long-haired, or with small to large whitish teeth. **Asci** *(27–)35–100(–130) × (4–)5–12(–15) µm, 8- up to 128-spored, some of the lower spores inverted (~1/8–3/4 of spores, strongly mixed if polysporous); **apex** (†) hemispherical to slightly (rarely medium) truncate, with (0.4–)0.7–4(–6) µm thick apical dome (but thin-walled in *O. concoloris*), often with distinct apical chamber; **base** L-, T-, Y- or h-shaped. **Ascospores** *(3.4–)5–20(–30) × (1–)1.5–4(–6) µm, cylindrical, clavate, ellipsoid, fusoid, obovoid, subglobose, cashew-shaped, heart-shaped, triangular, sperm-shaped, apex rounded to subacute, rarely acute to acuminate, straight to strongly curved (C- to L-shaped or helicoid); **SBs** affixed to apical, subapical or lateral spore wall, (1–)1.5–5(–6.5) × (0.2–)0.4–1.5(–2.5) µm, cylindrical to subulate or tear-shaped to ampulliform, sometimes globose, apically narrowed to a small or wide point, filum absent or exceptionally very short, straight or sometimes curved. **Paraphyses** not or often slightly, rarely strongly inflated at the apex, clavate-capitate, exceptionally sublageniform, terminal cells (0.5–)1–2(–2.5)× longer than lower cells, unbranched or sometimes branched near apex. Cortical cells of **ectal excipulum** at flanks of textura (globulosa-)angularis(-prismatica), cells isodiametric or vertically elongated, near base */†(5–)7–20(–30) × (4–)6–15(–20) µm, (†) thin-walled to slightly, sometimes medium to strongly gelatinized, common walls †(0.3–)0.5–1.5(–3) µm thick, near margin of t. angularis to t. porrecta, oriented at a high to low angle, with or without 1–10 µm up to 30–100(–200) µm long **glassy processes**, rarely with septate, 60–210(–300) µm long **hairs**. **SCBs** globose, or mixed with crystalloid ones; **VBs** consistently absent; **carotenoids** in **LBs** present in some taxa. **Exudate** (0.1–)0.5–3(–10) µm thick, continuous, cloddy, or granular, loosely or firmly attached, hyaline to bright yellow, rarely absent. — **ANAMORPH**: trinacrium-like*,* descalsia-like, dwayaangam-like, sometimes vermispora-like. **Conidiophores** ~1.5–30 µm long. **Conidiogenous cells** monoblastic or sympodial. **Conidia** staurosporous, rarely phragmosporous.

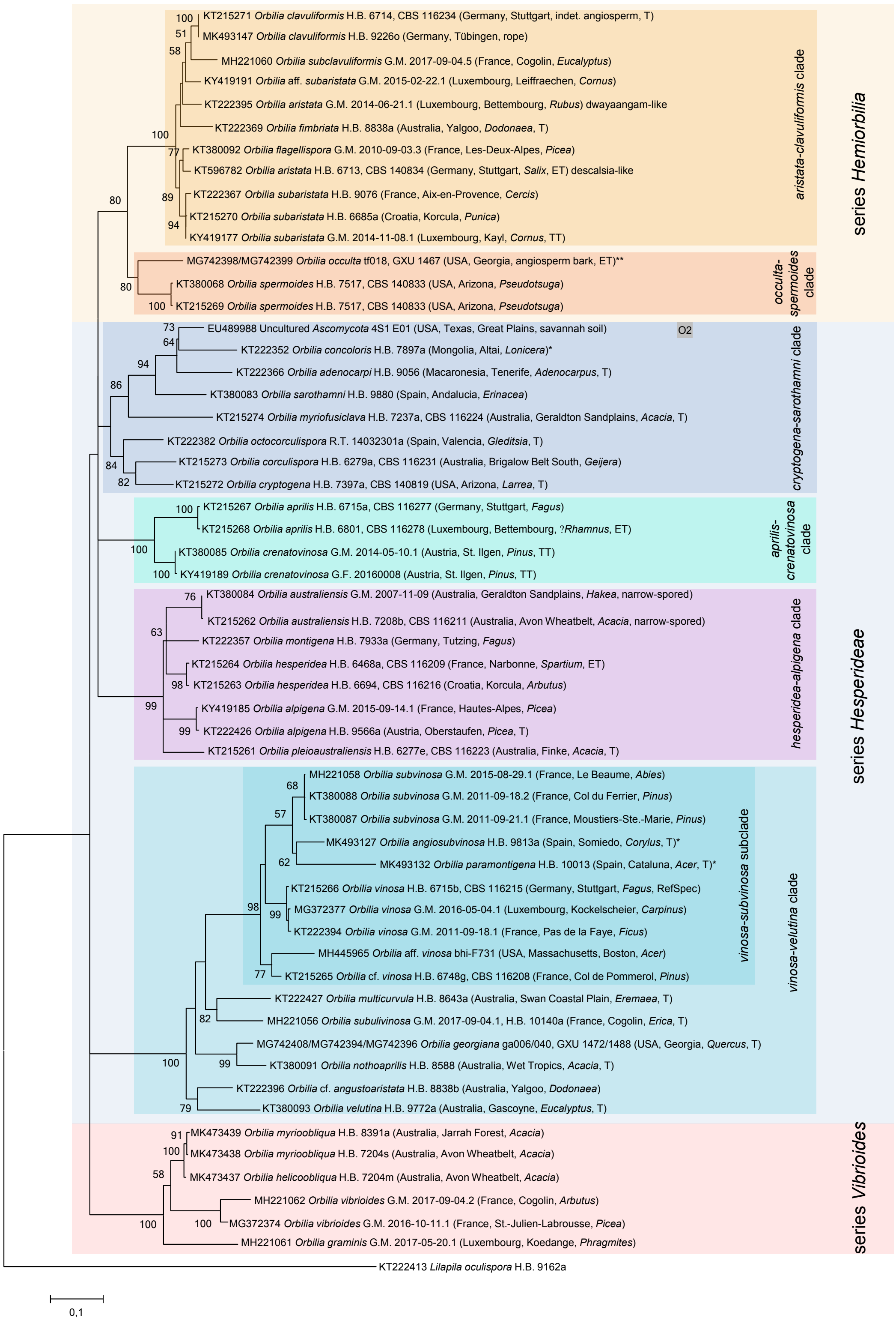
Habitat: on wood and bark of gymno- & angiosperms, also caulicolous, foliicolous, acicolous, or bryicolous, in boreal to tropical, humid to arid climates, always desiccation-tolerant.

Recognized series: *Hemiorbilia*, *Hesperideae*, *Vibrioides*, with 81 recognized species plus 15 unnamed ('affinis') and 1 of uncertain affinity.

Taxonomic remarks. Members of section *Hemiorbilia* are characterized by asci with a more or less hemispherical apex (dead state) with distinct apical wall thickening and often also with apical chamber. The apical thickening is usually congophilous by staining rose-red in CR_{SDS}, while a pale red (dextrinoid) reaction in IKI or MLZ was observed only in those species with an extraordinarily thick apical wall (*O. nothovinosa*, *O. vibrioides*). In some species the apex is partially medium truncate (e. g., *O. myrioauris*) and/or the apical thickening rather thin (e. g., *O. octocorculispora*) or even absent (*O. concoloris*). The spore bodies are mostly ± elongate, rod-shaped to subulate or tear-shaped to ampulliform, usually straight and rather thick, apically attached to a narrow or wide point, but never with a filum.

Section *Hemiorbilia* is morphologically rather sharply delimited, e. g., against species with thin-walled truncate ascus apices (subgenera *Habrostictis* and *Orbilia*). However, exceptions occur. Particularly some species included in section *Ovoideae* of subgenus *Orbilia* are morphologically hardly separable from section *Hemiorbilia* because of an inconsistent or even predominant (*O. clavipisca*) presence of ascus apical thickenings. Also section *Lentiformes* comprises taxa with a similar ascus apex structure, but differs in SB morphology, being either ± lens-shaped and very broadly attached, or ± lantern-shaped and narrowly attached, mostly with a short to long filum.

Series delimitation. Section *Hemiorbilia* includes three series, *Hesperideae*, *Hemiorbilia*, and *Vibrioides*, which are mainly separated by ascospore morphology and the thickness of the apical ascus wall, although spore shape is rather diverse within each series. Polyspory characterizes various members of series *Hesperideae* and *Vibrioides*, but is entirely absent in series *Hemiorbilia*. In series *Hemiorbilia* only a few of the lower



Phylogenetic analysis 9. Phylogram of section *Hemiorbilia* inferred from ML analysis of combined ITS1-5.8S-ITS2+LSU (D1–D2) rDNA dataset (57 sequences, 1309 positions, aligned with MUSCLE) using the GTR+G+I model in MEGA6 (500 replicates). An environmental strain from GenBank represents an unidentified species (O2). The tree is rooted with *Lilapila oculispora*. RefSpec = reference specimen, T = type, ET = epitype, TT = topotype. * = without LSU, ** = only partial LSU (D1).

spores are inverted in the asci, while in the other two series the proportion of inverted and not inverted spores is more equal. Glassy processes inconsistently occur in many species but are absent in series *Vibrioides*. Cashew-shaped or falcate ascospores occur in about 20 % of the species of series *Hesperideae* and in > 50 % of series *Vibrioides*, but are absent in series *Hemiorbilia*. The main characteristic of series *Hemiorbilia* is the basal tail of the spores which, however, also occurs in some multispored taxa of series *Hesperideae*. A pruinose disc and margin is characteristic of 64–128-spored species of series *Vibrioides* but not observed in 8–16-spored species of that group.

Anamorph. Members of section *Hemiorbilia* are characterized by anamorphs with staurosporous, sometimes 3-dimensional conidia formed on short conidiophores. These include different conidial types that are defined by the number and orientation of arms and by different branching types. Trinacrium-like conidia with one stipe and two arms are the prevalent case, but higher branching types (descalsia- and dwayaangam-like) also occur in two series (for series *Vibrioides* no certain connections to anamorphs are known), whereby descalsia-like conidia are so far only known in series *Hemiorbilia*. Rarely vermispora-like phragmoconidia are formed in series *Hesperideae* (*O. myriofusiclava*, *O. georgiana*).

Phylogeny. In our phylogenetic analysis of SSU+ITS+LSU in Baral et al. (2017b), section *Hemiorbilia* formed a monophyletic clade though without support and partially high distance among the clades. When analysing ITS+LSU, ITS, or LSU (Phyls 9–12, S13) seven main clades can be recognized. Except for the unsupported *cryptogena-sarothamni* clade, which received strong support in the ITS tree (Phyl. 10), and the medium supported *occulta-spermoides* clade, all received very strong support in the combined analysis (Phyl. 9). These seven clades clustered unresolved within section *Hemiorbilia*, with two exceptions: (1) the two clades which constitute series *Hemiorbilia* clustered with medium support in a clade when analysing ITS+LSU; (2) the *hesperidea-alpigena* clade and the *aprilis-crenatovinosa* clade clustered in a medium supported clade in the analysis of ITS (Phyl. 10, in some not shown analyses under the same conditions even strongly supported).

Morphologically these clades differ from each other only to some extent. For instance, series *Hemiorbilia* includes species with distinct, more or less thin ascospore tails and consistently 8-spored asci. However, an 8-spored sample with long and thin spore tails (*O.* cf. *angustoaristata*) is found in the *vinosa-velutina* clade, in which otherwise only species with very indistinct spore tails occur. *O. occulta*, the type species of series *Hemiorbilia*, and *O. spermoides* clustered distant from the bulk of series *Hemiorbilia* though having long and thin spore tails. Despite these discrepancies we included all these taxa in series *Hemiorbilia* because of their high morphological similarity.

In the overlapping 362 nt of available SSU sequences (V8–V9) the observed variation was 1–1.5% as a maximum, (see Phyl. S11). Many species of section *Hemiorbilia* are identical in this region, for instance, *O. aprilis*, *O. hesperidea*, and *O. aristata*, although belonging to different relationships. Also to other sections of *Orbilia* the differences in this gene region are few or even absent regarding some taxa of section *Lentiformes*. Therefore, the V8–V9 region is of little use in phylogenetic analyses of the genus *Orbilia*.

The rDNA gene regions which are available at present do not permit any conclusion about where section *Hemiorbilia* might be positioned within the genus *Orbilia* and which of its clades comprises a majority of taxa with plesiomorphic characters. From a morphological point of view it would seem logical that long and thin spore tails represent an apomorphic character. With this hypothesis it can be concluded that polyspory, which occurs in many members of section *Hemiorbilia* but so far in none of series *Hemiorbilia*, was an ancestral character state within the group.

Specific nucleotide positions. Molecular motifs in the SSU V8–V9, ITS, or LSU D1–D3 specific to the entire section *Hemiorbilia* have not been found. Two positions in the LSU D1–D2 (292: AGCTC**A**AA, 591: GAGG**T**CCGCG) are consistent within section *Hemiorbilia* and concur with most remaining *Orbilia* spp., except for section *Lentiformes* which here agrees with almost all basal genera (292: AGCTC**T**AAA, 591: GAGG**A**CCGCG, see also under section *Lentiformes*, p. 549).

A rare deviation near the 5'-end of LSU is unique for section *Hemiorbilia* (pos. 70: CAAC**C**GGGA), but occurs there only in some of its members: *O. vinosa* (including H.B. 6748g), *O.* aff. *vinosa* (bhi-F731), *O. multicurvula*, *O. nothoaprilis*, *O. georgiana*, *O. crenatovinosa*, *O. spermoides*, *O. occulta*, *O.* cf. *angustoaristata*, series *Vibrioides*, and *O. gemma*. All other orbiliaceous LSU sequences have instead CAAC**A**GGGA, including most members of series *Hemiorbilia* and *Hesperideae*, even *O. subvinosa* and *O. aprilis* which are closely related to *O. vinosa* and *O. crenatovinosa*, respectively.

Ecology. All members of section *Hemiorbilia* are desiccation-tolerant and occur worldwide, ranging from boreal to tropical and from humid to arid areas. They mainly inhabit woody but also herbaceous substrates including leaves, rarely hepatics.

Key to species of section *Hemiorbilia*

1. Asci 32- up to 128-spored 2
1. Asci 8- or 16-spored .... **key C**

2. Ascus apical wall immature †0.5–2.5(–3.5) µm thick; exudate never forming warts on the hymenium; crystalloid SCBs present or absent .... **key A**
2. Ascus apical wall immature †(2–)3–4(–6) µm thick; rough yellowish exudate often provoking a warted hymenium and radial ribs at the margin; crystalloid SCBs absent; all species from western Australia .... **key B**

Key A (series *Hesperideae* p.p., asci 32–128-spored)

1. SBs narrowly rod-shaped, spores *6.8–12.8 × 3.2–4.6 µm .... see ***O. macroasca*** (section *Lentiformes*), p. 507
1. SBs elongate tear-shaped to ± globose, if rod-shaped then spores narrower 2

2. SBs (sub)globose, often laterally inserted (somewhat below the middle) but also apically; spores clavate-oblong, with obtuse apex and slightly tapered, ± curved base, *6.8–11.5 × 2.2–3 µm; asci 64-spored; bark of *Acacia*, subtropical arid .... ***O. myrioauris***, p. 670
2. SBs strictly apical 3

3. Spores predominantly distinctly curved 4
3. Spores straight or only slightly (exceptionally strongly) curved 8

4. Spores *6.8–9.5(–10) × 1.3–1.5(–1.6) µm, quite consistently strongly falcate; SBs vermiform to subulate; asci 32-spored; apothecia with prominent teeth made up of long glassy processes; bark of *Eremaea* & *Hibbertia*, subtropical semihumid western Australia .... ***O. multicurvula***, p. 636

4. Spores min. *2–2.5 µm wide; apothecia without teeth 5

5. Spores *2–2.7 µm wide, fusoid-clavate, slightly to strongly curved near base; asci 64-spored 6
5. Spores *3–4.5 µm wide, ± cashew-shaped, or ± lunate with a thin tail; asci 32–64-spored 7

6. Spores †9–12 × 2.3(–2.4) µm, slightly to medium curved, with obtuse apex and distinct thick tail; bark of *Acacia*, subtropical semiarid western Australia .... ***O. myriohesperidea***, p. 589
6. Spores *(5–)6–8.5(–10.5) × (2–)2.2–2.5(–2.7) µm, slightly to very strongly curved, with obtuse to acute apex and ± attenuated base; bark of *Acacia*, *Jacksonia*, subtropical semihumid to semiarid western Australia .... ***O. myriofusiclava***, p. 653

7. Spores *(8–)9.5–13(–16) × (3–)3.5–4.5 µm, ± cashew-shaped, without tail; SBs tear-shaped; asci 32-spored; wood of *Larrea*, subtropical (semi)arid western North America .... ***O. cryptogena***, p. 662
7. Spores *(5.7–)6.3–7(–8) × (3–)3.3–3.6 µm, with ellipsoid-lunate head and an abrupt, thin, strongly bent tail; SBs almost globose; asci 64-spored; bark of *Acacia*, (sub)tropical (semi)arid western Australia .... ***O. myriomuscula***, p. 666

8. Spores *1.3–2.5 µm wide 9
8. Spores *2.7–4.5 µm wide 11

9. Spores *5.5–8 × 1.7–2.5 µm, ellipsoid-fusoid, without tail-like base; asci (64–)128-spored; apothecia ± hairy; wood of *Eucalyptus*, subtropical semiarid western Australia .... ***O. velutina***, p. 638
9. Spores *9–14.5 µm long, often with a tail-like base or tail; asci 32–64-spored; apothecia smooth 10

10. Asci 32-spored; spores *12–14.5 × 1.8–2 µm; wood of *Allocasuarina*, subtropical arid central Australia .... ***O. multivinosa***, p. 633
10. Asci 64-spored; spores †9–12 × 2.3(–2.4) µm; bark of *Acacia*, subtropical semiarid western Australia .... ***O. myriohesperidea***, p. 589

11. Asci 64-spored, †(9.5–)10–11.5(–12.5) µm wide; spores *(9–)10–12.5(–15) × 3.5–4(–4.5) µm, straight, with ellipsoid head and abrupt, thick tail; bark of *Acacia*, (sub)tropical (semi)arid western Australia .... ***O. myrioaustraliensis***, p. 564
11. Asci 32-spored, †(6.5–)7–9(–9.5) µm wide; spores *(2.7–)2.9–3.5(–3.8) µm wide 12

12. Spores †13–16 µm long, consistently with a distinct tail ~4.5–6.5 × 0.9–1.4 µm; bark of *Acacia*, subtropical semiarid western Australia .... ***O.* aff. *macrocarpa***, p. 570
12. Spores max. *12.5 µm long 13

13. Apothecia 0.4–1 mm diam., 0.2–0.4 mm high, often laterally compressed, with a 20–50 µm protruding margin; spores †8–12 µm long, with or without a short tail; bark of *Acacia*, subtropical (semi)arid western Australia .... ***O. macrocarpa***, p. 568
13. Apothecia 0.2–0.5 mm diam., 0.1–0.2 mm high, ± round, margin 0–10 µm protruding 14

14. Spores not attenuated in a tail-like base, *5–8(–8.5) µm long; with only globose SCBs; bark & wood of *Cytisus*, supra(sub)mediterranean semihumid southern Europe .... ***O. sarothamni***, p. 668
14. Spores often attenuated in a tail-like base or a distinct tail, usually longer than 7 µm; with crystalloid SCBs 15

15. Spores *(5.7–)7–8.7(–10.5) µm long, rarely with a distinct tail; SBs 1.5–2 µm long; petioles of *Livistona*, subtropical subhumid eastern Australia .... ***O. palmicola***, p. 567
15. Spores *(8.3–)9–11.5(–12.5) µm long, often with a distinct, rather narrow tail; SBs (2–)2.5–3 µm long; wood of *Acacia*, subtropical (semi)arid western & central Australia .... ***O. multiaustraliensis***, p. 564

Key B (series *Vibrioides* p.p., asci 32–128-spored)

1. Most of the spores slightly to strongly curved; asci (32–)64-spored 2
1. Spores ± straight, exceptionally slightly bent below, max. 7(–9) µm long; asci (32–)64–128-spored 6

2. Spores *(10–)11–16(–17) × (1.4–)1.5–1.7 µm, slightly to strongly falcate to geniculate; SBs apically attached, 2.8–4(–4.5) µm long; bark of *Acacia*, subtropical semiarid .... ***O. angustoobliqua***, p. 764
2. Spores max. 12 µm long, min. 1.7 µm wide 3

3. Spores *(4–)4.5–5.5 × 1.7–1.9(–2.1) µm, strongly curved (falcate to helicoid); SBs apically attached, 2.2–2.8 µm long; asci *9.7–10.7 µm wide [†8.5–9.5(–10) µm]; bark of *Acacia*, subtropical semiarid .... ***O. curvatiobliqua***, p. 761
3. Spores *6–12 µm long; asci *11–12 µm wide [†(8–)9–11(–11.5) µm] 4

4. Spores predominantly distinctly helicoid, *(6–)6.5–10.5(–12.8) × (1.8–)2–2.3(–2.5) µm; SBs apically attached, 3–4(–4.3) µm long; bark & wood of *Acacia*, subtropical semiarid .... ***O. helicoobliqua***, p. 760
4. Spores not or only indistinctly or exceptionally helicoid 5

5. Spores *6–8(–9.5) × (1.7–)1.8–2.1(–2.4) µm, ± L-shaped, often constricted in middle part (dumbbell-shaped); SBs predominantly subapically attached, 2–3.2 µm long; asci *(55–)60–80(–88) µm long (†45–58 µm), pars sporifera *30–57 µm long; bark & wood of *Acacia*, subtropical semiarid .... ***O. anguliobliqua***, p. 758
5. Spores *(6.5–)7.5–10(–11.7) × (1.8–)2–2.5(–2.6) µm, falcate (C- to L-shaped), also ± straight, never constricted; SBs apically attached, 3–4 µm long asci *78–105 µm long (†73–85 µm), pars sporifera *52–70 µm long; wood of *Eucalyptus*, subtropical arid .... ***O. allantoobliqua***, p. 762

6. SBs consistently apically attached 7
6. SBs consistently subapically attached 8

7. Asci 128-spored; spores *(5–)5.5–7(–8) × (1.6–)1.7–1.9(–2.2) µm; SBs 1.7–2.5(–3) µm long; bark of *Acacia*, subtropical semiarid .... ***O. paraobliqua***, p. 757
7. Asci 64-spored; spores *(5.8–)6.5–8(–9) × 2.2–2.4 µm; SBs (2.3–)2.6–3.8 µm long; bark of *Acacia*, subtropical semiarid (compare also *O. allantoobliqua*).. ***O.* cf. *paraobliqua***, p. 757

8. Asci 128-spored, *12.5–15.7 µm wide; spores *4.3–5.8 × 2–2.3 µm, cylindrical; bark of *Acacia*, subtropical arid.... ***O. pleistoobliqua***, p. 755
8. Asci (32–)64-spored, *8.5–12(–12.5) µm wide; spores *(4.3–)4.5–6.5(–7) × (1.8–)2–2.7(–3.2) µm, cylindrical to ± clavate; bark & wood of various angiosperms, leaves of *Cycadales*, (sub)tropical semihumid to arid.. ***O. myrioobliqua***, p. 753

Key C (section *Hemiorbilia*, asci 8- or 16-spored)

1. SBs laterally attached (at the ± protruding central part).. 2
1. SBs apically or subapically attached 5

2. Apothecial margin ± smooth; spores heart-shaped to triangular; asci 8–16-spored (series *Hesperideae*)..3
2. Apothecial margin dentate by long glassy processes; spores ± triangular or like a bird's head; asci 8-spored; subtropical semihumid western Australia (series *Hemiorbilia*) 4

3. Asci 16-spored; crystalloid SCBs present; spores heart- to kidney-shaped, *(5–)6–8(–9.5) × 3–4.2(–4.5) µm; bark or rarely wood of predominantly *Fabales*, temperate to tropical, humid to arid atlantic and southern Europe, eastern Asia, Australia, Africa, Macaronesia .... ***O. corculispora***, p. 656
3. Asci 8-spored; crystalloid SCBs absent; spores ± triangular to almost heart-shaped, *(6–)7–9(–10.5) × 4.2–5.5 µm; wood of *Pinus*, *Gleditsia*, *Ulex*, mediterranean semihumid southern Europe .... ***O. octocorculispora***, p. 660

4. Spores *(3.5–)4–6(–7) × (3.3–)3.5–4 µm, basal end short tapered, without a tail; bark & wood of *Chamelaucium* & *Verreauxia* .... ***O. triangulispora***, p. 744
4. Spores *(6–)7–8(–9) × 2.8–3.3(–3.8) µm, basal end attenuated in a very short tail (max. half as long as head); bark of *Banksia*. .... ***O. aviceps***, p. 742

5. Spores with a rather abrupt, thin or thick tail, i. e., a cylindrical or constricted basal end which is at least 3 × longer than wide, base of tail sometimes swollen; asci always 8-spored .... **key D (series *Hemiorbilia*)**
5. Spores without an abrupt tail but often with a gradually attenuated, tail-like base, if with distinct tail then asci 16-spored ... . **key E (series *Hesperideae* & *Vibrioides* p.p.)**

Key D (series *Hemiorbilia*, asci 8-spored)

1. Spore tail 2/3 up to 3 × the length of head, predominantly < *0.8 µm wide at its narrowest part, basal end sometimes swollen to 1–2 µm; apothecial margin nearly always with short to long glassy processes 2
1. Spore tail max. 2/3 the length of head, predominantly > *0.7 µm wide at its narrowest part, basal end swollen or not; glassy processes absent or present 19

2. Spore head predominantly < *2.6 µm wide, symmetrical, tail usually shorter than head 3
2. Spore head predominantly > *2.6 µm wide, symmetrical or asymmetrical 10

3. Spores *5–9 µm long, head broadly ellipsoid or fusoid..4
3. Spores *12–21 µm long, head elongate, narrowly ellipsoid.. 5

4. Apothecia with very prominent teeth; spores *5.5–7 × 1.6–1.7(–1.9) µm, head broadly ellipsoid, tail *2–3.2 × 0.2–0.3 µm; bark of *Eucalyptus*, subtropical semihumid western Australia .... ***O. nanosperma***, p. 737
4. Apothecia ± smooth; spore tail †~ 1–2 × 0.5 µm..***O. aprilis***, p. 645 (key H)

5. Spores †12.3–14 × 1.8–2.1 µm, tail 2.5–3.5 µm long; leaves of *Dryas*, (sub)alpine humid Europe .... ***O.* cf. *angustoaristata***, p. 701
5. Spore tail 3.5–8 µm long 6

6. SBs mainly rod-shaped to subulate, (2–)2.5–3.5 × 0.4–0.5 µm; spores *12–15(–17) × 1.6–2.4 µm, tail never inflated at base; crystalloid SCBs present; glassy processes 0–20 µm long; bark & wood of *Acacia* & *Pittosporum*, temperate subhumid eastern and subtropical arid central Australia .... ***O. angustoaristata***, p. 700
6. SBs cylindrical to tear-shaped, min. 0.6–0.8 µm wide..7

7. Spores *(11–)12–16.5(–18) × (2.3–)2.4–2.6(–2.7) µm, tail 4–7(–8) µm long; SBs (0.8–)1–1.2(–1.4) µm wide, often dumbbell-shaped; only globose SCBs present; glassy processes 0–10(–20) µm long; bark of *Cornus*, *Frangula*, warm-temperate humid eastern North America, cold-temperate central Europe .... ***O. clavuliaristata***, p. 706
Similar collections were on *Phragmites* (Luxembourg) and *Euphorbia* (Macaronesia, p. 709). A doubtful Pyrenean collection on *Cornus* mentioned under *O. frullaniae* differs in wider, tear-shaped SBs, less distinct spore tails, and crystalloid excipular SCBs (p. 704).
7. Spores *2–2.4 µm wide; SBs max. 1 µm wide (but overmature wider)..8

8. Spores *11.5–13.5 × 2–2.2 µm; SBs 1.6–2.2 µm long, ± tear-shaped; glassy processes 6–16 µm long, forming a crenulate margin; apothecia light cream-orange; bark of unidentified angiosperm, subtropical humid eastern Asia............................***O. brevicauda***, p. 705
8. Spores *(11.5–)14–21 × 2.1–2.5 µm; SBs 2–3.8 µm long, cylindrical to tear-shaped; glassy processes 20–60 µm long, forming distinct teeth at the margin; apothecia bright rose-red 9

9. SBs 2–3 µm long; spores *(11.5–)14–16(–17.5) µm long; lower (1–)2(–4) spores inverted; only globose SCBs present; on *Frullania* (on *Prunus*), cold-temperate humid subatlantic Europe .... ***O. frullaniae***, p. 704

A similar collection on *Cornus* bark from the Pyrenees possesses crystalloid SCBs (p. 704).

9. SBs 3–3.8 µm long; spores *14–17(–21) µm long; lower 0(–1) spores inverted; with or without crystalloid SCBs; bark of *Dodonaea*, subtropical semiarid western Australia .... ***O.* cf. *angustoaristata***, p. 701

A collection on bark of *Eucalyptus* (Pl. 526: 2), mentioned under *O. pseudoflagellispora* (section *Aurantiorubrae*, p. 951) and *O. flagellispora*, differs in slightly larger spores (*19–22 × 2.2–2.6 µm) with often one septum (overmature) and always slightly inflated tail base.

10. Spore heads strongly asymmetrical (± triangular), tail base always distinctly swollen; western Australia 11

10. Spore heads bilateral symmetrical or only slightly inequilateral 12

11. Spores *(13–)14–18(–19) × 3.8–4.7 µm (in profile view), often with a craw-like swelling below the head; marginal teeth 60–110 µm broad, 7–10 per apothecium; bark & wood of *Chamelaucium* & *Eucalyptus*, subtropical semihumid .... ***O. aviaristata***, p. 740

11. Spores *(18.5–)20–25 × 2.8–3.3(–3.6) µm (in profile view), never with a craw-like swelling; marginal teeth 20–80 µm broad, 15–22 per apothecium; bark & wood of *Acacia*, subtropical semiarid .... ***O. aviflagellata***, p. 738

12. Margin with 60–210 µm long, narrow hairs with thick walls and a septate lumen up to the apex; spores *19–21 × 3.9–4.2(–4.7) µm, with long and thin tails; bark of *Dodonaea*, subtropical semiarid western Australia .... ***O. fimbriata***, p. 728

12. Margin with 10–100 µm long glassy processes without lumen; spore heads predominantly < 3.8 µm wide 13

13. Spore heads subglobose to ovoid, ~1.2–1.8 × longer than wide; SBs 1.8–2.5 µm long 14

13. Spore heads ~2–3(–4)× longer than wide; SBs mostly > 2.5 µm long; SCBs never crystalloid 16

14. Apex of paraphyses uninflated or slightly spathulate, without exudate (or only fine granules); spores *(9–)12–17(–18.5) × 3.2–3.8(–4) µm, tail distinctly longer than head; crystalloid SCBs present in both paraphyses and excipulum; bark of conifers, cold-temperate to boreal (sub)humid western North America, orosubmediterranean humid southern Europe .... ***O. spermoides***, p. 734

14. Apex of paraphyses partly slightly to strongly capitate-clavate, covered by 0.3–3 µm thick refractive exudate; angiosperm bark 15

15. Spores *(9.5–)10–12(–13) × (2.8–)3–3.4(–3.6) µm, apex obtuse, tail shorter or only very slightly longer than head; crystalloid SCBs present in ectal excipulum; bark of *Cornus*, *Malus*, *Vitis*, temperate to subtropical humid eastern North America .... ***O. occulta***, p. 730

15. Spores *13–17 × 2.8–3 µm, apex subacute to acute, tail much longer than head; only globose SCBs present; bark of *Acacia*, subtropical semihumid western Australia .... ***O. austroocculta***, p. 733

16. Spores *(9.7–)10–12.5(–14) × 2.8–3.4 µm, head ellipsoid(-subfusoid), tail (2–)3–5.3(–6) µm long, shorter than head or only exceptionally slightly longer, basally uninflated; glassy processes 10–40 µm long; bark of *Ulex*, stems of *Rubus*, temperate humid, atlantic to subcontinental Europe .... ***O. breviaristata***, p. 724

A tropical humid eastern Australian collection on *Phragmites* deviates by shorter spores due to a shorter tail of 2.5–3.5 µm length (p. 725).

16. Spores min. *13–18 µm long, tail slightly to much longer than head, if shorter then basally inflated 17

17. Spore head 9–12.5 µm long, elongate-ellipsoid(-subfusoid), 3–4 × longer than wide; spores *(14–)16–26.5(–28.5) × (2.3–)2.6–3.3(–3.6) µm, tail base slightly to very strongly bulbous (*0.7–2.5 µm thick); apothecia with prominent teeth or nearly without; bark (& wood, rarely leaves) of gymno- & angiosperms, temperate to submediterranean (semi)humid Europe, subarctic to boreal humid Northern and subtropical semiarid Middle America .... ***O. flagellispora***, p. 695

17. Spore head 7–10 µm long, broadly ellipsoid(-subfusoid), 2–3 × longer than wide 18

18. Apothecial margin usually with prominent whitish teeth; spores *(16–)18.5–24.5(–27) × (2.5–)3–3.5(–3.8) µm, tail (10–)11–15(–16.5) µm long, base slightly to often distinctly inflated to *0.5–1.8 µm; bark (& wood) of various angio-, rarely gymnosperms, (sub)mediterranean semihumid to (oro)temperate humid, atlantic to subcontinental Europe, subtropical semiarid Macaronesia .... ***O. subaristata***, p. 719

18. Apothecial margin smooth or often with small, inconspicuous teeth; spores *(13–)14–22(–23) × (2.5–)2.7–3.3(–3.5) µm, tail (6–)8–12(–13) µm long, base not or only slightly inflated to *0.3–0.8 µm; bark (& wood) of various angio- & gymnosperms, boreal to submediterranean (sub)humid Europe, central Asia, western North America .... ***O. aristata***, p. 709

19. Spores *9–12.5 × 4.3–4.8 µm, tail much shorter than head; SBs 3–3.5 × 2–2.2 µm; margin with 20–30 µm long glassy processes; bark of *Eucalyptus*, warm-temperate humid eastern Australia .... ***O. megaocculta***, p. 727

19. Spores max. *3.8 µm wide; SBs max. 1.4 µm wide.......... 20

20. With small crystalloid SCBs in paraphyses and marginal excipulum; spores *(9–)11–14(–15) × 2.4–2.7 µm, SBs (3–)4–5(–5.5) µm long; wood of *Frangula*, temperate humid central Europe .... ***O. breviclava***, p. 689

20. Consistently without crystalloid SCBs 21

21. SBs 2–3 µm long 22

21. SBs 3–6 µm long 25

22. Margin with 4–30 µm long glassy processes; spores *9–12 × 2.3–2.6 µm; SBs 2.2–2.5 µm long; petioles of *Livistona*, subtropical subhumid eastern Australia .... ***O. parviclava***, p. 688

22. Margin without glassy processes 23

23. Spores (11–)12–17(–19) × (2.1–)2.3–2.8(–3.2) µm, western North America ....see ***O. navajoana* (series *Hesperideae*)**, p. 571

23. Spores *9–13 µm long.......... 24

24. Spores *9–12(–13) × 2.1–2.4 µm, with fusoid head; wood of *Melaleuca*, subtropical subhumid eastern Australia .... ***O.* aff. *parviclava*** (Pl. 318: 2)

24. Spores *10.5–13 × 2.4–3 µm, with cylindrical head; wood of *Larrea*, subtropical semiarid western North America .. ***O.* aff. *breviclava***, p. 690

25. Spores *11–14 µm long; margin without glassy processes .... compare ***O*. *breviclava*** (on *Frangula*), p. 689, and ***O*. cf. *subclavuliformis*** (on *Pinus*), p. 691
25. Spores *13–21 µm long 26

26. Spore tail always distinctly inflated at the base, spore head ellipsoid, *3.3–3.8 µm wide; SBs 3–4 µm long; glassy processes 20–70 µm long; bark & wood of *Salix*, orotemperate humid southwestern Europe .... ***O*. *asturiensis***, p. 686
26. Spore tail never inflated (or spores distinctly narrower); SBs 4–6 µm long 27

27. Spore head ellipsoid, *(2.5–)2.8–3.5(–3.7) µm wide; glassy processes always present, 3–5 up to 10–25(–40) µm long; wood & bark of gymno- & angiosperms, atlantic to continental, temperate to mesosubmediterranean (semi)humid Europe, hemiboreal to cold-temperate humid eastern & western North America .... ***O*. *clavuliformis***, p. 680
27. Spore head (sub)cylindrical, *2.2–2.7(–3) µm wide; glassy processes absent or up to 5(–7.5) µm long; wood & bark of gymno- & angiosperms, temperate humid to subtropical semihumid Europe, Macaronesia .... ***O*. *subclavuliformis***, p. 690

Key E (series *Hesperideae* & *Vibrioides* p.p., asci 8- or 16-spored)

1. Spores < 6 µm long, strongly cashew-shaped; asci 8-spored 2
1. Spores > 6 µm long 3

2. SBs filiform, 1.8–2.8 × 0.3–0.4 µm, turning tear-shaped only when overmature; spores *3.4–4.2(–4.7) × (1.4–)1.5–1.8(–1.9) µm; terminal cells of paraphyses 4–9.5 µm long; culms of *Phragmites* & *Ammophila*, temperate humid, atlantic to subcontinental Europe .... ***O*. *graminis***, p. 750
Collections on wood & bark of *Pinus sylvestris* from orosubmediterranean Europe differ in slightly larger spores of */†(3.8–)4.2–5.3(–5.8) × 1.5–1.8(–2.2) µm and slightly longer terminal cells of paraphyses (7.5–12 µm), p. 751.
2. SBs tear-shaped to globose, 1–2 × 0.7–1.3 µm; spores *(3.5–)3.8–5(–5.3) × (1.8–)2–2.5(–3.3); terminal cells of paraphyses 6–15 µm long; wood & bark of gymno- & angiosperms, orotemperate humid to subtropical semihumid Europe, Macaronesia, western North America .... ***O*. *vibrioides***, p. 747

3. Paraphyses spathulate to lageniform, firmly covered also laterally by a thin exudate; spores *(6.5–)8–11(–11.5) × (1.5–)1.6–1.8(–2) µm cylindric(-clavate); SBs ± ampulliform, 1.5–2.7 × 0.7–1 µm; marginal hairs 7–20 µm long, 0–1-septate, glassy processes absent; asci without apical thickening; wood of *Abies*, *Lonicera*, temperate to boreal (sub)humid western North America, central Asia .... ***O*. *concoloris***, p. 672
3. Paraphyses not spathulate-lageniform, usually loosely covered by thick cloddy exudate; asci with apical thickening 4

4. Spores often distinctly curved, without tail 5
4. Spores ± straight, sometimes with curved tail 8

5. Spore width < 2.3 µm; crystalloid SCBs present or absent; asci 8-spored; western Australia 6
5. Spore width > 2.7 µm; crystalloid SCBs present; asci 8–16-spored; Europe, America 7

6. Spores consistently strongly falcate, *(8–)10–13.5(–14.5) × (1.6–)1.8–2(–2.2) µm; SBs pear-shaped; crystalloid SCBs absent; bark of *Banksia*, subtropical semihumid .... ***O*. *curvatinavajoana*** (series *Hesperideae*), p. 575
6. Spores ± helicoid, *15–18 × 1.4–1.6(–1.7) µm; SBs ± subulate; crystalloid SCBs present; bark of *Acacia*, subtropical semiarid .... ***O*. *helicovinosa***, p. 630

7. Asci 16-spored; spores *(6–)6.5–8(–8.5) × 2.8–3.6 µm; SBs broadly tear-shaped, without filum; wood & bark of *Baccharis*, subtropical subhumid southeastern Northern America .... ***O*. *subcryptogena***, p. 665
7. Asci 8-spored; spores *11–18.7 × 3.5–5 µm; SBs rod-shaped, with short filum; bark of *Cercis* & *Ulmus*, southern & eastern Europe .... see ***O*. *cercidicola*** (section *Lentiformes*), p. 501

8. SBs ± globose, sometimes with a triangular upper part and/or a short filum .... see **section *Ovoideae* (subgenus *Orbilia*)**, compare also ***O*. *arizonensis*** (Pl. 213: 2)
8. SBs rod- to tear-shaped or ampulliform, min. 2 × as long as wide, without a filum .... (**series *Hesperideae***) 9

9. Asci 16-spored .... **key F**
9. Asci 8-spored 10

10. Spores min. *(2–)2.2–2.4 µm wide .... **key G**
10. Spores *1.3–2.2 µm wide .... **key H**

Key F (series *Hesperideae* p.p., asci 16-spored)

1. Spores *(11.5–)13–19(–21.5) × 1.6–2 µm; apothecial margin smooth, without glassy processes; wood of *Eucalyptus*, subtropical semiarid western Australia .... ***O*. *pleiovinosa***, p. 632
1. Spores min. *2–2.4 µm wide 2

2. Spores narrowly cylindrical to fusoid, *9.5–19 µm long, length/width ratio predominantly 4(–6) 3
2. Spores broadly (fusoid-)ellipsoid(-clavate), *6–13.5 µm long, length/width ratio 2–3 9

3. Without crystalloid SCBs; spores *(9.5–)11–14(–16) × (2–)2.2–2.6(–2.8) µm, base slightly to strongly attenuated; without glassy processes; wood of angiosperm shrubs, subtropical to temperate, semiarid to subhumid western North America .... ***O*. *pleionavajoana***, p. 573
3. With crystalloid SCBs 4

4. Spores *9.5–10.5 × 2–2.4 µm, SBs ?2 × 1 µm; *Larrea*, subtropical semiarid western North America .... ***O*. aff. *pleionavajoana***, p. 575
4. Spores *(10–)12–18.5 µm long 5

5. Spores *3–4(–4.5) µm wide 6
5. Spores *2–3(–3.2) µm wide 7

6. Spores with a distinct short tail-like base or tail; SBs 3–4.5 × 1–1.2 µm; wood of *Eucalyptus*, subtropical semiarid western Australia .... ***O*. aff. *pleioaustraliensis***, p. 562
6. Spores without a tail-like base; SBs ~2.5 × 1.5 µm; wood of *Parkinsonia*, subtropical semiarid western North America .... ***O*. aff. *megahesperidea***, p. 592

7. Margin with short glassy processes forming indistinct teeth; SBs 0.8–1 µm wide; spores *2–2.6 µm wide; wood & bark of *Acacia*, (sub) tropical arid western & central Australia .... ***O*. *pleiocoronohesperidea***, p. 586
7. Margin without glassy processes; SBs min. 1.2–1.3 µm wide 8

8. Spores *2.8–3(–3.2) µm wide; petioles of *Livistona*, subtropical subhumid eastern Australia .... ***O*. *pleiohesperidea***, p. 582
8. Spores *(2–)2.2–2.5(–2.6) µm wide; wood of *Acacia*, subtropical semiarid western Australia .... ***O*. aff. *pleiocoronohesperidea***, p. 588

9. Apothecia 0.2–0.8 mm diam., 0.13–0.3 mm high; spores *(7.5–)9–12(–13.5) × (2.7–)3.2–4.2(–4.7) µm; SBs 2.5–4.5 µm long; wood & bark of angiosperms, subtropical sub- and semihumid to arid Australia .... ***O*. *pleioaustraliensis***, p. 560
9. Apothecia 0.07–0.35 mm diam., 0.06–0.1 mm high; spores *(6–)7–9(–10.2) × (2.3–)2.5–3.5(–4) µm; SBs 2–3 µm long; culms of *Juncus roemerianus*, temperate humid eastern North America .... ***O*. *junci*** (?series *Vibrioides*), p. 766

Key G (series *Hesperideae*, asci 8-spored, spores predominantly > *(2–)2.2 µm wide)

1. With crystalloid SCBs (sometimes only in marginal excipulum) 2
1. Without crystalloid SCBs 10

2. Spores *(2.7–)3–4(–4.3) µm wide; SBs (0.9–)1.2–2(–2.3) µm wide; without glassy processes 3
2. Spores *(2–)2.3–3(–3.3) µm wide; SBs 0.6–1.5 µm wide; sometimes with glassy processes 6

3. Spores *(6.2–)7–9(–11) × (4–)4.5–5.5(–6) µm, broadly ellipsoid to ovoid; SBs tear- to pear-shaped, 3–5.5 × 1.7–2.3 µm; wood (& bark) of angio- & gymnosperms, temperate humid to semiarid western North America .... ***O*. *arizonensis***, p. 553
A sample from eastern North America on wood of *Carya* mentioned under *O. eremaeae* (section *Ovoideae*) has similar spores but almost globose SBs (p. 1286).
3. Spores predominantly > 9 µm long and < 4.5 µm wide 4

4. Spores *(8–)9–14(–16) × (2.5–)2.7–4(–4.3) µm, narrowly to broadly ellipsoid-fusoid; SBs 2.5–5.5 × 1–1.8 µm; wood & bark of various angiosperms, (sub)tropical semihumid to arid western & central Australia .... ***O*. *australiensis***, p. 556
4. Spores predominantly > 14 µm long, cylindric-clavate 5

5. Spores *(11.2–)14–17(–19.5) × (2.7–)3–3.5(–4) µm; SBs *4–5.8 × 1.3–2.3 µm; bark of *Ephedra*; subtropical semiarid western North America .... ***O*. *macrohesperidea***, p. 590
5. Spores *(14.5–)16–20(–21) × 3.4–4.4 µm; SBs 3–4 × 1.7–2 µm; bark of *Pittosporum*, temperate subhumid eastern Australia .... ***O*. *megahesperidea***, p. 591

6. With 3–40 µm glassy processes; spores *(12–)14–18(–19) µm long 7
6. Without glassy processes; spores *(7.5–)9–27(–30) µm long 8

7. Spores *(2–)2.3–3 µm wide; wood & bark of *Acacia*, petioles of *Livistona*, (sub)tropical sub- and semihumid to arid Australia .... ***O*. *coronohesperidea***, p. 583
7. Spores *(1.8–)2–2.4(–2.7) µm wide; Europe & North America .... see under 9 (*O. angiosubvinosa*)

8. Spores *(13–)18–27(–30) × 2–2.7(–3) µm; SBs 2.5–3.8 µm long; bark of *Adenocarpus*, supramediterranean semihumid Macaronesia .... ***O*. *adenocarpi***, p. 674
8. Spores max. 18–19 µm long; SBs partly longer than 4 µm 9

9. Spores *(7.5–)9–15(–18) × (1.9–)2.2–3(–3.3) µm; SBs 2.5–5 µm long; wood & bark of gymno- & angiosperms, warm-temperate to thermo-mediterranean humid to semiarid southern Europe, Macaronesia, Australia, western & southern North America .... ***O*. *hesperidea***, p. 576
Spore shape varies between cylindric-clavate and fusoid. If the spores are fusoid and > 2.7 µm wide compare *O. australiensis* (p. 556). Two collections on *Larrea* mentioned under *O. navajoana* (p. 572) deviate from *O. hesperidea* by < 3 µm long SBs.
9. Spores *(12.5–)14–17(–19) × (1.8–)2–2.4(–2.7) µm; SBs (2.7–)3.5–5.5(–7) µm long; wood of angiosperms, submediterranean (semi) humid Europe, mild-maritime humid western North America .... ***O*. *angiosubvinosa***, p. 620

10. SBs 4.5–5.5 µm long; spores *2.4–3.5 µm wide 11
10. SBs (1.8–)2.2–4(–4.7) µm long; spores *2–3 µm wide 12

11. Spores *13–15.5 × 2.4–2.9 µm, fusoid-clavate; glassy processes absent; wood of *Acacia*, tropical subhumid northern Australia .... ***O*. cf. *hesperidea***, p. 578
11. Spores *(13–)15–19(–21.5) × (2.7–)3–3.5(–3.7) µm, clavate with basal tail; glassy processes present; wood & bark of gymno- & angiosperms, temperate to submediterranean (semi)humid Europe, hemiboreal North America .... ***O*. *clavuliformis*** (series *Hemiorbilia*), p. 680

12. Spores *(6–)7–9(–9.8) × 2.1–2.5 µm; SBs (1.8–)2.3–2.8(–3.2) µm long; glassy processes 20–80 µm long; bark of *Eucalyptus*, *Polylepis*, subtropical (sub)humid montane South America .... ***O*. *colombiana*** (series *Hemiorbilia*), p. 679
12. Spores predominantly over 9 µm long; without glassy processes 13

13. Spores *(11–)12–17(–19) × (2.1–)2.3–2.8(–3.2) µm; SBs 2–2.8(–3) µm long; wood of angiosperms, cold-temperate to boreal (sub) humid western North America .... ***O*. *navajoana***, p. 571

13. Spores *(7.5–)9–13(–14) × (2–)2.2–2.7(–3) µm; SBs (2–)2.3–4(–4.7) µm long; boreal to mediterranean Europe 14

14. SBs (2–)2.3–3.2(–3.5) µm long; wood of gymnosperms, orotemperate to orosubmediterranean humid .... ***O. alpigena***, p. 595
14. SBs (2.5–)3–4(–4.7) µm long; wood of angiosperms 15

15. Spores *(2–)2.2–2.7(–3) µm wide, SBs 0.8–1.3 µm wide, boreal humid to mesomediterranean semihumid .... ***O. montigena***, p. 592
15. Spores *1.8–2.4 µm wide, SBs 0.5–0.7(–1.1) µm wide, orotemperate humid .... ***O. paramontigena***, p. 599

Key H (series *Hesperideae*, asci 8-spored, spores predominantly < *2.2 µm wide)

1. Glassy processes 40–200 µm long, forming distinct teeth at the margin; spores *(10.5–)12–14.5(–15.5) × (1.5–)1.6–1.8 µm; SBs 4–6 × 0.3–0.5 µm; bark & wood of *Proteaceae*, inflorescence stem of *Xanthorrhoea*, subtropical semihumid southwestern Australia .... ***Orbilia astrovinosa***, p. 629
1. Glassy processes absent or max. 20(–40) µm long, margin smooth to distinctly crenulate 2

2. Spores *6.5–12(–13) µm long; SBs (1.3–)1.5–3(–4) µm long 3
2. Spores *(10–)11–23(–30) µm long; SBs (2–)3–5(–6.5) µm long 9
If measurements intermediate see *O. hesperidea* (with crystalloid SCBs, p. 576) and *O. paramontigena* (without crystalloid SCBs, p. 599).

3. Glassy processes 10–40 µm long, margin with distinct whitish teeth; spores *(8.7–)9.5–12(–13) × (1.3–)1.4–1.6 µm; SBs 1.8–2.2 × 0.5–0.8 µm; excipular cells with small crystalloid SCBs; wood of *Pinus*, orotemperate humid subcontinental Europe .... ***O. crenatovinosa***, p. 643
3. Glassy processes absent or max. 12 µm long, margin therefore smooth or only finely crenulate 4

4. SBs 1.4–2.2(–2.5) µm long 5
4. SBs 2–3(–4) µm long 7

5. Spores ± cylindrical, *9–11.2 × 1.7–2 µm; paraphysis tips very slightly spathulate-lageniform, firmly covered also laterally by thin (0.2 µm) exudate; glassy processes absent; *Picea* wood, temperate humid subcontinental Europe .... ***Orbilia* aff. *concoloris***, p. 673
5. Spores fusoid-clavate; paraphysis tips uninflated or slightly clavate, loosely covered by (0.3–)0.5–2 µm thick cloddy-granular exudate.... 6

6. Spores *(6–)6.5–9.5(–10.5) × 1.5–2.2 µm; often with 1–10 µm long glassy processes; conidia trinacrium-like; bark & wood of angiosperms (rarely gymnosperms), atlantic to continental, temperate humid to mesomediterranean semihumid Europe .... ***O. aprilis***, p. 645
6. Spores *7.5–11 × 1.4–1.7 µm; without glassy processes; conidia vermispora-like; wood of angiosperms, warm-temperate to subtropical humid eastern North America .... ***O. georgiana***, p. 642

7. Excipular cells with globose and crystalloid SCBs; glassy processes 2–5 µm long; spores *8–11 × 1.7–1.9 µm; SBs 2–3 × 0.3–0.5 µm; wood of *Acacia*, tropical (sub)humid eastern Australia .... ***O. nothoaprilis***, p. 640
A similar collection from northeastern Australia (wood & bark of indet. angiosperm, Pl. 284: 2) differs in the slightly longer and narrower spores (*10–12 × 1.6–1.7 µm) and longer SBs (3–4 × 0.4–0.5 µm).
7. Excipular cells with only globose SCBs; glassy processes absent; SBs 0.5–0.7 µm wide 8

8. Spores *9–10 × 2–2.2 µm; SBs 2.3–3 µm long; herbaceous stems of *Anigozanthos*, subtropical semihumid western Australia .... ***O.* aff. *nothoaprilis***, p. 642
8. Spores *10–13 × 1.8–2.4 µm; SBs 3.5–4.5 µm long; wood of *Acer*, orotemperate humid southern Europe .... ***O. paramontigena***, p. 599

9. Spores *(14–)16–22(–30) × 1–1.3 µm; crystalloid SCBs present; wood of *Erica*, mediterranean semi- to subhumid Macaronesia .... ***O.* cf. *subulivinosa*** (Pl. 278), p. 634
9. Spores distinctly wider (min. *1.3–1.7 µm) 10

10. Spores *11–17 × 1.3–1.7 µm; SBs 2–4.2 µm long; asci *4–6.5 µm wide 11
10. Spores *10–22 × (1.3–)1.6–2.2 µm; SBs (3–)4–6(–7) µm long; asci *4.8–7 µm wide 12

11. Asci *5.5–6.5 µm wide; margin without glassy processes; wood of *Arctostaphylos patula*, cold-temperate subhumid western North America .... ***O.* cf. *vinosa*** (Pl. 259: 4)
11. Asci *4–4.5 µm wide; margin with distinct glassy processes; bark of *Pinus strobus*, cold-temperate humid eastern North America .... ***O.* cf. *vinosa*** (Pl. 259: 5)

12. Ascus apical dome immature †(1.8–)2–2.5(–3.5) µm thick; SCBs globose; wood & bark of angiosperms, subtropical semihumid to humid western and eastern Australia .... ***O. nothovinosa***, p. 627
12. Ascus apical dome immature †(0.8–)1–1.5(–2) µm thick 13

13. Ascospores *(15–)18–22.5(–25) × (1.3–)1.5–1.9(–2) µm; SCBs globose; wood & bark of *Erica*, mesomediterranean semihumid southern Europe .... ***O. subulivinosa***, p. 634
13. Ascospores *(10–)12–19(–22) × (1.6–)1.8–2.2(–2.7) µm; SCBs globose but often also crystalloid (small) 14

14. Conidia triradiate (2-armed, trinacrium-like); ascospores *(10–)11.5–18(–19) µm long, often < *2 µm wide; apothecia with a smooth or only very finely crenulate margin, pale to bright rose or orange; wood & bark of gymno- & angiosperms, boreal to mediterranean, humid to semiarid Europe, western Asia, Macaronesia, Africa, North America .... ***O. vinosa***, p. 599
14. Conidia twice dichotomously branched (4-armed, dwayaangam-like); ascospores *(12–)14–20(–22) µm long, often > *2 µm wide; apothecia often with a distinctly crenulate margin, usually bright orange(-red), rarely rosaceous 15

15. Conidia (presumed) with outwards curved arms; wood (rarely bark) of angiosperms, boreal to orotemperate or orosubmediterranean humid Europe .... ***O. arachnovinosa***, p. 622
15. Conidia with straight, parallel or diverging arms 16

16. Conidia *10.5–12.5(–13.5) µm wide in central part, at ends (13–)17–30(–36) µm wide when arms diverging; arms mainly *3.3–4.5 µm wide; wood of gymnosperms, (orotemperate to) orosub- (to suprasub-)mediterranean humid southern Europe ..... ***O. subvinosa***, p. 616

16. Conidia *10–11 µm wide in central part, at ends 12–21 µm wide when arms diverging; arms mainly *3–3.5 µm wide; wood of angiosperms, orosub- to suprasubmediterranean (semi)humid southern Europe .... ***O. angiosubvinosa***, p. 620

Series *Hesperideae*

Orbilia subgenus ***Hemiorbilia*** section ***Hemiorbilia*** series ***Hesperideae*** Baral & E. Weber, **ser**. **nov**., MB 815005 – Type species: *Orbilia hesperidea* Rolland

Etymology: named after the type species, *O. hesperidea*.

Latin diagnosis: *Apothecia (luteo-)aurantiaca vel aurantio-rosea, margine laevi vel ± dentato. Asci 8- ad 128-spori, apice in statu emortuo hemisphaerico, leniter ad modice crassitunicato. Ascosporae *(5–)6–25(–30) × (1–)1.5–4.5(–6) µm, subcylindricae ad fusoideo-clavatae vel ellipsoideae ad obovoideae, etiam semicirculares vel forma corculi, apice rotundato ad subacuto, raro acuto vel acuminato, rectae vel curvatae, in statu vivo corpusculum refringens lacrimi- ad ampulliformem vel bacilliformem ad subulatum continentes. Paraphyses ad apicem haud inflatae vel leniter ad modice (raro valde) clavato-capitatae. Habitat ad lignum vel corticem putridum ramorum gymno- vel angiospermarum, in aere prominentium, raro ad folios vel caules herbarum, in zona boreale ad tropica, humida ad arida.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–1(–1.3)((–1.5)) mm diam., light to bright orange to brick-red, also yellow-orange, orange-rose, or rose(-lilaceous), margin smooth to finely rough or crenulate, also whitish pubescent or with whitish teeth or hairs, sessile or with a short stipe. **Asci** *(35–)40–110(–135) × (4–)5–12(–16) µm, 8- up to 128-spored, lower spores inverted (1/4–3/4 of spores, strongly mixed if polysporous), rarely only 0–1 spores inverted; **apex** (†) hemispherical to slightly (rarely medium) truncate, with 0.4–1 or usually 0.7–2.5(–3.5) µm thick dome (but thin-walled in *O. concoloris*), often with distinct apical chamber; **base** L-, T-, Y- or h-shaped. **Ascospores** *(5–)6–25(–30) × (1–)1.5–4.5(–6) µm, cylindric- to fusoid-clavate or ellipsoid-fusoid to obovoid, falcate to comma- or cashew-shaped, heart-shaped, apex rounded to subacute (mostly obtuse), rarely acute to acuminate, partially with a tail-like base or sometimes distinct tail 3–5 × as long as wide, straight to slightly (rarely medium to strongly) curved, especially towards base; **SBs** mostly affixed to apical, rarely subapical or lateral spore wall, (1–)2–5.5(–6.5) × (0.2–)0.5–1.8(–2.5) µm, rod-shaped to vermiform or subulate, globose, tear- or pear-shaped to ampulliform, straight (rarely slightly flexuous), apically narrowed to a small or wide point, rarely with a very short filum. **Paraphyses** uninflated or slightly to medium (exceptionally strongly) clavate-capitate at the apex, rarely lageniform, terminal cells 0.5–1.5(–2)× as long as lower cells. **Ectal excipulum** cells near base *(5–)8–18(–30) × (4–)6–15(–20) µm, near margin of t. angularis to t. prismatica or t. porrecta, outer part oriented at a high to often medium or low angle, with or without 1–40 or rarely 30–150(–200) µm long **glassy processes**, rarely with up to 95 µm long septate **hairs**. **SCBs** globose or mixed with crystalloid ones. **Exudate** (0.1–)0.5–4(–10) µm thick, continuous to cloddy or granular, loosely attached, hyaline to bright yellow, rarely absent. — **ANAMORPH**: trinacrium-like, also dwayaangam- or vermispora-like. **Conidiophores** short (~1.5–30 µm). **Conidiogenous cells** monoblastic or sympodial. **Conidia** *12–22.5 × 2.5–3.2 or mostly *25–59 × 3.3–6.2 µm when phragmosporous, 3–9-septate, straight or curved in upper part; *14–55 × 12.5–75(–92) µm when trinacrium-like (2-armed), arms straight or somewhat curved downwards; *20–65 × 10.5–77 µm when dwayaangam-like (4-armed), arms straight or outwards curved.

Habitat: on wood and bark of angio- and gymnosperms, sometimes palm petioles or herbaceous stems and leaves, from boreal to tropical, humid to arid climates.

Recognized species: 47, plus 12 unnamed species (‘affinis’).

Taxonomic remarks. Series *Hesperideae* is characterized by ascospores which typically lack a distinct basal tail. Many of the included species are polysporous and only here some species possess distinct spore tails. Distinct, often pale reddish crystalloid SCBs are often present, but various species are without them. Glassy processes are usually absent but in some species they are short, and in two (*O. multicurvula*, *O. astrovinosa*) very long. *O. velutina* is extraordinary in having long hairs with a septate lumen. The exudate over the paraphyses and marginal cells is usually rather thick, externally rough, often ± yellow, but especially in *O. macrohesperidea*, *O.* aff. *macrocarpa*, *O. myriohesperidea* and *O. myrioaustraliensis* it is thin or even absent. *O. curvatinavajoana* deviates from the remaining species by asci with only 1–3 inverted lower spores.

The ascospores vary from narrowly or broadly ellipsoid- to cylindric-fusoid or fusoid-clavate. In some species the spores inconsistently or rather regularly possess a distinct short tail but, in contrast to series *Hemiorbilia*, all of these species are multispored and lack glassy processes. For instance, *O. multiaustraliensis* and *O. myrioaustraliensis* resemble taxa such as *O. breviaristata* or *O. megaocculta* in spore shape, while *O.* aff. *macrocarpa* and *O. myriohesperidea* resemble *O. parviclava* or *O. subclavuliformis*.

The longest spores of up to 30 µm were noted in *O.* cf. *subulivinosa* (Pl. 278) and *O. adenocarpi*, the former showing also the narrowest spores (1–1.3 µm), while in *O. velutina*, *O. myriomuscula*, and *O. corculispora* the spores are the shortest (~6–7.5 µm). *O. arizonensis* possesses about the widest spores (4–6 µm) and SBs (1.3–2.5 µm), and that even when considering the whole genus *Orbilia*. Some species are extraordinary in their consistently (*O. curvatinavajoana*, *O. multicurvula*, *O. cryptogena*, *O. subcryptogena*) or partially (*O. myriofusiclava*) strongly curved, falcate or cashew-shaped spores, and one has helicoid spores (*O. helicovinosa*). The spores of *O. myriomuscula* resemble mice with thin curved tails, while *O. corculispora* and *O. octocorculispora* possess triangular to heart-shaped spores in which the SBs are laterally inserted. A lateral insertion of SBs is also characteristic of the clavate spores of *O. myrioauris*.

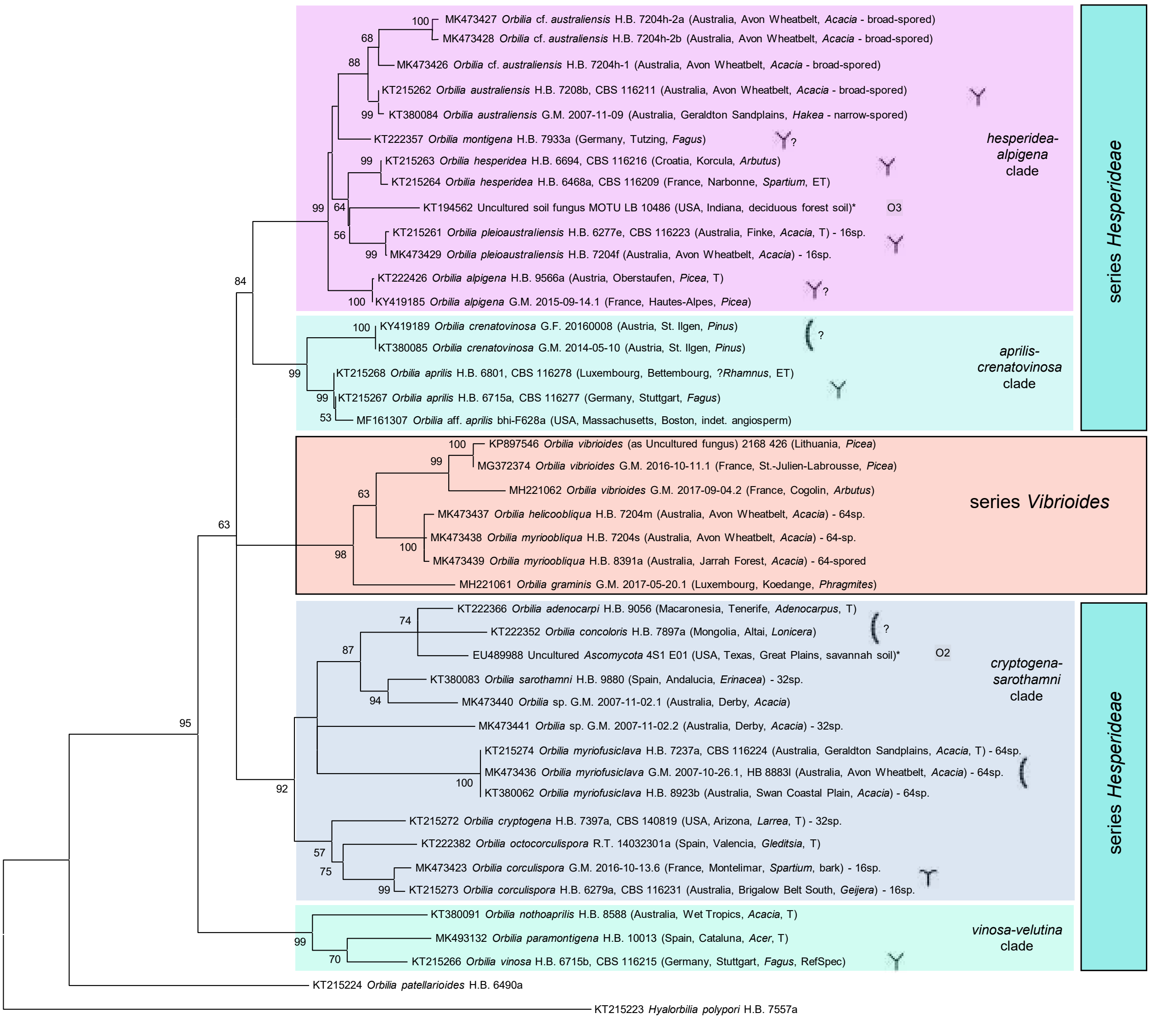
Species delimitation. Various aggregates exist in series *Hesperideae*, in which the limits between the species were difficult to assess. For instance, a rather high variation in ascospore size was noted in *O. australiensis* and the similar *O. hesperidea*, with some intermediate collections that were difficult to assign. In the *O. vinosa* aggregate, differently shaped conidia, being sometimes found on the natural substrate, provide the main morphological character to distinguish *O. vinosa*, *O. subvinosa*, and *O. arachnovinosa*, and their absence in many of the collections made a determination almost impossible.

Anamorph. In about a dozen species of series *Hesperideae* trinacrium-like anamorphs were observed, either in pure culture or on the natural substrate. Many of them resemble *Trinacrium robustum*, a species characterized by distinctly tapered conidial arms, whereas in *O. aprilis* (anamorph *T. tothii*), *O. vinosa* and *O. velutina* the arms often taper only slightly or not at all. Evident differences in conidial size and shape could not be found among those taxa with tapered arms, apart from how strongly the arms are narrowed towards their ends. In the absence of molecular data, the type of *T. robustum* cannot unequivocally be connected to a teleomorph.

Trinacrium-like conidia with arms curved downwards as in *T. incurvum* are connected to *O. corculispora*. Dwayaangam-like anamorphs were confirmed for *O. subvinosa* and possibly also occur in *O. angiosubvinosa* and *O. arachnovinosa*. *O. myriofusiclava*, *O. georgiana*, and possibly also *O. crenatovinosa* and *O. concoloris* are extraordinary in producing vermispora-like conidia.

Phylogeny. Series *Hesperideae* is circumscribed here in a wide sense, based predominantly on morphological criteria, since molecular data were absent in about 30 of the included ~60 taxa, and correlations between morphology and DNA data were not observed in various cases. Our phylogenetic analyses of ITS+LSU, ITS, or LSU (Phyls 9, 10, S13) provide evidence for a core group of series *Hesperideae* with high bootstrap support, here called *hesperidea-alpigena* clade, representing *O. australiensis*, *O. pleioaustraliensis*, *O. hesperidea*, *O. alpigena*, and *O. montigena*. Another strongly supported clade is formed by *O. angiosubvinosa*, *O. georgiana*, *O. multicurvula*, *O. nothoaprilis*, *O. paramontigena*, *O. subulivinosa*, *O. subvinosa*, *O. velutina*, and *O. vinosa*, here called *vinosa-velutina* clade, in which, however, also *O.* cf. *angustoaristata* of series *Hemiorbilia* clustered (Phyls 9, S13). Although *O. aprilis* and *O. crenatovinosa* are morphologically very similar to *O. nothoaprilis* and species around *O. vinosa*, they form a remote clade of their own (*aprilis-crenatovinosa* clade) which did not cluster with the *vinosa-velutina* clade in our analyses, except for the combined tree in Baral et al. (2017b), where they formed a weakly supported clade, or in our LSU analysis (S13), where they clustered unsupported. Instead, the *aprilis-crenatovinosa* clade clustered medium supported with the *hesperidea-alpigena* clade when analysing ITS (Phyl. 10).

Species of the *vinosa-velutina* clade are characterized by rather long and narrow, cylindrical to fusoid, partially clavate spores (except for *O.* cf. *angustoaristata* with a thin spore tail and *O. velutina* with very short spores), but some species intergrade with taxa of the *hesperidea-alpigena* clade in having wider spores, and also with the *aprilis-crenatovinosa*- clade which has rather short and narrow spores. The high molecular distance between the *vinosa-velutina* clade and the *aprilis-crenatovinosa* clade is



Phylogenetic analysis 10. Phylogram of series *Hesperideae* and *Vibrioides* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (43 sequences, 669 positions, aligned with MUSCLE, a short intron in the ITS1 of G.M. 2007-11-02.2 was deleted) using the TN+G+I model in MEGA6 (500 replicates). For a detailed tree of the *vinosa-velutina* clade see Phyl. 11. 3 environmental strains from GenBank are included, 2 of them representing unidentified species (O2, O3). The tree is rooted with *Hyalorbilia polypori* and *O. patellarioides*. Asci 8-spored except when otherwise stated; RefSpec = reference specimen, T = type, ET = epitype, * = without ITS1 and partial 5.8S.

surprising since the included species closely concur in both their anamorphs and teleomorphs. Because of this morphological resemblance and the lack of a sharp limit between these three clades, we refrained from recognizing different series for them.

Also the *cryptogena-sarothamni* clade received strong support only when analysing ITS (Phyl. 11). It is divided in our combined analysis into two medium supported subclades (Phyl. 9): *O. corculispora*, *O. octocorculispora*, and *O. cryptogena* clustered in one subclade, and *O. adenocarpi*, *O. concoloris*, *O. myriofusiclava*, and *O. sarothamni* in another subclade. The latter subclade is morphologically heterogeneous, since *O. adenocarpi* resembles *O. vinosa*, *O. concoloris* can easily be mistaken as a member of series *Regales* (section *Aurantiorubrae*), and *O. myriofusiclava* and *O. sarothamni* are reminiscent of *O. multiaustraliensis*. The latter species is without DNA data but is thought to be a close relative of *O. australiensis* and *O. pleioaustraliensis* which cluster in the *hesperidea-alpigena* clade.

In several clades of series *Hesperideae*, straight and curved ascospores occur mixed, indicating that spore curvature is of minor taxonomic importance above the species level. On the other hand, the similarity in ascospore shape between the 8-spored *O. vibrioides* and *O. graminis* (series *Vibrioides*) is correlated with similar molecular data, and also the similar spores of the 64-spored *O. curvatiobliqua* indirectly supports this correlation by sequences of two other species of this group with multispored asci but differently shaped spores. On the other hand, the 32-spored *O. cryptogena* has similar but larger spores and clustered in another clade. We assume that, based on a comparable spore morphology, two species without molecular data would cluster with their morphological siblings: the 16-spored *O. subcryptogena* with cashew-shaped spores and tear-shaped SBs with *O. cryptogena*, and the 64-spored *O. myrioauris* near the 16-spored *O. corculispora* because of its partially laterally inserted SBs.

Specific nucleotide positions. A remarkable symmetric pair of nucleotides is found in the SSU V8–V9 (pos. 154 & 166) which separates *O. australiensis*, *O. pleioaustraliensis*, *O. alpigena*, *O. cryptogena*, and *O. corculispora*, which cluster in two different clades (Phyl. 9), by **G**AGTCATCAGCT**C**, a motif being also characteristic of section *Habrostictis*, from all remaining sequences within section *Hemiorbilia* (including *O. hesperidea* and *O. myriofusiclava*) which have **A**AGTCATCAGCT**T** in concordance with any other member of *Orbiliomycetes* with available SSU data. In stem-loop B8 of 5.8S (pos. 121–134), the *vinosa-velutina* clade has **CTC**GGTATTCCG**GC** (in *O. subulivinosa* **TCC**GGTATTCCG**GC**) in contrast to the remaining taxa of section *Hemiorbilia* which mainly have **ATT**GGTATTCCG**AT** (in *O. sarothamni* **ACT**GGTATTCCG**GT**) (Tab. 18).

At pos. 1–4 of ITS2 (downstream of GAGCGTC), the general motif in section *Hemiorbilia* is ATTA (including series *Vibrioides* except for *O. graminis* which has ATCA), but the *O. cryptogena-sarothamni* clade has consistently ATTG (except for the uncultured strain 4S1 E01 which has ATTA). The motif ATTG also occurs in the entire section *Ovoideae* and some members of section *Orbilia*, but is not found in other *Orbiliomycetes* (Tab. 20). In the ITS alignment of series *Hesperideae*, the *cryptogena-sarothamni* clade is easily distinguished from other clades of this series and also from the entire section *Hemiorbilia* by showing a large gap at pos. ~18–32 of ITS2 (other taxa have here 10–19 additional nucleotides). This large gap is also shared by two unidentified and undocumented Australian collections on *Acacia aneura* (2.XI.2007), one with 8-spored asci (G.M. 2007-11-02.1) clustering strongly supported with *O. sarothamni*, and that with 32-spored asci (?*O. multiaustraliensis* or *O. macrocarpa*, G.M. 2007-11-02.2) unresolved in series *Hesperideae* (shown only in Phyl 10). The gap region occurs, however, also in some other groups, particularly section *Arthrobotrys*.

In the LSU D1–D3, several positions are characteristic for the *vinosa-velutina* clade (including *O.* cf. *angustoaristata*) vs. all remaining members of section *Hemiorbilia* and a majority or almost all other *Orbilia* spp.: pos. 105 is GCAA**G**AGCT vs. GCAA**C**AGCT, pos. 306 and 317 **G**TTTCATCTAA**G** vs. **A**TTTCATCTAA**A**, pos. 670 A**C**GCGAG vs. A**T**GCGAG, and pos. 726 is TGGGAG**C** vs. TGGGAG**T** (TGGGAG**C** also occurs in *O. crenatofalcata* and the entire section *Orbilia*).

The strongly supported *vinosa-subvinosa* subclade is recognizable in the LSU D2 (alignment of Phyl. S13) at pos. 439 and 489: AGACT**C**GC and GC**G**GGCCA vs. AGACT**T**GC and GC**A**GGCCA in other strains of section *Hemiorbilia*, besides some other positions. This subclade is also recognizable at pos. 76 of ITS1 and pos. 388 of ITS2 (alignment of Phyl. 11): GTGG**T** and TCGGY**C** vs. GTGR**A** and TCGGY**T** in the remaining taxa of the *vinosa-velutina* clade.

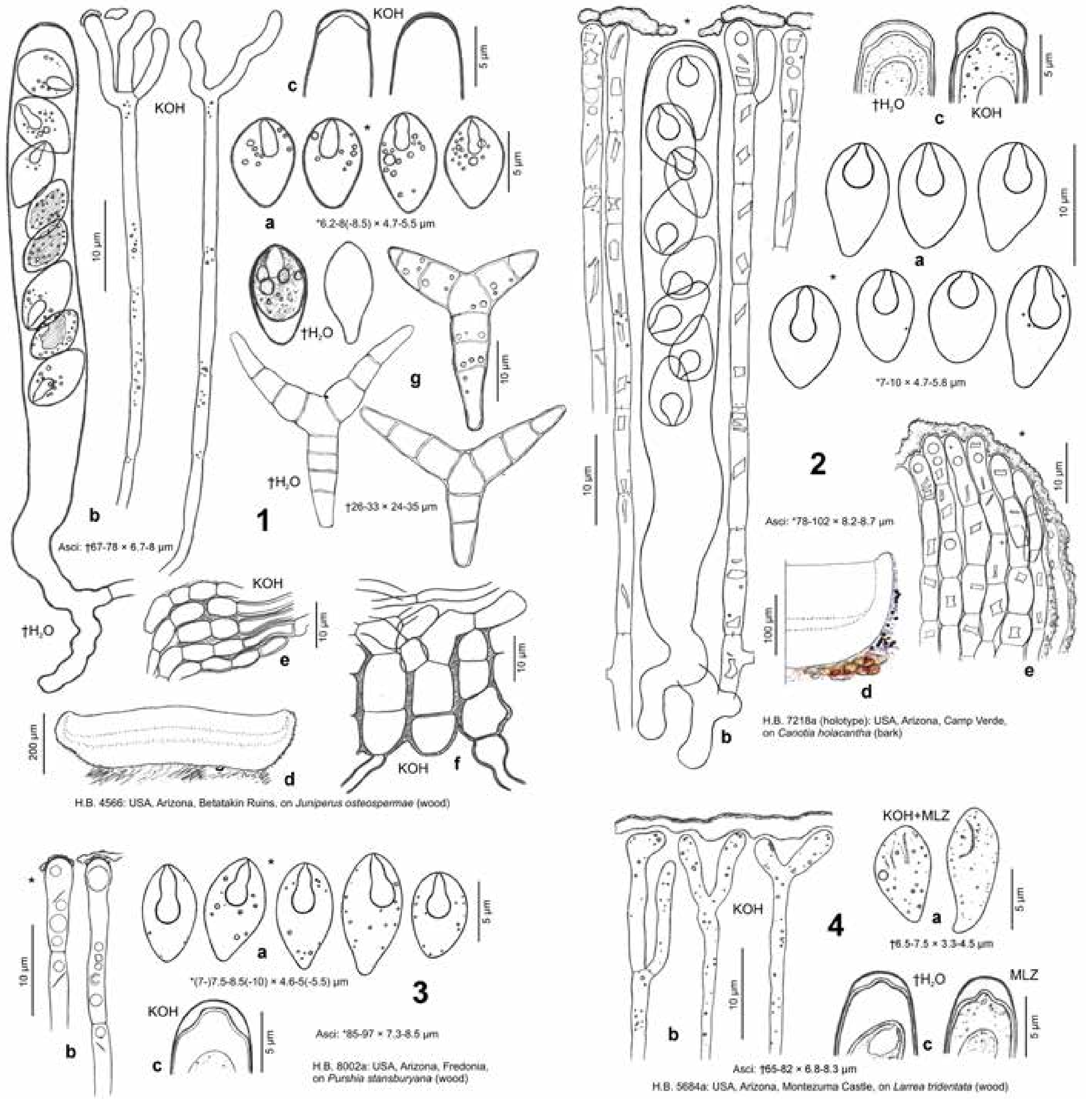
Ecology. Many species of series *Hesperideae* occur in subtropical to tropical, subhumid to arid regions, but many others were mainly collected in temperate to boreal-subalpine, humid regions. The apothecia grew on wood and bark of xeric branches and trunks of gymno- and angiosperm trees and shrubs. Some species occurred also on more or less herbaceous substrates: petioles of *Livistona* (*Orbilia australiensis*, *O. coronohesperidea*, *O. palmicola*, *O. parviclava*, *O. pleiohesperidea*), inflorescence stems of *Xanthorrhoea* (*O. astrovinosa*), stems of *Melilotus* (*O.* cf. *vinosa*), and stems of *Anigozanthos* and *Bambusa* (*O.* aff. *nothoaprilis*). Species of series *Hesperideae* occur worldwide. At present they were recorded in Europe, North America, Africa, Asia, and Australia.

Orbilia arizonensis Baral & G. Marson, **sp. nov.**, MB 813529 — Pls 213–214, Map 37

Etymology: named after the geographical origin of the first record, Arizona.
Typification: USA, Arizona, Montezuma Castle, branch of *Canotia holacantha*, 12.VI.2000, G. Marson (ex H.B. 7218a, M-0276434, holotype).

Latin diagnosis: *Apothecia 0.3–1.5 mm diam., sessilia, erumpentia, vivide aurantiaca vel lateritia, margine albido-pulverulenta vel irregulariter crenulata. Asci 8-spori. Ascosporae *6.2–11 × 4–6 µm, obovoideae, in statu vivo corpusculum refringens magnum lacrimi- vel saepe pyriformem, ad apicem affixum continentes. Cellulae vivae excipuli et paraphysium corpuscula crystalloidea continentes, excipulum marginale absque processis vitreis. Habitat ad corticem, raro lignum putridum ramorum siccorum fruticum angiospermarum vel arborum coniferarum in zona temperata humida ad semiarida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.9(–1.5) mm diam., 0.17–0.3 mm thick, light to deep pure or dirty orange to brick-red(-brownish), round to irregular elongate, scattered to (sub) gregarious; disc young concave, then flat, margin ± thick, 0–20 µm rising above disc, smooth, exterior whitish-powdered or irregularly crenulate; broadly sessile, slightly to strongly erumpent. **Asci** *78–97(–102) × 7.3–8.7 µm {2}, †(60–)65–90(–95) × 6.5–8(–8.7) µm {5}, 8-spored, spores (*) subbiseriate († uniseriate), (1–)3–5(–6) lower spores inversely oriented {3} (often mixed), pars sporifera *37–48 µm long; **apex** (†) hemispherical to slightly truncate, dome †0.9–1.5(–2) → (0.4–)0.8–1.2 µm thick {4}, with distinct apical chamber; **base**



H.B. 4566: USA, Arizona, Betatakin Ruins, on *Juniperus osteospermae* (wood)

H.B. 7218a (holotype): USA, Arizona, Camp Verde, on *Canotia holacantha* (bark)

H.B. 8002a: USA, Arizona, Fredonia, on *Purshia stansburyana* (wood)

H.B. 5684a: USA, Arizona, Montezuma Castle, on *Larrea tridentata* (wood)

Plate 213. **1–4**: *Orbilia arizonensis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum (**1e** submargin, with hyphoid outgrowths); **f**. id., at lower flanks, with anchoring hyphae; **g**. conidia from substrate.

with short to long, ± thick, flexuous stalk, Y-shaped or unbranched. **Ascospores** *(6.2–)7–9(–11)((–12)) × (4–)4.5–5.5(–6) µm {7}, †6.5–9.5(–10.5) × (3.3–)4.4–5 µm {2}, obovoid, apex rounded or obtuse, base slightly to strongly attenuated, rarely tail-like, straight to slightly inequilateral, rarely very slightly curved at base; **SBs** *3–5(–5.5) × (1.3–)1.7–2.3(–2.5) µm {4}, tear- to often pear-shaped, straight, apically narrowed to a small to wide point, overmature *2.5–3 × 2.5–2.7 µm. **Paraphyses** apically uninflated to slightly clavate-capitate, terminal cells *8–15(–20) × 2–3.2 µm {2}, †~6–16 × 1.7–2.8 µm {2}, lower cells *(8–)9.5–15.5(–18) × 1.5–2.2(–2.7) µm {2}, †~10–20 × 1.2–1.7 µm {1}; sometimes to frequently branched and often flexuous near apex {6}. **Medullary excipulum** pale rose, 20–85 µm thick, of medium loose to dense horizontal textura intricata-porrecta, with scattered to many inflated cells, sharply delimited. **Ectal excipulum** hyaline to very pale rose-orange, of slightly to medium gelatinized, vertically oriented t. angularis(-prismatica) from base to mid flanks, (30–)60–120 µm thick near base, cells */†(7–)10–19(–25) × 6–13 µm {3}; near margin (10–)20–40 µm thick (excl. covering hyphae), of t. prismatica oriented at 10–20°, marginal cortical cells */†(5–)7–10(–12) × 2.8–5(–6) µm {3}, running out into hyphae conglutinate by exudate, partially forming distinct irregular teeth, **glassy processes** absent. **Anchoring hyphae** sparse to very abundant, †1.5–3 µm wide, walls 0.2–0.4(–1) µm thick {3}, forming a covering layer on the flanks and margin of the ectal excipulum. **SCBs** in paraphyses and ectal excipulum crystalloid, subhyaline to pale orange, (1.5–)2–5(–6) × (0.5–)1–4(–5) µm, at margin and in paraphyses also globose. **Exudate** over paraphyses (0.2–)1–2(–3) µm thick, continuous to cloddy, ± loosely attached, disappearing in old apothecia; abundant also over margin. **— ANAMORPH**: trinacrium-like (presumed, from natural substrate {1}). **Conidiophores** not seen. **Conidia** Y-shaped, total size †26–33 × 24–35 µm, stipe †13–20 × 5–6 µm, 2–4-septate, arms tapering, †15–16 × 5.5–6.5 µm, (2–)3-septate {1}.

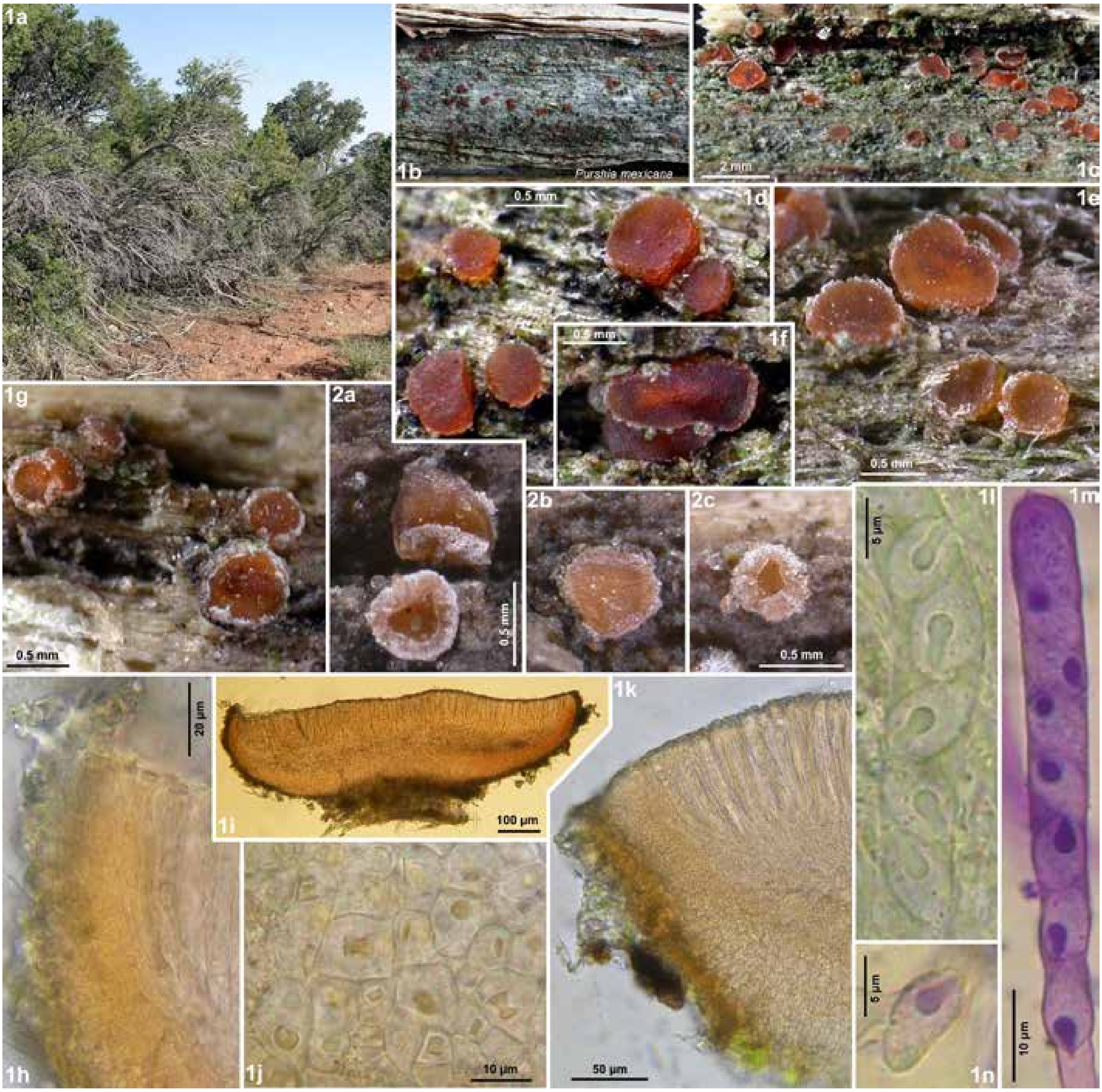


Plate 214. **1–2**: *Orbilia arizonensis*. – **1a**. subhumid montane shrubland with *Pinus edulis* (and *Juniperus osteosperma*), dead *Purshia* in foreground; **1b–g**, **2a–c**. rehydrated apothecia; **1j**. apothecium in median section; **1h–i**. marginal ectal excipulum in median section; **1k**. crystalloid SCBs in ectal excipulum (lower flanks); **1l–n**. asci and ascospores. – Living state (**1m–n** in CRB), except for asci in **1l–m**. — **1a–n**. H.B. 8002a: USA, Arizona, Fredonia, on *Purshia*; **2a–c**. H.B. 4566: USA, Arizona, Betatakin Ruins, on *Juniperus*.

Habitat: collected 0.2–2 m above the ground, partially to entirely decorticated, 6–23 mm thick branches of *Canotia holacantha* {1}, *Cercocarpus ledifolius* {1}, *Juniperus osteosperma* {1}, *Larrea tridentata* {1}, *Purshia stansburyana* {3}, on up to 0.5 mm deep medium decayed wood {5} or bark (bast) {1}, strongly greyed, green algae absent or sparse to abundant. **Associated**: *Caloplaca* sp. {1}, *Candelariella* sp. {1}, *Dothideales* {1}, *Hysterobrevium mori* {2}, *Odontotrema oregonensis* {1}, *Orbilia bicknellensis* {1}, *O. calyptrata* {2}, *O. cryptogena* {1}, *O. delphinus* {1}, *O. euonymi* {1}, *O. flexisoma* {1/2}, *O. ?gambelii* {1}, *O. lacrimispora* {2}, *O. ?lentiformis* {1}, *O. macrodelphinus* {4}, *O. maeandrina* {3}, *O. multigambelii* {1}, *O. multimaeandrina* {1}, *O. purshiae* {4}, *O. serpentina* {1}, *O. subovoidea* {1}, *O. ?vitalbae* {1}, *Patellaria* '*andina*' {1}, *P. atrata* {2}, *Symbiotaphrina desertorum* {1}. **Desiccation tolerance**: fully viable after 28(–30) months. **Altitude**: 975–2500 m a.s.l. **Geology**: Pennsylvanian-Permian and Tertiary (red) sand- and lime-, silt- or mudstone. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia arizonensis* is easily recognized by its extraordinarily wide ascospores and spore bodies. Within the *Orbiliomycetes* known at present only *O. megaocculta* has a comparable spore and SB width. The obovoid shape of ascospores and the pyriform shape of SBs are characteristic, also the conspicuous pale orange crystalloid SCBs. For the closely related *O. australiensis* see p. 556.

Variation. Spores and SBs varied somewhat in size among the collections, but this variation did not correlate with other features.

Anamorph. Trinacrium robustum-like conidia were once observed on the natural substrate. They are similar to those obtained in pure culture of the closely related *O. hesperidea* and *O. pleioaustraliensis*.

Map 37. Known distribution of *O. arizonensis* in North America.

Ecology. *O. arizonensis* grew on medium decayed wood (rarely bark) of xeric branches of several rather unrelated angiosperm shrubs, rarely also on gymnosperms, in cold-temperate subhumid pinyon-juniper woodlands and humid Douglas fir mixed forest of the Colorado Plateau and Southern Rocky Mountains, and in the warm-temperate semiarid Sonoran paloverde-mixed cacti desert scrub (Verde Valley at border between Mogollon Rim and Sonoran Desert) in the southwest of Northern America.

Specimens included. **USA**: **Arizona**, Navajo, 25.5 km WSW of Kayenta, Betatakin Ruins, 2045 m, fragment of *Juniperus osteosperma*, on wood, 5.X.1991, G. Marson (H.B. 4566, anam. substr.). – Grand Canyon, Kaibab Plateau, 28 km ESE of Fredonia, 13 km NNW of Jacob Lake, 2115 m, branch of *Purshia stansburyana*, on wood, 17.V.1995, G. Marson (H.B. 5295b ø). – ibid., branch of *P. stansburyana*, on wood, 15.VI.2003, G. Marson (H.B. 8002a). – 93 km SSE of Fredonia, S of North Rim, 2500 m, branch of *Cercocarpus ledifolius*, 17.V.1995, G. Marson (ø). – Coconino Plateau, 7.5 km ESE of Grand Canyon Village, 2205 m, branch of *P. stansburyana*, on wood, 16.VI.2003, G. Marson (H.B. 7462b). – Sonoran Desert, 65 km SSW of Flagstaff, 9 km NNE of Camp Verde, 4 km NE of Montezuma Castle, 1073 m, branch of *Canotia holacantha*, on bark, 12.VI.2000, G. Marson (ex H.B. 7218a, M-0276434, **holotype**). – ibid., 5.5 km NNE of Camp Verde, 975 m, branch of *Larrea tridentata*, on wood, 8.V.1995, G. Marson (H.B. 5684a).

Orbilia australiensis Baral & G. Marson, **sp. nov.**, MB 814365 — Pls 215–217, Map 38

Etymology: named after the continent Australia from which this species is so far known.

Typification: Western Australia, Barradale Roadhouse, twigs of *Acacia ?aneura*, 5.XII.2001, G. Marson (ex H.B. 7135a, MEL 2389218, holotype).

Latin diagnosis: *Similis* Orbiliae arizonensi *sed ascosporae breviores et angustiores*, *corpuscula refringentia angustiora*, *ab* O. hesperidea *gradatim differt ascosporis latioribus. Habitat ad lignum vel corticem leniter vel valde putridum ramulorum vel ramorum siccorum fruticum vel arborum angiospermarum*, *plerumque* Fabales, *in zona tropica vel subtropica humida ad arida Australiae occidentalis, septentrionalis et oridentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.18–)0.25–0.5(–0.8) × 0.18–0.5 mm diam., 0.1–0.25 mm high, light to bright brick-red-orange(-apricot), not or slightly translucent, round, rarely elliptical, scattered to subgregarious; disc flat, margin thin, 0–20(–30) µm protruding, smooth to ± rough; broadly sessile or with an obconical stipe 0.06–0.09 × 0.14–0.23 mm, superficial to slightly erumpent; dry bright brick-red. **Asci** *(50–)53–75(–82) {8} or 76–100 {2} × (6.5–)7–8.5(–9) µm {10}, †48–75 × 6–7.7 µm {5}, 8-spored, spores (*) biseriate, 2–6((–7)) lower spores inverted {14} (sometimes mixed), pars sporifera *34–42 µm long; **apex** (†) hemispherical, dome †1.2–2.2 → 0.7-2 µm thick {4}, with distinct apical chamber; **base** with short to medium long, thin or thick stalk, T-, L- or Y-shaped. **Ascospores** *((6.5–))(8–)9–14(–16)((–18)) {15} × (2.5–)2.7–3.5(–3.7) {14} or 3.2–4.3 µm {3}, †9–13(–15) × 3.5–4(–4.5) µm {2}, ellipsoid-fusoid to fusiform, apex obtuse, sometimes subacute or rounded, base mostly ± strongly attenuated, sometimes with a short tail-like end, straight or slightly curved at base; **SBs** *(2.5–)3–5(–5.5) × (0.9–)1.2–1.6(–1.8) ((–2.3)) µm {15}, pyriform to ampulliform, more rarely tear- or rod-shaped, apically narrowed to a small, sometimes wide point, straight, rarely slightly curved. **Paraphyses** apically uninflated to mostly slightly (rarely medium, exceptionally strongly) clavate-capitate (exceptionally spathulate to sublageniform), terminal cells *6–16(–20) × (2–)2.5–4(–4.8) µm {6}, lower cells *8–15 × (1.6–)1.8–2.5(–3) µm {5}; not or quite often branched at upper septum. **Medullary excipulum** hyaline to pale orange, 15–50 µm thick, of medium dense textura intricata with some or many inflated cells, sharply delimited. **Ectal excipulum** hyaline, of thin-walled († slightly gelatinized), vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks or margin, 25–110 µm thick near base, cells *(8–)10–25(–30) × 7–17(–20) µm {5}; 15–25(–30) µm thick near margin, of t. angularis or prismatica oriented at a 10–70° angle to the surface, marginal cortical cells *5–13 × 2.5–6(–8) µm {6}; **glassy processes** absent {9}. **Anchoring hyphae** sparse to abundant, */†1.8–3.3 µm wide, walls 0.2–0.3 µm thick {3}. **SCBs** in paraphyses and ectal excipulum globose, 1–3.6 µm diam., together with crystalloid SCBs {11}, hyaline or (especially in marginal excipulum) pale to light orange, 2.5–9 × 1.5–4 µm. **Exudate** over paraphyses 0.3–4 µm thick, granular-cloddy, hyaline to pale yellowish, ± loosely attached; over margin and flanks 0.7–7 µm thick. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1} but no data available).

Habitat: collected 0.1–3 m above the ground, corticated to decorticated, (1–)2–30(–100) mm thick twigs and branches of *Acacia* sp. {8}, *A. ?aneura* {1}, *A. cyperophylla* {1}, *Banksia cuneata* {1}, *B. grandis* {1}, *Calothamnus* sp. {1}, *Dodonaea viscosa* subsp. *angustissima* {1}, *Hakea* sp. {1}, *Jacksonia* sp. {2}, on 0.1–0.5 mm deep slightly to strongly decayed wood {10} and bark {15} (periderm & bast), greyed, green algae absent or sparse to abundant. **Associated**: *Acanthostigma ?minutum* {1}, *Amandinea* sp. {1}, *Caloplaca* sp. {3}, *Capronia* sp. {1}, *Claussenomyces* sp. {3}, *Coccomycetella* spp. {4}, *Durella* sp. {1}, *D.* aff. *connivens* {2/1}, *Gloniopsis* sp. {1}, *G. praelonga* {5}, *Hysterium angustatum* {1}, *Hysterobrevium mori* {2}, *Lecidea* sp. {1}, *Mycocalicium* sp. {1}, *Orbilia albidorosea* {1}, *O. allantoobliqua* {1}, *O. amberina* {1}, *O. anguliobliqua* {1}, *O. ?angustoaristata* {1}, *O. austrocylindrica* {1}, *O. austroobtusispora* {1}, *O. aviflagellata* {1}, *O. commarosa* {1}, *O. curvatiobliqua* {1}, *O. curvativitalbae* {2}, *O. eucalypti* {5}, *O. fimbriata* {1}, *O. helicoobliqua* {2}, *O. hesperidea* {4}, *O. kingsiana* {1}, *O. ?macrocarpa* {1}, *O. macrotrapeziformis* {1}, *O. microserpens* {2}, *O. multiaustraliensis* {1}, *O. multiserpens* {1}, *O. myrioeuonymi* {1}, *O. myriofusiclava* {5}, *O. myriolilacina* {2}, *O. myriomuscula* {1}, *O. myrioobliqua* {10}, *O. nothovinosa* {3/1}, *O. paraobliqua* {2}, *O. pleioaustraliensis* {3}, *O. pleioaustrocylindrica* {1}, *O. ?pleiocoronohesperidea* {1}, *O. ?pleiohesperidea* {1}, *O. pleiovinosa* {1}, *O. pleiovirgula* {1}, *O. ?pubescens* {1}, *Patellaria ?andina* {1}, *P. atrata* {1}, *Proliferodiscus griseoviolaceus* {1}, *Symbiotaphrina desertorum* {2/1}, *?Triblidium* sp. {3}. **Desiccation tolerance**: fully viable for at least 21 months. **Altitude**: 37–540 m a.s.l. **Geology**: Precambrian, Silurian & Jurassic-Cretaceous sedimentary rock, Cenozoic regolith; granite, granulite with granitic gneiss. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia australiensis* is characterized by comparatively large, (ellipsoid-)fusoid ascospores and conspicuous, pale orange crystalloid SCBs. *O. arizonensis* differs in shorter and wider spores, wider SBs, and larger apothecia, and in occurring in North America. *O. hesperidea* differs in narrower, subcylindrical spores with obtuse apices; yet, some collections have fusoid spores and are then not sharply separable from *O. australiensis*.

A few collections included in *O. hesperidea* (Pl. 237: 2, 5) show a spore width at the upper end of the range and appear to be intermediate to narrow-spored populations of *O. australiensis*,

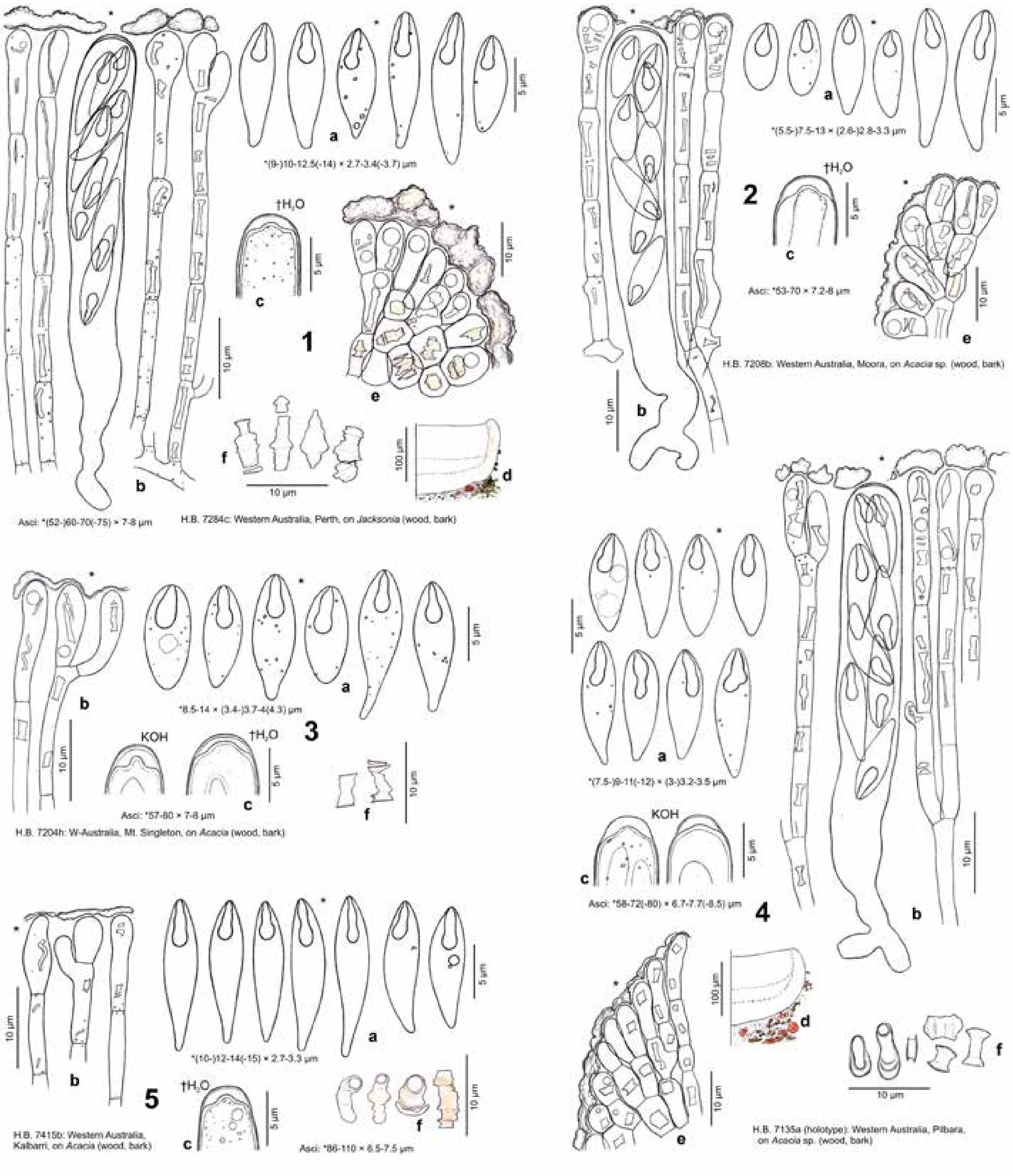


Plate 215. **1–5**: *Orbilia australiensis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. crystalloid SCBs in excipular cells (flanks and margin).

but their cylindric-ellipsoid-clavate spore shape with an obtuse apex fits better typical *O. hesperidea*. However, also collections with fusoid spores similar as in *O. australiensis* though with a width of only *2.2–2.7 µm were included by us in *O. hesperidea*. In three samples (H.B. 7204, 6452, 8883) *O. australiensis* and *O. hesperidea* grew in association. In two of them, the two species were sharply separated into two populations based on spore width and partly also spore shape, but in H.B. 6452 the two populations could not very clearly be separated.

Variation. Rather great variability in size and shape of the ascospores is noted within the present concept of *O. australiensis*. In several collections including the holotype (Pls 215: 1–4; 216: 7), the spores are partly or consistently rather short and thick (*~8–14 × 2.7–4 µm), mainly fusoid with obtuse (to subacute) apex and tapered base, though ellipsoid spores also sometimes occur. Three of them are extraordinary

Plate 216. **1–10**: *Orbilia australiensis*. – **1a**. semihumid Eucalypt open woodland with predominant *Jacksonia*; **2a–b**. dead corticated or decorticated xeric branches of *Jacksonia*, **1b–d**, **2a–d**, **3a–b**, **d–e**, **9a**. rehydrated apothecia; **3c**, **8a**. dry apothecia; **2f**, **4**. apothecia in median section; **2e**. id., marginal ectal excipulum; **5**. id., crystalloid SCBs in basal excipular cells; **3f–g**, **6**. asci with mature spores; **2g**, **8b**. ascus apices; **7**, **9b**, **10**. ascospores. – Living state, except for asci in **2g**, **3f–g**, **6**, **8b** (all in H_2O). — **1a–d**. H.B. 7284c: Western Australia, Perth, on *Jacksonia*; **2a–g**. H.B. 8611b: ibid., on *Jacksonia*; **3a–g**. 3.IX.2006: ibid., on *Banksia*; **4**. H.B. 8478f: ibid., on *Acacia*; **5**. H.B. 8660a: ibid., on *Banksia*; **6**. H.B. 8923c: Moora, on *Acacia*; **7**. H.B. 8883d: Mt. Singleton, on *Acacia*; **8**. 9.XI.2007: Geraldton Sandplains, on *Hakea*; **9**. H.B. 9695e: Gascoyne, on *Acacia*; **10**. H.B. 8838d: Yalgoo, on *Dodonaea*.

in their wide spores (*3.2–4.3 µm, Pls 215: 3; 216: 7; IVV: H.B. 6452d). In many other specimens the spores tend to be longer and especially narrower (*9.5–15 × 2.5–3.5 µm), and generally have a ± fusiform shape (Pls 215: 5; 216: 3, 6, 8–10). However, such spores may also occur in the first-mentioned group.

rDNA data suggest that two species are involved in our concept of *O. australiensis* (see below). However, since a sharp morphological limit could not be drawn, we refrained from splitting the species. The sequence of the broad-spored taxon became available only very recently, and it was confused with *O. myriobliqua* (H.B. 7204s) in the same collection, when the extract was done. Given that it belongs to H.B. 7204h, it would probably be representative also for the two other samples with extraordinarily broad spores.

Not included collections. Three very sparse samples from eastern Australia (Pl. 217: 1–2, H.B. 6809c [unillustrated]) differ in smaller spores and the absence of crystalloid SCBs. They probably represent a different species and should be recollected (see also a similar collection mentioned under *O. parviclava* in series *Hemiorbilia*, Pl. 320: 2).

Anamorph. In a pure culture of H.B. 7208b we obtained a few trinacrium robustum-like conidia when flooding an agar block with water. These closely resembled those of *O. pleioaustraliensis*, but were not documented.

Phylogeny. Sequences of *O. australiensis* s.l. were available from three collections from western Australia, two with comparatively narrow ascospores (ITS+LSU, from apothecia: spores *2.7–2.9 µm wide, IVV: 9.XI.2007; SSU+ITS+LSU, from pure culture: spores *2.6–3.3 µm wide, H.B. 7208b, Pl. 215: 2), and one from H.B. 7204, presumably H.B. 7204h with broad ascospores (Pl. 215: 3, spores *3.4–4.3 µm), in the following as *O.* cf. *australiensis* (ITS+LSU, from apothecia). The S1506 intron is present in the two more narrow-spored *O. australiensis* strains but absent in *O.* cf. *australiensis*. In the ITS the two samples of *O. australiensis* differ by 1 nt and 2 gaps (but 1 sequence is incomplete in the ITS2) and in the intron by 5 out of 315 overlapping nt (1.7 %), while in the LSU D1–D2 they are identical. *O.* cf. *australiensis* differs from them by 3.5 % in the ITS and 1 nt in the D2 of LSU.

The apothecia from which the sequence of *O.* cf. *australiensis* (uploaded as 7204h1) was taken were thought to belong to *O. myriobliqua*, but this seems very unlikely. The problem is that *O. myriobliqua* and *O. australiensis* occurred in this collection of *Acacia* branches together with at least 13 further *Orbilia* species. All three apothecia of *O. australiensis* that were examined in 2003 had broad ascospores. However, two further sequences from H.B. 7204 (ITS+LSU, 7204h-2a & -2b), also gained under the name *O. myriobliqua*, both possess the S1506 intron and resulted in another genotype of the *O. australiensis* complex. They differ from the above three sequences by 5.8–6.8 % in the ITS, 6.4–6.8 % in the intron, and 0.5–0.9 % in the LSU D1–D2, and from each other by 1.3 % in the ITS (7 nt), 1.1 % in the intron, and 0.3 % in the LSU (2 nt in D1). Therefore, they could either represent the true wide-spored *O. australiensis* H.B. 7204h or an unknown species, but hardly any of the 15 other species of this sample, which mostly belong to other sections of *Orbilia*.

When analysing (SSU+)ITS+LSU, ITS, or LSU, *O. australiensis* always clustered with high support in the *hesperidea-alpigena* clade, though without a supported association with any of its members (Baral et al. 2017b, Phyls 7, 9–10, S13). In the intron region (Phyl. S12), *O. australiensis* clustered highly supported with *O. pleioaustraliensis*, because other members of the *hesperidea-alpigena* clade do not possess the intron. The distance to these other members lies at 6–11 % in the ITS region, the lowest percentage being to *O. hesperidea* (6–7 % to narrow-spored *O. australiensis* and 8–11.5 % to the three *O.* cf. *australiensis* sequences). *O. pleioaustraliensis* shows a distance of 8–9 % in the ITS (9.5–11.5 % to the three *O.* cf. *australiensis* sequences) and ~12–13 % in the intron (overlapping 392 nucleotides). In the LSU (D1–D2) the distance to *O. hesperidea* is 2.8–3 % and to *O. pleioaustraliensis* 4.5 %.

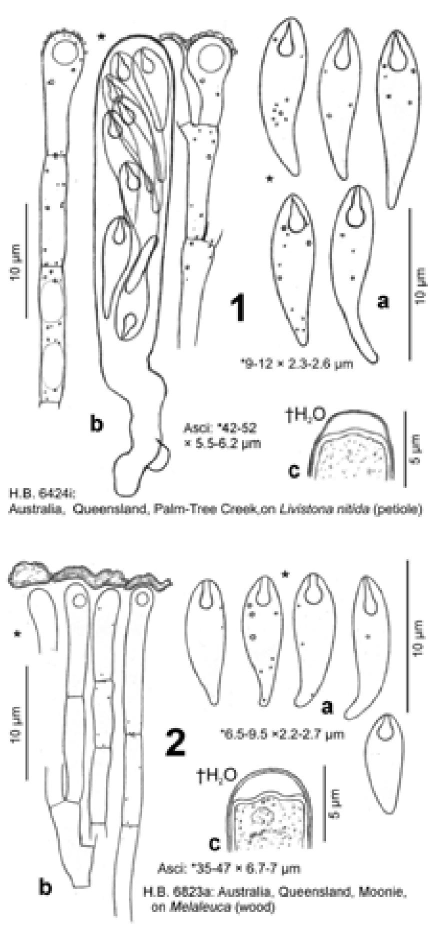
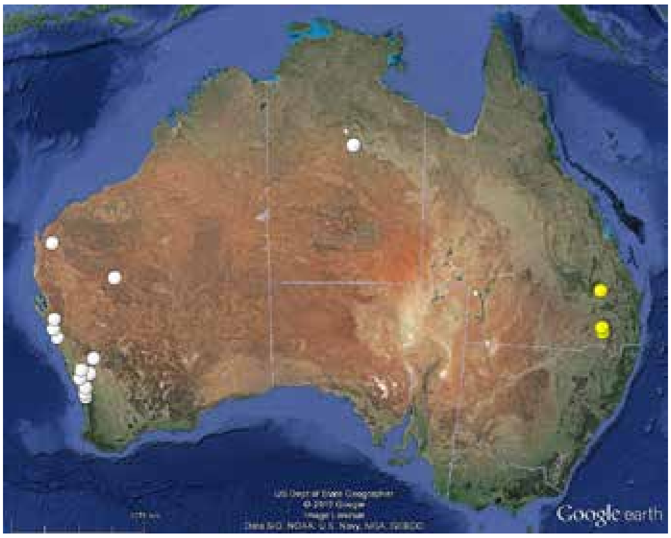


Plate 217. **1–2**: *Orbilia* aff. *australiensis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices.

Ecology. *O. australiensis* grew on slightly to strongly rotten wood and bark of xeric twigs and branches of various trees and shrubs, mainly of *Fabales* and *Proteales*, also *Sapindales* (*Dodonaea*). It is known from various sites of western and southwestern Australia, where it occurs in subtropical semiarid open acacia and other shrublands, and semihumid eucalypt (open) woodlands. A single collection is from northern Australia in a tropical arid open acacia shrubland (mulga). The not included collections from eastern Australia (Great Dividing Range) are in subtropical to warm-temperate semihumid eucalypt (open) woodlands.

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Acacia cyperophylla*, on wood, 28.X.2007, G. Marson (H.B. 9695e). – Carnarvon (border to Gascoyne), 137 km SE of Exmouth, 18 km ENE of Barradale Roadhouse, 95 m, twigs of *A.* ?*aneura*, on bark & wood, 5.XII.2001, G. Marson (MEL 2389218, **holotype**; **isotype** in H.B. 7135a). – Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, trunk of *Dodonaea viscosa* subsp. *angustissima*, on bark, 8.XI.2007, G. Marson (H.B.



Map 38. Known distribution of *O. australiensis* in Australia (yellow = not included collections).

8838d ø). – Geraldton Sandplains, 54 km N of Moora, 16.5 km N of Watheroo, Midlands Road, 292 m, twig of *Calothamnus*, on bark, 25.X.2007, G. Marson (ø). – 67 km N of Geraldton, 19 km N of Northampton, 273 m, branch of *Hakea*, on bark, 9.XI.2007, G. Marson (G.M. 2007-11-09.1 ø; sq.: KT380084). – 80 km NNW of Northampton, 29 km ENE of Kalbarri, near meander of Murchison, 160 m, twig of *Acacia*, on bark & wood, 9.XII.2001, G. Marson (H.B. 7415b). – Swan Coastal Plain, 150 km N of Perth, 13 km WNW of Moora, Dandaragan Road, 235 m, branch of *Acacia*, 24.X.2007, G. Marson (H.B. 8923c ø). – border to Jarrah Forest, 30 km NE of Perth, 4 km NE of Upper Swan, W of Walyunga, 76 m, branch of *Banksia cuneata*, on wood & bark, 2.IX.2006, G. Marson (H.B. 8660a ø). – ibid., branch of *Acacia*, on bark, 2.IX.2006, G. Marson (H.B. 8478f). – ibid., branches of *Jacksonia*, on wood & bark, 2.IX.2006, G. Marson (H.B. 8611b). – ibid., 37 m, twig & branch of *Jacksonia*, on wood & bark, 23.XI.2001, G. Marson (H.B. 7284c). – 54 km NNE of Perth, 11 km NE of Muchea, 187 m, bark of *Banksia grandis*, 3.IX.2006, G. Marson (ø). – Avon Wheatbelt, 68 km NE of Moora, 14 km S of Dalwallinu, 1.5 km S of Pithara, 327 m, twig of *Acacia*, on wood & bark, 24.XI.2001, G. Marson (ex H.B. 7208b, mixture in MEL 2389226 [type of *O. myriooblıqua*], CBS 116211, anam. cult.; sq.: KT215262). – 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig of *Acacia*, on wood & bark, 24.XI.2001, G. Marson (H.B. 7204h; sq.: MK473426, MK473427, MK473428). – ibid., twig of *Acacia*, on bark & wood, 26.X.2007, G. Marson (H.B. 8883d). – Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 271 m, branch of *Acacia*, on bark, 4.IX.2006, G. Marson (H.B. 8391b). – **Northern Territories**, Davenport Murchison Ranges, 118 km NNW of Tennant Creek, 23 km NNW of Banka Banka Station, 300 m, branch of *Acacia*, on wood, 7.X.1998, G. Marson (H.B. 6452d ø).

Not included. **AUSTRALIA**: **Queensland**, Brigalow Belt South, 69 km SSW of Theodore, 15 km N of Taroom, Palm-Tree Creek, Roy Staines Bridge, 200 m, petioles of *Livistona nitida*, 22.X.1998, G. Marson (H.B. 6424i ø). – 80 km N of Goondiwindi, 10 km S of Moonie, 278 m, branch of *Melaleuca*, on wood, 23.X.1998, G. Marson (H.B. 6823a ø). – 100 km S of Miles, 22.5 km NW of Moonie, 305 m, branch of *Casuarina cunninghamiana*, on wood, 23.X.1998, G. Marson (H.B. 6809c).

Orbilia pleioaustraliensis Baral & G. Marson, **sp. nov.**, MB 814368 — Pls 218–220, Map 39

Etymology: referring to the 16-spored asci and the otherwise close similarity with *O. australiensis*.

Typification: Australia, Northern Territories, Yulara, twigs of *Acacia jennerae*, 10.X.1998, G. Marson (ex H.B. 6277e, MEL 2389200A, holotype; ex-type culture: CBS 116223; sq.: KT215261).

Latin diagnosis: *Similis* Orbiliae australiensi *sed asci 16-spori. Habitat ad lignum vel corticem putridum ramulorum vel ramorum siccorum fruticum vel arborum angiospermarum in zona tropica vel subtropica subhumida ad arida Australiae occidentalis, centralis et orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.6(–0.8) mm diam., 0.13–0.23(–0.3) mm high, (light to) bright (dirty) orange(-rose) to brick-red, round, sometimes elliptical, scattered to gregarious (in ± small groups); disc slightly concave to flat, margin distinct, rising 0–30 µm above disc, ± glabrous; broadly sessile, ± erumpent, slightly to entirely immersed, sometimes deeply hidden in clefts. **Asci** *(70–)75–110(–120) × (8–)9–10(–11) µm {9}, †(48–)60–97(–110) × (6–)7–8.5 µm {9}, 16-spored (rarely 2–8 spores aborted), spores (*) 3–4-seriate, (5–)6–11(–12) lower spores inversely oriented {9} (slightly to strongly mixed), pars sporifera *45–60 µm long; **apex** (†) hemispherical (to slightly truncate), dome †1–1.7(–2) → 0.7–1 µm thick {6}, with wide apical chamber; **base** short- to rather long-stalked, L-, Y- or h-shaped. **Ascospores** *(7.5–)9–12(–13.5) × (2.7–)3.2–4.2(–4.7) µm {9}, †9–12(–13) × 3–4 µm {3}, ellipsoid(-clavate) to fusoid(-clavate), apex rounded to obtuse, base sometimes rounded, mostly distinctly tapered, sometimes or often with a distinct tail-like base or short, thick tail *1.5–3(–4) × (0.7–)1–1.3(–1.8) µm, straight, base sometimes slightly to medium curved; **SBs** (2.5–)3–4(–4.5) × (1.1–)1.3–1.6(–1.8) µm {7}, pear-shaped to ampulliform, rarely rod-shaped, apically narrowed to a small to wide point. **Paraphyses** apically slightly to medium (rarely strongly) clavate(-capitate), often flexuous, terminal cells (4.5–)6–20(–28) × (1.8–)2.5–4.5(–5.8) µm {6}, †2–3.5 µm wide {1}, lower cells (9.5–)11–15(–23) × 1.4–2.7 µm {4}; rarely to frequently branched at upper septum. **Medullary excipulum** pale orange(-rose), 15–40(–70) µm thick, of medium dense textura intricata or globulosa-angularis (with many inflated cells), sharply or indistinctly delimited. **Ectal excipulum** hyaline, near margin light to bright orange-rose, of (*) thin-walled, vertically oriented t. globulosa-angularis(-prismatica) from base to submargin, 25–130 µm thick near base, cells *9–20(–24) × 6–13(–15) µm {5}; 25–40(–60) µm thick at mid flanks, 20–40 µm near margin, upper margin of t. prismatica oriented at a 20–50° angle, marginal cortical cells *7–12(–14) × 3–5 µm {2}, walls (†) medium gelatinized, **glassy processes** absent. **Anchoring hyphae** abundant, */†2–4 µm wide {2}, walls 0.2–0.4 µm thick {2}, sometimes covering flanks and margin by a 3–10 µm thick hyaline layer. **SCBs** in paraphyses and cells from lower flanks to margin globose, low-refractive, mostly together with crystalloid ones {8}, refractive, pale to bright orange(-rose), 2.5–5.5 µm diam. **Exudate** over paraphyses 0.5–2(–4) µm thick, continuous to cloddy, very pale yellowish, loosely attached, marginal external hyphae immersed in hyaline exudate, sometimes with light honey-yellow exudate between hyphae and excipular cells. **— ANAMORPH**: trinacrium-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** not seen. **Conidia** Y-shaped, total size *28–32 × 18–24 µm {1}, †22 × 25 µm {1}, stipe *14–20 × 6–7 µm, †12 × 5 µm, 2–3-septate, arms tapering, *9.5–14 × 5–6.5 µm, †14–14.5 × 5 µm, 2(–3)-septate.

Habitat: collected 0.2–3 m above the ground or lying on ground, partially to often entirely decorticated, 1.5–20 mm thick twigs and branches of *Acacia* sp. {4}, *A. cyperophylla* {1}, *A. estrophiolata* {1}, *A. jennerae* {1}, *Atriplex* sp. {1}, *Melaleuca* sp. {1}, *Pittosporum phillyreoides* {1}, *Vachellia farnesiana* {1}, on 0.1–1 mm deep strongly decayed wood {9} and bark (periderm & bast) {3}, ± greyed, green algae absent or sparse. **Associated**: *Amandinea* sp. {1}, *Baggea* sp. {1}, *Caloplaca* sp. {1}, *Claussenomyces* sp. {1}, *Coccomycetella* spp. {4}, *Dacrymyces* sp. {2}, *Exidia* sp. {1}, *Gloniopsis* sp. {1}, *Hyalorbilia ?erythrostigma* {4}, *Hysterobrevium mori* {3}, *Hysteropatella* sp. {1}, *Orbilia allantoobliqua* {1}, *O. amberina* {1}, *O. anguliobliqua* {1}, *O. angustoaristata* {2}, *O. australiensis* {3}, *O. austroobtusispora* {1}, *O. austropleiomicrosoma* {1}, *O. aviflagellata* {1}, *O. barrowensis* {1}, *O. corculispora* {1}, *O. coronohesperidea* {1}, *O. curvatimyriella* {1}, *O. curvatiobliqua* {1}, *O. farnesianae* {1}, *O. helicoobliqua* {2}, *O. hesperidea* {2}, *O. lanternae* {1}, *O. ?livistonae* {2}, *O. megahesperidea* {1}, *O. microserpens* {1}, *O. multiaustraliensis* {2}, *O. multiaustrocylindrica* {1}, *O. ?multigambelii* {1}, *O. multiserpens* {3/1}, *O. myriella* {2/1}, *O. myrioauris* {1}, *O. myriofusiclava* {2}, *O. myriolilacina* {2}, *O. myriomuscula* {1}, *O. myrionamibica* {1/1}, *O. myrionanosoma* {1}, *O. myriooblıqua* {2}, *O. ?myrioolneyae* {1}, *O. myriopseudoregalis* {1}, *O. nothovinosa* {1}, *O. octocercocarpi* {2}, *O. paraobliqua* {2}, *O. ?parviclava* {1}, *O. pleioaustrocylindrica* {1}, *O. pleiocoronohesperidea* {1/1}, *O. ?pleioserpens* {1}, *O. pleiovinosa* {1}, *O. pleistooblıqua* {1}, *O. ?saguarina* {1}, *Patellaria ?andina* {1}, *Ostropales* {3}, *Peniophora* sp. {1}, *?Stictis* sp. {1}, *Symbiotaphrina*

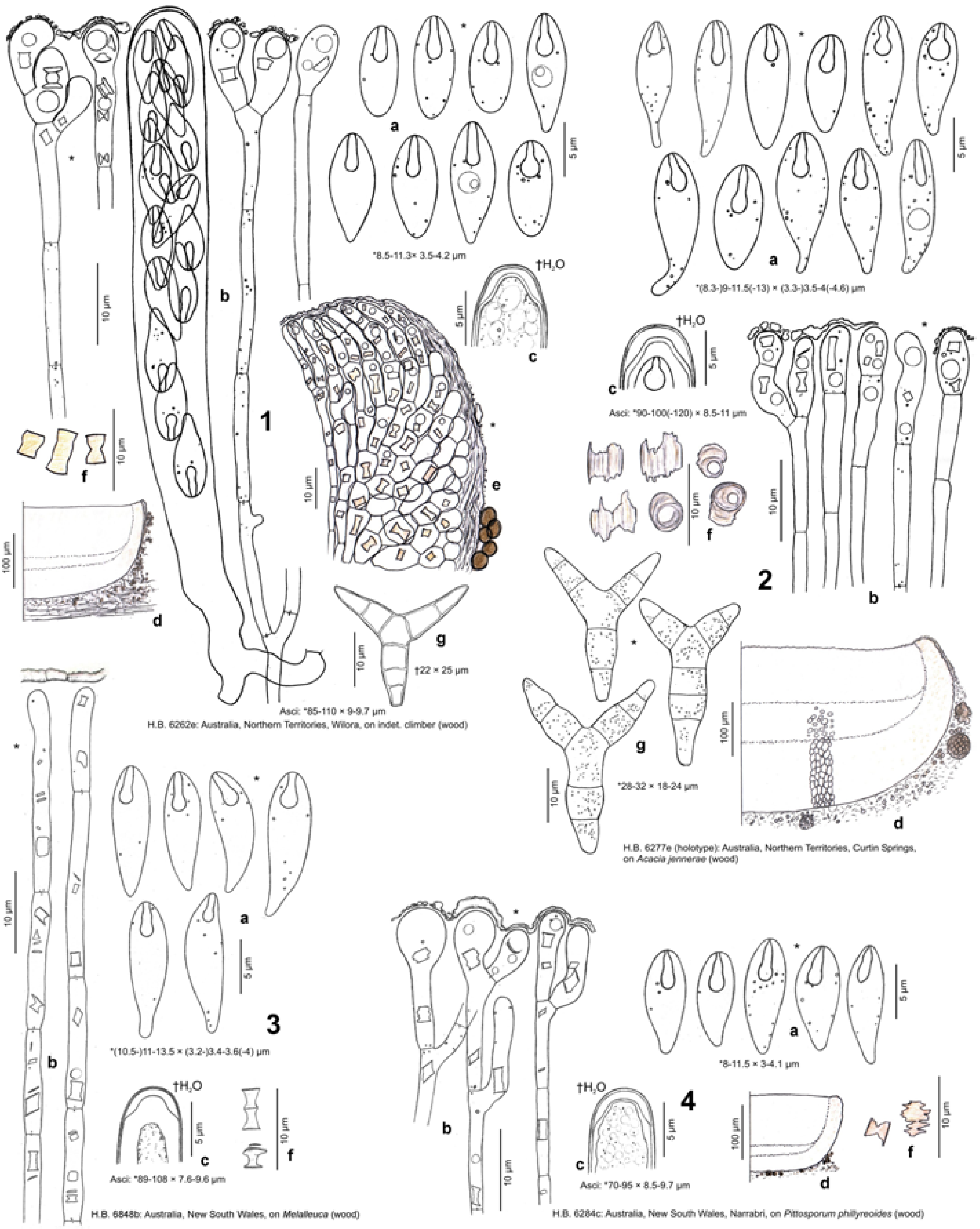


Plate 218. **1–4**: *Orbilia pleioaustraliensis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. crystalloid SCBs in ectal excipular cells (margin and flanks); **g**. conidia (**1** from substrate, **2** from culture).

desertorum {3}, ?*Triblidium* sp. {3}, *Tryblidaria* sp. {1}, *Xylobolus* sp. {1}. **Desiccation tolerance**: ± fully viable for 33 months. **Altitude**: 13–613 m a.s.l. **Geology**: Archean, Mesoproterozoic, Devonian, Carboniferous & Cretaceous sediments, Cenozoic regolith (ochre to red-brown sand and gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleioaustraliensis* is characterized by 16-spored asci, by which it differs from the otherwise very similar 8-spored *O. australiensis*, also it resembles the 32-spored *O. multiaustraliensis*. These taxa sometimes even grew in close association. Both *O. australiensis* and *O. pleioaustraliensis* differ from North American *O. arizonensis* especially in distinctly narrower ascospores and spore bodies.

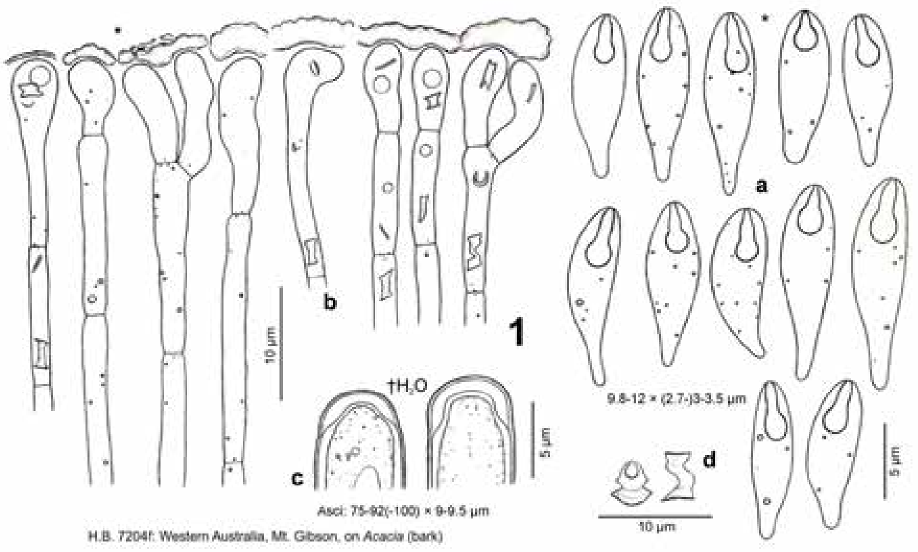


Plate 219. **1**: *Orbilia pleioaustraliensis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. crystalloid SCBs in marginal ectal excipulum.

Variation. A few 8-spored asci were very exceptionally observed within an apothecium among the 16-spored ones. In such asci the spores were longer (*12–14 × 3.4–3.6 µm) and the SBs slightly larger. The reverse case (a 16-spored ascus among 8-spored asci) was never observed in apothecia of *O. australiensis*. Some variation in spore size and presence of attenuated or tailed spore bases is noted among but also within collections.

Not included collection. A single apothecium on *Eucalyptus* (IVV: H.B. 9772b) deviates in extraordinarily long spores (*13.5–16.5 × 3.2–3.7 µm) which resemble those in Pl. 218: 3, also in the partial presence of a distinct tail and in narrower SBs (3–4.5 × 1–1.2 µm). Typical *O. pleioaustraliensis* occurred at the same site on *Acacia* (IVV: H.B. 9695b) and showed the characteristic spore size (*9.8–12.3 × 3.6–4.1 µm), while the here associated *O.* aff. *pleiocoronohesperidea* (Pl. 240) differs in much narrower spores.

Anamorph. Conidia were obtained in pure culture of *O. pleioaustraliensis* when flooded by water (Pl. 218: 2g). They resemble *Trinacrium robustum* and are also very similar to those of *O. australiensis*. A single conidium found on the natural substrate in another collection (Pl. 218: 1g) concurs with those from culture.

Phylogeny. Sequences of two samples of *O. pleioaustraliensis* were available: H.B. 6277e (Finke, holotype, from pure culture; Avon Wheatbelt, H.B. 7204f, from apothecia) comprises ITS and LSU (the former also SSU). The S1506 intron is present in the former but absent in the latter sample. The two sequences differ in the ITS by 3 nt and in the LSU D1–D2 also by 3 nt. In analyses of SSU+ITS+LSU, ITS+LSU, ITS, or LSU (Phyls 7, 9–10, S13) the species is found with high support in the *hesperidea-alpigena* clade, with an ITS distance of 8.2–10.5 % to the other included species. Although *O. pleioaustraliensis* differs from *O. australiensis* merely in 16-spored asci, the two species show a distance of 8.2 % to each other and do not cluster in a clade of their own (see also under *O. australiensis*, p. 559).

Ecology. *O. pleioaustraliensis* was found on rotten wood and bark of xeric twigs and branches of various angiosperm trees and shrubs or climbers. It is at present known from nine sites: in subtropical semiarid to arid open acacia shrublands of western Australia, in (sub)tropical arid open acacia shrublands of central Australia (around Macdonnell Ranges), and in subtropical subhumid eucalypt woodlands of eastern Australia (New England Range). Some of the collections contained only a few apothecia, whereas others were rather abundant, for instance, about 250 apothecia in the collection on *Pittosporum*. The not included collection on wood of *Eucalyptus* was in a subtropical semiarid acacia open woodland in the Gascoyne ecoregion of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Carnarvon, 117 km NNE of Carnarvon, 7 km SSE of Minilya Roadhouse, Barrabiddy Creek, 13 m, branch of *Vachellia farnesiana*, on wood, 6.XI.2007, G. Marson (H.B. 8997f ø). – 183 km SSE of Carnarvon, 10 km W of Overlander Roadhouse, 12 km NE of Hamelin Pool, Denham-Hamelin Road, 67 m, twig of *Acacia*, on bark, 7.XII.2001, G. Marson (H.B. 7215c). – ibid., twig of *Acacia*, on bark & wood, 6.XI.2007, G. Marson (H.B. 8727f). – Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *A. cyperophylla*, on wood, 28.X.2007, G. Marson (H.B. 9695b). – Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig & branch of *Acacia*, on bark, 24.XI.2001, G. Marson (H.B. 7204f; sq.: MK473429). – ibid., twig of *Acacia*, 26.X.2007, G. Marson (H.B. 8883e ø). – **Northern Territories**, Burt Plain, 31 km SW of Barrow-Creek Hotel, 3.7 km WSW of Wilora, 480 m, branch of *Atriplex*, on wood, 8.X.1998, G. Marson (H.B. 6262e, anam. substr.). – MacDonnell Ranges, SE of Waterhouse Range, 50 km SW of Alice Springs, 613 m, branch of *Acacia estrophiolata*, on wood, 10.X.1998, G. Marson (ø). – Finke, 100 km E of Yulara, 24 km ENE of Curtin Springs Roadhouse, 28 km NNE of Mt. Connor, 480 m, twigs of *A. jennerae*, on wood, 10.X.1998, G. Marson (ex H.B. 6277e, MEL 2389200A, **holotype**, CBS 116223, anam. cult.; sq.: KT215261). – **New South Wales**, Brigalow Belt South, 38 km SSW of Goondiwindi, 34 km SSW of Boggabilla, 230 m, branch of *Melaleuca*, on wood, 23.X.1998, G. Marson (H.B. 6848b ø). – 20 km SW of Narrabri, 248 m, twigs & branches of *Pittosporum phillyreoides*, on wood, 24.X.1998, G. Marson (H.B. 6284c).

Not included. **AUSTRALIA**: **Western Australia**, Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Eucalyptus*, on wood, 28.X.2007, G. Marson (ex H.B. 9772b, mixture in MEL 2389281 [type of *O. velutina*]).

Map 39. Known distribution of *O. pleioaustralieneis* in Australia.

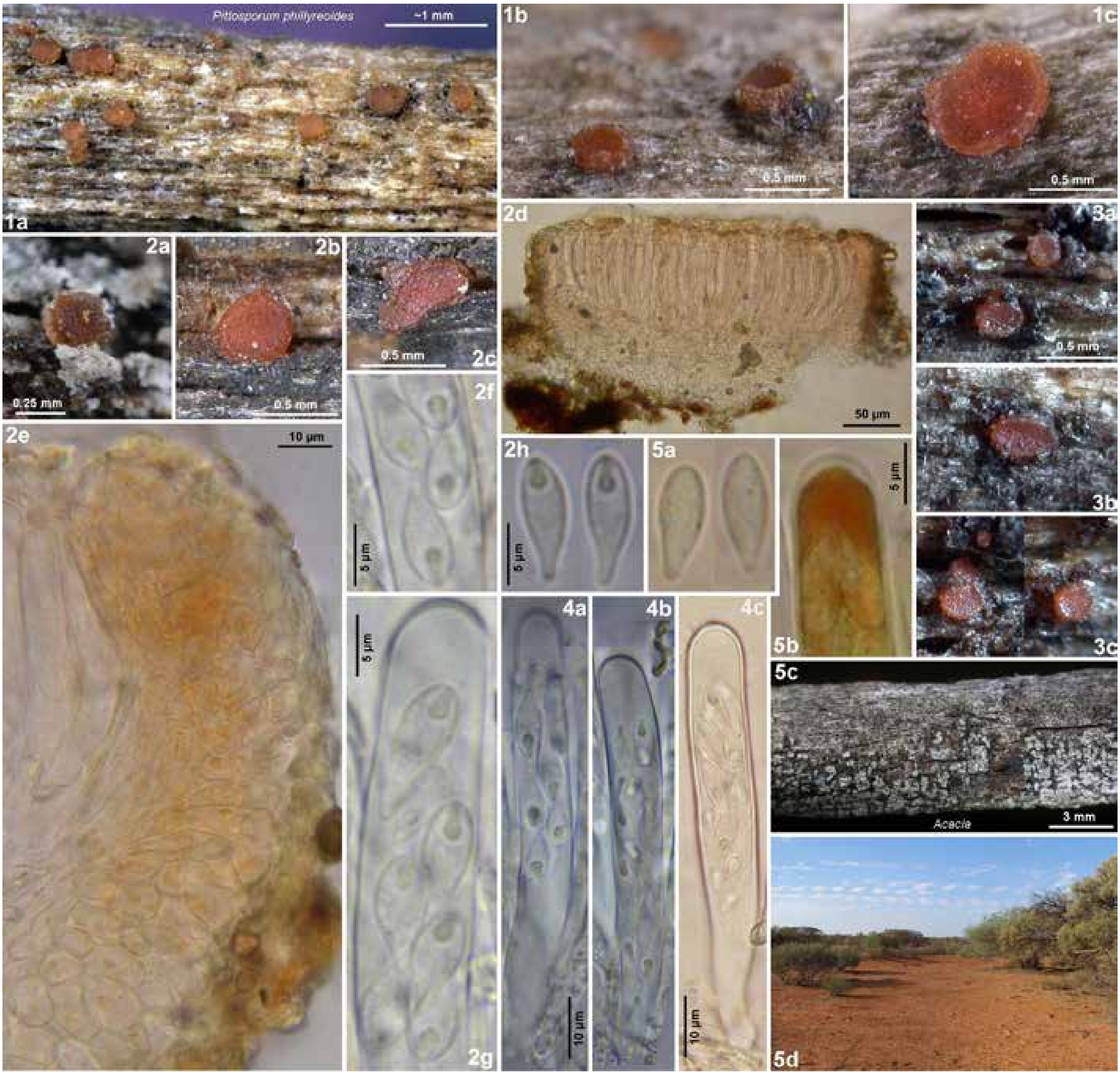


Plate 220. **1–5**: *Orbilia pleioaustraliensis*. – **5d**. semiarid acacia shrubland; **5c**. dead corticated xeric *Acacia* branch; **1a–c**, **2a–c**, **3a–c**. rehydrated apothecia; **2d**. apothecium in median section; **2e**. id., marginal ectal excipulum; **4a–c**. asci; **5b**. ascus apex; **2f–g**, **4a**, **5a**. ascospores. – Living state, except for **5a** (in KOH), **5b** (in KOH+IKI). — **1a–c**. H.B. 6284c: Western Australia, Narrabri, on *Pittosporum*; **2a–h**. H.B. 8727f: ibid., Carnarvon, on *Acacia*; **3a–c**. H.B. 6277e (holotype): Northern Territories, Curtin Springs, on *Acacia*; **4a–c**. H.B. 8883e: Western Australia, Mt. Singleton, on *Acacia*; **5a–d**. H.B. 7215c: ibid., Carnarvon, on *Acacia*.

Orbilia multiaustraliensis Baral & G. Marson, **sp**. **nov**.,
MB 813531 — Pls 221–222

Etymology: referring to the 32-spored asci and the similarity with *O. australiensis*.

Typification: Australia, Northern Territories, Yulara, branch of *Acacia jennerae*, 10.X.1998, G. Marson (ex H.B. 6277j, MEL 2389203A, holotype).

Latin diagnosis: *Similis* Orbiliae pleioaustraliensi *sed asci 32-spori, ascosporae cauda longiore et angustiore praeditae. Habitat ad lignum putridum rami sicci* Acaciae *in zona subtropica (semi)arida Australiae occidentalis et centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.22–0.4(–0.5) mm diam., 0.13–0.2 mm high, bright brick-red-orange, round to elliptical, subgregarious in rather small groups; disc slightly concave to flat, margin distinct or indistinct, 0–10 µm rising above disc, ± smooth, externally somewhat powdered; broadly sessile, erumpent between wood fibres, partially to entirely immersed. **Asci** *90–112 × 8.3–9 {T} or 74–97 × 9–10 µm {1}, †(62–)70–77(–82) × (6.5–)7–8.5(–9.5) µm {2}, 32-spored, spores 4-seriate, lower spores inversely oriented (somewhat mixed) {2}, pars sporifera *50–65 µm long; **apex** (†) hemispherical to slightly truncate, dome †0.7–1 → 0.3 {1} or 1–2 → 0.8–1.3 {2} µm thick, with slight apical chamber; **base** ± unstalked or with short thick stalk, L-, Y- or h-shaped. **Ascospores** *(8.3–)9–11.5(–12.5) × (2.7–)2.9–3.5 µm {2}, †7.5–10 × 2.7–3 µm {T}, ellipsoid-fusoid, apex obtuse to subacute, base with a short to medium long tail (1–)2–3(–4)((–5.5)) × 0.4–0.7 µm (exceptionally without), †0.2–0.3 µm wide, sometimes gradually attenuated, straight to slightly curved at base; **SBs** *(1.4–)1.7–2.2 × 1–1.2 {1} or 2.5–3 × 1.4–1.5 {T} µm, pear-shaped to ampulliform, apically narrowed to a minute or mostly ± wide point; with some minute LBs. **Paraphyses** apically uninflated to medium clavate-capitate, terminal cells *(6–)8–12(–17) × 2.8–4.2 µm {2}, lower cells *(8–)14–20(–23) × 1.5–2.3(–3) µm {2}, sometimes branched at upper septum. **Medullary excipulum** hyaline, 15–30 µm thick, of dense horizontal textura intricata-porrecta with many inflated cells, rather sharply delimited. **Ectal excipulum** hyaline, pale orange near margin,

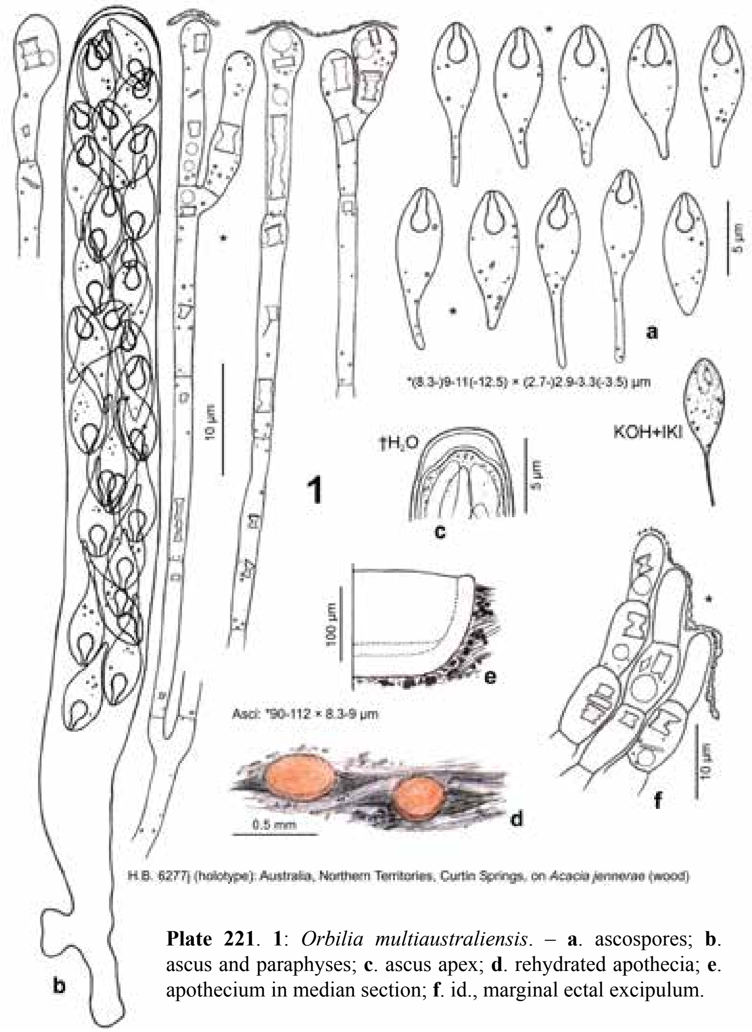


Plate 221. **1**: *Orbilia multiaustraliensis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., marginal ectal excipulum.

of (†) thin-walled or slightly gelatinized, irregularly vertically oriented t. angularis from base to mid flanks, 30–40 µm thick near base, cells *(6–)8–13(–16) × 6–11 µm {2}; 25 µm thick near margin, of t. prismatica oriented at a 10–20° angle to the surface, marginal cortical cells */†7–11 × 3–4.5 µm {2}, **glassy processes** absent. **Anchoring hyphae** sparse, †1.5–2.5 µm, wall 0.2–0.7 µm thick {T}. **SCBs** in paraphyses and ectal excipulum globose, mixed with crystalloid ones, pale orange. ones {2**Exudate** over paraphyses 0.5–1 µm thick, continuous, rough, over margin and flanks granular, thin. **— ANAMORPH**: unknown.

Habitat: lying ± on the ground or 2.5–3 m above, 7–20 mm thick decorticated branches of *Acacia cyperophylla* {1}, *A. jennerae* {1}, on 0.3 mm deep very decayed wood {2}, strongly greyed, no algae. **Associated**: *Baggea* sp. {1}, *Coccomycetella* spp. {3}, *Hysterobrevium mori* {1}, *Orbilia allantoobliqua* {1}, *O. anguliobliqua* {1}, *O. angustoaristata* {1}, *O. australiensis* {1}, *O. austropleiomicrosoma* {1}, *O. coronohesperidea* {1}, *O. multiserpens* {1}, *O. myriella* {1}, *O. myrionamibica* {1}, *O. pleioaustraliensis* {2}, *O. pleiocoronohesperidea* {1/1}, *O. pleiovinosa* {1}, *Ostropales* {1}, *Symbiotaphrina desertorum* {1}. **Desiccation tolerance**: fully viable for 38 months. **Altitude**: 480–540 m a.s.l. **Geology**: Mesoproterozoic sedimentary rock (red-brown sandstone), Cenozoic regolith. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia multiaustraliensis* is very close to *O. palmicola*, from which it differs in distinctly longer SBs, also in the frequent presence of a spore tail. The tail is already present within the living premature asci, when the spores are still devoid of a spore body. Therefore, *O. multiaustraliensis* cannot be considered as a more mature stage of *O. palmicola*. *O. pleioaustraliensis* mainly differs in 16-spored asci and spores with shorter and thicker tails. *O. myrioaustraliensis* differs in larger apothecia, 64-spored asci, and spores with thicker, always distinct tails. *O. macrocarpa* differs in larger and thicker apothecia with strongly protruding margin, a thinner ascus apical dome, spores without distinct tails, and in the presence of yellow LBs in paraphyses, medullary and lower ectal excipulum, finally in occurring on bark. *O.* aff. *macrocarpa* (Pl. 229) has prominent spore tails similar as *O. multiaustraliensis*, but its spores are much longer, and its other features closely match *O. macrocarpa*.

Variation. The paratype concurred quite well with the holotype, except for distinctly shorter and narrower SBs and slightly shorter and wider asci.

Ecology. *O. multiaustraliensis* was found on rotten wood of xeric branches of *Acacia*. The species is known from two subtropical collection sites: from a semiarid acacia woodland in a dry riverbed (Gascoyne) of western Australia, and from an acacia shrubland in the arid sand dunes (Finke, south of MacDonnell Ranges) of central Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Acacia cyperophylla*, on wood, 28.X.2007, G. Marson (H.B. 9695d). – **Northern Territories**, Finke, 100 km E of Yulara, 24 km ENE of Curtin Springs Roadhouse, 28 km NNE of Mt. Connor, 480 m, branch of *A. jennerae*, on wood, 10.X.1998, G. Marson (ex H.B. 6277j, MEL 2389203A, **holotype**).

Orbilia myrioaustraliensis Baral & E. Weber, **sp. nov.**, MB 814367 — Pls 223–224

Etymology: named after the 64-spored asci and a similarity with the 32-spored *O. multiaustraliensis.*

Typification: Western Australia, Tuckanarra, branch of *Acacia*, 27.X.2007, G. Marson (ex H.B. 8881a, MEL 2389262, holotype).

Latin diagnosis: *Similis* Orbiliae multiaustraliensi *sed asci 64-spori, ascosporae latiores, etiam caudae ascosporarum. Habitat ad corticem putridum ramorum siccorum* Acaciae *in zona (sub)tropica (semi)arida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–0.7(–1) × 0.3–0.5 mm, 0.18–0.28(–0.4) mm high, light to bright orange, non-translucent, round to elliptical, scattered; disc slightly concave to flat, margin distinct, 25–40 µm protruding, ± smooth; sessile on an obconical base or with a distinct stipe up to 0.25 × 0.35 mm, slightly immersed; dry hysterioid or 3–4-angular, light to bright dirty orange. **Asci** *120–130 × 12–13 µm {2}, †95–120 × (9.5–)10–11.5(–12.5) µm {2}, 64-spored (54–58 spores counted), spores †4–5-seriate, lower spores inverted (strongly mixed), pars sporifera *100 µm long, †75–85 µm; **apex** (†) hemispherical irrespective of the viewing direction, dome †0.5–0.7 → 0.3–0.4 µm thick {1} (KOH 1–1.6 → 0.8–1 µm), immature with large, wide and high apical chamber; **base** with very short to medium long, thick stalk, L-, Y- or h-shaped. **Ascospores** *((7–))(9–)10–12.5(–15) × 3.5–4(–4.5) µm {2}, †(8.5–)9–13(–15) × 3–3.8 µm {2}, with ellipsoid(-fusoid) head and abrupt, cylindrical, basally sometimes slightly inflated tail */†(2–)3–5(–7) × 0.8–1.2 µm {2}, apex obtuse (to subacute), tail straight to slightly, exceptionally very strongly curved; **SBs** *(2.3–)2.6–3.2 × (1.2–)1.3–1.6(–1.8) µm {T}, tear-shaped, apically narrowed to a ± small point. **Paraphyses** apically slightly (rarely medium) clavate, terminal cells *10–18 × 2.5–3.5 µm {T}, †7.5–15(–22) × (1.8–)2.5–4.3 µm {1}, lower cells *10–19 × 2–3(–3.5) µm {T}, †11–17(–22) × 1.5–2 µm {1}; rarely to quite frequently branched at upper septum. **Medullary excipulum** 30–70 µm thick, of dense textura intricata with medium abundant inflated cells, sharply delimited. **Ectal excipulum** of hyaline, (†) slightly gelatinized, indistinctly to vertically oriented t. angularis(-prismatica) from base to mid flanks, 30–80 µm

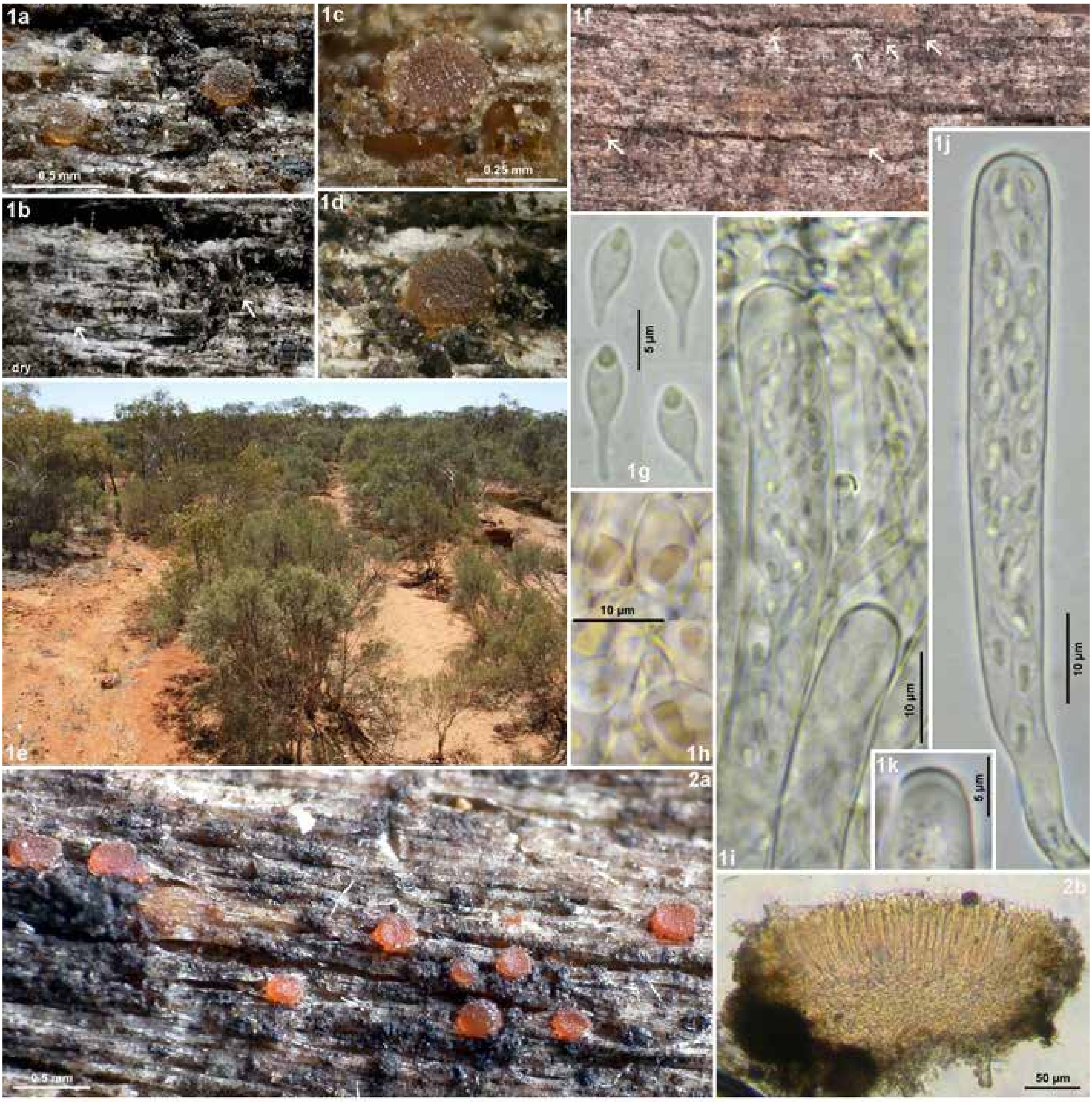


Plate 222. **1–2**: *Orbilia multiaustraliensis*. – **1e**. arid acacia open woodland; **1f**. closeup of branch (rehydrated); **1a**, **c–d**, **2a**. rehydrated apothecia; **1b**. dry apothecia (same sector as **1a**); **2b**. apothecium in median section; **1g**. ascospores (3 overmature); **1h**. crystalloid SCBs in marginal ectal excipulum; **1i–j**. asci and paraphyses; **1k**. ascus apex. – Living state, except for **1k**, **2b** (in KOH). — **1a–k**. H.B. 9695d: Western Australia, Gascoyne, on *Acacia*; **2a–b**. H.B. 6277j (holotype): Australia, Northern Territories, on *Acacia*.

thick near base, cells */†8–13(–15) × 6–8(–9) µm {2}, containing pale to light yellow-orange **LBs** 0.3–1.8 µm diam. (carotenoids, also in paraphyses) {3}; 20–40 µm thick near margin, of t. prismatica-porrecta oriented at a 0–20° angle to the surface, hyphae firm-walled, undulating and somewhat free in the outer layer, marginal cortical cells †8–16 × 3–4.3(–5) µm {1}, curved inwards; **glassy processes** absent. **Anchoring hyphae** abundant, †2–3(–4) µm wide, walls 0.2–0.3 µm thick {1}, forming a dense hyaline layer up to 35 µm thick near base (inner part light yellow), at flanks 20 → 10 µm thick. **SCBs** in paraphyses and marginal cells globose, 2.5 µm diam., mostly also with crystalloid (rod-shaped), pale yellow-orange SCBs in paraphyses (1.5–2 × 0.7–1.1 µm) and marginal excipulum {T}. **Exudate** over paraphyses 0.1–0.3 µm thick, granular, scattered, hyaline, loosely attached, over margin and flanks 0.2–1 µm thick, granular-cloddy. — **ANAMORPH**: unknown.

Habitat: collected 0.7–1.5 m above the ground, corticated, 8–12 mm thick branches of *Acacia* sp. {3}, on medium to strongly decayed bark {3} (bast), often on edges of bark, strongly greyed, without algae. **Associated**: ?*Baggea* sp. {1}, *Dinemasporium* sp. {1}, *Orbilia coronohesperidea* {1}, *O. myriomuscula* {1}, *O. phanosoma* {1}, *O. pleiocoronohesperidea* {1}, *O. pleioserpens* {3}, ?*Teichospora* sp. {1}. **Desiccation tolerance**: many submature asci still viable after 8 months. **Altitude**:: 467–690 m a.s.l. **Geology**: Precambrian sedimentary rock (red-brown gravel), mafic basaltic volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia myrioaustraliensis* closely resembles *O. multiaustraliensis*, from which it mainly differs in 64-spored asci and wider spores with thicker tails. *O.* aff. *macrocarpa* (Pl. 229) differs in much narrower spore heads

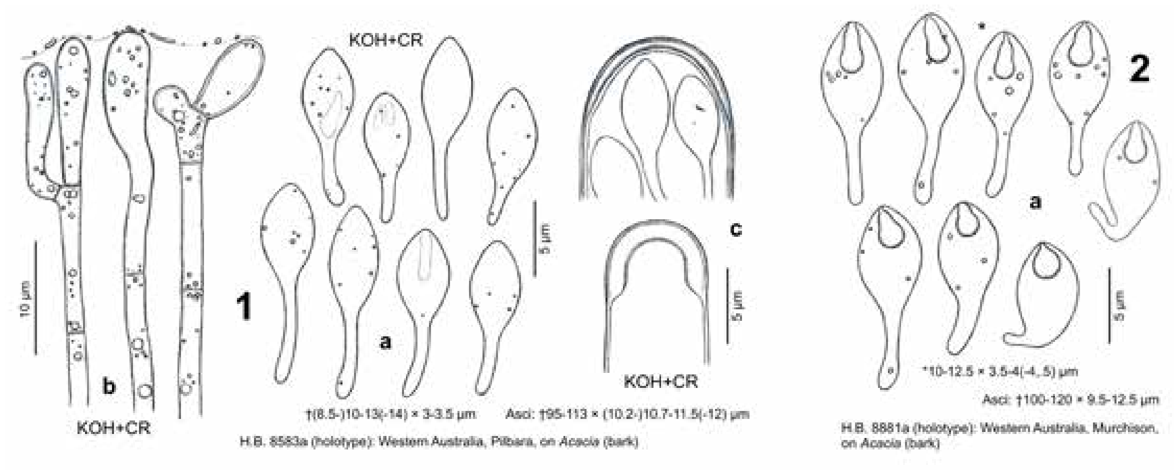


Plate 223. **1–2**: *Orbilia myrioaustraliensis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices.

and 32-spored asci. *O. myriohesperidea* differs in much narrower spores.

Ecology. *O. myrioaustraliensis* was found on strongly rotten bark of dead xeric branches of *Acacia* in subtropical semiarid to tropical arid open acacia shrublands in dry riverbeds of the Murchison and Pilbara ecoregions in the mid west of Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Pilbara, N of Karijini, 1.5 km SW of Wittenoom, delta of Wittenoom Gorge, 467 m, branch of *Acacia*, on bark, 28.XI.2001, G. Marson (H.B. 8583a). – 49 km NW of Newman, northern border of Ophthalmia Range, 690 m, branch of *Acacia*, on bark, 28.X.2007, G. Marson (H.B. 8879c ø). – Murchison, 72 km SW of Meekatharra, 17 km W of Reedy, E of Tuckanarra, 493 m, branch of *Acacia*, on bark, 27.X.2007, G. Marson (ex H.B. 8881a, MEL 2389262, **holotype**).

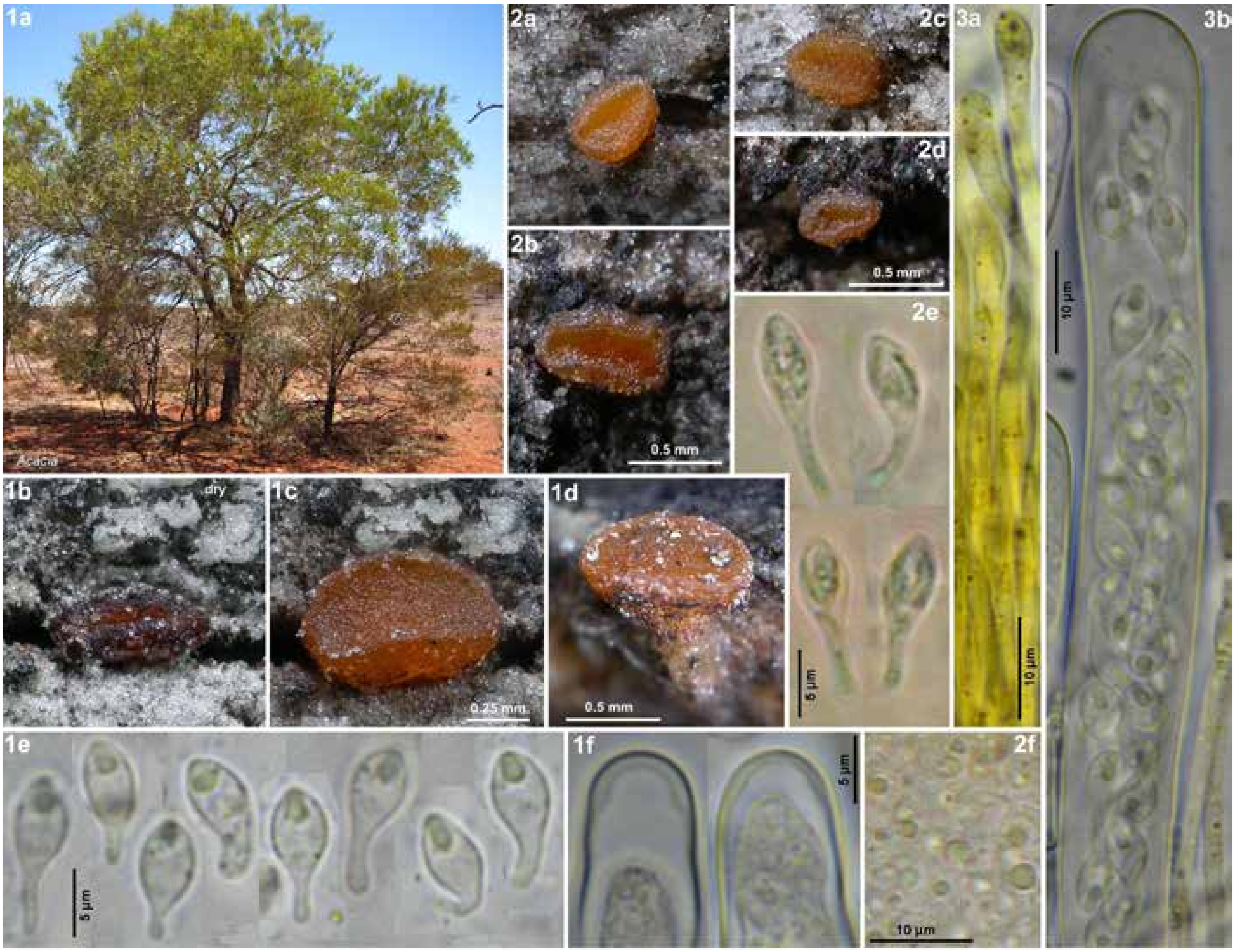


Plate 224. **1–3**: *Orbilia myrioaustraliensis*. – **1a**. semiarid acacia shrubland; **1c–d**, **2a–d**. rehydrated apothecia; **1b**. dry apothecium; **2f**. lipid bodies in ectal excipulum; **1f**. ascus apices; **3a**. paraphyses with carotenoids; **3b**. mature ascus; **1e**, **2e**. ascospores. – Living state, except for **1f**, **2e** (in H_2O), **2f** (in KOH). — **1a–f**. H.B. 8881a (holotype): Western Australia, Murchison, on *Acacia*; **2a–f**. H.B. 8583a: Pilbara, on *Acacia*; **3a–b**. H.B. 8879c: ibid., on *Acacia*.

Orbilia palmicola Baral, **sp. nov.**,

MB 813542 — Pls 225–226

Etymology: named after the substrate, the palm *Livistona nitida*.

Typification: Australia, Queensland, Taroom, leaves of *Livistona nitida*, 22.X.1998, G. Marson (ex H.B. 6424a, BRI AQ799184, holotype).

Latin diagnosis: *Similis* Orbiliae multiaustraliensi *sed ascosporae et corpuscula refringentia minora, ascosporae indistincte caudatae. Habitat ad petiolos putridos siccos* Livistonae nitidae *in zona subtropica subhumida Australiae orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.4 × 0.2–0.3 mm, 0.1–0.13 mm high, light to bright orange, ± round, scattered; disc flat, margin distinct, 0–10 µm rising above disc, smooth; broadly sessile, erumpent between host fibres. **Asci** *60–85 × 8–9.2 µm, †50–80 × 6.4–8 µm, exactly 32-spored, spores ± 4-seriate, lower spores inversely oriented (strongly mixed), pars sporifera *45–53 µm long; **apex** (†) hemispherical to slightly truncate, dome †H_2O 1 → 0.5 µm thick (KOH 1–1.5 → 0.6–1 µm), with apical chamber; **base** without or with or without short, thick or thin, flexuous stalk, L-, Y- or h- shaped. **Ascospores** *(5.7–)7–8.7(–10.5) × (2.7–)2.9–3.2 µm, †7–8 × 2.8–3 µm, broadly fusoid-clavate, apex rounded or often obtuse to subacute, base often tail-like, straight to very slightly curved at base; **SBs** *1.5–2 × 1–1.2 µm, tear-shaped to ampulliform, apically narrowed to a small to wide point, with some ± small LBs. **Paraphyses** apically uninflated to slightly clavate, rarely slightly spathulate, terminal cells *6–17 × 2–3.2 µm, lower cells *10–15 × 1.4–2 µm, basal cells *7–10 × 2–2.5 µm; not infrequently branched near apex. **Medullary excipulum** hyaline, 10–15 µm thick, of dense textura intricata with a few or many inflated cells, quite sharply delimited. **Ectal excipulum** hyaline, light orange near margin, of thin-walled, irregularly oriented t. angularis from base to mid flanks, 20–40 µm thick near base, cells *5–14 × 4–10 µm; 15–25 µm thick near margin, of t. prismatica-angularis oriented at a 10–45° angle to the surface, (†)

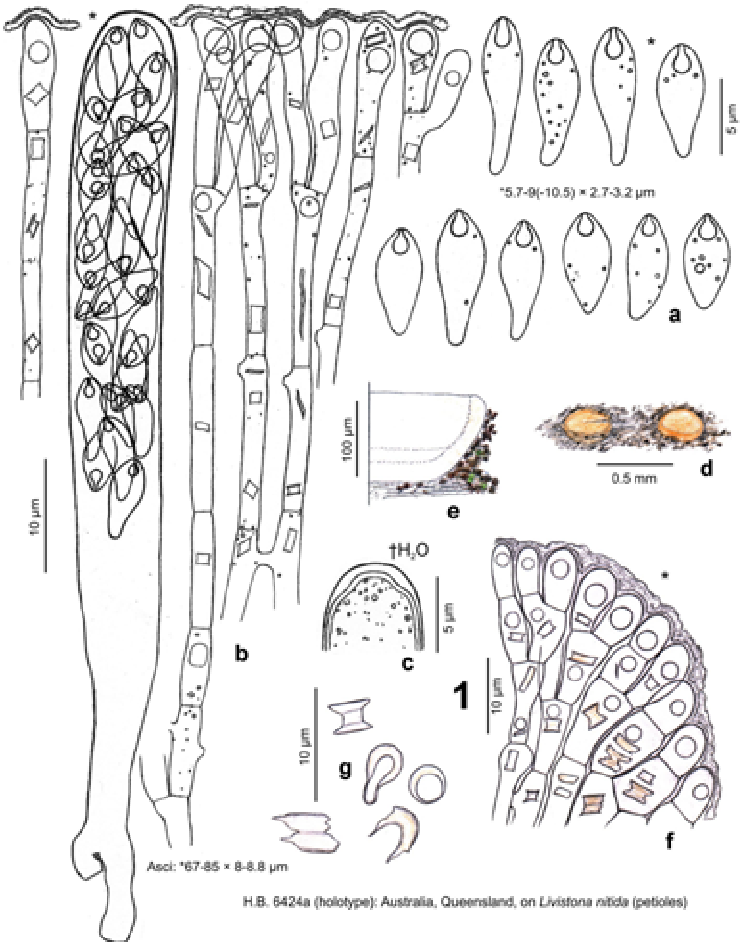


Plate 225. **1**: *Orbilia palmicola*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., ectal excipulum at margin; **g**. crystalloid SCBs in ectal excipular cells.

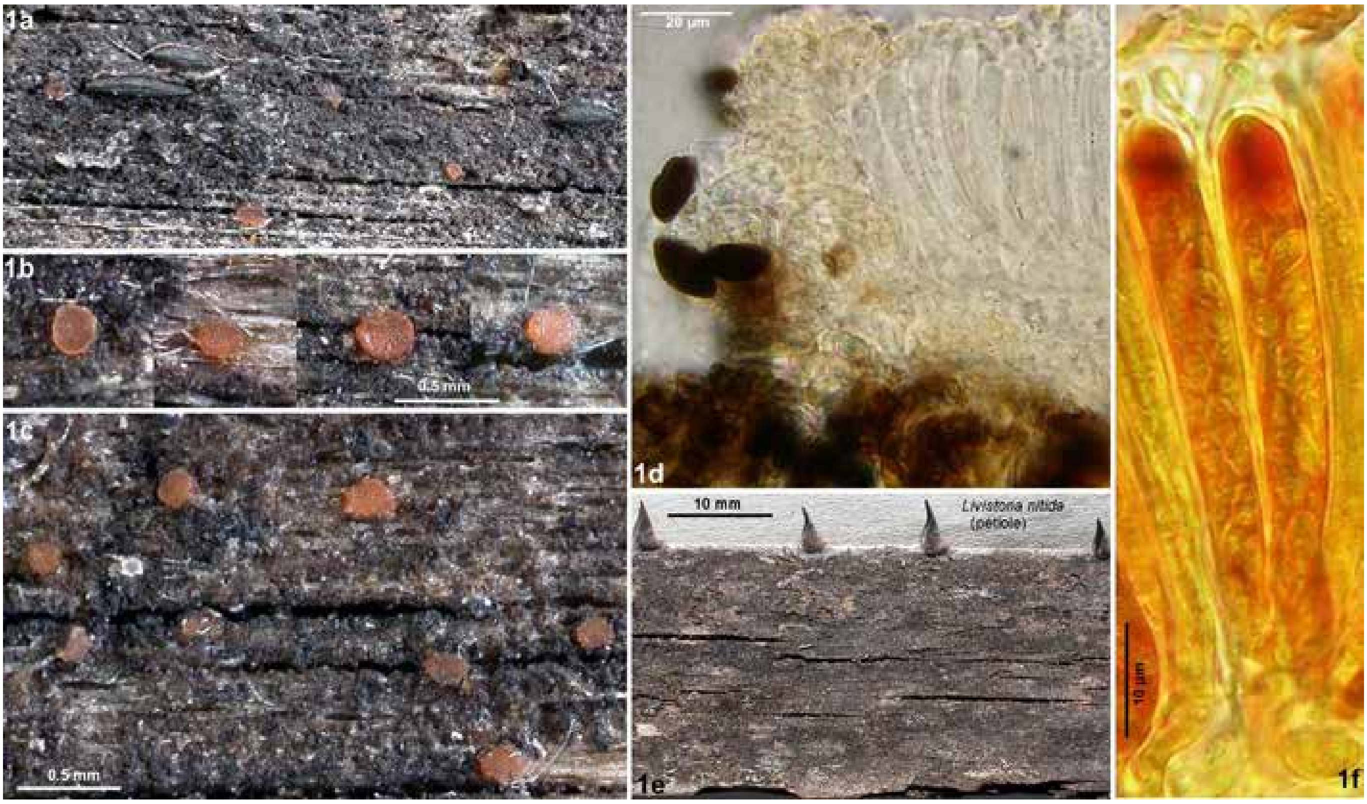


Plate 226. **1**: *Orbilia palmicola*. – **1e**. dead xeric petiole of *Livistona nitida* (upper side); **1a–c**. rehydrated apothecia (**1a** with *Gloniopsis* sp.); **1d**. apothecium in median section; **1f**. asci and paraphyses (in IKI). – Dead state (**1d** in KOH, **1f** in KOH+IKI). — **1a–f**. H.B. 6424a (holotype): Australia, Queensland, on *Livistona*.

slightly gelatinized, marginal cortical cells *6–12 × 3–4.5 µm, **glassy processes** absent. **Anchoring hyphae** sparse, †2–2.5 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and ectal excipulum globose, and crystalloid, pale orange. **Exudate** over paraphyses 0.4–1.5(–2) µm thick, continuous, rough, loosely attached; over margin and flanks 1–2 µm thick, rough-cloddy. **— ANAMORPH**: unknown.

Habitat: collected 0.2–2 m above the ground, still-attached, 15–28 mm broad dead petioles of *Livistona nitida*, always on rather strongly decayed upper side, slightly to strongly greyed, green algae sparse. **Associated**: *Gloniopsis* sp., *Mellitiosporiella* sp., *Orbilia acaciae*, *O. ?australiensis*, *O. ?commarosa*, *O. coronohesperidea*, *O. ?dixiensis*, *O. livistonae*, *O. multiserpens*, *O. myrioeuonymi*, *O. parviclava*, *O. pleiohesperidea*, *?Phaeotrichoconis* sp. **Desiccation tolerance**: fully viable for at least 9 months. **Altitude**:: 200 m a.s.l. **Geology**: Jurassic sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia palmicola* appears to be closely related to *O. pleioaustraliensis*, from which it differs in 32-spored asci and smaller ascospores with much smaller SBs. *O. multiaustraliensis* mainly differs in spores with thinner tails and longer SBs. *O. myriofusiclava* is also similar, but its spores are distinctly narrower and often curved, and have a bit more acute apices, also the asci are 64-spored.

Ecology. *O. palmicola* grew ± scattered over rather large areas of rotten, attached, hanging, xeric petioles of *Livistona* in a subtropical subhumid savannah eucalypt woodland in the Palm-Tree Creek at the Great Dividing Range of eastern Australia.

Globose, hyaline, single cells were observed in close proximity to some apothecia, which might be pollen grains or oospores (see Fig. 117). Most of them were infected by haustoria of mycelia which seem to belong to the *Orbilia*. A few conidia of *Trinacrium* sp. were observed in proximity to infected cells, but their connection to *O. palmicola* could not be confirmed.

Specimens included. **AUSTRALIA**: **Queensland**, Brigalow Belt South, 69 km SSW of Theodore, 15 km N of Taroom, Palm-Tree Creek, Roy Staines Bridge, 200 m, petioles of *Livistona nitida*, 22.X.1998, G. Marson (BRI AQ799184, **holotype**; MEL 2389207 & H.B. 6424a, **isotypes**).

Orbilia macrocarpa Baral & G. Marson, sp. nov.,
MB 813532 — Pls 227–228

Etymology: named after the comparatively large and thick apothecia.

Typification: Western Australia, Meekatharra, branch of *Acacia*, 26.XI.2001, G. Marson (ex H.B. 8697d, MEL 2389249, holotype).

Latin diagnosis: *Similis* Orbiliae multiaustraliensi *sed ascosporae cauda breviore praeditae, apothecia majores, margine projecto. Habitat ad corticem putridum ramorum siccorum* Acaciae *in zona subtropica (semi)arida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.27–)0.4–1 × (0.24–)0.3–0.5 mm, 0.2–0.4 mm high, light to bright orange(-brick-red), non-translucent, round to often elongate (laterally compressed), scattered to gregarious in small groups; disc slightly concave to flat, margin distinct, ± thick, 20–50 µm protruding, smooth to very slightly rough; broadly sessile, superficial or erumpent from cracks in periderm; dry usually hysterioid with ± closed disc. **Asci** †(80–)90–100(–110) × 7.3–8.8 µm {2}, 32-spored, spores †4-seriate, lower spores inverted {2} (strongly mixed), pars sporifera †64–75 µm; **apex** (†) hemispherical, dome †0.8–1.3 → 0.3–0.8 µm thick {1}, with apical chamber; **base** with short, thick, flexuous stalk, ?L-shaped. **Ascospores** *8.8 × 3.5 µm, †8–12 × 2.7–3.5 µm {2}, (ellipsoid-)fusoid to fusiform(-clavate), apex subacute to acute, base strongly attenuated, with or without a distinct tail or tail-like end, straight to sometimes slightly curved; **SBs** *~3.3 × 1-1.2 µm, narrowly tear-shaped (subulate). **Paraphyses** apically slightly to strongly clavate (rarely moniliform), terminal cells †7–20 {2} × 2–3 {1} or 3–4.5 µm {1}; sometimes branched at upper septum, lower half with light yellow-orange **LBs** (carotenoids) in the cells. **Medullary excipulum** pale to light yellowish to orange (or hyaline in lower part), 30–100 µm thick, of medium dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** hyaline, of (†) thin-walled to slightly gelatinized, vertically oriented t. angularis-prismatica from base to mid flanks, 90–200 µm thick near base, cells †(6–)9–15(–18) × (5–)6–11 µm {2}, common walls 0.5–1 µm; 50 µm thick on lower flanks, 20–30 µm near margin (up to 70 µm at protruding part including covering layer), pale to bright yellowish-orange, of t. prismatica-porrecta oriented at a 0–40° angle to the surface, marginal cortical cells †9–14 × 2.7–5 µm {1}, firm-walled (walls 0.2–0.4 µm thick); **glassy processes** absent. **Anchoring hyphae** sparse to abundant, †2–3(–4) µm wide, walls 0.2–0.3 µm thick {2}, forming a hyaline to light yellow-ochre, 10–20 µm thick t. intricata-porrecta at flanks and margin. **SCBs** no data available. **Exudate** over paraphyses and margin 0.2–1 µm thick, granular, loosely attached. — **ANAMORPH**: unknown.

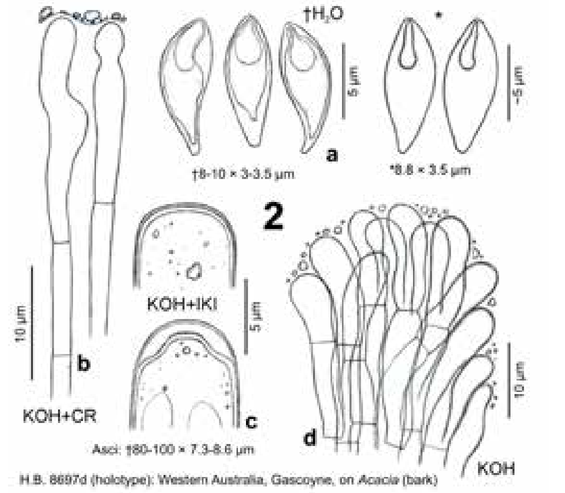


Plate 227. **1**: *Orbilia macrocarpa*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section.

Habitat: collected ~2 m above the ground, ± corticated, 4–15 mm thick branches of *Acacia* sp. {2}, on strongly decayed bark (bast) {2}, usually in cracks of periderm, rarely on inner surface of detaching bark, strongly greyed, no algae. **Associated**: *Orbilia anguliobliqua* {1}, *O. corculispora* {1}, *O. microserpens* {1}, *O. ?multiserpens* {1}, *O. ?multivirgula* {2}, *O. myriella* {1}, *O. myriomuscula* {1}, *O. myrioobliqua* {1}, *O. ?navajoana* {1}, *O. pleioungulata* {1}, *O. ?pseudeuphorbiae* {1}, *Ostropales* {1}, *Rhizodiscina* sp. {1}. **Desiccation tolerance**: unknown but certainly during min. 1 year. **Altitude**: 157–560 m a.s.l. **Geology**: Mesoproterozoic and Cretaceous sedimentary rock (red-brown sandstone). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia macrocarpa* differs from *O. multiaustraliensis* in larger and thicker apothecia with a strongly protruding margin, and in growing on bark, also in spores with shorter tails. The species was almost exclusively studied in the dead state, therefore, the vital characters are unknown, except for the spore bodies. *O.* aff. *macrocarpa* (Pl. 229) concurs very well with the present taxon, but differs in distinctly longer spores and an almost absent exudate *O. myriofusiclava* has similar apothecia but differs in 64-spored asci, smaller, often curved spores, and very abundant exudate.

Variation. Some variation between the two collected populations need to be mentioned: the holotype differs from the paratype in shorter and wider spores which are ± without a tail-like base, also in the paraphyses being apically only slightly inflated and therefore narrower. The other features are very similar between the two collections, and we are not in doubt that they are conspecific.

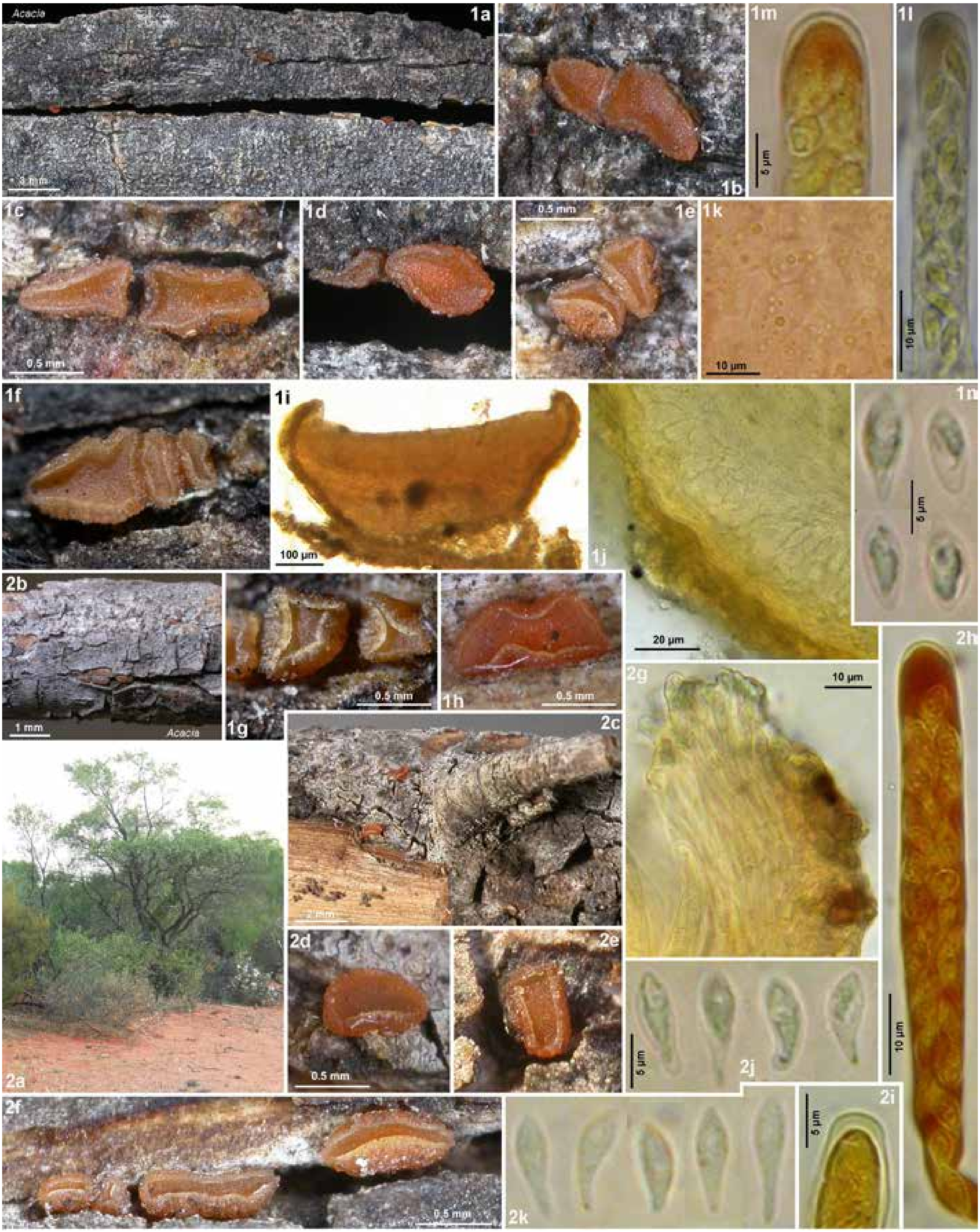


Plate 228. **1–2**: *Orbilia macrocarpa*. – **2a**. semiarid acacia shrubland; **1a**, **2b–c**. branches of *Acacia* (apothecia in cracks of bark, rehydrated), **1b–h**, **2d–f**. rehydrated apothecia; **1i**. apothecium in median section; **1j**, **2g**. id., ectal excipulum (flanks and margin); **1k**. lipid bodies in ectal excipulum (lower flanks); **1l**, **2h**. asci; **1m**, **2i**. ascus apices; **1n**, **2j–k**. ascospores. – All in dead state (**1n**, **2g**, **j** in H2O; **1j–k**, **2k** in KOH; **1l–m**, **2h–i** in KOH+IKI). — **1a–n**. H.B. 8697d (holotype): Western Australia, Gascoyne, on *Acacia*; **2a–j**. H.B. 9033d: ibid., Yalgoo, on *Acacia*.

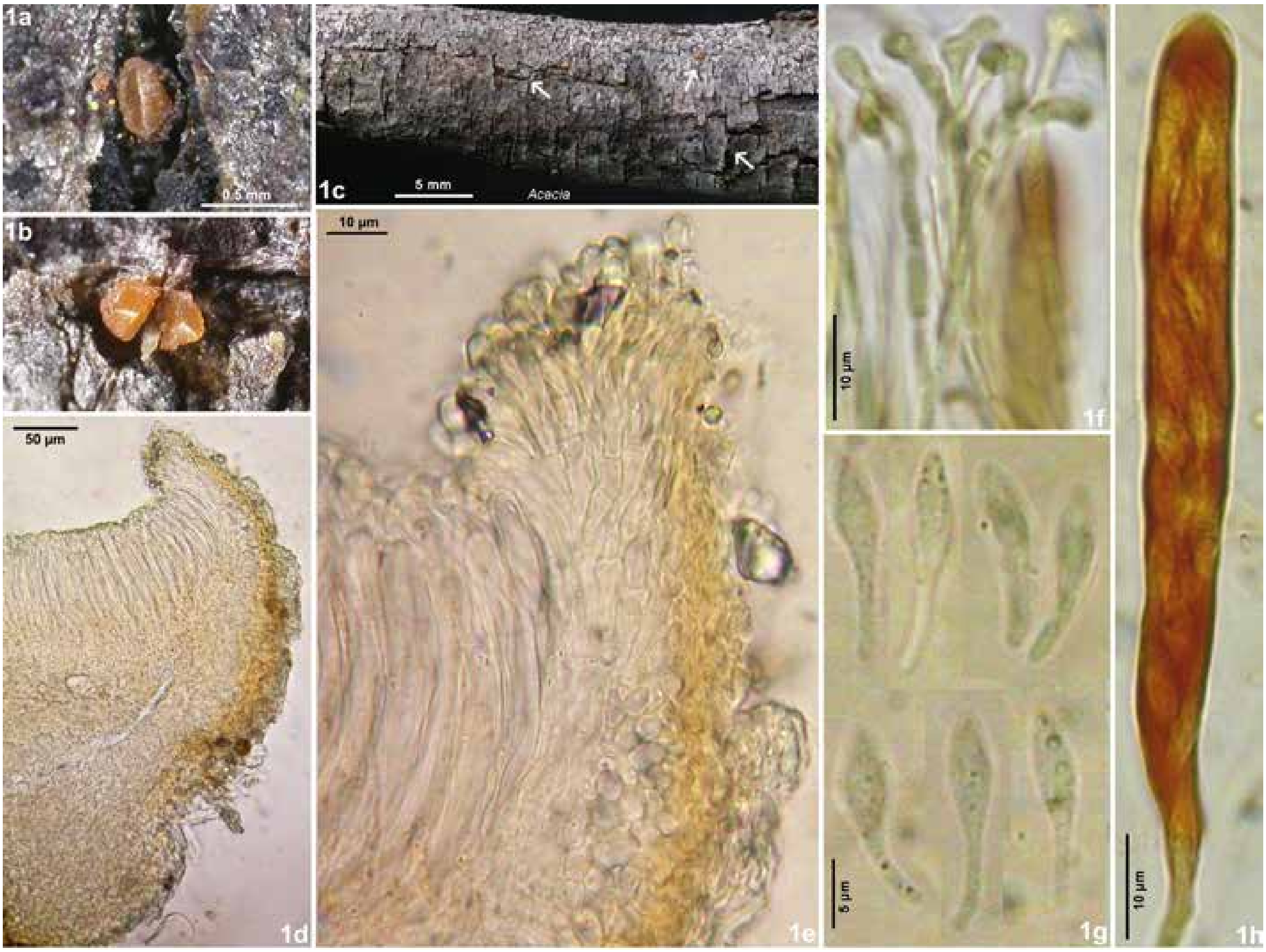


Plate 229. **1**: *Orbilia* aff. *macrocarpa*. – **1c**. dead corticated xeric branch of *Acacia*; **1a–b**. rehydrated apothecia (**1b** after a median section was taken); **1d**. apothecium in median section; **1e**. id., marginal ectal excipulum; **1h**. mature ascus; **1f**. paraphyses; **1g**. ascospores. – All in dead state (**1d–e**, **g** in KOH; **1f**, **h** in KOH+IKI). — **1a–h**. H.B. 7415f: Western Australia, Kalbarri, on *Acacia*.

Ecology. *O. macrocarpa* grew on rotten bark of xeric *Acacia* branches. The two known collections derive from subtropical semiarid to arid open acacia shrublands of western Australia (Yalgoo and Gascoyne ecoregion).

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, south-border of Collier Range, 175 km NE of Meekatharra, 41 km SW of Kumarina Roadhouse, 560 m, branch of *Acacia*, on bark, 26.XI.2001, G. Marson (ex H.B. 8697d, MEL 2389249, **holotype**). – Yalgoo, W of Toolonga, 200 km N of Geraldton, 15 km SSE of Wannoo Billabong Roadhouse, 157 m, branch of *Acacia*, on bark, 8.XII.2001, G. Marson (H.B. 9033d).

Orbilia aff. *macrocarpa* — Pl. 229

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4 × 0.25–0.28 mm, 0.33 mm high (receptacle 0.13–0.18 mm), bright orange, scarcely translucent, ± angular to laterally compressed, scattered; disc flat, margin very distinct, 40–60 µm protruding, finely whitish pubescent; sessile on a small hidden stipe 0.1 × 0.17 mm, erumpent from cracks. **Asci** †100–110 × 8–8.5 µm, 32-spored (25–30 spores counted), spores †4-seriate, lower spores inverted (± mixed), pars sporifera †60–88 µm long; **apex** (†) hemispherical, dome †0.8–1.2 µm thick, with slight apical chamber; **base** with medium long and thin, flexuous stalk, L-shaped. **Ascospores** †13–16 × 2.8–3 µm, with a fusoid, 7.5–9 µm long head and a distinct tail 4.5–6.5 × 0.9–1.2(–1.6) µm, apex obtuse to subacute, tail straight to slightly curved, sometimes slightly inflated at base; **SBs** only sometimes faintly seen, ?narrowly tear-shaped. **Paraphyses** apically slightly to medium clavate, sometimes moniliform, terminal cells †10–20 × 2.5–3.5 µm, lower cells †8–18 × 1.4–1.8 µm; frequently branched near apex, containing pale yellow-orange **LBs** (carotenoids) in lower part, hymenium pale orange. **Medullary excipulum** pale orange, 60 µm thick, of medium dense textura intricata with many inflated cells, sharply delimited mainly at flanks. **Ectal excipulum** very pale orange, of slightly gelatinized, indistinctly vertically oriented t. angularis from base to submargin, ~170 µm thick near base, cells †8–12 × 7–12 µm; 50 µm thick on lower flanks, 15–20 µm at submargin, 30–40 µm at upper margin, here of thin-walled t. prismatica oriented at a 10–20° angle to the surface, marginal cortical cells †8–13 × 3–4.5 µm, ± firm-walled (walls 0.2–0.3 µm thick); **glassy processes** absent. **Anchoring hyphae** rather sparse, †2–3 µm wide, walls 0.2–0.3(–0.5) µm thick, forming a 10–20 µm thick layer of yellowish-orange (externally hyaline) hyphae over flanks and margin. **SCBs** no data available. **Exudate** over paraphyses absent; over margin and flanks 0.1 µm thick, continuous. — **ANAMORPH**: unknown.

Habitat: corticated, 11 mm thick branch of *Acacia* sp., on medium decayed bark, in cracks of periderm, ± greyed, without algae. **Associated**: *Gloniopsis* sp., *Hysterobrevium mori*, *Orbilia australiensis*, *O. commarosa*, *O.* ?*pleiohesperidea*. **Desiccation tolerance**: unknown but certainly during min. 1 year. **Altitude**: 160 m a.s.l. **Geology**: Silurian sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. The collection differs from *O. multiaustraliensis* in distinctly longer ascospores, and in larger and thicker apothecia with a strongly protruding pubescent margin, also in growing on bark. The spores are consistently provided with a distinct, rather long tail. A new species is not proposed here because merely two apothecia were available, and no vital characters could be studied. Moreover, separation from *O. macrocarpa* (Pls 227–228) is not certain. The apothecia were accidentally discovered when the associated *O. commarosa* was restudied almost 5 years after it was collected.

Ecology. *O.* aff. *macrocarpa* was found on medium rotten bark of a dead xeric branch of *Acacia* in a subtropical semiarid acacia shrubland at the border of Murchison Gorge of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Geraldton Sandplains, 80 km NNW of Northampton, 29 km ENE of Kalbarri, near meander of Murchison, 160 m, branch of *Acacia*, on bark, 9.XII.2001, G. Marson (H.B. 7415f).

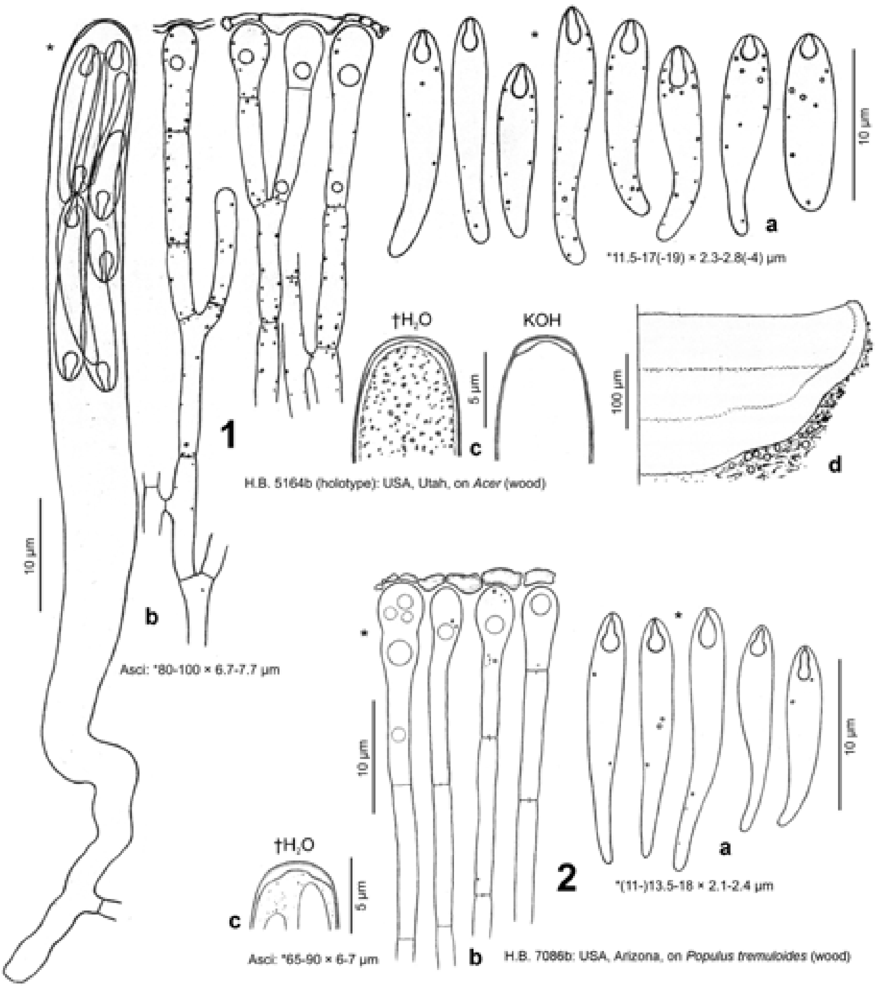


Plate 230. **1–2**: *Orbilia navajoana*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section.

Orbilia navajoana Baral & G. Marson, **sp. nov.**, MB 813544 — Pls 230–231, Map 40

Etymology: referring to the type locality, the Navajo trail in Bryce Canyon.

Typification: USA, Utah, Bryce Canyon, branch of *Acer*, 25.VIII.1994, G. Marson (ex H.B. 5164b, M-0276537, holotype).

Latin diagnosis: *Apothecia 0.2–0.7 mm diam., sessilia, erumpentia, aurantiaca, margine laevi vel subtiliter aspero. Asci 8-spori. Ascosporae *11–19 × 2.1–3.2 µm, subcylindrico- ad fusoideo-clavatae, apice obtusae, ad basim attenuatae et plerumque leniter curvatae, in statu vivo corpusculum refringens lacrimi- ad ampulliformem, ad apicem affixum continentes. Cellulae vivae exciputi marginalis et paraphysium corpuscula globosa continentes, excipulum marginale absque processis vitreis. Habitat ad lignum putridum ramorum siccorum angiospermarum vel coniferarum in zona temperata subhumida ad boreale humida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.25–0.5(–0.7) mm diam., 0.12–0.22 mm high, light to bright orange(ochraceous), non-translucent, round (to elliptical), scattered to gregarious; disc medium concave to flat, margin distinct, medium thick, 0–10 µm protruding, smooth to finely rough; broadly sessile, slightly to half erumpent. **Asci** *(65–)80–90(–100) × 6–8(–8.8) µm {4}, †(55–)60–85 × 5–7 µm {4}, 8-spored, spores *3–4-seriate, 2–6 lower spores inverted {3} (often mixed), pars sporifera *34–42 µm long; **apex** (†) hemispherical to slightly truncate, dome †0.5–1.1 → 0.5–0.7 µm thick {3}, with slight apical chamber, wall sometimes almost unthickened, even when immature; **base** with short to long, ± thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(11–)12–17(–19) × (2.1–)2.3–2.8(–3.2) µm {4}, subcylindric- to fusoid-clavate, apex rounded to mainly obtuse, medium to strongly attenuated in a 0.7–1.5 µm wide tail-like base, straight to mostly slightly, sometimes medium curved near base; **SBs** *2–2.8(–3) × 1–1.3 µm {2}, tear-to pear-shaped, also ampulliform, apically narrowed to a small to wide point. **Paraphyses** apically slightly to medium capitate-clavate, terminal cells *6–18 × (2–)2.5–3.7 µm {2}, †(2.2–)2.5–3(–3.7) µm wide {1}, lower cells *(6.5–)9–15(–20) × 1.4–2.3 µm {2}, †1.2–1.5 µm wide {1}; rarely or frequently branched near apex. **Medullary excipulum** 60–70 µm thick, of medium dense textura intricata(-globulosa), sharply delimited. **Ectal excipulum** pale to light orange (especially towards margin), of thin-walled to slightly gelatinized, vertically oriented t. angularis(-prismatica) from base to mid flanks, 20–70 µm thick near base, cells *8–25 × 6–13.5 µm {2}; 30–60 µm thick at flanks, 15–30 µm near margin, of t. porrecta oriented at a 20–30° angle to the surface, marginal cortical cells *8–13 × 2–4 µm {2}; **glassy processes** absent. **Anchoring hyphae** abundant, *2.5–3.5 µm wide, walls 0.2–0.4 µm thick {1}. **SCBs** globose {5}, 0.8–2.2 µm diam. in paraphyses, 2–3.5 µm in ectal excipulum (near margin). **Exudate** over paraphyses and marginal excipulum 0.5–2 µm thick, cloddy-continuous, loosely attached. **— ANAMORPH**: trinacrium-like (presumed, from natural substrate {1}, only 1 conidium seen). **Conidiophores** not seen. **Conidia** Y-shaped, †24 × 42 µm, stipe 12 × 6 µm, 2-septate, arms 21–22 × 7 µm, 3-septate, strongly tapered {1}.

Habitat: collected up to 3 m above the ground, decorticated, 13–35 mm thick branches of *Acer* sp. {1}, *Juniperus osteosperma* {2}, *Populus tremuloides* {1}, *Salix ?bebbiana* {1}, on 0.2–0.5 mm deep medium to very decayed wood {4}, strongly greyed, with many green algae. **Associated**: *?Amandinea* sp. {1}, *Diplolaeviopsis* sp. {1}, *Hysterium* sp. {1/1}, *Hysteropatella* sp. {1}, *Mellitiosporiella macrospora* {1}, *M. pulchella* {1}, *Odontotrema* sp. {1}, *O. oregonensis* {1}, *Orbilia calyptrata* {1}, *O. cupularis* {1}, *O. delphinus* {1}, *O. dixiensis* {1}, *O. flexisoma* {1}, *O. gambelii* {2}, *O. macrodelphinus* {1}, *O. microsoma* {2}, *O. multimaeandrina* {1}, *O. ophiosoma* {1}, *O. tremuloidis* {1}, *Perrotia flammea* {1}, *Phragmiticola* sp. {1}, *Sclerococcum* sp. {1}, *Unguiculariopsis* sp. {1}. **Desiccation tolerance**: a few mature asci still alive after 17 months, excipular cells and some paraphyses even after 33 months. **Altitude**: 2068–2825 m a.s.l. **Geology**: Permian and Upper Cretaceous sand-, lime- and mudstone; mafic volcanic lava with basalt, andesite & rhyolite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia navajoana* is characterized by rather long, subcylindric- to fusoid-clavate spores with short, tear-shaped SBs. It differs from both *O. vinosa* and *O.*

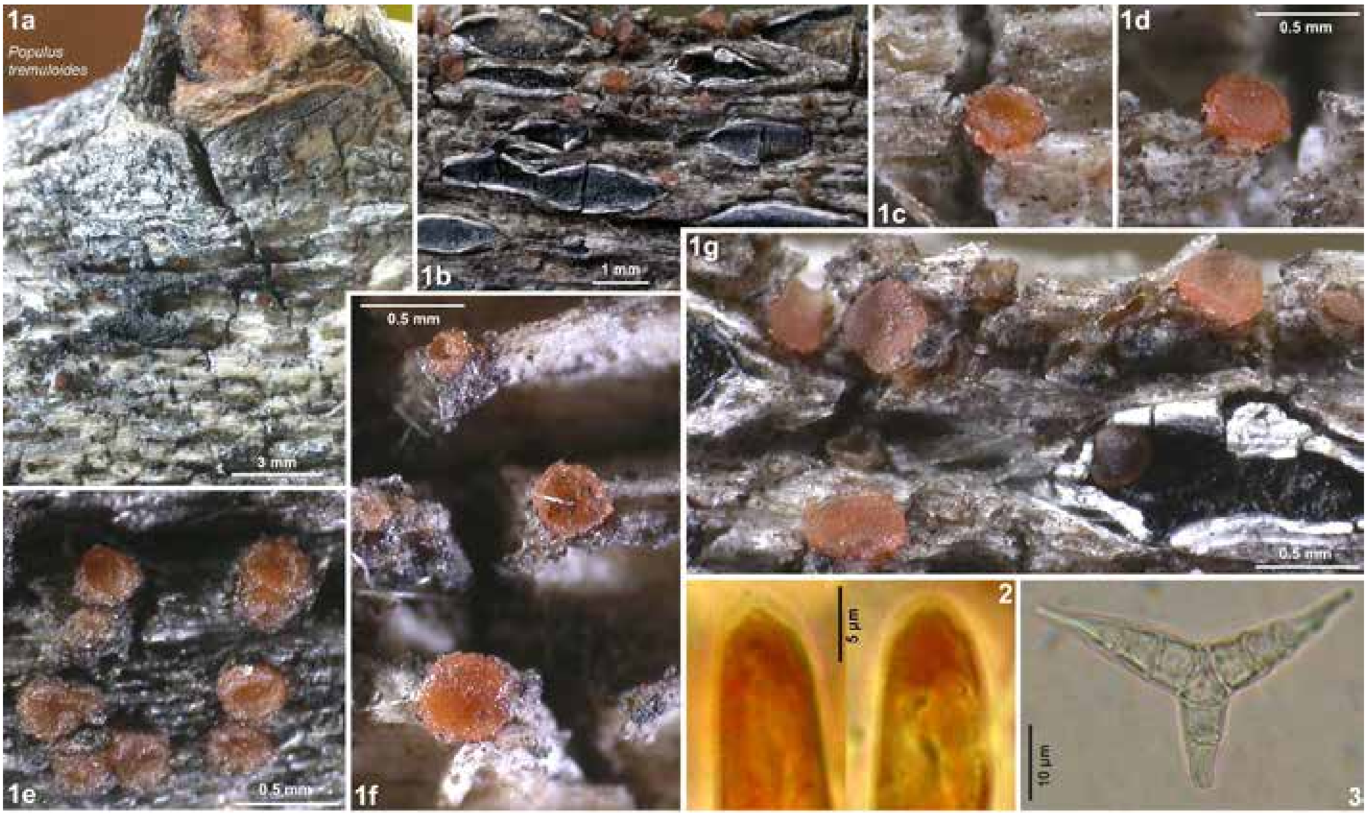


Plate 231. **1–3**: *Orbilia navajoana*. – **1a**. detail of decorticated xeric branch of *Populus tremuloides*; **1b–g**. rehydrated apothecia (with *Mellitiosporiella pulchella*); **2**. ascus apices. **3**. conidium from substrate. – Dead state (**2** in KOH+IKI, **3** in H_2O). — **1a–g**. H.B. 7086b: USA, Arizona, San Francisco Peaks, on *Populus*; **2**. H.B. 5362: ibid., Grand Canyon, on *Juniperus*; **3**. H.B. 5164b (holotype): USA, Utah, Bryce Canyon, on *Acer*.

hesperidea in the consistently shorter SBs, from the former also in wider spores, and from the latter in the consistent absence of crystalloid SCBs. The ascus apical thickening is also thinner than in these two species.

Variation. The spores of *O. navajoana* vary to some extent in length and especially width. The only abundant collection (on *Populus*) showed the narrowest spores, whereas the two on *Juniperus* had the widest spores (IVV: H.B. 5362, 8097c).

Not included collections. Two samples on *Larrea* from the Sonoran Desert scrub (IVV: H.B. 5658d, H.B. 5687f) have spores and SBs very similar to *O. navajoana*, but are not included because they possess crystalloid SCBs in the ectal excipulum and sometimes also in the paraphyses. For the similar Macaronesian *O. adenocarpi* see p. 674.

A sparse Australian specimen on *Acacia* (IVV: H.B. 9033a) was only studied in the dead state: it has similar ascus and spore dimensions but deviates in a hairy margin with thin-walled ~15–30 µm long projecting hairs.

Anamorph. The trinacrium robustum-like conidium observed in the holotype resembles those of *O. alpigena* and *O. montigena*.

Ecology. *O. navajoana* was collected on ± rotten wood of xeric branches of various trees including gymnosperms. The apothecia were mostly very sparse, only the sample on *Populus* was rich. It is so far only known from the mountainous southwest of Northern America (Colorado Plateau) from cold-temperate subhumid to humid pinyon-juniper woodlands and ponderosa pine forests and from a boreal Douglas fir mixed forest. The not included collections are from a subtropical semiarid Sonoran paloverde-mixed cacti desert scrub in western North America and from a subtropical semiarid acacia shrubland in western Australia.

Specimens included. **USA**: **Utah**, Utah Mts., Dixie Forest, 27 km SSE of Torrey, 18 km S of Grover, 2825 m, branch of *Salix ?bebbiana*, 15.V.1995, G. Marson (H.B. 5410c ø). – Bryce Canyon, 33 km SE of Panguitch, 8 km WSW of Tropic, Navajo Trail SE of Sunset Point, 2300 m, branch of *Acer*, on wood, 25.VIII.1994, G. Marson (ex H.B. 5164b, M-0276537, **holotype**, anam. substr.). – **Arizona**, Grand Canyon, Coconino Plateau, 3.5 km N of Tusayan, 2075 m, branch of *Juniperus osteosperma*, on wood, 17.VI.2003, G. Marson (H.B. 8097c ø). – 3 km N of Tusayan, 2068 m, branch of *J. osteosperma*, on wood, 28.VIII.1994, G. Marson (H.B. 5362). – Mogollon Rim, 23 km NW of Flagstaff, 10.5 km WNW of Humphreys Peak, 2450 m, branches of *Populus tremuloides*, on wood, 12.VI.2000, G. Marson (H.B. 7086b).

Not included. **USA**: **Arizona**, Sonoran Desert, 82 km NW of Phoenix, SE of Wickenburg, 615 m, branch of *Larrea tridentata*, on wood, 4.V.1995, G. Marson (H.B. 5658d). – 17.5 km NNE of Lukeville, Organ Pipe, Ajo Mountain

Map 40. Known distribution of *O. navajoana* in North America (yellow = not included collections on *Larrea*).

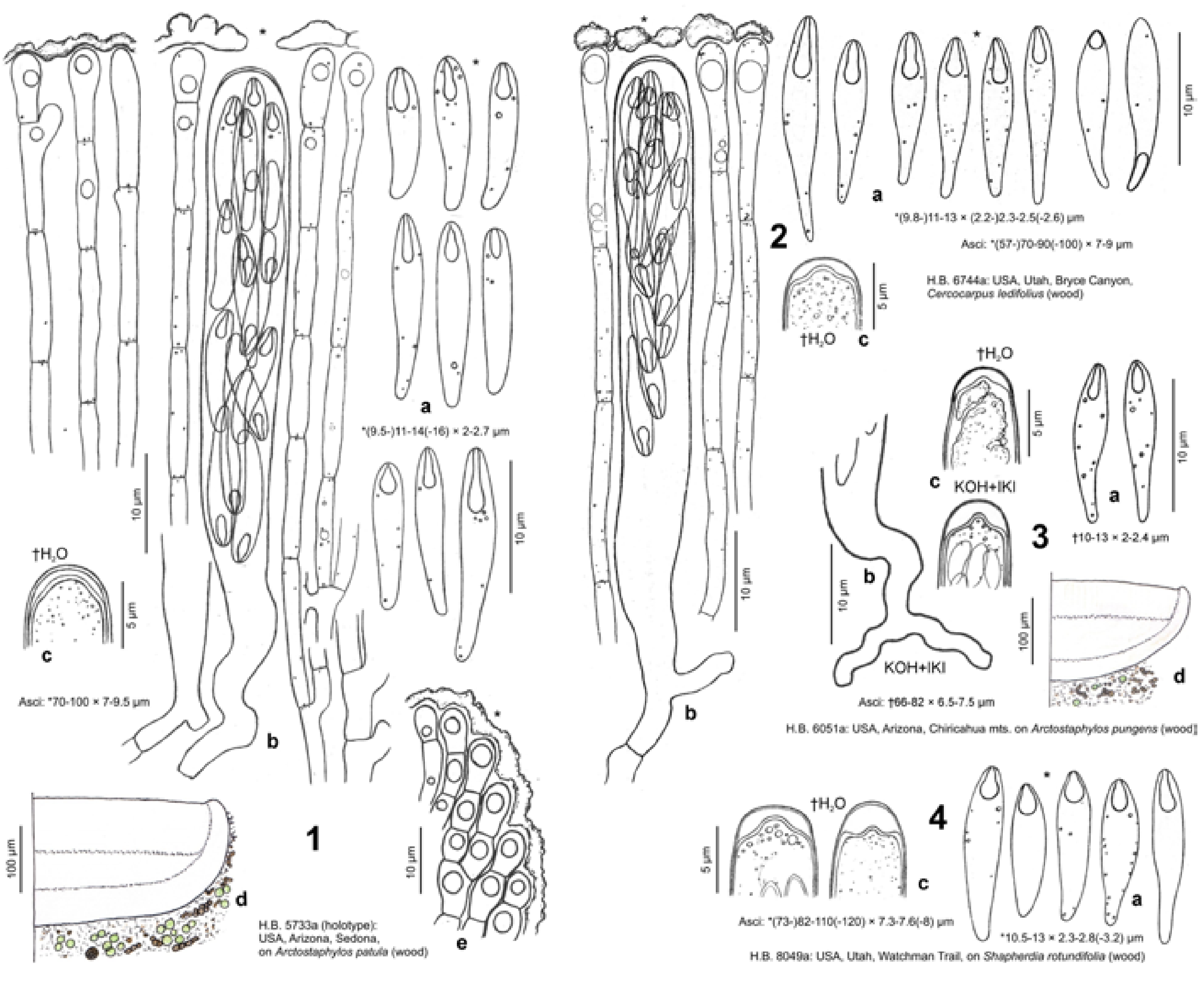


Plate 232. **1–4**: *Orbilia pleionavajoana*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum.

Trail, 710 m, branch of *L. tridentata*, 5.V.1995, G. Marson (H.B. 5687f ø). — **AUSTRALIA**: **Western Australia**, Yalgoo, 200 km N of Geraldton, W of Toolonga, 15 km SSE of Wannoo Billabong Roadhouse, 157 m, branch of *Acacia*, on bark, 8.XII.2001, G. Marson (H.B. 9033a ø).

Orbilia pleionavajoana Baral & G. Marson, **sp. nov.**, MB 813547 — Pls 232–233, Map 41

Etymology: a 16-spored relative of *O. navajoana*.

Typification: USA, Arizona, Sedona, branches of *Arctostaphylos patula*, 8.V.1995, G. Marson (ex H.B. 5733a, M-0276562, holotype).

Latin diagnosis: *Similis* Orbiliae navajoanae *sed asci 16-spori. Habitat ad lignum putridum ramulorum et ramorum siccorum fruticum angiospermarum in zona subtropica ad temperata semiarida ad subhumida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.25–)0.35–0.7(–1.2) mm diam., 0.14–0.26 mm high, light to bright or deep (yellow-) orange (apricot) to brick- or blood-red, ± round, sometimes elliptical, scattered to mostly ± gregarious; disc flat, margin distinct, smooth, 0–20 µm protruding; broadly sessile, slightly to strongly immersed in biofilm or fibres; dry bright to deep orange to blood-red. **Asci** *(57–)70–100(–120) × 7–8.5(–9.5) µm {4}, †66–82 × 6.5–7.5 µm {1}, 16-spored, spores 4–6-seriate, 4–8 lower spores inversely oriented {3} (± mixed), pars sporifera *37–50(–55) µm long; **apex** (†) hemispherical to slightly truncate, dome immature †0.7–0.9 {T+1}, 1–1.3 {1} or 1.3–2 µm {1} thick, mature 0.7–0.8 or 1–1.3 µm thick, with slight to distinct apical chamber; **base** with short to medium long, ± thick, flexuous stalk, ± L- or Y-shaped. **Ascospores** *(9.5–)11–14(–16) × (2–)2.2–2.6(–2.8)((–3)) µm {4}, 10–13 × 2–2.4 µm {1}, subcylindrical or cylindric- to fusoid-clavate, apex rounded or obtuse (to subacute), base slightly to strongly attenuated, sometimes or often tail-like, straight to very slightly curved near base; **SBs** *(2.3–)2.6–3.5(–4) × (0.7–)0.9–1.3(–1.5) µm {4}, tear- to pear-shaped, also ampulliform or subulate, apically narrowed to a small to mostly wide point. **Paraphyses** apically slightly to medium clavate-capitate, terminal cells *5.5–20 × 2.3–3.8 µm {2}, lower cells *(7.5–)10–18 × 1.5–2(–2.4) µm {2}; rarely branched near apex; hymenial layer very pale rose-orange to light pink. **Medullary excipulum** very pale rose(-orange), 30–60 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** (very) pale rose-orange, of thin-walled (externally slightly thick-walled), vertically oriented t. globulosa-angularis-prismatica from base to mid flanks, 30–100 µm thick near base, cells */†6–21 × 6–12(–15) µm {3}; 20–40 µm thick at mid flanks, 10–35 µm at margin, of t. prismatica oriented irreglarly at a 20–60° angle to the surface, marginal cortical cells */†(5–)7–11 × (2–)3–4.5(–6) µm {3}, **glassy processes** absent {4}. **Anchoring hyphae** sparse to medium abundant, */†2–3(–3.7) µm wide, walls 0.2–0.3(–0.4) µm thick {2}. **SCBs** globose {2}, 1 per cell, in paraphyses 1–2.7 µm diam., in excipulum 2.5–4 µm, crystalloid SCBs absent {3}. **Exudate** very pale yellowish-chlorinaceous, over paraphyses (0.5–)1–3(–4) µm thick {3}, continuous though broken into large clods, loosely attached; over margin and flanks rough, 2–5 µm thick. — **ANAMORPH**: unknown.

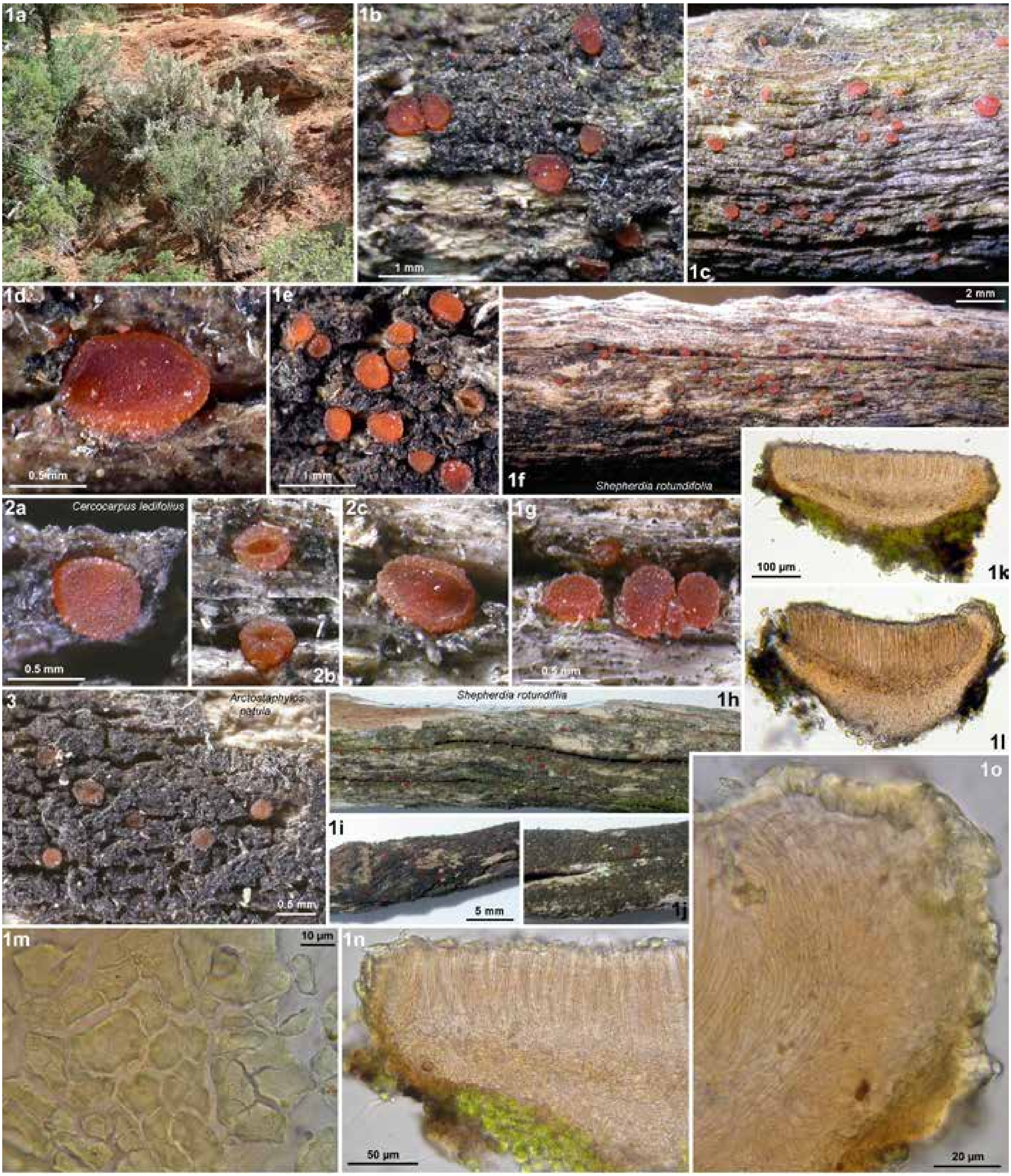


Plate 233. **1–3**: *Orbilia pleionavajoana*. – **1a**. semiarid mountain shrub with *Cercocarpus intricatus*, *Shepherdia rotundifolia* etc.; **1h–j**. decorticated xeric branches of *Shepherdia rotundifolia*; **1b–g**, **2a–c**, **3**. rehydrated apothecia; **1k–l**, **n**. apothecia in median section; **1o**. id., marginal region; **1m**. cloddy exudate on marginal excipulum (external view). – Dead state (in H_2O). — **1a–m**. H.B. 8049a: USA, Utah, Zion, on *Shepherdia*; **2a–c**. H.B. 6744a: ibid., Bryce Canyon, on *Cercocarpus*; **3**. H.B. 5733a (holotype): USA, Arizona, Sedona, on *Arctostaphylos*.

Habitat: collected 0.2–1.5 m above the ground, decorticated, 4–22 mm thick twigs and branches of ± dead shrubs of *Arctostaphylos patula* {1}, *A. pungens* {1}, *Cercocarpus ledifolius* {1}, *Parkinsonia microphylla* {1}, *Shepherdia rotundifolia* {1}, on 0.3–1.5 mm deep medium to strongly decayed and eroded wood {4}, on upper side, often along longitudinal cleft, often strongly greyed and covered by green algae. **Associated**: *Claussenomyces* sp. {1}, *Coccomycetella* sp. {1}, *Cryptodiscus foveolaris* {1}, *Dacrymyces* sp. {2}, *Diplolaeviopsis* sp. {1}, *Durella* sp. {2}, *D.* ?*connivens* {1}, *Gloniella* sp. {1}, *Gloniopsis subrugosa* {1}, *Hysterium* sp. {1}, ?*Hysteropatella* sp. {1}, *Mellitiosporiella pulchella* {2/1}, *Orbilia* ?*dixiensis* {1}, *O. hesperidea* {1}, *O. maeandrina* {1}, *O. pluristomachia* {1}, *O. vibrioides* {1}, *Ostropales* {1}, *Parmelia* sp. {1}, *Perrotia flammea* {2}, *Phragmiticola* sp. {4}, ?*Pragmopora* sp. {1}, *Propolis farinosa* {1}, ?*Triblidium* sp.

{1}. **Desiccation tolerance**: fully viable for at least 22 months, after 31 months still many immature and some mature asci alive. **Altitude**: ~1165–2300 m a.s.l. **Geology**: Triassic-Jurassic-Cretaceous red sand- and limestone, Oligocene felsic volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleionavajoana* differs from *O. navajoana* mainly in 16-spored asci, but perhaps also ecologically. The two taxa deviate from the similar taxon pair *O. hesperidea* (8-spored) and *O. pleiohesperidea* (16-spored) mainly in the absence of crystalloid SCBs.

Variation. The studied collections closely concur, except for some variation in apothecial size and spore shape. Abnormal ascospores over 14 µm long, with 4.5–4.8 µm long SBs, are formed inside asci with reduced spore numbers, e.g., in 10-spored asci.

Not included collection. A sample on *Larrea* (IVV: H.B. 5687g) differs from *O. pleionavajoana* in possessing crystalloid SCBs and slightly smaller spores (*9.5–10.5 × 2–2.4 µm), and probably represents a different species.

Ecology. *O. pleionavajoana* was found on ± rotten wood of xeric twigs and branches of various angiosperm shrubs in the mountainous southwest of Northern America. The collection sites include a subtropical semiarid paloverde-mixed cacti desert scrub in the Sonoran Desert, warm-continental subhumid manzanita chaparral scrublands in the Mogollon Rim and Sonoran and Chihuahuan Desert, a warm-temperate semiarid pinyon-juniper woodland cold-temperate subhumid ponderosa pine forest at the southern border of Utah Mountains. In the holotype collection, *O. hesperidea* grew in a close but separate population.

Specimens included. **USA**: **Utah**, Utah Mts., Bryce Canyon, 33 km SE of Panguitch, 8 km WSW of Tropic, Navajo Trail SE of Sunset Point, 2300 m, branches of *Cercocarpus ledifolius*, on wood, 20.VI.2000, G. Marson (H.B. 6744a). – Zion, south entrance, Pine Creek, The Great Arch, 1590 m, branches of *Shepherdia rotundifolia*, on wood, 14.VI.2003, G. Marson (H.B. 8049a). – **Arizona**, Mogollon Rim, 37 km SSW of Flagstaff, ~1 km NE of Sedona, 1320 m, branches of *Arctostaphylos patula*, on wood, 8.V.1995, G. Marson (M-0276562, **holotype**; H.B. 5733a, **isotypes**). – Sonoran Desert, 40 km NNE of Tucson, 11 km NE of Catalina, Casa del Oro, Biosphere, 1165 m, on *Parkinsonia microphylla*, 7.V.1995, G. Marson (ø). – Chihuahuan Desert, 150 km ESE of Tucson, NW end of Chiricahua Mts., E of parking area, ~1700 m, branches of *Arctostaphylos pungens*, on wood, 26.V.1996, G. Marson (H.B. 6051a).

Not included. **USA**: **Arizona**, Sonoran Desert, 17.5 km NNE of Lukeville, Organ Pipe, Ajo Mountain Trail, 710 m, branch of *Larrea tridentata*, 5.V.1995, G. Marson (H.B. 5687g ø).

Map 41. Known distribution of *O. pleionavajoana* in North America.

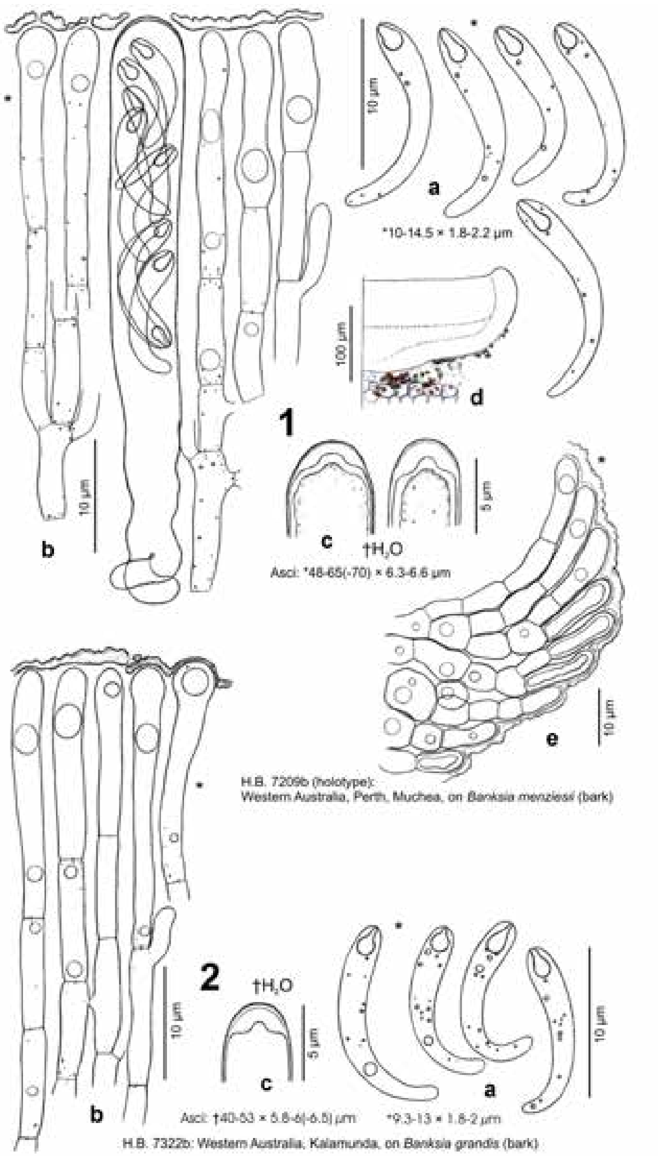


Plate 234. **1–2**: *Orbilia curvatinavajoana*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

Orbilia curvatinavajoana Baral & G. Marson, **sp. nov.**, MB 813548 — Pls 234–235

Etymology: referring to the strongly curved ascospores and a similarity with *O. navajoana*.

Typification: Western Australia, Muchea, trunk of *Banksia menziesii*, 23.XI.2001, G. Marson (ex H.B. 7209b, MEL 2389227, holotype).

Latin diagnosis: *Similis* Orbiliae navajoanae *sed ascosporae valde arcuatae. Habitat ad corticem siccum putridum ramorum vel truncorum* Banksiae *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.45 mm diam., 0.12–0.13 mm high, light orange(-rose-red), rarely pale yellowish-cream, medium translucent, ± round, (very) scattered; disc slightly concave to flat, margin distinct, 0–10 µm protruding, smooth; sessile, almost superficial to half immersed; dry bright orange-red to apricot. **Asci** *48–70 × 6–6.6 µm {2}, †(40–)44–59(–64) × 5.5–6(–6.5) µm {2}, 8-spored, spores *2–4-seriate, 1–2(–3) lower spores inverted {2} (not mixed), pars sporifera *~28–30 µm long; **apex** (†) hemispherical to slightly truncate, dome †1.2–2 → 1–1.5 µm thick {2}, with distinct apical chamber; **base** with very short to medium long, thin or thick, flexuous stalk, L, T- or h-shaped. **Ascospores** *(8–)10–13.5(–14.5) × (1.6–)1.8–2(–2.2) µm {2} [actual length ~(11–)12–15.5 µm], cylindric-clavate, apex rounded to obtuse, gradually tapered towards

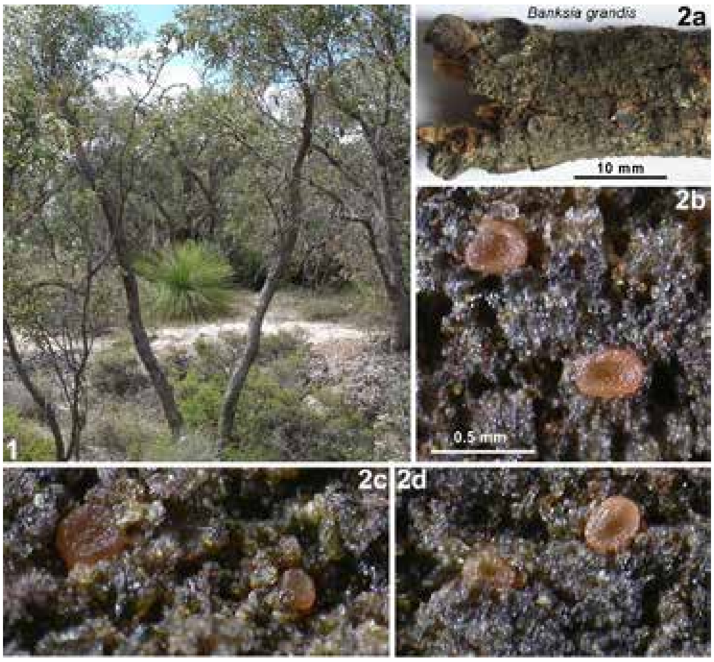


Plate 235. **1–2**: *Orbilia curvatinavajoana*. – **1**. semihumid open banksia-eucalypt woodland with *Xanthorrhoea*; **2a**. dead corticated xeric branch of *Banksia grandis*; **2b–d**. rehydrated apothecia (after 4.5 years). — **1**. H.B. 7209b (holotype): Western Australia, Perth, Muchea, on *Banksia menziesii*; **2a–d**. H.B. 7322b: ibid., Kalamunda, on *Banksia grandis*.

0.9–1.3 µm wide base, medium to very strongly curved (falcate, especially near base); **SBs** *(1.5–)1.8–2.5(–2.7) × 1–1.2(–1.4) µm {2}, pear-shaped to ampulliform, apically narrowed to a small to wide point. **Paraphyses** apically uninflated to slightly clavate-capitate, sometimes sublageniform, terminal cells *(11–)13–22(–28) × (2.2–)2.5–3.5 µm {2}, lower cells *(6–)8–13 × 1.7–2.7 µm {2}; very rarely branched at upper septum. **Medullary excipulum** hyaline, 30–40 µm thick, of medium loose or dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a 5 µm thick t. porrecta. **Ectal excipulum** hyaline, of (†) medium gelatinized, ± distinctly vertically oriented t. globulosa-angularis-prismatica from base to mid flanks or margin, 30–40 µm thick near base, cells *10–20 × 5–15 µm {2}; 25 µm thick at mid flanks, 15–30 µm near margin, here of t. (angularis-)prismatica oriented at a 45–70° angle to the surface, outer layer and uppermost margin of t. prismatica-porrecta oriented at 10–45°, marginal cortical cells *9–20 × 3.5–4.5 µm {2}, (†) slightly to strongly gelatinized (thick-walled), **glassy processes** absent. **Anchoring hyphae** ± sparse, */†2–3.5(–4) µm wide, walls 0.2–0.5 µm thick {2}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.5–3 µm diam. **Exudate** over paraphyses 0.3–1.5 µm thick, granular-cloddy, hyaline to pale chlorinaceous, loosely or later firmly attached; over margin and flanks 1–3 µm, also between cortical cells. **— ANAMORPH**: unknown.

Habitat: collected (0–)1–3 m above the ground, on 10–24 mm thick, corticated branches or a standing, sometimes still-living, ~15–20 cm thick trunk of *Banksia menziesii* {1}, *B. grandis* {1}, on medium to strongly decayed bark (periderm & bast) {2}, on very uneven surface, also along longitudinal cleft, partially detaching, slightly to strongly greyed, green algae sparse to abundant. **Associated**: *Exidia* sp. {1}, *Gloniopsis praelonga* {1}, *Orbilia aviceps* {2}, *O. eucalypti* {1}, *O.* ?*pleioserpens* {1}, ?*Teichospora* sp. {1}. **Desiccation tolerance**: fully viable for at least 16 months. **Altitude**: 188–370 m a.s.l. **Geology**: Archean granulite with granitic gneiss, granite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia curvatinavajoana* resembles the North American *O. navajoana* in size and shape of ascospores and SBs, but sharply differs in a strong spore curvature, also in much less inverted spores within the asci. *O. multicurvula* is perhaps closely related due to its very similar spore shape, but differs in narrower spores with vermiform to subulate SBs.

Ecology. *O. curvatinavajoana* was collected on ± rotten bark of dead xeric branches of *Banksia* in a subtropical semihumid open banksia-eucalypt woodland and open eucalypt forest (jarrah-marri) in the Darling Range of southwestern Australia. The two known collections consist of only a few rather remotely growing apothecia.

Specimens included. **AUSTRALIA**: **Western Australia**, Jarrah Forest, Darling Range, 54 km NNE of Perth, 11 km NE of Muchea, 188 m, trunk of *Banksia menziesii*, on bark, 23.XI.2001, G. Marson (ex H.B. 7209b, MEL 2389227, **holotype**). – 28 km E of Perth, 8 km ESE of Kalamunda, 4 km E of Bickley, junction of Lockwood and Gunjin Road, 370 m, branch of *Banksia grandis*, on bark, 13.XII.2001, G. Marson (H.B. 7322b).

Orbilia hesperidea Rolland, Bull. Soc. Mycol. Fr. 17: 118, pl. 4 fig. 1 (1901) — Pls 236–239, Map 42

Etymology: after the type substrate (hesperidoids = *Citrus*), collected in 'plantations d'orangers' (in reference to the Garden of Hesperides).
Typification: France, Antibes, branches of *Citrus aurantium*, II.1900, L. Rolland (PC, herb. Boudier, holotype); France, Languedoc-Roussillon, Narbonne, branch of *Spartium junceum*, 21.IX.1999, H.O. Baral (ex H.B. 6468a, M-0291758, epitype, designated here, MBT385113, ex-epitype culture: CBS 116209; sq.: KT215264).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–0.8(–0.9)((–1.4)) mm diam., (0.08–)0.1–0.2 mm thick, pale rose to mostly light to bright (dirty) (ochraceous-)orange(-rose) to apricot, also amber-yellow, not (or slightly) translucent, round or sometimes ± compressed, scattered to often gregarious; disc slightly concave to flat, margin indistinct or mostly ± thick, (0–)10(–20) µm protruding, smooth or rough; sessile, slightly or half immersed in rows between wood fibres; dry bright orange-red (or olivaceous-yellow). **Asci** *(36–)40–50 {6} or 50–75(–85) {17} or 75–103 {1} × (5.5–)6–8(–8.5) µm {20}, †35–42 {1} or 46–75(–84) {7} × (4.7–)5–7.3 {9} µm, 8-spored, spores ± 4-seriate, (2–)3–5(–6) lower spores inversely oriented {17} (sometimes mixed), pars sporifera *(19–)23–35 µm long; **apex** (†) hemispherical to very slightly truncate, dome 1.2–1.5(–2.5) → 0.7–1.3 µm thick {8}, or only 0.4–0.8 µm thick irrespective of maturity {3}, with or without distinct apical chamber; **base** with short to medium long, ± thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(7.5–)9–11(–12.5) {5} to (9–)11–15(–18)((–19.5)) {21} × (1.9–)2.2–3(–3.3) {24} µm, †(9.3–)10–15(–18.5) × (2–)2.2–2.8(–3.2) µm {7}, subcylindric-clavate to fusoid(-clavate), rarely fusiform, apex rounded or obtuse, rarely subacute, base slightly to strongly attenuated, often with a tail-like end, rarely with a distinct tail, straight to slightly (rarely medium) curved near base; **SBs** *(2.5–)3–4.5(–5) × (0.8–)1–1.3(–1.5) µm {23}, rod-shaped to ampulliform or subulate, also pear- or tear-shaped, apically narrowed to a ± wide (rarely small) point; overmature *2–3 × 1.5–1.7 µm, broadly tear-shaped. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cells *6.5–15(–19) × (1.8–)2.2–3.5(–4) µm {6}, †7–18 × 1.7–2.8(–3.5) µm {T}, lower cells *6–15(–17.5) × 1.5–2.5(–3) µm {5}, †7–14 × 1–1.6 µm {T}; unbranched or sometimes branched near apex; hymenium pale rose. **Medullary excipulum** subhyaline, 20–70 µm thick, of dense textura intricata with many inflated cells, medium to sharply delimited. **Ectal excipulum** pale rose, of (†) thin-walled or distinctly gelatinized (common walls 0.5–1.5(–3) µm), ± vertically oriented t. angularis from base to mid flanks, 25–50 µm thick near base, cells *7–17.5 × 6–12 µm {3} †(6–)10–16(–26) × 6–11(–17) µm {2}; 10–30 µm thick near margin, upper margin of t. prismatica(-angularis) to t. prismatica(-porrecta) oriented at a 20–60° angle to the surface, marginal cortical cells *(4–)6–11 × (2.3–)3–4.5(–5.5) µm {3}, †2–3.2 µm wide, **glassy processes** absent {18}. **Anchoring hyphae** ± abundant, */†1.8–3 µm wide, walls 0.2–0.3(–0.4) µm thick {2}. **SCBs** in paraphyses and excipular cells (flanks and margin) crystalloid {21}, hyaline to light yellowish-orange, (1–)2–6(–9) × (0.5–)1–3.5(–4.5) µm, also some globose present. **Exudate** pale to bright chlorinaceous to sulphur-yellow, rarely hyaline, over paraphyses (1–)1.5–4(–6) µm thick, broken into clods, loosely attached; over margin and flanks 2–5(–7) µm thick, rough-cloddy, firmly attached. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1} and natural substrate {3}). **Conidiophores** not seen. **Conidia** Y-shaped, European specimens: total size */†19–28 × 19–26 µm {2}, stipe */†10.5–17 × 4.5–5.2 µm, 2–3-septate, arms tapering, */†10–15 × 4–4.5(–5.5) µm, (1–)2–3-septate; Australian specimen: total size *25–30 × 29.5–38 µm {1}, stipe *16–17.5 × 4–5 µm, 2–3-septate, arms tapering, *16–20.5 × 4–4.5 µm, 2-septate.

Habitat: collected 0.1–3 m above the ground, decorticated, rarely corticated, 2–70 mm thick twigs and branches, also 10–30 cm thick living trunks, rarely cones, of *Acacia* sp. {5}, *Arbutus unedo* {3}, *Arctostaphylos patula* {1}, *Bystropogon odoratissimus* {1}, *Calicotome villosa* {1}, *Calothamnus* sp. {1}, *Campsis* (?)*radicans* {1}, *Citrus aurantium* {1}, *Erica arborea* {3}, *Eucalyptus* sp. {1}, *Juniperus phoenicea* {1}, *Lonicera implexa* {1}, *Myrtus communis* {1}, *Olea europaea* {2}, *Parkinsonia microphylla* {1}, *Periploca laevigata* {2}, *Pinus halepensis* {3}, *Quercus coccifera* {1}, *Q. ilex* {1}, *Q. pubescens* {1}, *Spartium junceum* {1}, *Vitis* sp. {1}, on 0.1–2 mm deep (medium to) strongly decayed wood {26}, more rarely bark {10} (periderm or bast), sometimes with abundant beetle or ant galleries, sometimes on detaching bark, medium to strongly greyed, with or without a few to many green algae. **Associated**: *Amandinea* sp. {2}, *Arthonia crozalsiana* {1}, *Caloplaca* sp. {1}, *Claussenomyces* sp. {1}, *Coccomycetella* sp. {1}, *Cryptodiscus foveolaris* {2}, *Dacrymyces* sp. {2}, ?*Deltopyxis* sp. {1}, *Diplolaeviopsis* sp. {2}, *Durella* sp. {2/1}, *D. atrocyanea* {1}, *D.* ?*connivens* {1}, *Gloniella* sp. {1}, *Gloniopsis praelonga* {1}, *Holmiella* sp. {1}, *Hyalorbilia subfusispora* {1}, *H. texensis* {1}, *Hysterium* sp. {1}, *H. angustatum* {2}, *H. pulicare* {1}, ?*Hysterobrevium smilacis* {1}, ?*Hysteropatella* sp. {2}, *Mellitiosporiella pulchella* {2}, *Naemacyclus fimbriatus* {1}, *Orbilia amberina* {1}, *O. anguliobliqua* {1}, *O. aprilis* {3}, *O. australiensis* {4}, *O. austroobtusispora* {1}, *O. aviflagellata* {1}, *O. cejpii* {1}, *O. coniferarum* {1}, *O. curvatiobliqua* {1}, *O.* ?*dixiensis* {1}, *O. gambelii* {1}, *O. helicoobliqua* {2}, *O. microlentiformis* {1}, *O. microserpens* {1}, *O. multiserpens* {1}, *O. myriofusiclava* {1}, *O. myriolilacina* {2}, *O. myriomuscula* {1}, *O. myrioobliqua* {3}, *O. myriosphaera* {2}, *O. nothovinosa* {1}, *O. obtusispora* {1}, *O. paraobliqua* {2}, *O. pleioaustraliensis* {2}, *O. pleioaustrocylindrica* {1}, *O.* ?*pleiomesaverdiana* {1}, *O. pleionavajoana* {1}, *O.* ?*pleioungulata* {1}, *O. polyspora* {1}, *O. subaristata* {1}, *O. subulivinosa* {1}, *O. vibrioides* {1}, *O. vinosa* {3}, *Ostropales* {1}, }, ?*Parmelia* sp. {1}, *Patellaria* '*andina*' {1/1}, *Perrotia flammea* {1}, *Phragmiticola* sp. {2}, ?*Pragmopora* sp. {1}, *Proliferodiscus griseoviolaceus* {1}, *Propolis* ?*farinosa* {2}, *P. viridis* {5}, *Schismatomma* sp. {1}, *Symbiotaphrina* ?*desertorum* {1}, ?*Triblidium* sp. {2}. **Desiccation tolerance**: fully viable for at least 22 months, some conidia still alive after 3 years. **Altitude**: 1–410 m a.s.l. (Europe), 35–1320 m (North America), 222–380 m (Australia). **Geology**: Archean-Paleoproterozoic and Pennsylvanian-Permian sand-, lime- & mudstone, Cretaceous limestone & siliceous shale, Miocene limestone; gneiss, mica schist, basaltic flow. **Phenology**: XII–VI, VIII–IX (N-hemisphere, throughout the year, long-lived).

Taxonomic remarks. *Orbilia hesperidea* is characterized by ± straight, subcylindric-clavate but also fusoid ascospores with ± attenuated, often slightly curved bases but only exceptionally with short distinct tails, and ± obtuse apices containing medium long, rod-shaped to ampulliform SBs. Further diagnostic characters include the consistent presence of crystalloid SCBs and absence of glassy processes. The crystalloid SCBs permit clear separation from the following species in which only globose SCBs occur: *O. montigena* and *O. alpigena* from montane to subalpine Europe (the latter also deviates by shorter SBs), *O. clavuliformis* and *O. subclavuliformis* from temperate to mediterranean Europe (both having distinct spore tails), and *O. navajoana* from mountainous southwestern North America (also deviating by shorter SBs).

Four Australian species are similar to *O. hesperidea*: *O. coronohesperidea* differs in the presence of glassy processes and somewhat longer spores, *O. megahesperidea* in distinctly larger spores, and *O. pleiohesperidea* in 16-spored asci. *O. australiensis* differs in wider, never subcylindric-clavate spores, but intermediate collections occur. For the similar Macaronesian *O. adenocarpi* (p. 674) and the cosmopolitan *O. vinosa* (p. 599) and related species see there.

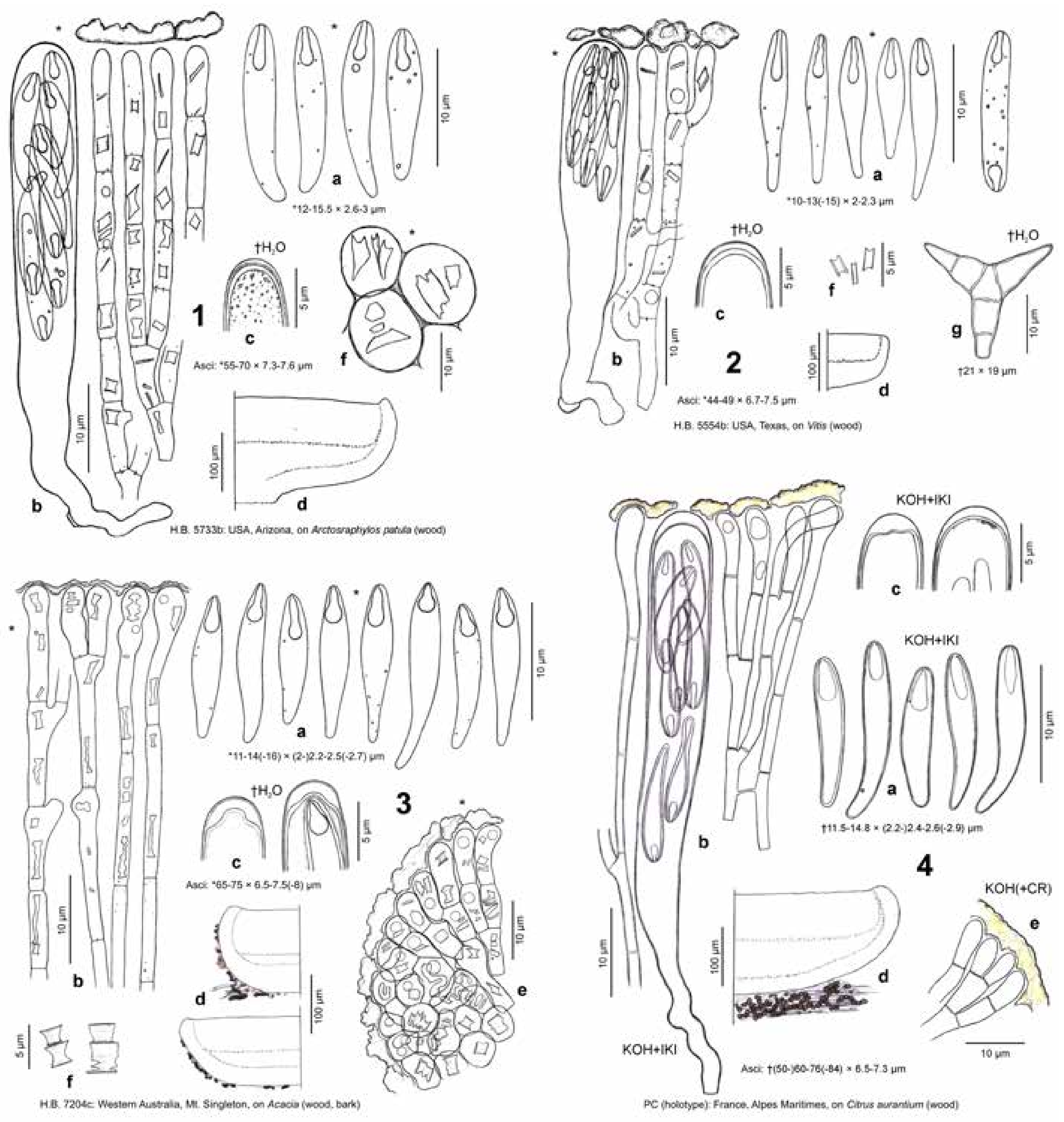
Variation in *O. hesperidea* is especially evident concerning ascus length, whereas ascus width varies only slightly and hardly correlates with ascus length. Even within a single collection (Pl. 237: 4), ascus size differed between populations collected from two closely growing trees, although spore size hardly differed (*9–12 × 2–2.7 vs. *11–12.5 × 2–2.3 µm, respectively). With *75–103 µm the longest asci were observed in a specimen from southern France (Pl. 237: 2). Two North American collections differ in much thinner apical domes, even when immature (Pl. 236: 1–2), whereas a third (on *Parkinsonia*, IVV: H.B. 8476c) showed †1.3 → 0.8 µm thick domes comparable to European and Australian specimens.

Also spore size strongly varies, particularly in length (e.g., between Pl. 237: 3–4 and 6). Within one collection (Pl. 237: 5) such variation was observed between different populations; the long-spored population in this sample is also exceptional in the frequent presence of distinct spore tails. Spore width varies between *2.2–2.5 and *2.5–3 µm, rarely only *1.9–2.3 µm (Pls 236: 2; 238: 6e).

Spore shape in *O. hesperidea* is usually cylindric-ellipsoid-clavate, with rounded to obtuse spore apices, especially in European collections, though a few fusoid spores may also occur. Exclusively fusoid spores with ± subacute apices were noted in a number of specimens from North America (Pl. 236: 2) and Australia (Pls 236: 3; 239: 1b, 3g). Such fusoid-spored populations are not always sharply separated from populations of *O. australiensis*, which sometimes grew in association. It remains unclear whether they belong to the scope of *O. hesperidea* as we assume here, or deserve distinction as a separate taxon.

Also the spore bodies in *O. hesperidea* show some variation in length and width, yet without apparent correlation to other features. In some collections the paraphyses are apically sometimes branched (e.g., in the holotype), while they are predominantly unbranched in many others. Apothecial size and colour varied from rarely small and pale rose (Pl. 234: 2) to usually rather large and bright orange.

Type studies. Although Rolland (1901) described *O. hesperidea* from a living collection, which is obvious from the distinct SBs in the drawn spores (Fig. 151: 2), no information on SCBs is available from his description. Rolland gave an ascus size of 70 × 7 µm and a spore size of *20 × 4 µm, but the present reexamination of the rather rich holotype revealed much smaller spores (Pl. 236: 4a). Rolland's figure is without a scale, but the spores inside the drawn ascus have a size of *~12.5–17 × 2.1–2.5 µm when taking an ascus length of 70 µm. Also the spore bases were found to be less tapered than Rolland illustrated, who named the spores 'napiform' (like a turnip or root). Rolland described the spore body as an 'ovoid guttule', which he figured a good distance from the spore apex without a visible connection. In the present reexamination, the SBs could be seen as a transparent region which extends up to the spore apex where it narrows to a point. Contrary to Rolland's



H.B. 5733b: USA, Arizona, on *Arctosraphylos patula* (wood)

H.B. 5554b: USA, Texas, on *Vitis* (wood)

H.B. 7204c: Western Australia, Mt. Singleton, on *Acacia* (wood, bark)

PC (holotype): France, Alpes Maritimes, on *Citrus auranlium* (wood)

Plate 236. **1–4**: *Orbilia hesperidea*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. crystalloid SCBs in excipular cells; **g**. conidium from substrate.

illustration, the lower spores are consistently inversely oriented within the asci. The observed micromorphology of the revised type material would also fit *O. montigena*. However, the mediterranean habitat excludes that species. Rolland mentioned that the inhabited wood was strongly greyed by a black yeast ('ad lignum torula infuscatum'). In order to fix the name we here designate a specimen from France (Narbonne, on *Spartium*, ex H.B. 6468a, Pls 237: 2; 238: 1), from which an ascospore isolate (CBS 116209) and a sequence were gained, as **epitype** *O. hesperidea*.

Not included collections. A very sparse, unillustrated Australian sample (on *Salix babylonica*) was only studied in the dead state (spores †15–16 × 2.7 µm, similar as in Pl. 237: 5a left). Another Australian collection (on *Acacia*, Pl. 237: 7) lacks crystalloid SCBs and has longer SBs (4.5–5.5 µm); with its fusoid spores this specimen resembles narrow-spored populations of *O. australiensis*.

Anamorph. The conidia obtained in pure culture of a sample from southern France developed only after flooding with water. They resemble *Trinacrium robustum* and are similar to those seen in *O. arizonensis* and *O. pleioaustraliensis*. Conidia more or less similar to the culture were found on the natural substrate.

Phylogeny. Sequences from pure cultures of two European collections of *O. hesperidea* were available (H.B. 6468a from France, H.B. 6694 from Croatia), both comprising SSU, ITS, and LSU. The S1506 intron is absent in both. In the ITS region

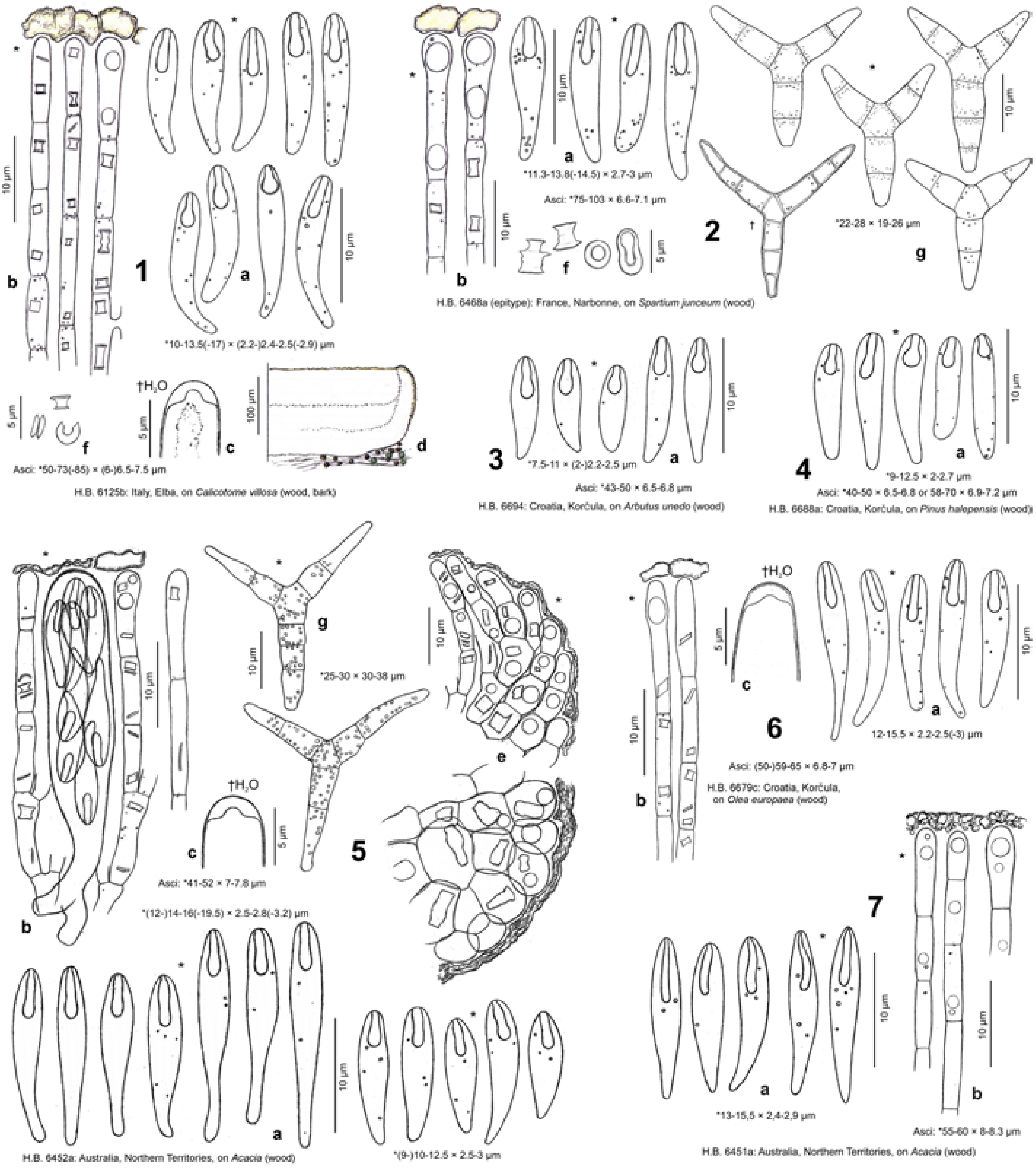


Plate 237. **1–6**: *Orbilia hesperidea*; **7**: *O.* cf. *hesperidea*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., ectal excipulum (margin and mid flanks); **f**. crystalloid SCBs in excipular cells; **g**. conidia from substrate (but in **2g** 4 living conidia from culture).

they show a distance of 1.2 % to each other, while the LSU (D1–D2) differs by 1 nt. When analysing SSU+ITS+LSU, ITS+LSU, ITS, or LSU, (Phyls 7, 9–10, S13), *O. hesperidea* clustered highly supported with *O. australiensis*, *O. pleioaustraliensis*, *O. alpigena* and *O. montigena* in the *hesperidea-alpigena* clade. The ITS distance to other species of this clade lies at 6.7–10 %, the lowest percentage being to *O. australiensis* (6.7–7 %).

Ecology. *O. hesperidea* inhabits ± rotten wood and bark of xeric branches of both gymno- and angiosperm trees and shrubs in the thermo- and mesomediterranean belt of southern Europe, where it was never found in more montane regions. Macaronesian records were made in inframediterranean semiarid to semihumid *Euphorbia atropurpurea* and *E. canariensis* scrubs (*Periploco laevigatae-Euphorbietum canariensis*) in the northeastern and eastern part of Tenerife. *O. hesperidea* also occurs in the southwest of Northern America, in the subtropical semiarid Sonoran paloverde-mixed cacti desert scrub and the subhumid warm-continental manzanita chaparral scrubland of adjacent

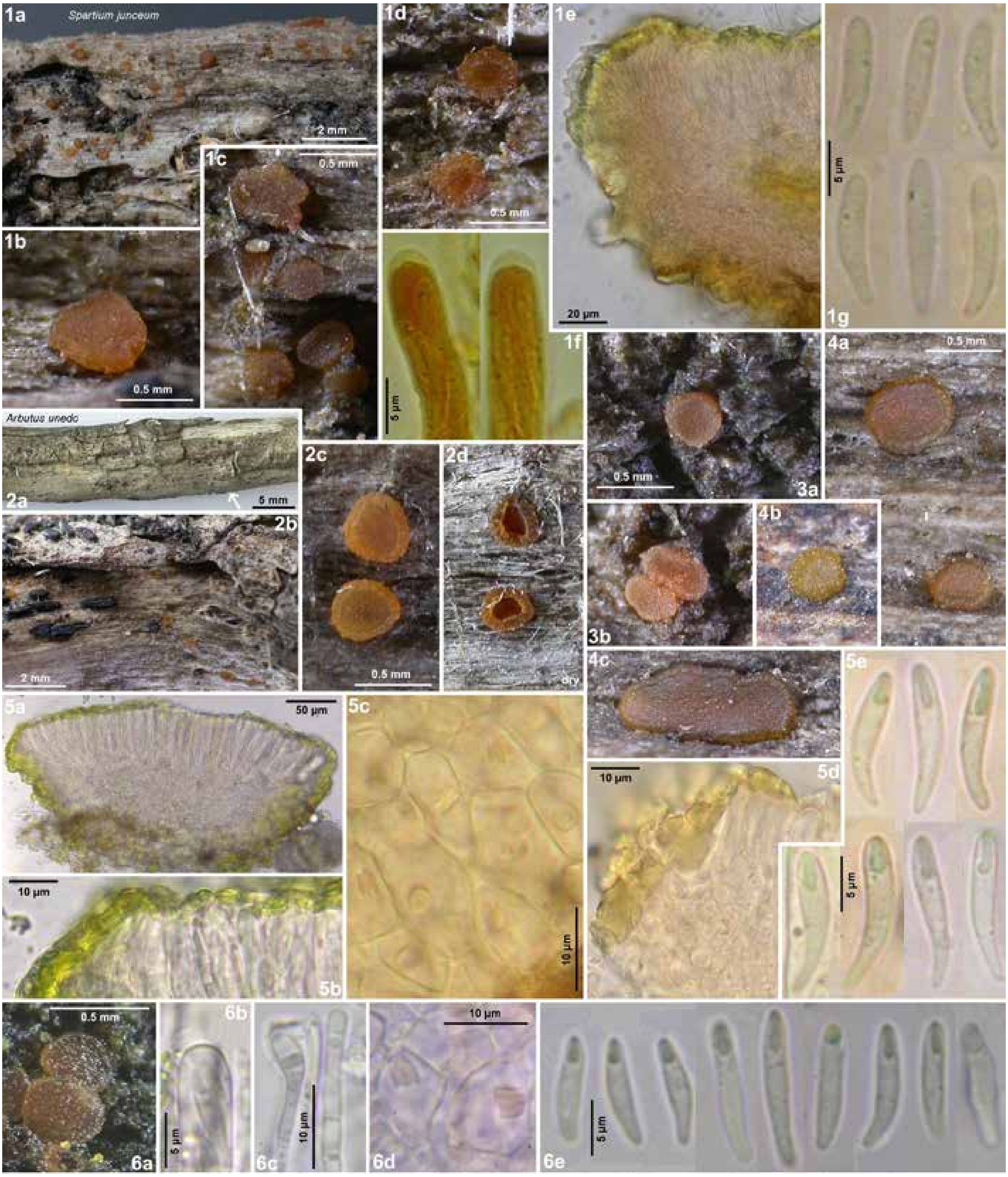


Plate 238. **1–6**: *Orbilia hesperidea* (Europe). – **2a**. dead, partially decorticated xeric branch of *Arbutus unedo*; **1a–d**, **2b–c**, **3a–b**, **4a–c**, **6a**. rehydrated apothecia; **2d**. dry apothecia; **1e**, **5a**. apothecia in median section; **5b**, **d**. id., marginal region, with covering exudate; **5c**, **6d**. crystalloid SCBs in excipular cells at flanks; **1f**, **6b**. ascus apices; **6c**. paraphyses; **1g**, **5e**, **6e**. ascospores. – Living state, except for **1e** (in H_2O), **1g** (in KOH), **1f** (in KOH+IKI); **5a–b**: illuminated by Luxeon-LED. – **6a–e**: phot. S. Tello. — **1a–g**. H.B. 6468a (epitype): France, Narbonne, on *Spartium*; **2a–d**. H.B. 6694: Croatia, Korčula, on *Arbutus*; **3a–b**. H.B. 6679c: ibid., on *Olea*; **4**. H.B. 6693: ibid., on *Quercus*; **5a–e**. 9103a: Greece, Peloponnes, on *Olea*; **6a–e**; 13.I.2013: Spain, Huelva, on *Eucalyptus*.

Mogollon Rim, also in subtropical humid to warm-temperate subhumid areas of the south (Oak and Coastal Prairies). In subtropical southwestern Australia the species occurred in semiarid eucalypt woodlands, and in tropical northern Australia in a winter-dry (savannah) eucalypt woodland and an arid acacia shrubland. Not included records are from a subtropical humid open eucalypt woodland in southwestern Australia and a tropical wet and dry (savannah) eucalypt woodland in northern Australia.

Specimens included. **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Alpes Maritimes**, ENE of Cannes, WSW of Antibes, Golfe Juan, 'Clos des Hirondelles' (not located), ?100 m, branches of *Citrus aurantium*, on wood, II.1900, L. Rolland (herb. Boudier, PC, **holotype**, H.B. 6873 ø). – **Var**, 10 km

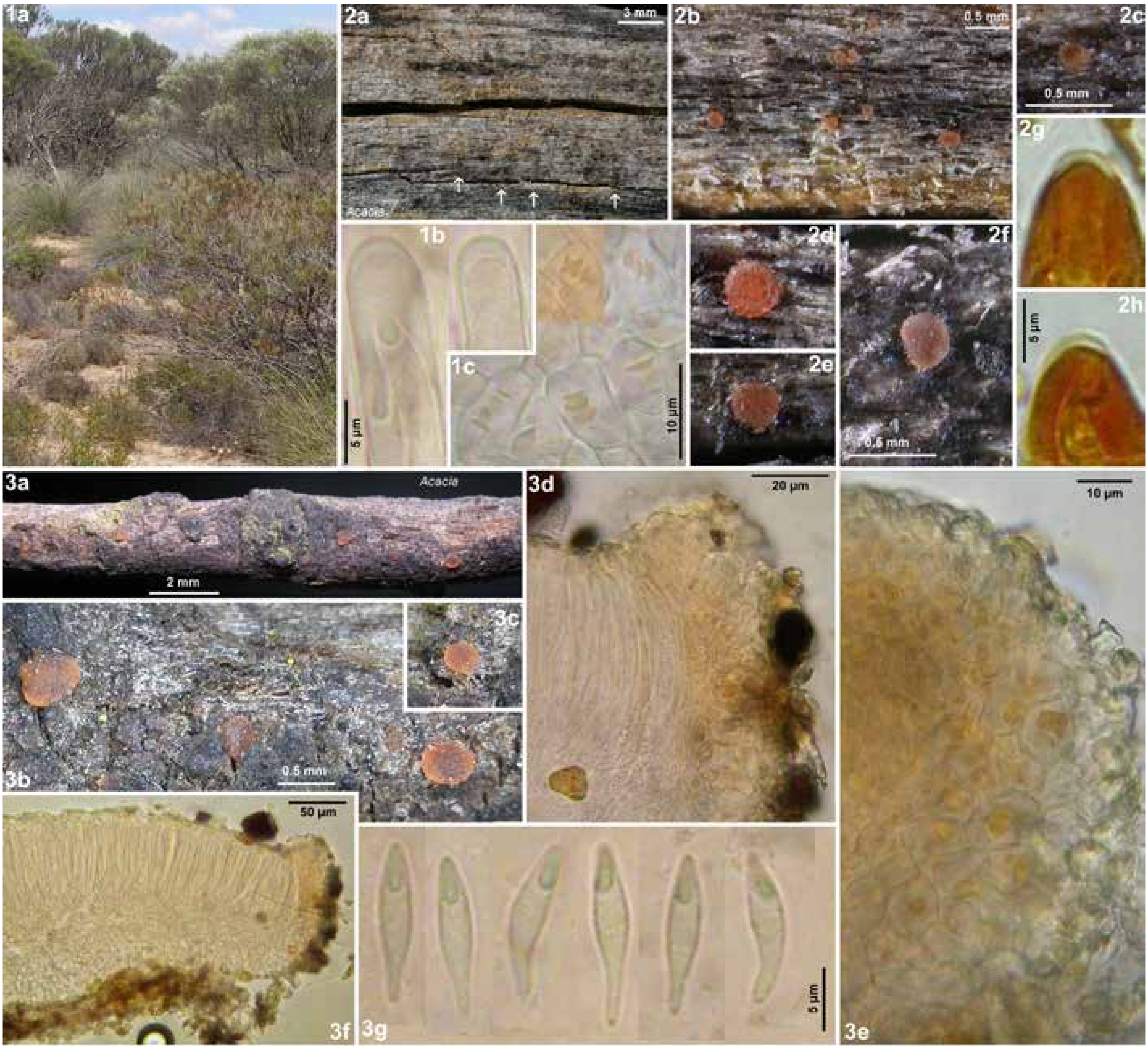
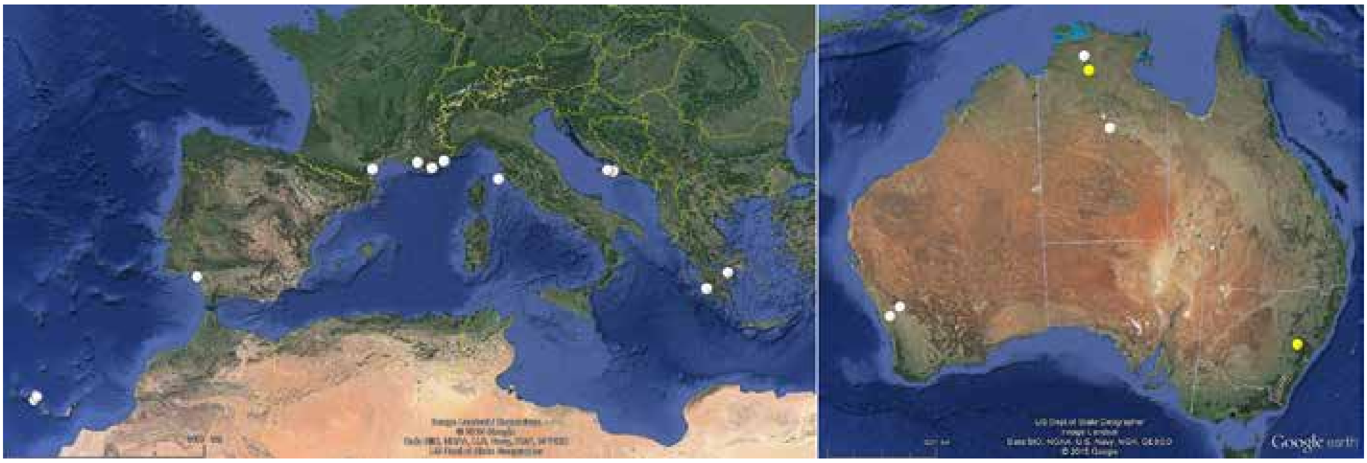


Plate 239. **1–3**: *Orbilia hesperidea* (Australia). – **1a**. semiarid Eucalypt open woodland; **2a**, **3a**. partly or entirely decorticated xeric branches of *Calothamnus* and *Acacia* (rehydrated); **2b–f**, **3b–c**. rehydrated apothecia; **3f**. apothecium in median section; **3d–e**. id., marginal ectal excipulum; **1c**. crystalloid SCBs in excipular cells; **1b**, **2g–h**. ascus apices; **3g**. ascospores. – Living state, except for **1b** (in H_2O), **2g–h** (in IKI). — **1a–c**. H.B. 8966c: Western Australia, Moora, on *Calothamnus*; **2a–h**. H.B. 6452a: Australia, Northern Territories, Banka Banka, on *Acacia*; **3a–g**. H.B. 8883b: Western Australia, Mt. Singleton, on *Acacia.*

W of Cogolin, 5 km NW of Gorbière, SW of Capelude, 380 m, branch of *Erica arborea*, on wood, 4.IX.2017, G. Marson (H.B. 10140c). – **Bouches-du-Rhône**, 11 km SE of Aix-en-Provence, 1.3 km NW of Fuveau, NW of Le Cros du Pont, 285 m, trunk of *Quercus pubescens*, on bark, 30.VI.1992, C. Roux (C.R. 21227, doc. vid.). – **Languedoc-Roussillon**, **Aude**, 15 km SSW of Narbonne, 3.7 km NNW of Sigean, Reserve africaine, 9 m, branch of *Spartium junceum*, on wood,



Map 42. Known distribution of *O. hesperidea* in Macaronesia, southern Europe, and Australia (yellow = not included collections).

21.IX.1999, H.O. Baral (ex H.B. 6468a, M-0291758, **epitype**, anam. cult., anam. substr., CBS 116209; sq.: KT215264). – ibid., cones of *Pinus halepensis* (H.B. 6523d ø). — **SPAIN**: **Andalucía**, **Huelva**, 24 km E of Huelva, 10 km S of Bonares, 80 m, trunk of *Eucalyptus*, on wood, 13.I.2013, D. Merino, D. Estrada & S. Tello (S.T. 1301201302, doc. vid.). — **ITALY**: **Toscana**, **Livorno**, Isola d'Elba, 4.5 km WNW of Portoferraio, Capo d'Enfola, 40 m, twigs & branches of *Calicotome villosa*, on wood & bark, 23.IV.1998, D. Triebel & G. Rambold (M-0229710, H.B. 6125b ø). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 3 km E of Korčula, Badija island, east-coast, 3 m, branch of *Pinus halepensis*, on wood, 8.VI.2000, H.O. Baral (ø). – ibid., turističko-sportski centar, 4 m, branch of *P. halepensis*, on wood, 8.VI.2000, H.O. Baral (H.B. 6688a ø). – 2.5 km W of Korčula, N of Vrbovica, NW of Vrh glave, 2 m, branches of *Arbutus unedo*, on wood, 9.VI.2000, H.O. Baral (H.B. 6694, CBS 116216; sq.: KT215263). – ibid., branch of *Quercus ilex*, on wood (H.B. 6693). – ibid., branch of *Myrtus communis*, on wood, 22.VIII.2000, N. Matočec (CNF 2/4694, doc. vid.). – ibid., twigs of *Lonicera implexa*, on bark, 24.VIII.2000, N. Matočec (CNF 2/9334, H.B. 7028 ø). – 8 km W of Korčula, NE of Pupnat, Veli vrh, 450 m, branch of *Erica arborea*, on bark, 11.VI.2000, N. Matočec (CNF 2/4496, doc. vid.). – 11.5 km W of Korčula, 2 km W of Račišće, below Samograd cave, 40 m, branches of *Olea europaea*, on wood, 4.VI.2000, H.O. Baral (H.B. 6679c). – ibid., Samograd cave, 120 m, branch of *Arbutus unedo*, on wood, 4.VI.2000, N. Matočec (CNF 2/4487, doc. vid.). – 9 km WNW of Vela Luka, Proizd island, U. Bili bok, 1 m, branch of *A. unedo*, on wood, 23.VIII.2000, N. Matočec (CNF 2/4696, doc. vid.). – 2.5 km SSE of Čara, E of Zavalatica, v. Žitna cove, 10 m, twig & branch of *Juniperus phoenicea*, on wood, 21.VIII.2000, N. Matočec (CNF 2/4680, doc. vid.). – ibid., branch of *Erica arborea*, on wood, 24.VIII.2000, N. Matočec (ø, doc. vid.). — **GREECE**: **Peloponnese**, 12 km NNE of Kyparissia, 2 km S of Elia, 20 m, branch of *Olea europaea*, on bark & wood, 4.VI.2009, S. Helleman (H.B. 9103a). – 8.5 km SE of Korinthos, 2 km SSE of Isthmia, Kalamaki beach, 1 m, twig of *Quercus coccifera*, on bark, 1.VI.2009, S. Helleman (ø). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Anaga, 6 km NE of Tegueste, 2.3 km E of Punta de Hidalgo, 1.2 km NW of Chinamada, Andén de la Cruz, 345 m, branch of *Bystropogon odoratissimus*, on wood, 20.V.2013, L. & C. Quijada (TFC Mic. 24233, doc. vid.). – 9 km NE of Santa Cruz de Tenerife, 3 km NNW of San Andrés, Hoya el Laurel, 305 m, branch of *Periploca laevigata*, on wood, 5.III.2013, L. & C. Quijada (TFC Mic. 23914, doc. vid.). – Fasnia, 7.5 km SSW of Güímar, 1.5 km NE of Fasnia, Barranco de Herques (La Morra los Cardones), 346 m, branch of *P. laevigata*, on wood, 18.XII.2013, L. & C. Quijada (TFC Mic. 24430, non vid.). — **USA**: **Arizona**, Mogollon Rim, 37 km SSW of Flagstaff, ~1 km NE of Sedona, ~1320 m, branch of *Arctostaphylos patula*, on wood, 8.V.1995, G. Marson (H.B. 5733b). – Sonoran Desert, 82 km NW of Phoenix, ~1.5 km SE of Wickenburg, 615 m, branch of *Parkinsonia microphylla*, on wood, 4.V.1995, G. Marson (H.B. 8476c). – **Texas**, Coastal Prairies, 32 km N of Houston, Spring, Motel 6, 35 m, branch of *Campsis* (?)*radicans*, on wood, 20.VI.1996, G. Marson (ex H.B. 5552c, in M-0276419 [*Hyalorbilia texensis*]). – 65 km W of Austin, ~2 km WSW of Johnson City, 380 m, branch of *Vitis*, on wood, 18.VI.1996, G. Marson (H.B. 5554b, anam. substr.). — **AUSTRALIA**: **Western Australia**, Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig of *Acacia*, on bark & wood, 24.XI.2001, G. Marson (H.B. 7204c). – ibid., twig of *Acacia*, on bark, 26.X.2007, G. Marson (H.B. 8883b). – Geraldton Sandplains, 54 km N of Moora, 16.5 km N of Watheroo, Midlands Road, 292 m, twig of *Calothamnus*, on wood & bark, 25.X.2007, G. Marson (H.B. 8966c ø). – **Northern Territories**, Arnhem Plateau, 54 km ENE of Pine Creek, 6.3 km NE of Mary River Roadhouse, Kakadu, 222 m, branch of *Acacia*, on bark, 5.X.1998, G. Marson (H.B. 6295). – Davenport Murchison Ranges, 118 km NNW of Tennant Creek, 23 km NNW of Banka Banka Station, 300 m, branch of *Acacia*, on wood, 7.X.1998, G. Marson (H.B. 6452a, anam. substr.).

Not included. **AUSTRALIA**: **Northern Territories**, Daly Basin, 37 km ESE of Katherine, 11 km ESE of Cutta Cutta Caves, 180 m, branch of *Acacia*, on wood, 6.X.1998, G. Marson (H.B. 6451a). – **New South Wales**, South Western Slopes, 183 km NW of Sydney, 20 km SE of Mudgee, 537 m, twig of *Salix babylonica*, on wood, 25.X.1998, G. Marson (ø).

Orbilia pleiohesperidea Baral, **sp. nov.**, MB 813549 — Pls 240–241

Etymology: named after the similarity to *O. hesperidea* but deviating in 16-spored asci.

Typification: Australia, Queensland, Taroom, leaves of *Livistona nitida*, 22.X.1998, G. Marson (ex H.B. 6424d, BRI AQ799186, holotype).

Latin diagnosis: *Similis* Orbiliae hesperideae *sed asci 16-spori. Habitat ad petiolum putridum siccum* Livistonae nitidae *in zona subtropica subhumida Australiae orientalis.*

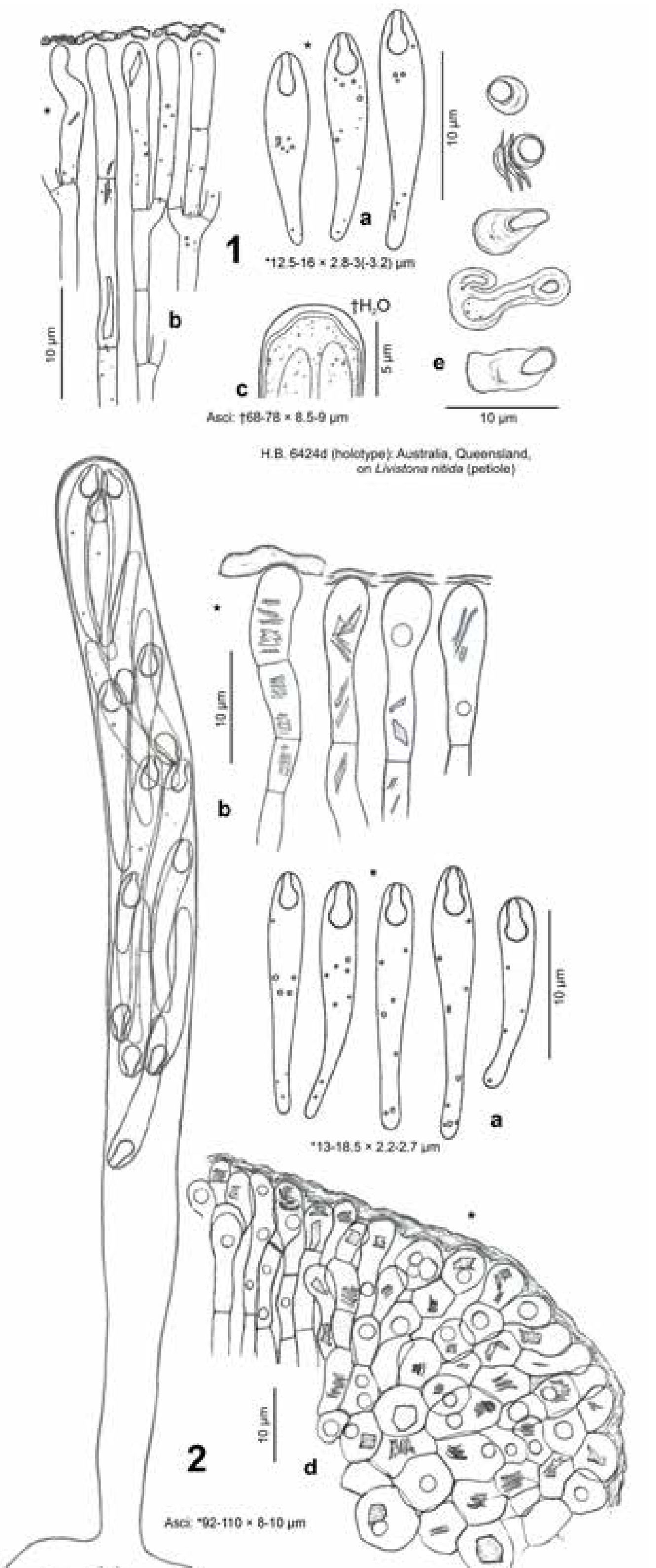


Plate 240. **1**: *Orbilia pleiohesperidea*; **2**: *O.* cf. *pleiohesperidea*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. median section of marginal ectal excipular cells; **e**. crystalloid SCBs in ectal excipular cells at flanks.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.35–0.45 mm diam., 0.14 mm high, light orange, round, scattered; disc flat to slightly convex, margin ± thick, not protruding, smooth; sessile, ± superficial. **Asci** †60–84 × 7.5–9 µm, 16-spored; **apex** (†) hemispherical (to slightly truncate), dome †0.8–1 → 0.5–0.7 µm thick,

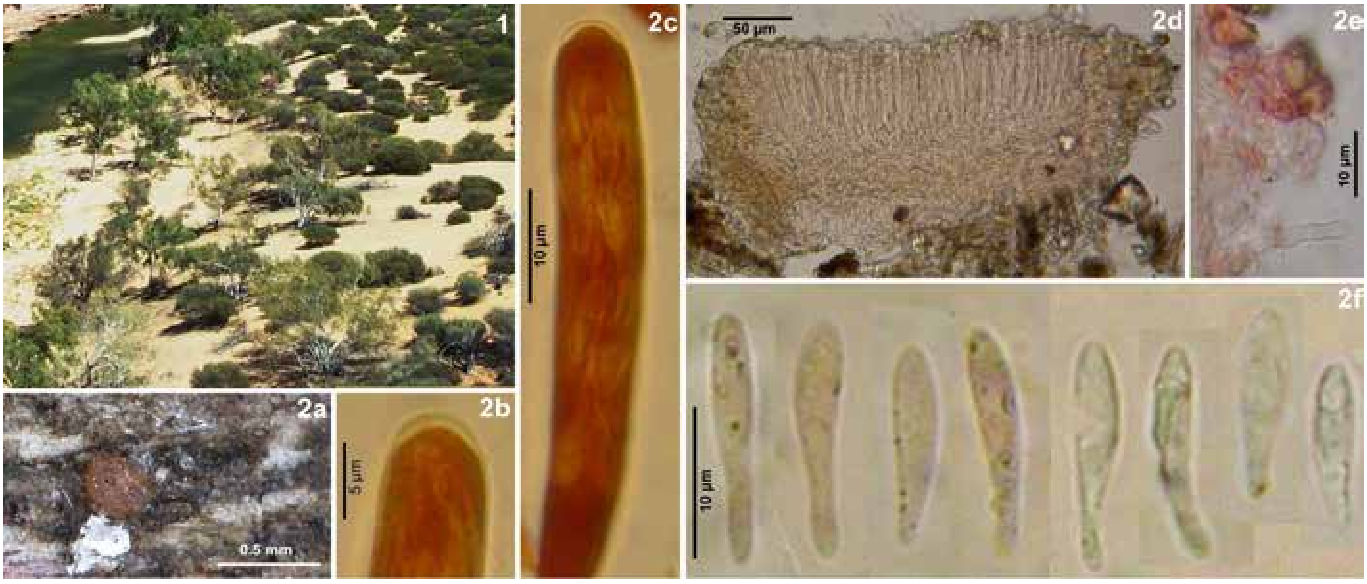


Plate 241. **1**: *Orbilia* cf. *pleiohesperidea*; **2**. *O. pleiohesperidea*. – **1**. ?semihumid Casuarina woodland; **2a**. rehydrated apothecium; **2d**. apothecium in median section; **2e**. marginal ectal excipulum with hair-like cortical hyphae; **2c**. mature ascus; **2b**. ascus apex; **2f**. ascospores. – Dead state (asci in KOH+IKI, spores left in KOH, right in H_2O). — **1**. H.B. 7415c: Western Australia, Kalbarri, on *Acacia*; **2a–f**. H.B. 6424d (holotype): Australia, Queensland, on *Livistona*.

with broad apical chamber; **base** with short to long, thin or thick, flexuous stalk, L-, Y-, or h-shaped. **Ascospores** *12.5–16 × 2.8–3(–3.2) µm, †12.2–15.5 × 2.5–3 µm, fusoid-clavate, apex obtuse, base medium to strongly attenuated in a tail-like end or distinct thick tail 3–4 × 1–1.2 µm, straight but often slightly curved near base; **SBs** *2.8–3.2 × 1.2–1.6 µm, pear-shaped to ampulliform, apically narrowed to a wide point. **Paraphyses** apically uninflated to slightly clavate, terminal cells *8–15 × 2–2.5 µm, lower cells *8–15 × 1.4–1.8 µm; often branched at upper septum. **Medullary excipulum** hyaline, 40 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** of (†) slightly gelatinized, vertically oriented t. angularis from base to mid flanks, 30–35 µm thick near base, cells †8–14 × 6–10 µm; 20 µm thick near margin, upper margin of hyphoid elements oriented at a 0–10° angle to the surface, marginal cortical cells near mid flanks †7–11 × 4–5 µm, at upper margin †8–12 × 2.5–3 µm; **glassy processes** absent. **Anchoring hyphae** abundant, †2–3 µm wide, walls 0.2–0.5(–0.8) µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) rod- or ring- to horseshoe-shaped, in excipulum 3.5–10 × 3–5 µm. **Exudate** over paraphyses 1–2.5 µm thick, cloddy, pale yellowish, loosely attached, over marginal excipulum 1.5–4 µm thick. **— ANAMORPH**: unknown.

Habitat: collected 0.2–2 m above the ground, petiole of *Livistona nitida*, on strongly decayed upper side, greyed, no algae. **Associated**: *Gloniopsis* sp., *Mellitiosporiella* sp., *Orbilia acaciae*, *O.* ?*australiensis*, *O.* ?*commarosa*, *O. coronohesperidea*, *O.* ?*dixiensis*, *O. livistonae*, *O. multiserpens*, *O. myrioeuonymi*, *O. palmicola*, *O. parviclava*. **Desiccation tolerance**: ascospores, paraphyses and excipular cells still viable after 9 months. **Altitude**: 200 m a.s.l. **Geology**: Jurassic sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleiohesperidea* is characterized by 16-spored asci and fusoid-clavate ascospores with a tail-like base or distinct thick tail. *O. hesperidea* mainly differs in 8-spored asci and ascospores only occasionally with tails. The North American *O. pleionavajoana* differs in lacking crystalloid SCBs. *O. pleiohesperidea* differs from *O. pleiocoronohesperidea* in much wider spores (values do not overlap) with sometimes thicker tails and rather short and thick SBs, also in the absence of glassy processes, though a deviating collection (*O.* aff. *pleiocoronohesperidea*, Pl. 246) also lacks them.

Not included collection. A somewhat intermediate sample on *Acacia* (Pl. 240: 2) deviates from *O. pleiohesperidea* in the marginal excipulum lacking hyphoid elements and in narrower, predominantly cylindric-clavate spores with rounded apices.

Ecology. The very sparse type collection was on petioles of *Livistona* in a subtropical subhumid (winter-dry, savannah) eucalypt woodland in the Palm-Tree Creek (Great Dividing Range, eastern Australia). The not included collection on *Acacia* was from a subtropical semihumid casuarina woodland on Silurian sedimentary rock in the Geraldton Sandplains of western Australia.

Specimens included. **AUSTRALIA**: **Queensland**, Brigalow Belt South, 69 km SSW of Theodore, 15 km N of Taroom, Palm-Tree Creek, Roy Staines Bridge, 200 m, petioles of *Livistona nitida*, 22.X.1998, G. Marson (ex H.B. 6424d, BRI AQ799186, **holotype**).

Not included. **Western Australia**, Geraldton Sandplains, 80 km NNW of Northampton, 29 km ENE of Kalbarri, near meander of Murchison, 160 m, branch of *Acacia*, 9.XII.2001, G. Marson (H.B. 7415c ø).

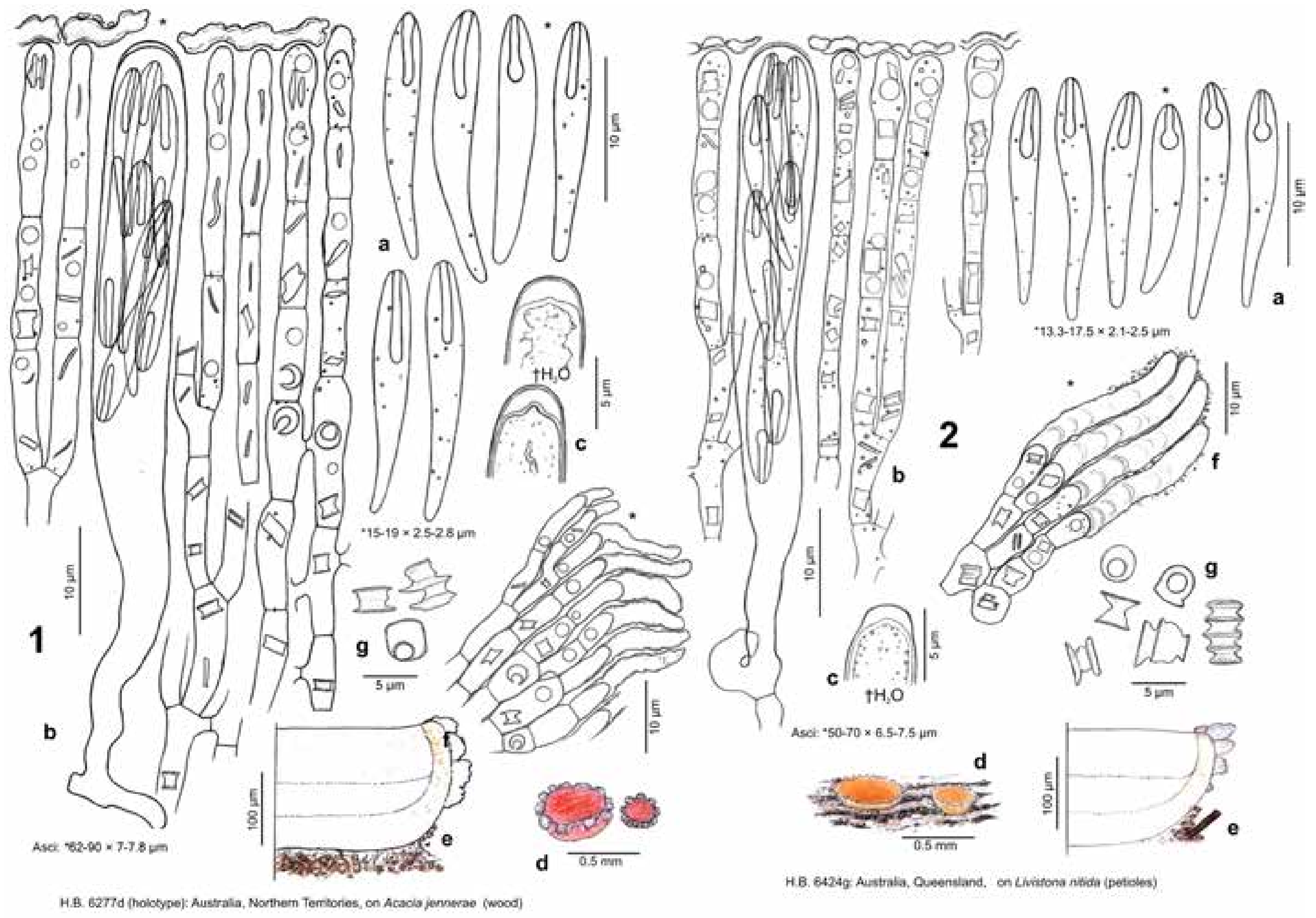
Orbilia coronohesperidea Baral, **sp. nov.**, MB 813551 — Pls 242–243, Map 43

Etymology: named after the similarity to *O. hesperidea* but margin with crown-like teeth.

Typification: Northern Territories, Curtin Springs Roadhouse, twig and branch of *Acacia jennerae*, 10.X.1998, G. Marson (ex H.B. 6277d, MEL 2389199, holotype).

Latin diagnosis: *Similis* Orbiliae hesperideae *sed excipulum marginale processis vitreis praeditum, ascosporae leniter longiores. Habitat ad lignum vel corticem putridum ramulorum vel ramorum siccorum* Acaciae *et ad petiolos putridos* Livistonae nitidae *in zona (sub)tropica arida ad semi- vel subhumida Australiae occidentalis, centralis et orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.5(–0.8) mm diam., 0.12–0.18(–0.21) mm high, light to bright (ochraceous-)orange or orange-rose, not or medium translucent, round (to elliptic), scattered to gregarious in small groups; disc flat (to slightly convex), margin distinct, finely to distinctly crenulate or with prominent whitish teeth, 5–15 µm protruding (incl. teeth); broadly sessile, superficial to slightly immersed, dry somewhat contracted, deep orange-red. **Asci** *50–70 {4} or 80–90 {T} × 6.5–7.8 µm {3}, †46–70 × 6–7(–7.5) µm {5}, 8-spored, spores *2–4-seriate, 2–4 lower spores inverted {3} (sometimes mixed), pars sporifera *30–42 µm long; **apex** (†) hemispherical to very slightly truncate, dome †1–1.8 → 0.5–1.2 µm thick {4}, with small apical chamber; **base** with short to medium to long, thick, flexuous stalk, L- to Y-shaped. **Ascospores**



H.B. 6277d (holotype): Australia, Northern Territories, on *Acacia jennerae* (wood)

H.B. 6424g: Australia, Queensland, on *Livistona nitida* (petioles)

Plate 242. **1–2**: *Orbilia coronohesperidea*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., marginal ectal excipulum, cortical cells with glassy processes; **g**. crystalloid SCBs in excipular cells.

*(12.2–)14–18(–19) × (2–)2.2–3 µm {5}, †15–18.5 × (2–)2.3–3(–3.5) µm {2}, subcylindric- to narrowly fusoid-clavate, apex rounded to obtuse, base slightly to mostly strongly attenuated in a tail-like end, straight to often slightly curved in middle part, also near base; **SBs** *4–5.5(–6.5) × 0.6–1.1 µm {3}, rod-shaped to subulate, apically narrowed to a wide point, straight; overmature *3–3.5 × 1.2–1.3 µm, ampulliform. **Paraphyses** apically uninflated to slightly clavate(-sublageniform), terminal cells *(7–)13–17(–21) × (1.8–)2.5–3.5(–4.5) µm {3}, lower cells *8–13 × (1.3–)1.8–2.5(–3) µm {3} (near base up to 4 µm wide); unbranched at upper septum, hymenium pale orange. **Medullary excipulum** subhyaline, 40–60 µm thick, of medium loose or dense textura intricata-globulosa, sharply delimited. **Ectal excipulum** pale orange (light orange at margin), of (†) thin-walled to medium gelatinized, vertically oriented t. globulosa(-prismatica) from base to mid flanks, 25–80 µm thick near base, cells *9–20 × 8–14 µm {2}; 20–25 µm thick near margin, of t. prismatica-porrecta oriented at a 10–45° angle to the surface, marginal cortical cells *6–12 × 3–4.5 µm {2}; **glassy processes** 3–20 {4} or 20–40 {2} × (2–)3–4(–5.5)((–7)) {5} µm, high-refractive, stratified or not, straight to irregularly curved, coherent to form ± distinct teeth. **Anchoring hyphae** medium abundant, *2.5–3 µm wide, walls 0.2–0.4 µm thick {1}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1–3 µm diam., also crystalloid {6}, in excipulum 3–6 × 1.5–5 µm, pale to light yellowish-orange-rose. **Exudate** over paraphyses 0.5–3 µm thick, cloddy, pale to light yellowish-chlorinaceous, loosely attached; over margin and flanks absent or 1–2 µm thick. **— ANAMORPH**: unknown.

Habitat: collected 0–2 m above the ground, on decorticated or partially corticated, 2.5–12 mm thick twigs and branches, also trunks, of *Acacia* sp. {3}, *A. jennerae* {1}, *Eucalyptus* sp. {1}, on 0.3–0.5 mm deep strongly decayed wood {4} or bark (periderm & bast) {3}, petioles of *Livistona nitida* {1}, strongly greyed, without algae. **Associated**: *Baggea* sp. {1}, *Coccomycetella* sp. {1}, *Dinemasporium* sp. {1}, *Gloniopsis* sp. {1}, *Hyalorbilia* ?*erythrostigma* {1}, *Lophiostoma* sp. {1}, *Mellitiosporiella* sp. {1}, *Orbilia acaciae* {1}, *O. angustoaristata* {1}, *O.* ?*australiensis* {1}, *O. austropleiomicrosoma* {1}, *O.* ?*commarosa* {1}, *O. corculispora* {1}, *O.* ?*dixiensis* {1}, *O. livistonae* {1}, *O. microserpens* {1}, *O. multiaustraliensis* {1}, *O. multiserpens* {2}, *O. myriella* {1}, *O. myrioaustraliensis* {1}, *O. myrioeuonymi* {1}, *O. myriofusoidea* {1}, *O. myrionamibica* {1}, *O. octocercocarpi* {1}, *O. octoserpentina* {1}, *O. palmicola* {1}, *O. parviclava* {1}, *O. pleioaustraliensis* {1}, *O. pleiocoronohesperidea* {3}, *O. pleiohesperidea* {1}, *O. pleioserpens* {2}, *O. serpentina* {1}, *Ostropales* {1}, *Patellaria* '*andina*' {2}, ?*Stictis* sp. {1}, *Symbiotaphrina desertorum* {1}, ?*Teichospora* sp. {1}, ?*Trimmatostroma* sp. {1}. **Desiccation tolerance**: fully viable for at least 9 months, after 17 months some mature asci still alive. **Altitude**: 200–480 m a.s.l. **Geology**: Precambrian and Jurassic-Cretaceous sedimentary rock, Cenozoic regolith; Archean granulite with granitic gneiss. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia coronohesperidea* differs from *O. hesperidea* in the presence of short to long glassy processes forming white, small to large teeth on the apothecial margin, and in somewhat longer ascospores. From *O. vinosa* it differs in wider spores, more distinct, orange crystalloid SCBs, and longer glassy processes. *O. angiosubvinosa* from ± temperate (semi)humid Europe and North America differs in slightly narrower spores and is characterized by dwayaangam-like conidia. *O. pleiocoronohesperidea* differs in 16-spored asci and slightly narrower spores.

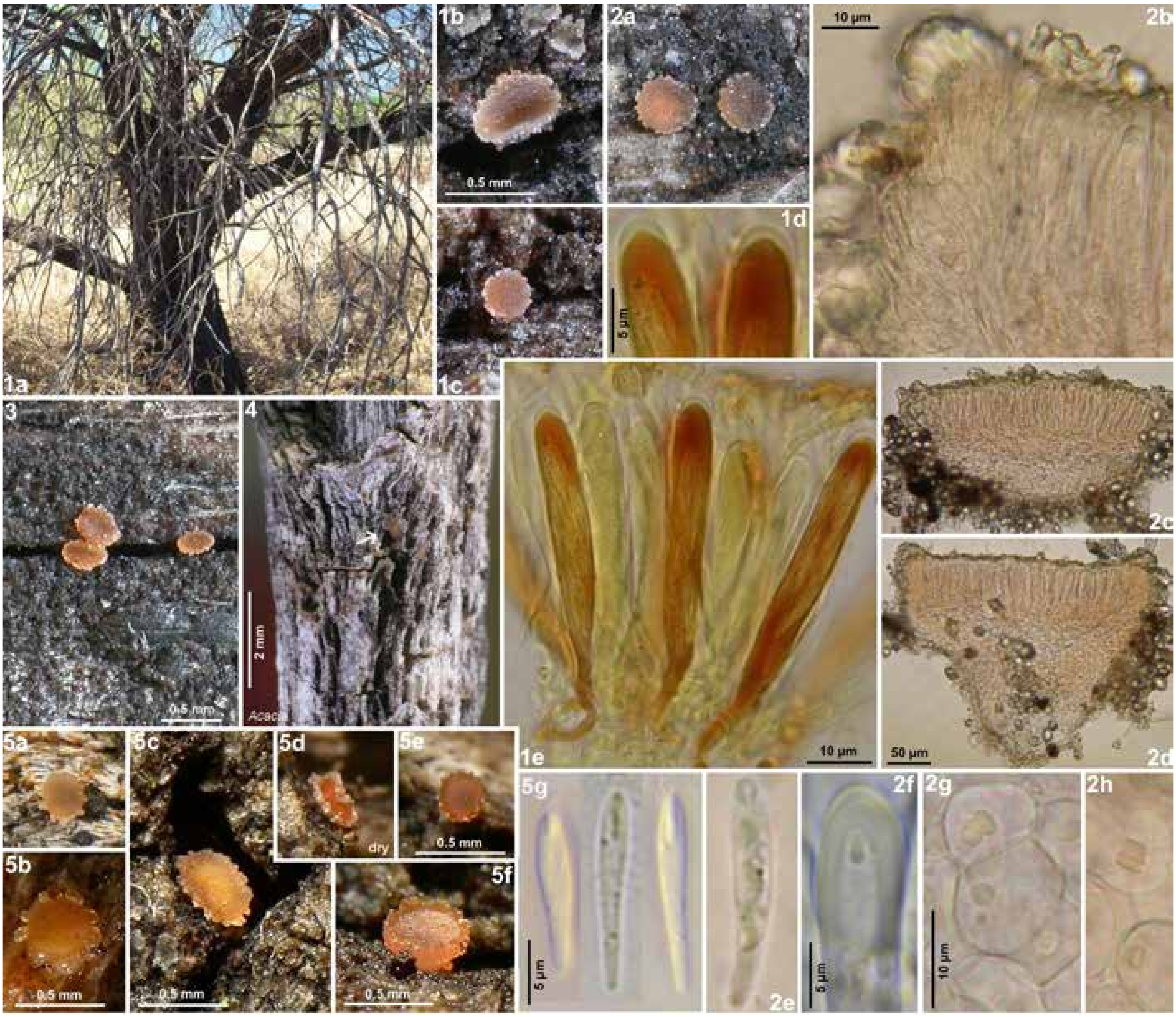
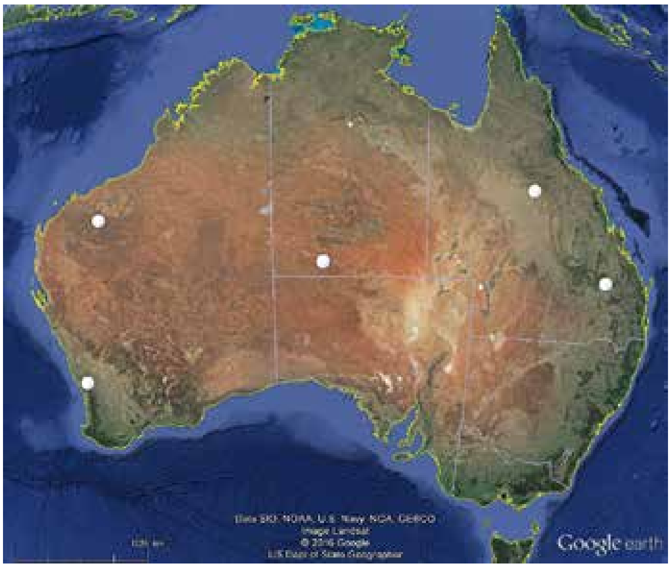


Plate 243. **1–5**: *Orbilia coronohesperidea*. – **1a**. arid acacia shrubland and hummock grassland, *Acacia* with dead attached branches; **4**. decorticated rotten xeric twig of *Acacia* (rehydrated); **1b–c**, **2a**, **3a**, **5a–c**, **e–f**. rehydrated apothecia; **5d**. apothecium in dry state; **2c–d**. apothecia in median section; **2b**. id., marginal ectal excipulum; **2g–h**. crystalloid SCBs in excipular cells; **1e**. asci and paraphyses; **1d**, **2f**. ascus apices; **2e**, **5g**. ascospores. – Living state, except for **1d–e** (in KOH+IKI), **2e**, ascus in **2f** (in H_2O). — **1a–e**. H.B. 8583c: Western Australia, Pilbara, on *Acacia*; **2a–h**. H.B. 8976a: ibid., on *Acacia*; **3**. H.B. 6424g: Australia, Queensland, on *Livistona*; **4**. 6609f: ibid., on *Acacia*; **5a–g**. 4.IX.2006: Western Australia, Bindoon, on *Eucalyptus*.

Variation. The collections on *Livistona* and *Eucalyptus* differ from those on *Acacia* in longer glassy processes and somewhat smaller, especially narrower spores. In the holotype (Pl. 242: 1) the asci were exceptionally long (*80–90 µm), but on a different twig in the same sample they measured only *62–65 µm.

Ecology. The often rather sparse collections of *O. coronohesperidea* originate from a few very remote areas of Australia. In eastern Australia the species was found on xeric, decayed, attached petioles of *Livistona* in a subtropical subhumid (winter-dry, savannah) eucalypt woodland (Great Dividing Range). Those samples on rotten wood and bark of xeric twigs and branches of *Acacia* are from (sub)tropical (semi)arid open acacia shrublands in western and (north)eastern Australia, e. g., in the dry delta of the Wittenoom Gorge of the Pilbara, and in central Australia south of MacDonnell Ranges, and that on bark of *Eucalyptus* from a subtropical semihumid eucalypt woodland (upper edge of Jarrah Forest ecoregion) in southwestern Australia.



Map 43. Known distribution of *O. coronohesperidea* in Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Pilbara, 1.5 km SW of Wittenoom, N of Karijini, delta of Wittenoom Gorge, 467 m, branch of *Acacia*, on bark & wood, 28.XI.2001, G. Marson (H.B. 8583c). – ibid., branch of *Acacia*, on bark & wood, 29.X.2007, G. Marson (H.B. 8976a). – Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 271 m, branch of *Eucalyptus*, on bark, 4.IX.2006, G. Marson (ø). – **Northern Territories**, Finke, 100 km E of Yulara, 24 km ENE of Curtin Springs Roadhouse, 28 km NNE of Mt. Connor, 480 m, twig & branch of *Acacia jennerae*, on wood, 10.X.1998, G. Marson (ex H.B. 6277d, MEL 2389199, **holotype**). – **Queensland**, Brigalow Belt South, 69 km SSW of Theodore, 15 km N of Taroom, Palm-Tree Creek, Roy Staines Bridge, 200 m, petiole of *Livistona nitida*, 22.X.1998, G. Marson (H.B. 6424g). – Desert Uplands, 29 km E of Hughenden, 13 km W of Prairie, 390 m, twigs of *Acacia*, on wood, 16.X.1998, G. Marson (H.B. 6609f).

Orbilia pleiocoronohesperidea Baral & G. Marson, **sp. nov.**, MB 813552 — Pls 244–245

Etymology: named after the similarity to *O. coronohesperidea* but with 16-spored asci.

Typification: Northern Territories, Curtin Springs Roadhouse, branches of *Acacia jennerae*, 10.X.1998, G. Marson (ex H.B. 6277l, MEL 2389204, holotype).

Latin diagnosis: *Similis* Orbiliae coronohesperideae *sed asci 16-spori, ascosporae paulo angustiores. Habitat ad lignum putridum ramorum siccorum* Acaciae *in zona tropica arida Australiae occidentalis et centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.6(–0.7) mm diam., 0.1–0.18(–0.22) mm high, pale to bright (brick-)orange-rose, not or slightly translucent, ± round, scattered to (sub)gregarious in small groups; disc slightly concave or usually flat, margin 5–20 µm protruding, ± distinctly whitish pruinose to denticulate or often with distinct small whitish teeth; broadly sessile or with obconical base, superficial to slightly erumpent; dry with hardly contracted brick-orange disc. **Asci** *52–64 × 7.4–7.7 µm {1} or 70–85 × 8–8.8 µm {T}, †46–70 {2} or 77–101 {T} × 6.3–7.5(–8) {3} µm, 16-spored, spores *~4–5-seriate, 8–10 lower spores inverted {1}, pars sporifera *55 µm long; **apex** (†) hemispherical, dome †1.5–2 → 0.8–1.3 µm thick {3}, with or without distinct apical chamber; **base** with short to long, thin or thick, flexuous stalk, L-, T-, Y- or h-shaped. **Ascospores** *(13–)14.5–18.5 × 2–2.2 {2} or 2.4–2.6 µm {T}, †12.5–17 × 1.8–2.1 µm {2}, narrowly fusoid- to cylindric-clavate, apex rounded to obtuse, base medium to strongly attenuated, usually tail-like, straight to slightly curved; **SBs** *3–3.5 {1} or 4–5(–5.5) {T} × 0.8–1 {2} µm, rod-shaped to subulate or slightly ampulliform, apically narrowed to a ± wide point, straight. **Paraphyses** apically uninflated to slightly clavate, sometimes sublageniform, terminal cells *(7–)10–16(–18) × 2.5–3.5 µm {2}, †8–12 × 2–2.8 µm {1}, lower cells *(8–)10–13.5 × 1.7–3.5 µm {2}, †9–11 × 2–2.2 µm {1}, unbranched near apex. **Medullary excipulum** pale rose-orange, 20–60(–80) µm thick, of medium loose to dense textura intricata, horizontally oriented, with many inflated cells, medium sharply delimited. **Ectal excipulum** of (†) slightly gelatinized, vertically oriented t. angularis(-prismatica) from base to submargin, 20–60 µm thick near base, cells *8–20(–25) × 7–13(–16) µm {2}, †8–18 × 4–12 µm {2}; 15–20 µm thick near margin, of t. prismatica-porrecta oriented at a 10–30° angle to the surface, marginal cortical cells *7–15 × 3–4 µm {1}, †9–11 × 2.5–3 µm {1}; **glassy processes** 2–10(–20) × 2.5–3.5(–4) µm {3}, high-refractive, slightly stratified, straight to irregularly curved, somewhat coherent to form ± distinct small teeth. **Anchoring hyphae** abundant, †2–3(–3.5) µm wide, walls 0.2–0.3(–0.5) µm thick {2}, sometimes forming strands. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1–2 µm diam., also crystalloid {3}, hyaline to pale orange, in excipulum 2.5–7 × 1.5–5 µm (from base to margin). **Exudate** over paraphyses 0.5–2 µm thick, cloddy-continuous, loosely attached, pale to light sulphur-yellow, over margin absent or 0.2–2 µm thick. **— ANAMORPH**: unknown.

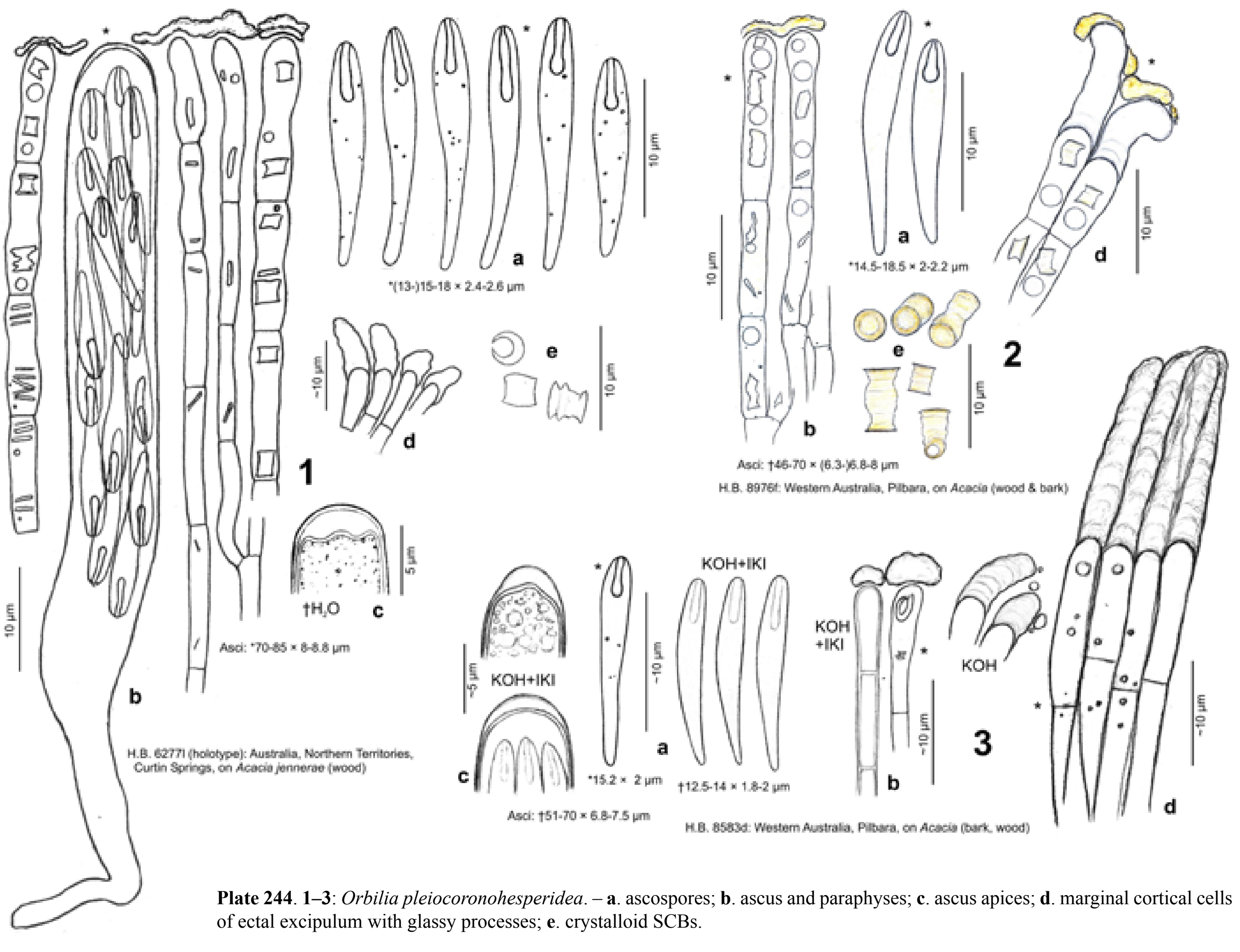


Plate 244. **1–3**: *Orbilia pleiocoronohesperidea*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal cortical cells of ectal excipulum with glassy processes; **e**. crystalloid SCBs.

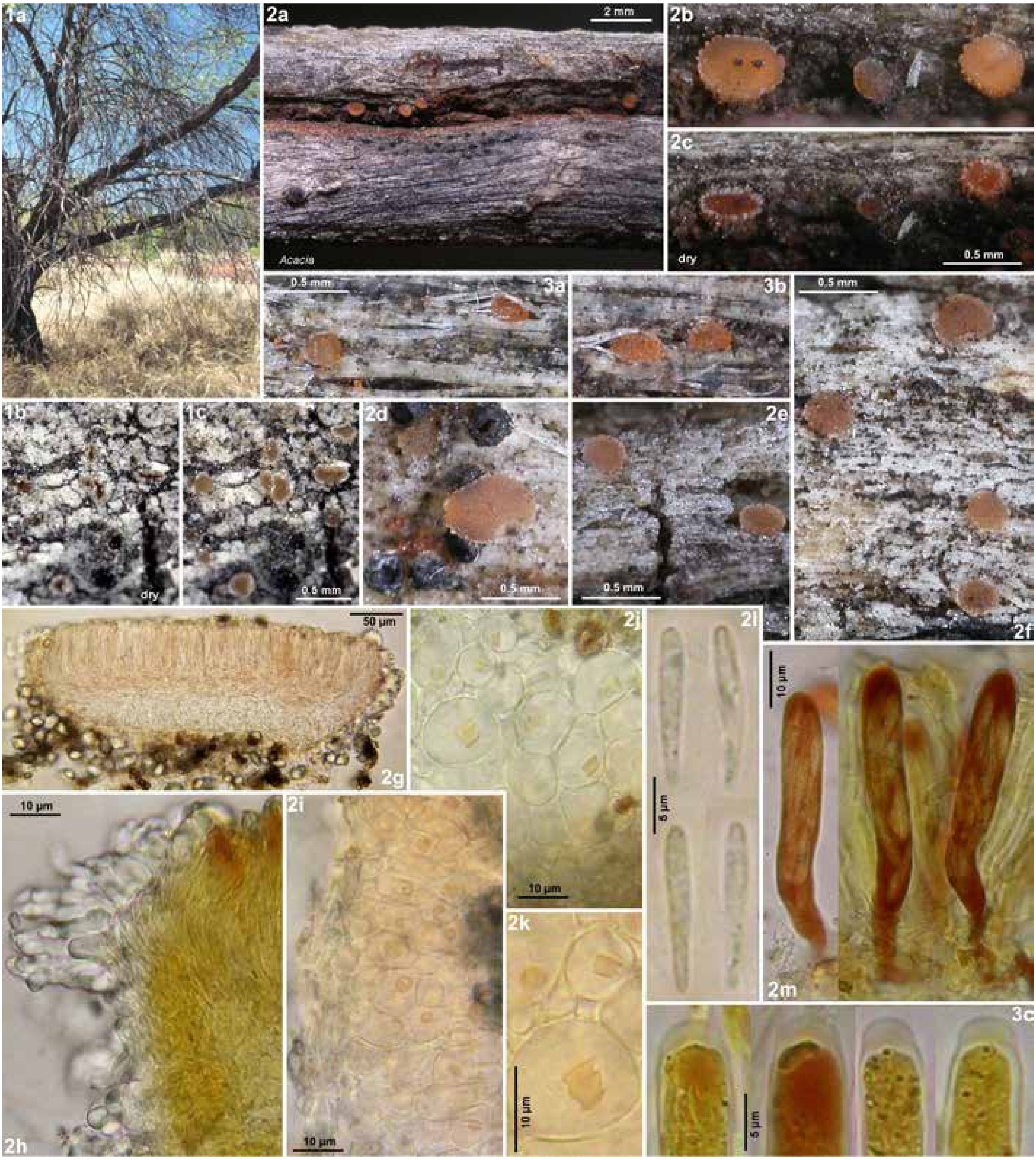


Plate 245. **1–3**: *Orbilia pleiocoronohesperidea*. – **1a**. arid acacia shrubland and hummock grassland; **2a**. decorticated xeric branch of *Acacia*; **1c**, **2b**, **d–f**, **3a–b**. rehydrated apothecia; **1b**, **2c**. dry apothecia (**1b–c** after almost 6 years); **2g**. apothecium in median section; **2h–i**. id., marginal ectal excipulum; **2j–k**. crystalloid SCBs in basal excipular cells; **2m**. asci and paraphyses; **3c**. ascus apices; **2l**. ascospores. – Living state, except for **2g**, **l** (in H_2O); **2h**, **m** (in IKI), **3c** (KOH+IKI). — **1a–b**. H.B. 8583: Western Australia, Pilbara, on *Acacia*; **2a–m**. H.B. 8976: ibid., on *Acacia*; **3a–c**. H.B. 6277l (holotype): Australia, Northern Territories, on *Acacia*.

Habitat: partially to entirely decorticated, 6–14 mm thick xeric branches of *Acacia* sp. {2}, *A. jennerae* {1}, on 0.3–0.5 mm deep very decayed wood {3} or bark {1}, strongly greyed, without algae. **Associated**: *Baggea* sp. {1}, *Coccomycetella* sp. {1}, *Dinemasporium* sp. {1}, *Hyalorbilia ?erythrostigma* {1}, *Lophiostoma* sp. {1}, *Orbilia angustoaristata* {1}, *O. austropleiomicrosoma* {1}, *O. coronohesperidea* {3}, *O. microserpens* {1}, *O. multiaustraliensis* {1}, *O. multiserpens* {1}, *O. myriella* {1}, *O. myrioaustraliensis* {1}, *O. myriofusoidea* {1}, *O. myrionamibica* {1}, *O. pleioaustraliensis* {1}, *O. pleioserpens* {2}, *Ostropales* {1}, *Patellaria* '*andina*' {1}, *Symbiotaphrina desertorum* {1}, ?*Teichospora* sp. {1}, ?*Trimmatostroma* sp. {1}. **Desiccation tolerance**: excipular cells and paraphyses, also many immature asci still viable after 14 months. **Altitude**: 467–480 m a.s.l. **Geology**: Archean & Paleoproterozoic sedimentary rock, Cenozoic regolith. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleiocoronohesperidea* is very similar to *O. coronohesperidea*, from which it merely differs in 16-spored asci and somewhat narrower ascospores.

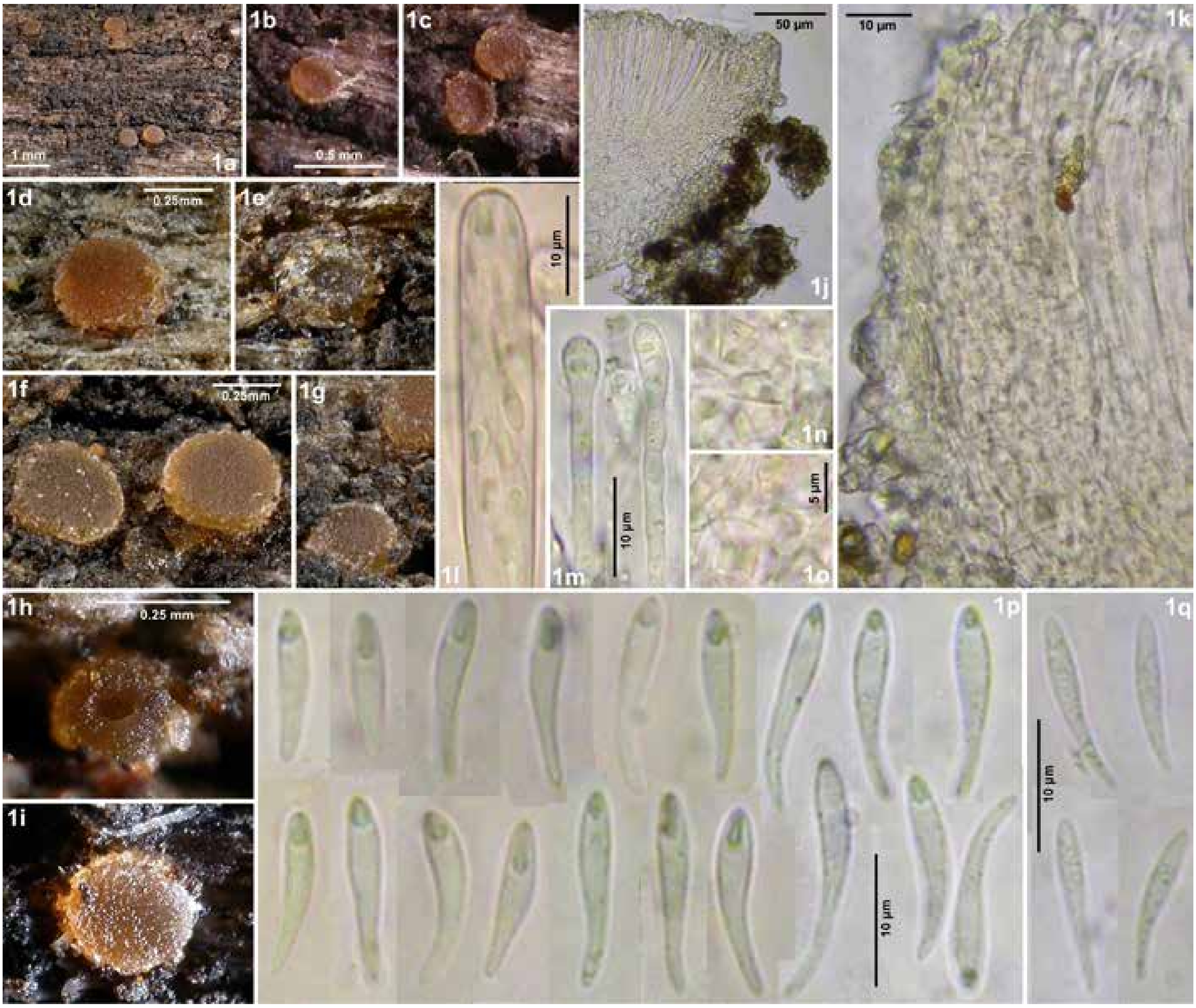


Plate 246. **1**: *Orbilia* aff. *pleiocoronohesperidea*. – **1a–i**. rehydrated apothecia; **1j**. apothecium in median section; **1k**. id., marginal ectal excipulum; **1n–o**. crystalloid SCBs in excipular cells; **1l**. ascus; **1m**. paraphyses; **1p–q**. ascospores. – Living state, except for **1q** (in KOH). — **1a–q**. H.B. 9695g: Western Australia, Gascoyne, on *Acacia*.

O. pleiohesperidea deviates in shorter and wider SBs and in the absence of glassy processes. A deviating collection in which glassy processes could not be observed is described below (Pl. 246): although the apothecia may show a crenulate margin, the marginal excipulum is composed merely of hyphoid elements here.

Variation. The two collections from Western Australia differ from the holotype from central Australia in narrower spores, but otherwise seem to fit very well.

Ecology. The three collections were made on rotten wood of xeric branches of *Acacia* sp. in tropical (to subtropical) arid open acacia shrublands of western (Pilbara desert) and central Australia (south of MacDonnell Ranges). *O. coronohesperidea* grew in association in all three collections but in separate populations. At the Pilbara site *O. coronohesperidea* grew predominantly on bark, whereas *O. pleiocoronohesperidea* was in 2001 always found on wood, but in 2007 mainly on bark.

Specimens included. **AUSTRALIA**: **Western Australia**, Pilbara, 1.5 km SW of Wittenoom, N of Karijini, delta of Wittenoom Gorge, 467 m, branch of *Acacia*, on wood, 28.XI.2001, G. Marson (H.B. 8583d). – ibid., branches of *Acacia*, on bark & wood, 29.X.2007, G. Marson (H.B. 8976f). – **Northern Territories**, Finke, 100 km E of Yulara, 24 km ENE of Curtin Springs Roadhouse, 28 km NNE of Mt. Connor, 480 m, branches of *Acacia jennerae*, on wood, 10.X.1998, G. Marson (ex H.B. 6277l, MEL 2389204, **holotype**).

Orbilia* aff. *pleiocoronohesperidea — Pl. 246

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.48 mm diam., 0.17–0.22 mm high, light orange(-red) or orange-brownish, round, scattered or in small groups; disc flat, margin thin, indistinct, 10–15 µm protruding, smooth or ± rough; broadly sessile, ± erumpent. **Asci** 75–87(–100) × 7.2–8.5 µm, †58–68 × 5.5–6.2 µm, 16-spored, spores *3–4-seriate, 7–8 lower spores inverted (hardly mixed), pars sporifera *60–65 µm long; **apex** (†) hemispherical (to slightly truncate), dome †1–1.2 → 0.7–0.9 µm thick, with indistinct apical chamber; **base** with short to long, thin or thick, flexuous stalk, h-shaped. **Ascospores** *(10–)11.5–16(–18) × (2–)2.2–2.5(–2.6) µm, †12–15 × 1.7–2.2 µm, fusoid-clavate, apex obtuse (rarely rounded), base medium to mostly strongly attenuated in a tail-like end or sometimes distinct thick tail 3–6(–7.5) × (0.8–)1–1.3(–1.5) µm, mostly slightly to medium curved near base; **SBs** *(2.5–)3–4(–4.5) × 1.2–1.3 µm, rod- to elongate tear-shaped, apically narrowed to a wide point, overmature 2.3–2.8 × 1.4–1.5 µm, tear-shaped to ampulliform. **Paraphyses** apically slightly clavate, terminal cells *(6–)8–15(–19) × 3–4 µm, lower cells *(11–)13–20 × 1.7–2.4 µm (up to 3 µm wide near apex); quite frequently branched at upper septum. **Medullary excipulum** hyaline, 30–50 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** of (†) thin-walled (to slightly gelatinized), vertically oriented t. globulosa-angularis from base to mid flanks, 50–90 µm thick near base, cells †8–18(–20) × 6–13 µm; 20–25 µm thick near margin, of t. prismatica-porrecta oriented at an 0–10° angle to the surface, marginal cortical cells */†7–12 × 3.5–4 µm; **glassy processes** absent. **Anchoring hyphae** sparse, *2–3 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and marginal ectal excipulum globose, 2 µm diam., but mainly crystalloid, very pale orange, at lower flanks absent. **Exudate** over paraphyses 0.2–0.3 µm thick, granular, loosely attached over gel, over marginal excipulum 0.5–1 µm thick. — **ANAMORPH**: unknown.

Habitat: collected 2.5–3 m above the ground, corticated, 16–20 mm thick branch of *Acacia cyperophylla*, on very decayed wood, ± greyed, no algae. **Associated**: *Coccomycetella* spp. {2}, *Hysterobrevium mori*, *Orbilia allantoobliqua*, *O. australiensis*, *O. multiaustraliensis*, *O. pleioaustraliensis*, *O. pleiovinosa*, *Ostropales*. **Desiccation tolerance**: paraphyses and excipular cells still viable after 34 months (and 57 months including a singular rehydration). **Altitude**: 540 m a.s.l. **Phenology**: long-lived.

Taxonomic remarks. This collection deviates from *O. pleiocoronohesperidea* in lacking glassy processes at the margin, also in slightly wider SBs. For the similar *O. pleiovinosa*, with which it grew in association, see under that species (p. 632).

Ecology. *O.* aff. *pleiocoronohesperidea* was found on rotten wood of a decorticated xeric branch of *Acacia* in a subtropical (almost tropical) semiarid (almost arid) acacia open woodland of western Australia

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, bridge over Gascoyne River, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Acacia cyperophylla*, on wood, 28.X.2007, G. Marson (H.B. 9695g).

Orbilia myriohesperidea Baral, **sp. nov.**, MB 813541 — Pl. 247

Etymology: named after the 64-spored asci and the ascospores resembling those of *O. hesperidea*.

Typification: Western Australia, Toolonga, branch of *Acacia*, 8.XII.2001, G. Marson (ex H.B. 9006b, MEL 2389272, holotype).

Latin diagnosis: *Similis* Orbiliae hesperideae *sed asci 64-spori. Habitat ad corticem putridum rami sicci* Acaciae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.35 mm diam., 0.19 mm high, bright orange-red, non-translucent, ± round, scattered; disc flat, margin distinct, 20–25 µm protruding, smooth; broadly sessile, ± superficial. **Asci** †81–90 × 8.5–9(–9.5) µm, 64-spored (~40–50 spores counted), spores ~8-seriate, lower spores inverted (strongly mixed); **apex** (†) hemispherical to slightly truncate, dome †1.3–1.6 → 0.8–1 µm thick, with slight apical chamber; **base** with short, ± thick, flexuous stalk, L-shaped. **Ascospores** †9–12 × 2.3(–2.4) µm, ellipsoid(-fusoid)-clavate, apex obtuse, base with a distinct cylindrical tail 2.5–4.5 × 0.9–1.2(–1.4) µm, straight to mostly slightly to medium curved or geniculate near base; **SBs** sometimes visible as a transparent region in spore apex (dead state), ?narrowly tear-shaped, ?2–2.5 × 0.6–0.8 µm. **Paraphyses** apically uninflated or slightly (to medium) clavate, terminal cells †(5–)8–15 × 3–4.2 µm; frequently branched at upper septum, hymenium pale orange. **Medullary excipulum** 30–40 µm thick, of medium dense textura intricata with some distinctly inflated cells in chains, sharply delimited. **Ectal excipulum** pale orange, of (†) thin-walled, vertically oriented t. angularis-prismatica at base and lower flanks, 30 µm thick near base, cells †10–16 × 6–9 µm; at mid flanks of t. prismatica oriented at a 20° angle, 20 µm thick at margin, of t. prismatica-porrecta oriented at 10°, marginal cortical cells †9–11 × 3–4 µm; **glassy processes** absent. **Anchoring hyphae** abundant, †1.3–2(–2.5) µm wide, walls 0.2–0.3 µm thick, forming at flanks a dense, hyaline, slightly gelatinized t. porrecta 20–25 µm thick. **SCBs** no data available. **Exudate** over paraphyses and margin 0.2–0.3 µm thick, continuous. — **ANAMORPH**: unknown.

Habitat: ± corticated, 9–10 mm thick xeric branch of *Acacia* sp., on strongly decayed bark (bast), greyed, green algae absent. **Associated**: *Orbilia myrionanosoma*. **Desiccation tolerance**: unknown but certainly min. 1 year. **Altitude**: 157 m a.s.l. **Geology**: Cretaceous sedimentary rock (red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia myriohesperidea* is readily recognized by its multispored asci and fusoid-clavate ascospores with thick tails. *O. myriofusiclava* differs in much shorter spores with more subacute apices and not forming such prominent tails, also in the presence of thick exudate. The species might also be closely related to the 32-spored *O.* aff. *macrocarpa* which has much larger spores with more fusoid heads (Pl. 229). *O.*

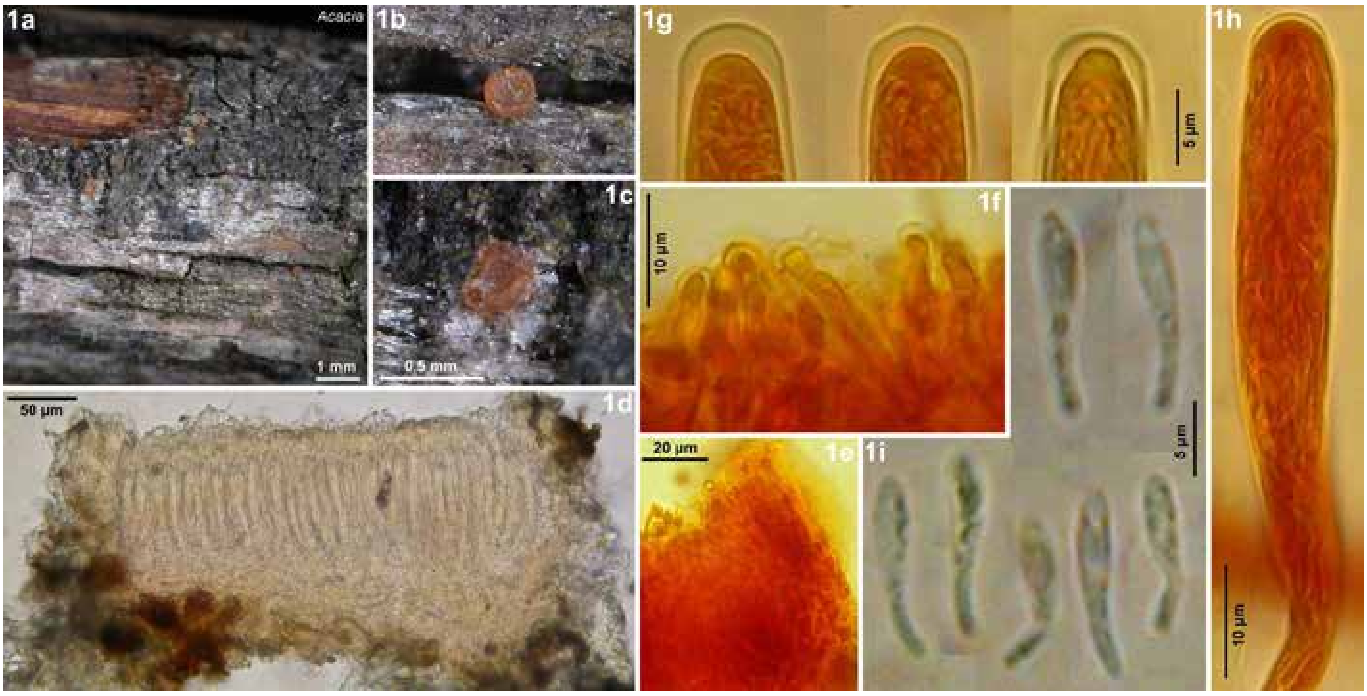


Plate 247. **1**: *Orbilia myriohesperidea*. – **1a**. dead corticated xeric branch of *Acacia* (rehydrated); **1b–c**. rehydrated apothecia (after > 7 years); **1d**. apothecium in median section; **1e**. id., marginal ectal excipulum, **1f**. paraphyses; **1g**. ascus apices; **1h**. mature ascus; **1i**. ascospores. – All in dead state (**1d**, **i** in KOH, **1e–h** in KOH+IKI). — **1a–i**. H.B. 9006b (holotype): Western Australia, Yalgoo, on *Acacia*.

myriohesperidea resembles *O. hesperidea* and *O. pleiohesperidea* in spore shape, the latter having a similar spore tail, but differ in 8- and 16-spored asci, respectively. No vital characters are known in this species, which was detected during a restudy of *O. myrionanosoma* more than 7 years after it was collected.

Ecology. *O. myriohesperidea* grew on rotten bark of a xeric branch of *Acacia* in a subtropical semiarid acacia shrubland in the Yalgoo ecoregion of the Darling Plateau (western Australia).

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 200 km N of Geraldton, 15 km SSE of Wannoo Billabong Roadhouse, W of Toolonga, 157 m, branch of *Acacia*, on bark, 8.XII.2001, G. Marson (ex H.B. 9006b, MEL 2389272, **holotype**).

Orbilia macrohesperidea Baral & G. Marson, **sp. nov.**, MB 813553 — Pls 248–249

Etymology: named according to the similarity to *O. hesperidea* but deviating in larger ascospores.

Typification: USA, Arizona, Wickenburg, branch of *Ephedra ?viridis*, 4.V.1995, G. Marson (ex H.B. 5894c, M-0276504, holotype).

Latin diagnosis: Similis *Orbiliae hesperideae sed asci, ascosporae et corpuscula refringentia latiora, excipulum marginale pilis brevissimis tenuitunicatis praeditum. Habitat ad corticem putridum ramorum siccorum* Ephedrae *in zona subtropica semiarida Americae septentrionalis.*

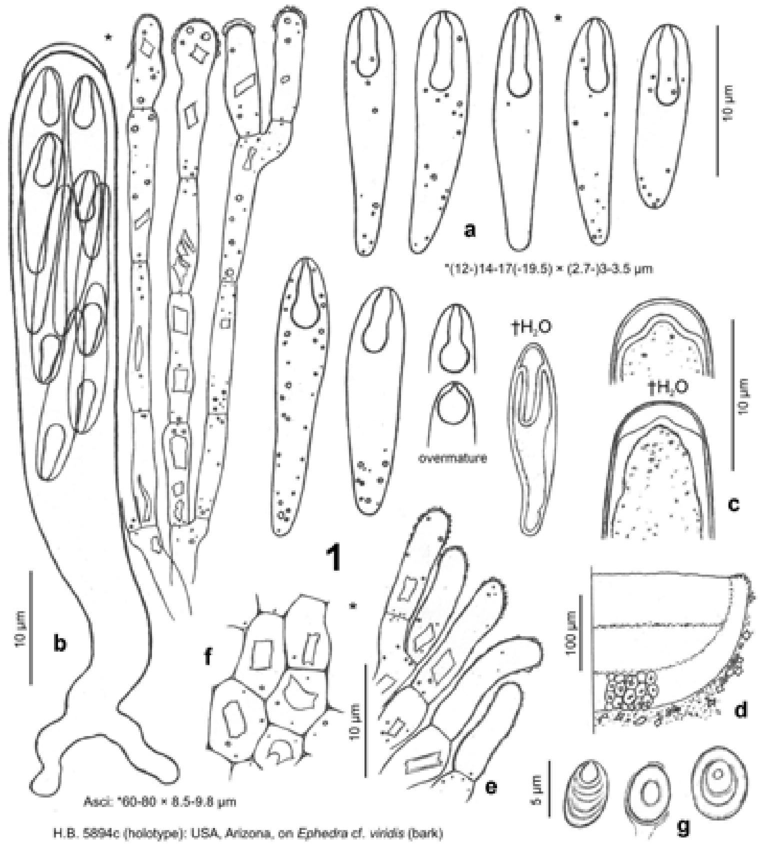


Plate 248. **1**: *Orbilia macrohesperidea*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum; **f**. id., mid flanks (cells containing crystalloid SCBs); **g**. crystalloid SCBs in basal excipular cells.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.5 mm diam., 0.15–0.18 mm high, pale (dirty) orange-ochraceous, non-translucent, round, scattered; disc slightly concave to flat, margin distinct, 0–5 µm protruding, slightly whitish pubescent; broadly sessile, ± superficial. **Asci** *57–80(–105) × 8.5–9.8 µm, †48–68 × 7.5–8.8 µm, 8-spored, spores *2–3-seriate, (3–)4(–7) lower spores inverted (sometimes mixed), pars sporifera *35–40 µm long; **apex** (†) hemispherical to slightly truncate, dome immature †1–1.4 µm thick, with small apical chamber; **base** with short, thick, flexuous stalk, Y- to h-shaped. **Ascospores** *(11.2)14–17(–19.5) × (2.7–)3–3.5(–4) µm, cylindrical to clavate or fusoid-clavate, apex rounded to obtuse, base slightly (to strongly) attenuated, sometimes tail-like, straight, sometimes slightly curved near base; **SBs** *4–5.8 × 1.3–2(–2.3) µm, pear-shaped to ampulliform, apically narrowed to a ± wide point, straight. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, rarely sublageniform, terminal cells *6–14 × 2.5–4 µm, lower cells *9–15 × 1.8–3 µm; sometimes branched at upper septum. **Medullary excipulum** subhyaline, 40–50 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** subhyaline, of (†) slightly gelatinized, vertically oriented t. angularis from base to submargin, 40–50 µm thick near base, cells *8–22 × 7–18 µm; 20–30 µm thick near margin, upper margin of t. porrecta oriented at a 40–50° angle to the surface, marginal cortical cells *8–15 × 3(–4) µm, forming ± free hair-like protrusions; **glassy processes** absent. **Anchoring hyphae** sparse, 2–3 µm wide, walls 0.2–0.3 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) crystalloid, refractive, in excipular cells 4–8 × 3–5 µm, pale yellowish(-orange). **Exudate** over paraphyses and marginal cells 0.1–0.5 µm thick, granular(-continuous), firmly attached. **— ANAMORPH**: unknown.

Habitat: partially decorticated, 10–13 mm thick xeric branches of *Ephedra ?viridis*, on strongly decayed bark (bast), greyed, with sparse algae. **Associated**: *?Baggea* sp., *Hysterobrevium mori*, *Melaspilea emergens*, *Orbilia calyptrata*, *O. lacrimispora*, *O. maeandrina*, *O. multiserpens*, *O. sonorensis*, *Peniophora* sp. **Desiccation tolerance**: many mature asci still viable after 28 months. **Altitude**: 615 m a.s.l. **Geology**: Oligo- & Miocene sand- & mudstone; volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia macrohesperidea* is similar to *O. hesperidea*, from which it differs in wider asci, ascospores and SBs, also in hair-like protrusions at the margin. For the similar Australian *O. megahesperidea* see below.

Ecology. *O. macrohesperidea* grew on rotten bark of xeric branches of *Ephedra* in a subtropical semiarid paloverde-mixed cacti desert scrub in the Sonoran Desert of the southwest of Northern America.

Specimens included. **USA**: **Arizona**, Sonoran Desert, 82 km NW of Phoenix, SE of Wickenburg, 615 m, branch of *Ephedra ?viridis*, on bark, 4.V.1995, G. Marson (ex H.B. 5894c, M-0276504, **holotype**).

Plate 249. **1**: *Orbilia macrohesperidea*. – **1a**. dead, corticated xeric branch of *Ephedra* with *Peniophora*; **1b–c**. rehydrated apothecia (after 11 years). — **1a–c**. H.B. 5894c (holotype): USA, Arizona, on *Ephedra*.

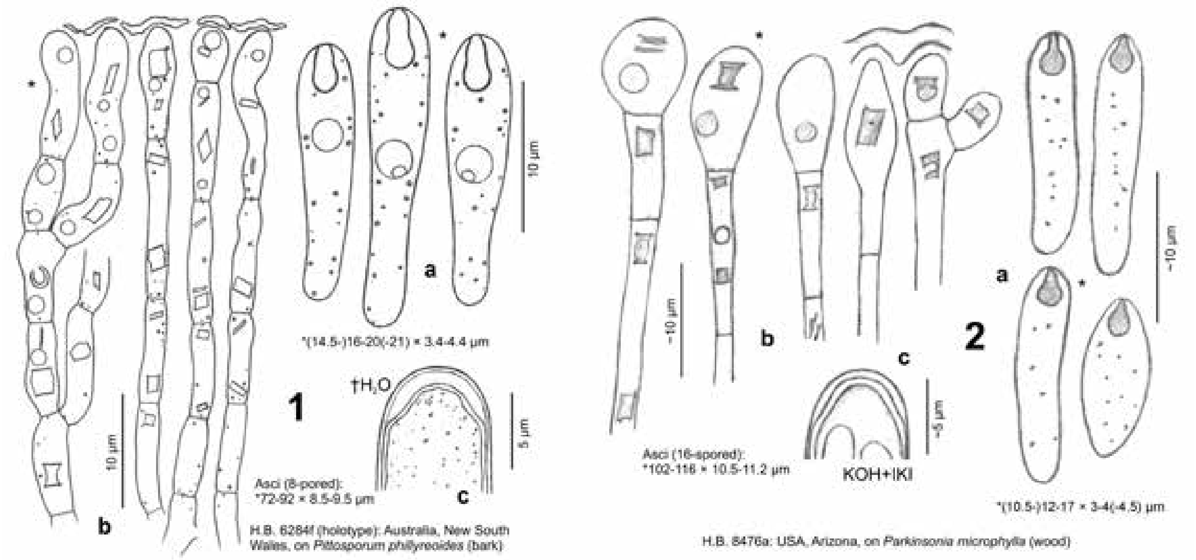


Plate 250. **1**: *Orbilia megahesperidea*; **2**: *O.* aff. *megahesperidea* (16-spored). – **a**. ascospores; **b**. paraphyses; **c**. ascus apex.

Orbilia megahesperidea Baral & G. Marson, **sp. nov.**, MB 813554 — Pls 250–251

Etymology: named after the similarity to *O. hesperidea* but with much larger ascospores.

Typification: Australia, New South Wales, Narrabri, twig and branch of *Pittosporum phillyreoides*, 24.X.1998, G. Marson (ex H.B. 6284f, MEL 2389205, holotype).

Latin diagnosis: *Similis* Orbiliae macrohesperideae *sed ascosporae leniter majores*, *basi leniter inflatae*, *corpuscula refringentia breviora*, *apothecia minuta*, *excipulum marginale absque pilis. Habitat ad corticem putridum ramorum siccorum* Pittospori phillyreoidis *in zona temperata subhumida Australiae orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.3 mm diam., ~0.2 mm high, light orange, round, barrel-shaped, scattered; disc flat, margin smooth; broadly sessile, superficial to slightly immersed. **Asci** *72–92 × 8.5–9.5 µm, 8-spored, spores 2–3-seriate, 3–5 lower spores inverted; **apex** (†) hemispherical, dome †1–1.2 µm thick, with small to large chamber; **base** with short, thick stalk, h-shaped. **Ascospores** *(14.5–)16–20(–21) × 3.4–4.4 µm, cylindric-clavate, apex rounded (to obtuse), base slightly to medium attenuated, sometimes dumbbell-shaped, straight to very slightly curved; **SBs** 3–4 × 1.7–2 µm, tear-shaped to pyriform or ampulliform, apically narrowed to a wide point. **Paraphyses** apically slightly (rarely medium) clavate, sometimes moniliform or spathulate, terminal cells *5–16 × 2.2–3.5 µm, lower cells *8–11 × 2–2.5(–3.3) µm (near base 7 × 3 µm); sometimes branched near apex. **Medullary excipulum** not examined. **Ectal excipulum** at flanks of t. angularis, margin not examined; **glassy processes** presumably absent. **Anchoring hyphae** not examined. **SCBs** in paraphyses and ectal excipulum globose, 1–1.5 µm diam., and angular, hyaline. **Exudate** over paraphyses 0.5–1.5 µm thick, cloddy, hyaline, loosely attached. **— ANAMORPH**: unknown.

Habitat: collected 248 m above the ground, partially decorticated, 4–15 mm thick twigs and branches of *Pittosporum phillyreoides*, on very rotten bark (periderm & bast), sometimes in clefts, strongly greyed, green algae very sparse. **Associated**: *Claussenomyces* sp., *Gloniopsis* sp., *Orbilia angustoaristata*, *O.* ?*livistonae*, *O. multiserpens*, *O.* ?*myrioolneyae*, *O. pleioaustraliensis*, *Polynema* sp., *Symbiotaphrina desertorum*, ?*Triblidium* sp., *Xylobolus* sp. **Desiccation tolerance**: fully viable (except for mature asci) for 25 months. **Altitude**: 615 m a.s.l. **Geology**: Cenozoic regolith; interlayered sedimentary and volcanic rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia megahesperidea* is characterized by large, cylindric-clavate, often slightly dumbbell-shaped ascospores with comparatively short and wide, ampulliform to pyriform SBs. From the similar North American *O. macrohesperidea* it deviates in slightly larger spores with ±

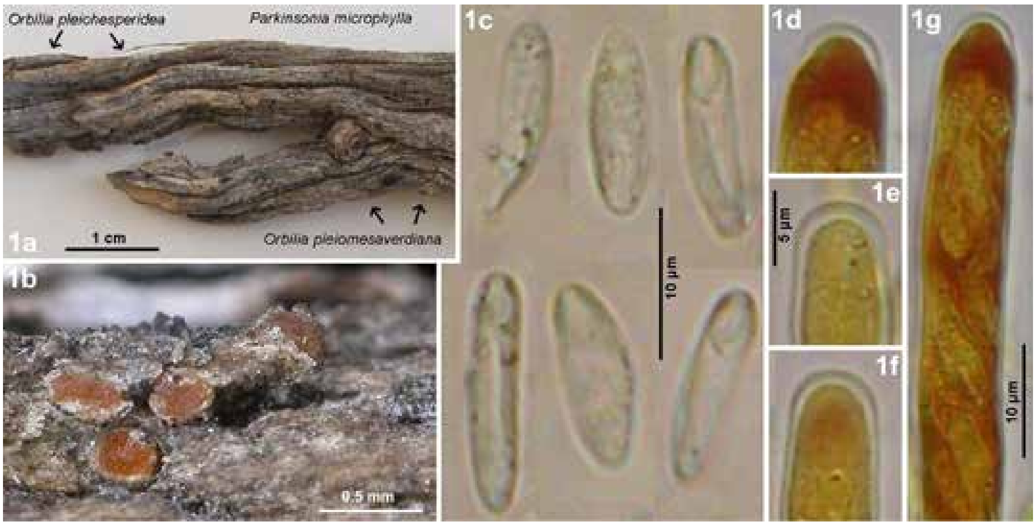


Plate 251. **1**: *Orbilia* aff. *megahesperidea*. – **1a**. decorticated xeric branch of *Parkinsonia microphylla*; **1b**. rehydrated apothecia (after 9 years); **1g**. mature ascus; **1d–f**. ascus apices; **1c**. ascospores. – Dead state (asci in KOH+IKI, spores in H_2O). — **1a–g**. H.B. 8476a: USA, Arizona.

inflated bases, and in shorter SBs, also in smaller yellow-orange apothecia with a smooth margin. The nucleus in the living spores is visible when stained in IKI (Pl. 250: 1a).

Not included collection. A deviating North American sample has similar ascospores but 16-spored asci (Pls 250: 2; 251).

Ecology. *O. megahesperidea* grew on rotten bark of a xeric branch of *Pittosporum phillyreoides* in a warm-temperate subhumid eucalypt woodland in eastern Australia west of the Great Dividing Range. The not included collection on wood of *Parkinsonia* (foothill paloverde) was from the subtropical semiarid Sonoran paloverde-mixed cacti desert scrub in the southwest of Northern America.

Specimens included. **AUSTRALIA**: **New South Wales**, Brigalow Belt South, 20 km SW of Narrabri, 248 m, twig & branch of *Pittosporum phillyreoides*, on bark, 24.X.1998, G. Marson (ex H.B. 6284f, MEL 2389205, **holotype**).

Not included. **USA**: **Arizona**, Sonoran Desert, 82 km NW of Phoenix, SE of Wickenburg, 615 m, branch of *Parkinsonia microphylla*, on wood, 4.V.1995, G. Marson (H.B. 8476a).

Orbilia montigena Baral & E. Weber, **sp**. **nov**., MB 813556 — Pls 252–253, Map 44

Etymology: referring to the montane distribution of the first collections.
Typification: Germany, Bayern, Spitzingsee, branch of *Sorbus aucuparia*, 3.VII.2005, P. Karasch (ex H.B. 7838b, M-0276517, holotype).

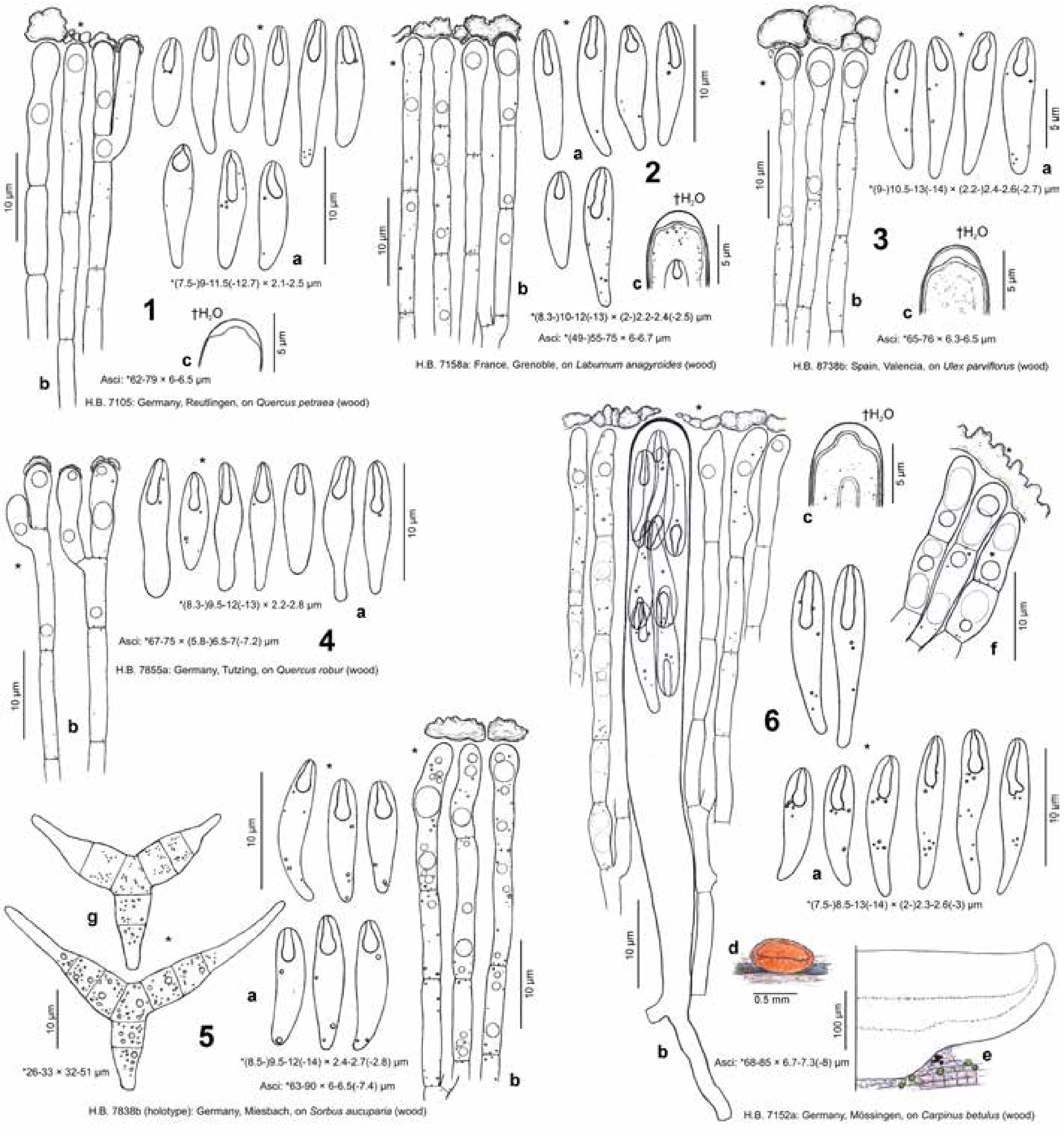


Plate 252. **1–6**: *Orbilia montigena*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium (rehydrated); **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. conidia from substrate.

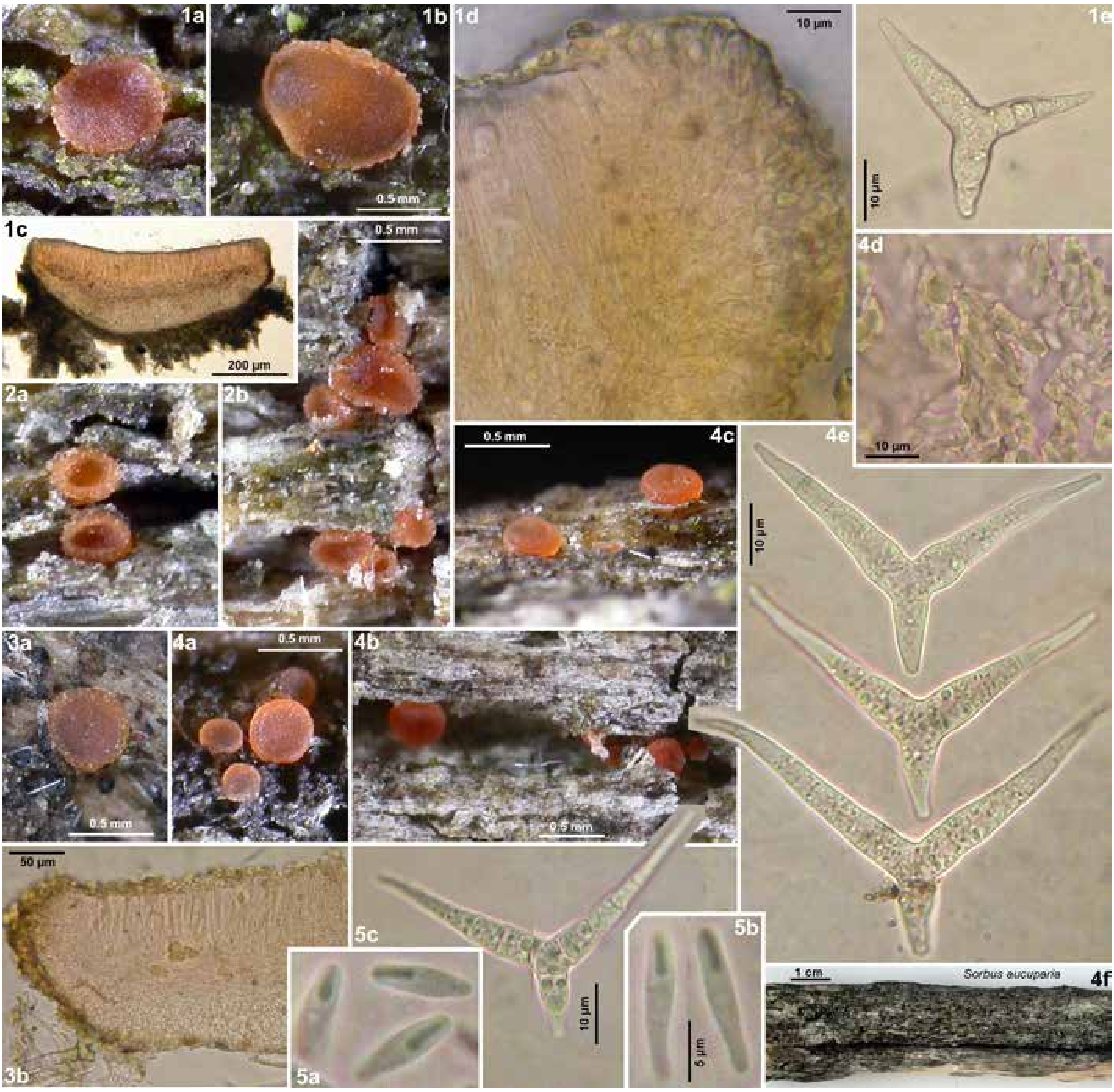


Plate 253. **1–5**: *Orbilia montigena*. – **4f**. decorticated xeric branch of *Sorbus aucuparia*; **1a–b**, **2a–b**, **3a**, **4a–c**. rehydrated apothecia; **1c**, **3b**. apothecia in median section; **1d**. id., marginal ectal excipulum; **4d**. exudate on margin (external view); **5a–b**. ascospores; **1e**, **4e**, **5c**. conidia from substrate. – Living state, except for **5c**, some conidial cells in **1e**. — **1a–e**. H.B. 7933a: Germany, Tutzing, on *Fagus*; **2a–b**. H.B. 7158a: France, Grenoble, on *Laburnum*; **3a–b**. H.B. 8738b: Spain, Valencia, on *Ulex*; **4a–f**. H.B. 7838b (holotype): Germany, Miesbach, on *Sorbus*; **5a–c**. H.B. 7855a: Germany, Tutzing, on *Quercus*.

Latin diagnosis: *Similis* Orbiliae hesperideae *sed cellulae excipuli et paraphysium absque corpusculis crystalloideis. Habitat ad lignum valde putridum ramulorum vel ramorum siccorum fruticum vel arborum angiospermarum in zona boreali ad mesomediterranea Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.4–0.8(–1.1) mm diam., 0.15–0.25(–0.33) mm high (receptacle 0.1–0.15 mm), light to bright orange(-red), rarely rose-red, scarcely translucent, round (to elliptical), subscattered to subgregarious; disc slightly (to medium) concave or flat, margin ± thick, 5–20 µm protruding, ± smooth or (very) finely to distinctly crenulate; broadly sessile or with a short and broad obconical stipe 0.06–0.1 × 0.25–0.4 mm, superficial or slightly immersed, sometimes immersed in clefts; dry bright (orange-)red, with contracted margin. **Asci** *(49–)60–82(–90) × (5.8–)6–7.2(–7.5)((–8.5)) µm {6}, †(44–)48–64(–85) {5} × (5–)5.3–6.3(–6.8) µm {3}, 8-spored, spores 2–4-seriate, ((1–))(2–)3–4(–5)((–6)) lower spores inversely oriented {8} (rarely to often mixed), pars sporifera *(25–)28–30(–37) µm; **apex** (†) hemispherical, dome †(0.5–)0.7–1(–1.2) µm thick {5}, usually with apical chamber; **base** with short to long, thin or thick, ± flexuous stalk, L-, h- or Y-shaped. **Ascospores** *((7.5–))(8.3–)9–13(–14)((–15.5))((–17)) × (2–)2.2–2.7(–3) µm {14}, subcylindric-fusoid or -ellipsoid to fusoid-clavate or clavate, apex rounded to obtuse, base sometimes tail-like, rarely with distinct short tail, straight or (very) slightly (to medium) curved near base; **SBs** *((2–)) (2.5–)3–4(–4.7) ((–5.5)) × 0.8–1.3 {7}, tear- to pear-shaped, or rod-shaped to vermiform or ampulliform, apically narrowed to a small to wide point, overmature *1.5–3 × 1.2–1.4(–1.6) µm. **Paraphyses** apically uninflated or slightly (rarely medium) clavate, sometimes sublageniform or spathulate, terminal cells *(7–)9–20((–25)) × ((1.5–))(1.7–)2–3((–3.5)) µm {5}, lower cells *(7–)9–14(–15)((–18)) × 1.6–2.6(–2.8) µm {5}; rarely to infrequently branched near apex; hymenium pale rose to orange. **Medullary excipulum** subhyaline to pale rose, 40–60 µm thick, of rather dense textura intricata with many inflated cells, medium to very sharply delimited from ectal excipulum (sometimes by a 10 µm thick yellowish t. porrecta). **Ectal excipulum** hyaline to pale rose, of (†) thin-walled (to slightly gelatinized), vertically oriented t. globulosa-angularis-prismatica from base to midflanks or submargin, (40–)50–80(–100)((–200)) µm thick near base, cells *(6–)8–16(–19) × (5–)6–11(–13) µm {5}; 20–30 µm thick at flanks, 25–40 µm thick near margin, of t. prismatica-angularis to prismatica-porrecta oriented at a 20–30 up to 50–70° angle to the surface, marginal cortical cells *(6–)7–10(–15) × 2.5–4.5(–5.2) µm {4}, †(7–)8–12(–13) × 2–2.5 or 3–4 µm {2}, **glassy processes** absent {8}. **Anchoring hyphae** medium to very abundant, */†2–3 µm wide, walls 0.2(–0.3) µm thick {4}, forming a dense, up to 70–100 µm thick, non-gelatinized t. intricata at base, also covering the flanks. **SCBs** globose {10}, in paraphyses 1–3 µm diam.; in excipular cells 1.5–3.5(–4) µm diam. **Exudate** hyaline to light chlorinaceous- or sulphur-yellow, over paraphyses (0.3–)1–3(–5) µm thick, broken into externally rough clods, usually loosely attached; over margin and flanks rough-cloddy to granular, 0.5–4 up to 5–10 µm thick. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {3}). **Conidiophores** not seen. **Conidia** Y-shaped, total size *(26–)30–34(–39) × (30–)35–50(–69) µm, †37 × 52 µm, stipe *10–15 × 5.5–6.5(–8.2) µm, (1–)2(–3)-septate, arms strongly and abruptly tapering, *(16–)19–33(–40) × 6–7(–8) µm, †5.5 µm wide, (2–)3–4(–5)-septate {3}.

Habitat: collected 0.5–4 m above the ground (rarely on the ground), 3–80 mm thick, still-attached, decorticated twigs and branches or logs of *Carpinus betulus* {1}, *Cornus mas* {1}, *Corylus avellana* {1}, *Fagus sylvatica* {1}, *Koelreuteria paniculata* {1}, *Laburnum anagyroides* {1}, *Populus alba* {1}, *P. tremula* {1}, *Quercus* sp. {1}, *Q. petraea* {1}, *Q. robur* {1}, *Robinia pseudoacacia* {2}, *Sorbus aucuparia* {1}, *Ulex parviflorus* {2}, on wood {16}, 0.5–1 or rarely 5–10 mm deep (medium to) strongly decayed, sometimes very eroded, ungreyed to strongly greyed, green algae sparse to abundant. **Associated**: *Durella connivens* {2}, '*Helotium*' *uvidulum* {2}, *Hyalorbilia hergiswiliana* {2}, *H. subfusispora* {1}, *Lecanora* sp. {1}, *Mycocalicium ?parietinum* {1}, *Orbilia aprilis* {2}, *O. arachnovinosa* {1}, *O. corculispora* {1}, *O. microsoma* {1}, *O. pleioeuonymi* {1}, *O. ?pleiogambelii* {1}, *O. pleiomicrosoma* {1}, *O. pleistoeuonymi* {1}, *O. polyspora* {1}, *O. vinosa* {1}, *Perrotia flammea* {1}, *Strossmayeria basitricha* (anamorph) {1}. **Desiccation tolerance**: some paraphyses, ascospores, and immature asci still alive after 22 months. **Altitude**: 150 m a.s.l. (hemiboreal Europe), 130–1585 m (central Europe), 255–1250 m (southern Europe). **Geology**: Lower to Upper Jurassic, Cretaceous & Tertiary marl-, lime- & sandstone, flysch, Quaternary glacial or fluviatile sand & gravel; serpentinite. **Phenology**: III, V–X, XII (throughout the year, long-lived).

Taxonomic remarks. *Orbilia montigena* resembles the mediterranean *O. hesperidea* in ascospore shape and in the absence of glassy processes, but differs in the consistent absence of crystalloid SCBs and in occurring in montane to subalpine climatic zones. *O. vinosa* differs from *O. montigena* in narrower and longer spores, longer SBs, and in the partial presence of crystalloid SCBs. For the morphological differences between *O. montigena* and *O. alpigena* see under the latter species (p. 595). The two species were at first believed to represent a single taxon, but differences in SB size and molecular data suggest that samples on coniferous wood need to be separated from those on angiosperm wood.

Variation. *O. montigena* varies somewhat in the size of asci, spores, and SBs. Spore shape was rather consistent, although a few spores showed tail-like bases in most of the collections.

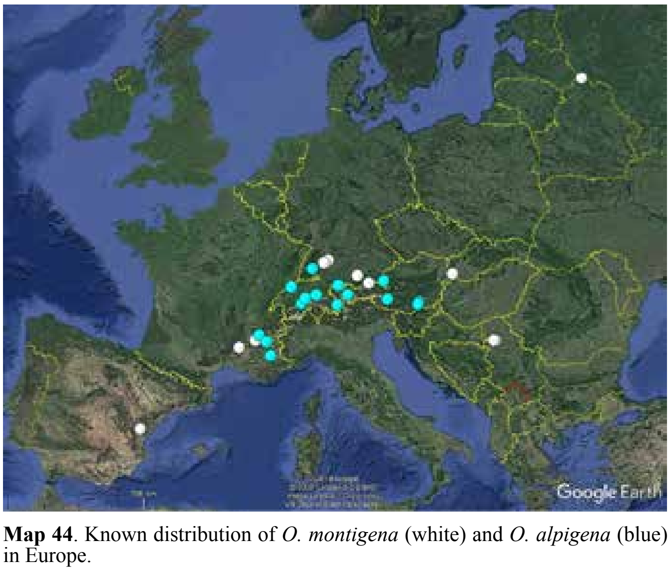
Not included collection. A sample on unidentified angiosperm wood from the lowlands of eastern North America studied by E. Crenson (pers. comm., IVV: 4.IX.2017) is not included in the description, particularly because of the geographical origin and the lack of data about SCBs, also because the margin is finely denticulate, perhaps by short glassy processes. In the spores and SBs this sample would well fit *O. montigena*.

Anamorph. Trinacrium-like conidia more or less indistinguishable from those associated with *O. alpigena* were repeatedly found in association with apothecia of *O. montigena*. Likewise indistinguishable appears to be the single conidium observed in the similar North American *O. navajoana*. Also the conidia of *O. hesperidea* are similar, but have narrower and shorter, also often less strongly tapered arms. Trinacrium-like conidia observed in the Slovakian sample on *Quercus* deviate in less tapered, obtuse arms and are therefore considered as uncertain.

Phylogeny. Sequences of two *O. montigena* samples (on *Fagus* from Bayern, montane; on *Quercus* from Slovakia, colline), gained from apothecia and comprising the ITS region (S1506 intron absent), concur by only 1 nt difference in the ITS2. The species shows an ITS distance of 9 % to *O. alpigena*. In our phylogenetic analysis of the ITS region, *O. montigena* clustered with high support in the *hesperidea-alpigena* clade (Phyls 9–10), with a distance of ~7.5–10.5 % to other members of the clade, the lowest percentage being to narrow-spored *O. australiensis*.

Ecology. *O. montigena* inhabits strongly rotten wood of xeric branches of various angiosperm trees and shrubs. The species was found in calcareous, orotemperate (montane: Schwäbische Alb, German and French Alps and Prealps) but also supratemperate (colline: Danubian floodplain, Fruška Gora), humid regions of central and southern Europe, where it occurred in rich deciduous forests, e.g., a thermophilous (xerophilous) pannonian oak grove with *Cornus mas*, a *Querco-Fagetum* with *Lilium martagon* and *Vincetoxicum officinale*, or one with *Tilia tomentosa* and *Staphylea pinnata*. The sample on *Sorbus* was in the subalpine *Pinus mugo* belt. In the Sebezh National Park of northwestern Russia *O. montigena* was found in the hemiboreal southern taiga. Two collections on *Ulex parviflorus* are from mesosub- or supramediterranean semihumid Massif central and Sistema Ibérico, but they did not differ in their micromorphology from typical samples from cooler sites. One sample from the lowlands of Fruška Gora was at a more suprasubmediterranean subhumid site.

Specimens included. **RUSSIA (West)**: **Pskov**, **Sebezh**, ~18 km SE of Sebezh, Lake Osyno, 150 m, branch of *Corylus avellana*, on wood, 16.VII.2006, V.A. Melnik, vid. E.S. Popov (LE 294850, as *O. vinosa*, doc. vid.). — **GERMANY**: **Baden-Württemberg**: Schwäbische Alb, 6 km E of Reutlingen, 3 km ENE of



Map 44. Known distribution of *O. montigena* (white) and *O. alpigena* (blue) in Europe.

Eningen, Hännersteigfels, 735 m, branch of *Quercus petraea*, on wood, 3.III.2002, H.O. Baral (H.B. 7105). – 4 km SSW of Mössingen, 1.5 km NE of Beuren, Dreifürstenstein, 850 m, branch of *Carpinus betulus*, on wood, 23.VI.2002, H.O. Baral (H.B. 7152a). – **Bayern**, **Oberbayern**, Mangfallgebirge, 16.5 km SSE of Miesbach, 2.7 km ESE of Spitzingsee, Taubenstein, ~1585 m, branch of *Sorbus aucuparia*, on wood, 3.VII.2005, P. Karasch (H.B. 7838b, M-0276517, **holotype**, anam. substr.). – Fünfseenland, 8 km NW of Tutzing, 3.5 km S of Andechs, Goaslweide, 720 m, branch of *Quercus robur*, on wood, 9.VII.2005, P. Karasch (H.B. 7855a, anam. substr.). – ibid., branches of *Fagus sylvatica*, on wood, 15.X.2005, H.O. Baral (H.B. 7933a, anam. substr.; sq.: KT222357). — **SLOVAKIA**: **Bratislava**, 10 km SE of Bratislava, 4.8 km S of Podunajské Biskupice, Topol'ové hony, 132 m, branch of *Cornus mas*, on wood, 18.V.2019, A. Polhorský (A.P. 19/22b, doc. vid.). – ibid., 130 m, log of *Quercus*, on wood, 5.VI.2019, A. Polhorský (A.P. 19/29, BRA-CR31732, doc. vid., sq.: MN611699). — **SERBIA**: **Vojvodina**, Fruška Gora, 13 km SW of Novi Sad, 3 km SSW of Beočin, Crveni Čot, 398 m, branch of *Populus alba*, on wood, 22.VII.2019, D. Savić (doc. vid.). — 12.5 km S of Novi Sad, Iriški venac, W of WWII memorial, 415 m, branch of *P. tremula*, on wood, 12.VII.2019, D. Savić (doc. vid.). – SW of WWII memorial, 493 m, branch of *Koelreuteria paniculata*, on wood, 25.IX.2019, D. Savić (doc. vid.). – ibid., 480 m, branch of *Robinia pseudoacacia*, on wood, 4.IX.2019, D. Savić (doc. vid.). – 15.5 km S of Novi Sad, 3.2 km NNW of Irig, Novo Hopovo, 255 m, *R. pseudoacacia*, on wood, 25.IX.2019, D. Savić (doc. vid.). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 48 km SW of Grenoble, 8.3 km N of Die, SW of Col de Rousset, 1250 m, branches of *Laburnum anagyroides*, on wood, 22.VIII.2000, G. Marson (H.B. 7158a). – **Ardèche**, 5 km E of Vallon-Pont-d'Arc, 4 km WNW of St.-Remèze, les Mouniers, 410 m, branch of *Ulex parviflorus*, on wood, 8.X.2002, G. Marson (H.B. 7317b ø). — **SPAIN**: **Com. Valenciana**, **Castellón**, 51 km W of Castellón, 6 km SE of Barracas, 980 m, twig of *U. parviflorus*, on wood, 27.XII.2007, J.P. Priou (H.B. 8738b).

Not included. **USA**: **New York**, 18 km NNE of New York, 5.5 km WNW of Bronx, Inwood Hill Park, 45 m, branch of indet. angiosperm, on wood, 4.IX.2017, E. Crenson (doc. vid.).

Orbilia alpigena Baral & E. Weber, **sp**. **nov**., MB 813557 — Pls 254–255, Map 44

Etymology: referring to its predominant occurrence in the region of the Alps.
Typification: Austria, Vorarlberg, Eineguntkopf, branches of *Picea abies*, 2.VII.2011, H.O. Baral (ex H.B. 9566a, M-0276432, holotype; sq.: KT222426).

Latin diagnosis: *Similis* Orbiliae montigenae *sed corpuscula refringentia ascosporarum breviora, habitat ad lignum ramulorum vel ramorum siccorum arborum coniferarum.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.25–)0.3–0.7(–0.8) mm diam., 0.15–0.2(–0.26)(–0.33) mm high (receptacle 0.1–0.15 mm), pale to bright orange-rose or orange-red, faintly translucent, round, scattered to subgregarious; disc flat to slightly convex, margin indistinct or thin to thick, 0–5 µm protruding, smooth to slightly rough; broadly sessile or with a short obconical stipe 0.06 × 0.2 mm, superficial; dry deep orange-red, margin scarcely raised. **Asci** *(52–)55–65(–75) × 5.5–6.5 µm {3}, †(42–)45–55(–57) × (4.7–)5–5.5(–5.8) µm {2}, 8-spored, spores 2–4-seriate, 3–5(–6) lower spores inversely oriented {5} (sometimes to often mixed); **apex** (†) hemispherical to slightly (rarely medium) truncate, dome †0.7–1.5(–2) → (0.3–)0.5–1.3 µm thick {4}, with or without apical chamber; **base** with short to long, medium thick, flexuous stalk, Y-, L- or h-shaped. **Ascospores** *((6–))(7.5–)9–13(–14) × (2–)2.2–2.7(–2.9) µm {8}, †8.5–13 × 2–2.5(–2.8) µm {3}, (cylindric-)fusoid to fusiform or fusoid- to fusiform-clavate, apex obtuse to subacute, base rarely tail-like or with a tail 1–3(–6) × 1–1.4 µm, straight to slightly curved near base; **SBs** *((1.8–))(2–)2.3–3.2(–3.5)((–4)) × (0.8–)1–1.5(–1.6) {7}, tear- to pear-shaped, apically narrowed to a ± small point. **Paraphyses** apically uninflated or slightly (to medium) clavate or ellipsoid, terminal cells *(6–)8–15(–19) × 2–3(–3.5) µm {3}, lower cells *7.5–13(–14.5) × 1.5–2.5 µm {2}; rarely to infrequently branched near apex; hymenium pale rose(-orange). **Medullary excipulum** pale rose, 50–90 µm thick, of rather dense textura intricata with many inflated cells, medium to sharply delimited from ectal excipulum (sometimes by a 5–10 µm thick yellowish t. porrecta). **Ectal excipulum** hyaline to pale rose, of (†) thin-walled (to slightly gelatinized), vertically oriented t. angularis from base to submargin, 40–100 µm thick near base, cells *7–14 × 6–12 µm {2}; 20–25 µm thick at flanks, 15–20(–40) µm near margin, of t. prismatica-angularis to prismatica-porrecta oriented at a (30–)50–80° angle to the surface, marginal cortical cells *5–10 × (2.5–)3–4.5 µm {2}, **glassy processes** absent {8}. **Anchoring hyphae** ± abundant, forming strands, *2–3 µm wide, walls 0.2–0.3 µm thick {1}. **SCBs** globose {7}, in paraphyses (1–)1.5–3 µm diam.; in excipular cells 1.8–3.2 µm diam. **Exudate** hyaline to pale yellow, over paraphyses 1–3(–4) µm thick, cloddy to continuous, externally ± rough, ± loosely attached; over margin and flanks rough-cloddy to granular, 2–3(–5) µm thick. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {5}). **Conidiophores** not seen. **Conidia** Y-shaped, total size *25–37 × 36–48 µm, †25 × 39 µm, stipe *10–11.5(–14.5) × 5.7–7.2 µm, †10.5 × 6 µm, 2-septate, arms strongly and abruptly tapering, *17.5–27 × 5.7–7.8 µm, †19–21 × 5–5.5 µm, 3(–4)-septate {3}.

Habitat: collected 1–2 m above the ground, corticated to decorticated, 3–28 mm thick, still-attached twigs and branches of *Picea abies* {13}, *Pinus sylvestris* {1}, on wood {14}, 0.2–0.3 mm deep medium to strongly decayed, often in old beetle galleries, strongly greyed or not, green algae sparse to abundant. **Associated**: *Amphosoma resinicola* {1}, *Cryptodiscus muriformis* {1}, *C. pini* {1}, *Hypogymnia physodes* {2}, *Lachnellula abietis* {1}, *L. resinaria* {1}, *Mellitiosporiella* cf. *macrospora* {1}, *Mellitiosporium propolidoides* {4}, *Orbilia aprilis* {1}, *O. cylindrospora* {1}, *O. euonymi* {4}, *O. flagellispora* {2}, *O. patellarioides* {1}, *O. subvinosa* {1}, *O. vinosa* {2}, ?*Pragmopora* sp. {1}, *Propolis hillmanniana* {1}, *P. rhodoleuca* {1}, *Pseudevernia furfuracea* {2}, *Resinomyces griseus* {1}, *Therrya* cf. *fuckelii* {1}, crustose lichens. **Desiccation tolerance**: fully viable for at least 1 month. **Altitude**: 870–1760 m a.s.l. **Geology**: Buntsandstein, Middle & Upper Jurassic and Cretaceous marl- & limestone, dolomite, Jurassic & Tertiary mud- & sandstone, molasse, Pleistocene till; amphibolite, gneiss, pelite, phyllite, mica schist. **Phenology**: IV–X (but probably throughout the year, long-lived).

Taxonomic remarks. Like *O. montigena*, *O. alpigena* resembles the mediterranean *O. hesperidea*, from which both differ in the absence of crystalloid SCBs and in the preference for montane to subalpine climatic zones. Morphologically, *O. montigena* cannot easily be distinguished from *O. alpigena*. The main indication for two separate taxa was suspected to lie in the length of spore bodies. *O. montigena* shows a distinct tendency to longer SBs, ranging at (2.5–)3–4(–4.7) µm compared to (1.8–)2–3.5(–4) µm in *O. alpigena*. This feature was found to correlate with the substrate: angiosperms in *O. montigena*, gymnosperms in *O. alpigena*. Furthermore, apothecia of *O. alpigena* are slightly smaller, never concave, with a hardly protruding, always ± smooth margin, and the spores are more fusoid, with a sometimes subacute apex and an always narrow attachment of the SBs.

Variation. *O. alpigena* varies somewhat in ascus length, thickness of apical dome, and in spore and SB size. Variation in spore length and shape was especially seen in the first collection of *O. alpigena* (H.B. 4801a), the spores showing sometimes distinct and rather long tails.

Anamorph. Trinacrium-like conidia were repeatedly found in association with apothecia of *O. alpigena*. They are rather characteristic in their very broad and strongly tapered arms and stipes. Therefore, we believe that it is possible to recognize the species from its anamorph even if no mature teleomorph is present. An unlocalized French, probably montane collection on a *Larix* branch consisted only of a single immature apothecium with asci with thick-walled apices and paraphyses with globose SCBs; the abundantly associated conidia obviously belonged to *O. alpigena* (Pl. 254: 4). However, conidia found in the very similar *O. montigena* and the North American *O. navajoana* appear to be indistinguishable.

Phylogeny. Sequences of *O. alpigena* were gained from apothecia of two collections (Vorarlberg and Hautes-Alpes),

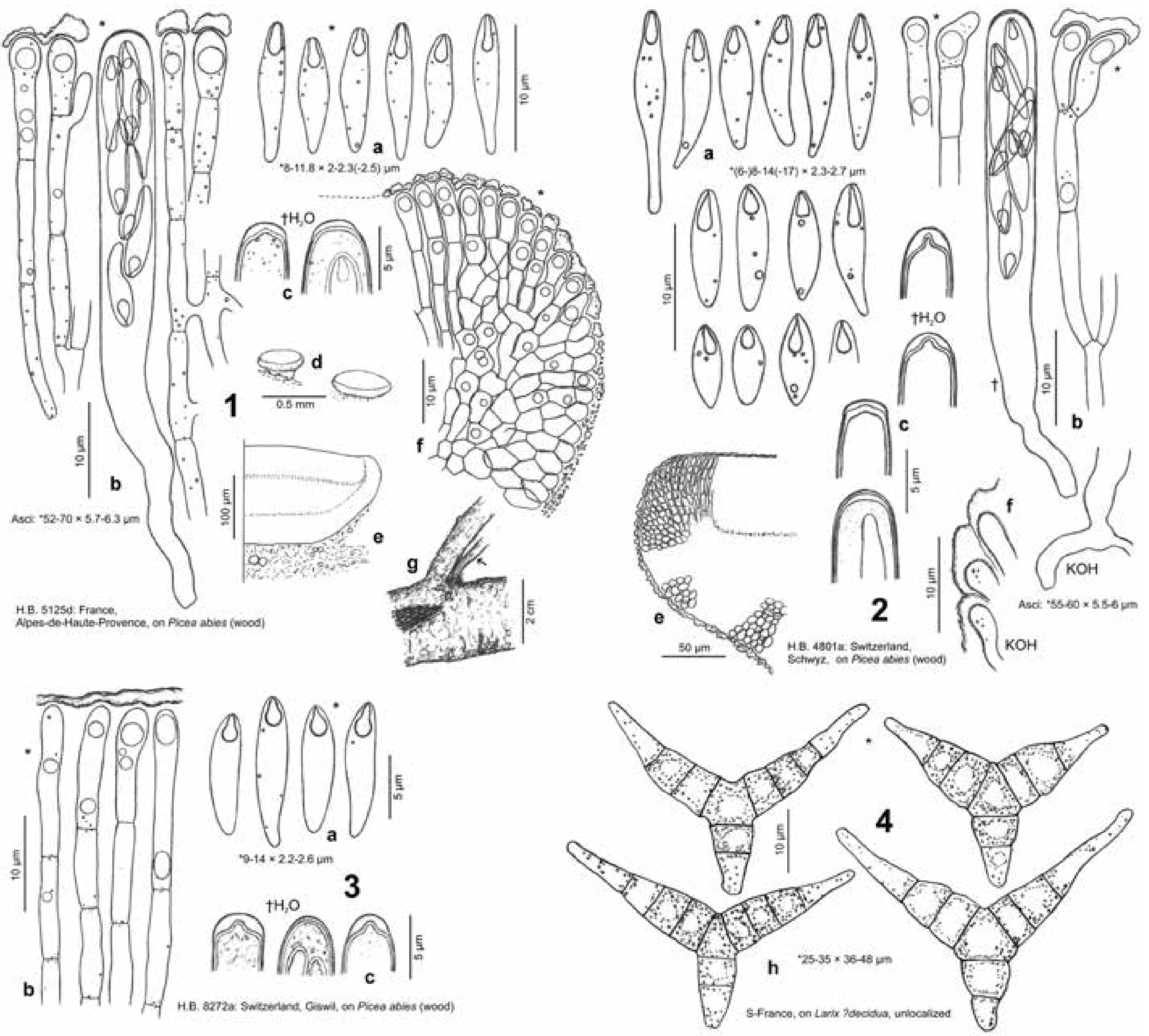


Plate 254. **1–4**: *Orbilia alpigena*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., ectal excipulum (margin and mid flanks); **g**. corticated xeric branch with a thin decorticated side twig; **h**. conidia from substrate (associated teleomorph immature).

comprising SSU (only Vorarlberg), ITS, and LSU (the S1506 intron is absent in both). In the ITS region and in the overlapping part of LSU (D1–D2) the two strains are completely identical. In our phylogenetic analyses, *O. alpigena* clustered highly supported in the *hesperidea-alpigena* clade (Phyls 9–10, S13), showing an ITS distance of 8.5–10.5 % to other members of the clade. The high distance of 9 % to *O. montigena*, with which it does not form a clade, confirms separation from that species.

Ecology. *O. alpigena* inhabits medium to strongly rotten wood of xeric branches of gymnosperm trees. The species was so far only found in central and southern Europe (Schwarzwald, Alps) where it appears to be restricted to montane to subalpine, orotemperate humid, rarely orosubmediterranean zones. It occurs in *Picea* forests, e. g., with *Vaccinium* and *Calluna*, or *Gentiana lutea*, on acidic but also calcareous soils.

Specimens included. **GERMANY**: **Baden-Württemberg**: Schwarzwald, 8.3 km WNW of Villingen, 1 km NW of Unterkirnach, E of Behringerhof, 870 m, branch of *Picea abies*, on wood, 19.VIII.2005, H.O. Baral (H.B. 7874a ø, anam. substr.). – **Bayern**, **Oberbayern**, 5.3 km NW of Bad Reichenhall, 2.8 km SW of Aufham, Steineralm, 1083 m, branch of *Picea abies*, on wood, 12.VIII.2018, H.O. Baral (H.B. 10170a, anam. substr.). — **SWITZERLAND**: **Jura**, 12 km NNW of Biel, 5 km ENE of Tramelan, NE of Orange, 880 m, branch of *P. abies*, on wood, 16.VI.2018, H.O. Baral (H.B. 10156). – **Bern**, 3.3 km NNW of Mürren, 2 km WSW of Lauterbrunnen, Grütschalp, 1760 m, branches of *P. abies*, on wood, 11.VI.2017, B. Senn-Irlet (B.S.I. 17/53, doc. vid.). – **Obwalden**, 8.5 km NE of Brienz, 7.5 km WSW of Giswil, Glaubenbielen, 1555 m, branch of *P. abies*, on wood, 17.VIII.2006, H.O. Baral (H.B. 8272a, anam. substr.). – **Schwyz**, 13 km S of Einsiedeln, 4 km SW of Oberiberg, SE of Ibergeregg, Schijenloch, 1500 m, branch of *P. abies*, on wood, 9.X.1992, G. Marson (H.B. 4801a). – **Graubünden**, 4.5 km SW of Zernez, Carolina, 1635 m, branch of *P. abies*, on wood, 23.VI.2018, B. Senn-Irlet (B.S.I. 18/75, doc. vid.). — **AUSTRIA**: **Vorarlberg** (border to Bayern), 7.7 km SSE of Oberstaufen, E of Falken-Hütte, Eineguntkopf, 1590 m, branches of *P. abies*, on wood, 2.VII.2011, H.O. Baral (ex H.B. 9566a, M-0276432, **holotype**; sq.: KT222426, anam. substr.). – **Tirol**, 7.7 km ESE of Landeck, 2.8 km ENE of Fließ, Pillermoor, 1542 m, branch of *P. abies*, on wood, 12.VI.2011, M. Bemmann (ø, doc. vid.). – **Steiermark**, 18 km NE of Wolfsberg, Freiländeralm, Hebalm, 1433 m, branch of *P. abies*, on wood, 3.V.2017, G. Friebes (GJO 86305, non vid.). – Koralpe, 13.5 km ESE of Wolfsberg, 3.5 km WSW of Glashütten, NE of Grünangerhütte, 1550 m, branch of *P. abies*, on wood, 6.V.2016, G. Friebes (G.F. 20160114, doc. vid.). – ibid., 17.IV.2017 (GJO 85614, non vid.). – **Kärnten**, 37 km NW of Spittal, 4.5 km WNW of Mallnitz, Tauerntal, 1670 m, branches of *P. abies*, on wood, 23.IX.2016, G. Friebes (G.F. 20160173, non vid.). — **FRANCE**: **Rhônes-Alpes**, **Isère**, 20

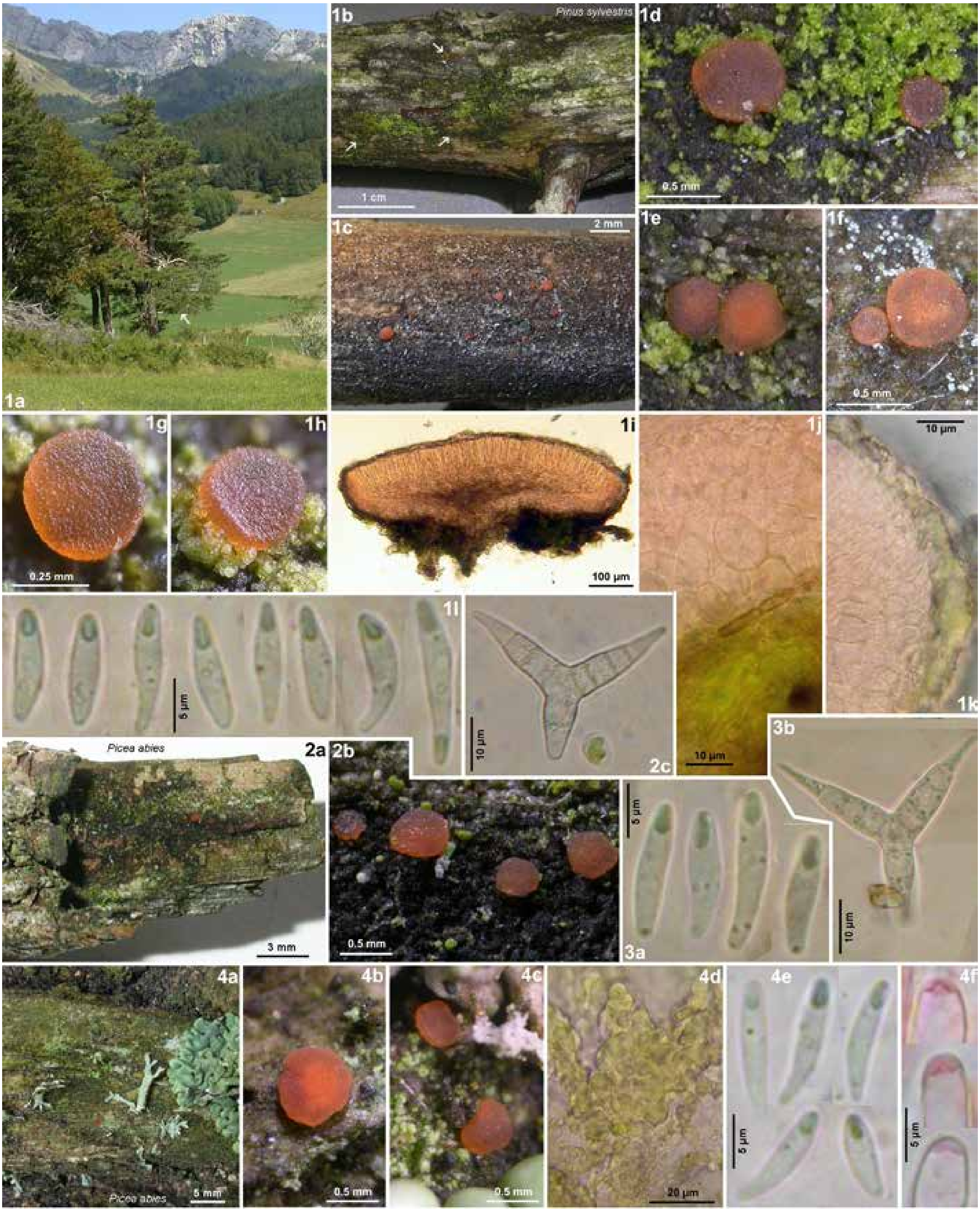


Plate 255. **1–4**: *Orbilia alpigena*. – **1a**. montane conifer forest; **1b**, **2a**, **4a**. (partly) decorticated xeric, rehydrated branches of *Pinus sylvestris* and *Picea abies* (**4a** with *Hypogymnia physodes* and *Pseudevernia prunastri*); **1c–h**, **2a–b**, **4b–c**. rehydrated apothecia; **1i**. apothecium in median section; **1j**. id., basal ectal excipulum; **1k**. id., marginal ectal excipulum; **4d**. marginal exudate (external view); **4f**. ascus apices; **1l**, **3a**, **4e**. ascospores; **2c**, **3b**. conidia from substrate. – Living state, except for **4f** (in $\mathrm{CR}_{\mathrm{SDS}}$), terminal conidial cells in **3b**. — **1a–l**. H.B. 9137b: France, Grenoble, on *Pinus*; **2a–c**. H.B. 8272a: Switzerland, Giswil, on *Picea*; **3a–b**. H.B. 7874a: Germany, Villingen, on *Picea*; **4a–f**. H.B. 9566a (holotype): Austria, Oberallgäu, on *Picea*.

km SW of Grenoble, 2 km SSE of Villard-de-Lans, W of Les Glovettes, 1200 m, branch of *Pinus sylvestris*, on wood, 11.VIII.2009, H.O. Baral (H.B. 9137b). – unlocalized, branch of *Larix* ?*decidua*, undated, G. Marson (ø, anam. substr.). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *Picea abies*, on wood, 17.VII.1994, G. Marson (H.B. 5125d). – **Hautes-Alpes**, 30 km N of Gap, 6.5 km E of Corps, 3.8 km ESE of Fallavaux, 1680 m, branch of *P. abies*, on wood, 14.IX.2015, G. Marson (G.M. 2015-09-14.1; sq.: KY419185).

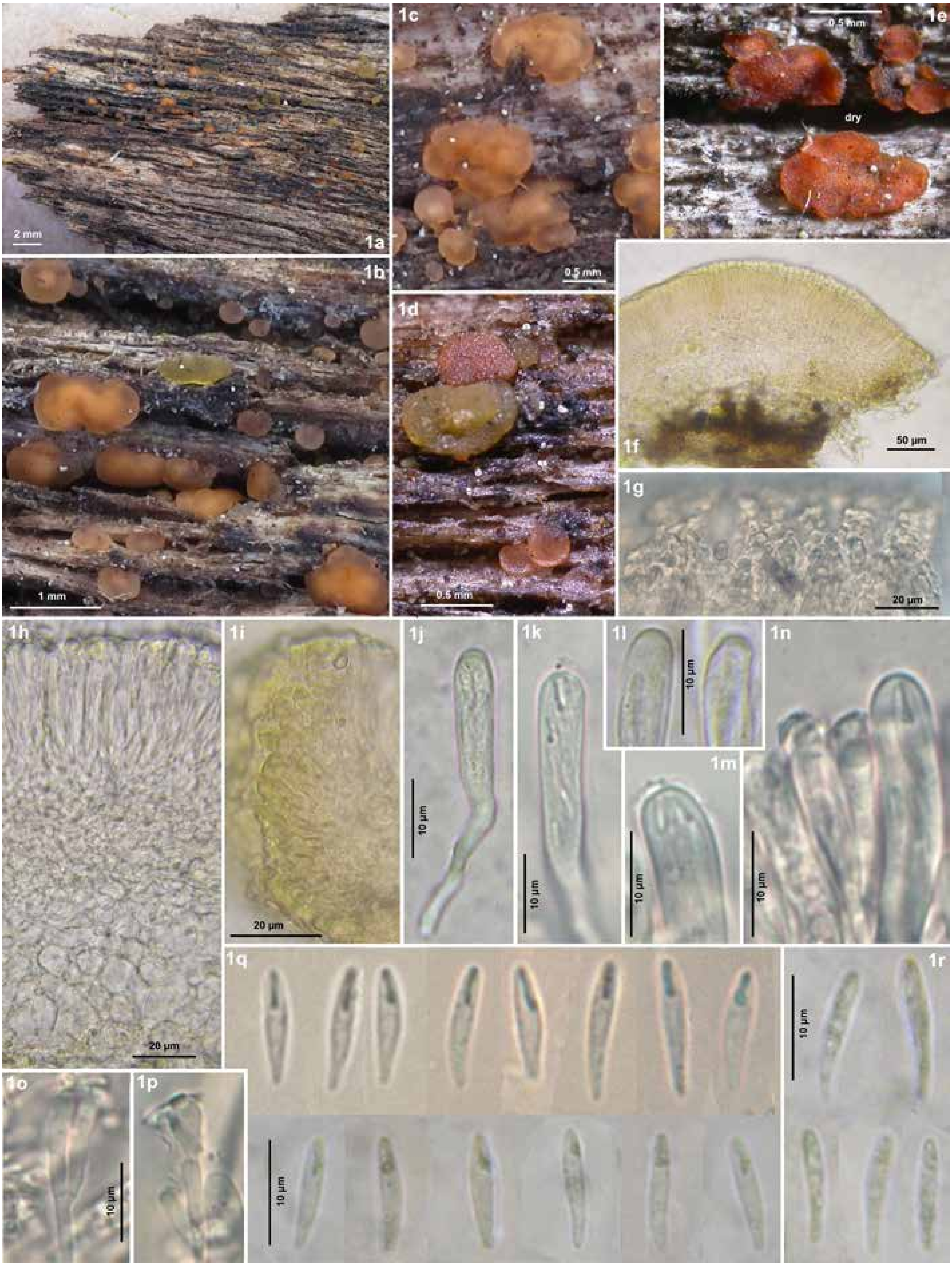


Plate 256. **1**: *Orbilia paramontigena*. – **1a–d**. rehydrated apothecia (**1b** & **d** with *Dacrymyces*); **1e**. dry apothecia; **1f**. apothecium in median section; **1i**. id., marginal ectal excipulum; **1h**. id., central part with hymenium, medullary and ectal excipulum; **1g**. margin in external view; **1j–k**. asci; **1l–n**. ascus apices; **1n–p**. paraphyses; **1q–r**. ascospores. – Living state, except for **1i–j**, **l**, **r**, upper part of **1h** (in H_2O). – **1a–c**, **g**, **k**, **m–p**, **q** (above row): phot. J. Bometón. — **1a–r**. Spain, Cataluña, on *Acer*.

Orbilia paramontigena Baral, Bometón & E. Weber, **sp. nov.**, MB 825631 — Pl. 256

Etymology: referring to the microscopical resemblance to *Orbilia montigena*. **Typification**: Spain, Cataluña, Ripoll, Gombrèn, branch of *Acer* sp., 19.VI.2016, J. Bometón, L. Sánchez, J. Ballarà (ex J.B. 658/16 & ex H.B. 10013, AH 52843, holotype; sq.: MK493132).

Latin diagnosis: *Similis* Orbiliae montigenae *sed ascosporae angustiores, corpuscula refringentia angustiora. Habitat ad lignum valde putridum rami sicci* Aceri *in zona orotemperata humida Europae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.8(–1.2) mm diam., 0.13–0.17 mm high (receptacle 0.11–0.12 mm), light orange-rose to bright orange, medium translucent, round to elongate-elliptical, undulating when large, subgregarious; disc flat, margin thin, 0–8 µm protruding, smooth; broadly sessile, superficial but often deeply immersed in clefts; dry bright orange-red, hardly margin. **Asci** *42–54 × 6–6.5 µm, †35–47 × 5–5.5 µm, 8-spored, spores 2–4-seriate, ~4 lower spores inversely oriented, pars sporifera *22–23 → 19 µm long; **apex** (†) ± hemispherical (subconico-subtruncate), dome †0.7–1 µm thick, no apical chamber seen; **base** with short to long, thin or thick, flexuous stalk, L-, T- or Y-shaped. **Ascospores** *10–13 × 1.8–2.4 µm, †9.5–12(–13) × 1.6–2(–2.2) µm, fusoid to fusoid-clavate, apex obtuse, base often tail-like, straight to sometimes slightly curved towards base; **SBs** *3.5–4.5 × 0.5–0.7 → 2.5–3.5 × 1–1.1 µm, vermiform with basal inflation, apically attached by a wide point. **Paraphyses** apically uninflated or usually slightly (to medium) clavate, terminal cells *7–12 × 2.3–3.5 µm, †2–2.5 µm wide, lower cells *5–11 × 1.7–2.6(–3) µm, *1.5–2 µm wide; unbranched near apex; hymenium hyaline to pale yellow. **Medullary excipulum** very pale orange, 30–40 µm thick, of dense textura intricata with many inflated cells, ± sharply delimited from ectal excipulum (sometimes by a 5–10 µm thick t. porrecta). **Ectal excipulum** hyaline, of (†) thin-walled, indistinctly vertically oriented t. globulosa-angularis from base to midflanks, 60–100 µm thick near base, cells *8–20(–23) × 7–14 µm; 20–40 µm thick at flanks, 15–20 µm near margin, of t. prismatica oriented at a 30–70° angle to the surface, marginal cortical cells *6–9 × 3–4.5 µm, slightly projecting and converging to form radial ribs, **glassy processes** absent or 1–3 × 3 µm. **Anchoring hyphae** sparse, †1.3–2 µm wide, walls 0.2 µm thick. **SCBs** globose, medium refractive, in paraphyses 1.5–2.7 µm diam.; in excipular cells 1.8–3 µm diam. **Exudate** pale yellow, over paraphyses 1–2 µm thick, cloddy, ± loosely attached; over margin and flanks 0.5–3 µm thick, firmly attached. **— ANAMORPH**: unknown.

Habitat: 60 mm thick, fallen, decorticated branch of *Acer* sp., on 0.5–1 mm deep strongly decayed wood, strongly greyed, green algae very sparse. **Associated**: *Dacrymyces* sp. **Desiccation tolerance**: many excipular cells and some immature asci still alive after 1 year. **Altitude**: 1235 m a.s.l. **Geology**: Cretaceous limestone, marl & clay. **Phenology**: VI (possibly throughout the year, long-lived).

Taxonomic remarks. *Orbilia paramontigena* resembles *O. montigena* (series *Hesperideae*), from which it differs in somewhat narrower ascospores containing distinctly narrower SBs. In SB size and shape the species resembles *O. vinosa*, but differs in distinctly shorter and slightly wider spores. In spore width *O. paramontigena* comes close to *O. angiosubvinosa*, which differs in longer spores and SBs and in possessing crystalloid SCBs. *O. paramontigena* is described as a new species mainly because of its deviating molecular data.

Phylogeny. A sequence gained from apothecia comprises the ITS region and the S1506 intron. When analysing the ITS, *O. paramontigena* clustered highly supported in the *vinosa-subvinosa* subclade of the *vinosa-velutina* clade (Phyls 9, 11), with a distance of 9–9.7% to *O. vinosa* and 12.5–13% to *O. subvinosa*, *O. angiosubvinosa*, and *O. nothoaprilis*. In comparison, the distance between *O. paramontigena* and *O. montigena* is 18%. In the intron region (Phyl. S12), *O. paramontigena* clustered highly supported with *O. subulivinosa*, distant from the *vinosa-subvinosa* subclade. Affiliation in the *vinosa-subvinosa* subclade is supported by specific nucleotides at pos. 76 and 388 (see under series *Hesperideae*, p. 553), whereas at pos. 482 the *vinosa-subvinosa* subclade has GCT**A** while *O. paramontigena* matches the remaining taxa of the *vinosa-velutina* clade (GCT**C**, rarely GCG**C**).

Ecology. *O. paramontigena* was collected on a decorticated, xeric branch of *Acer* in a thermophilous angiosperm woodland of *Quercus*, *Fagus*, *Acer*, and *Buxus* on a S-exposed slope in the orotemperate humid eastern Pyrenees.

Specimens included. **SPAIN**: **Cataluña**, **Girona**, 12 km NW of Ripoll, 2.2 km NNW of Gombrèn, Solell de la Molina, 1235 m, branch of *Acer*, on wood, 19.VI.2016, J. Bometón, L. Sánchez, J. Ballarà (ex J.B. 658/16, ex H.B. 10013, AH 52843, **holotype**; sq.: MK493132).

Orbilia vinosa (Alb. & Schwein.) P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 101 (1871) — Pls 257–262, Map 45

≡ *Peziza vinosa* Alb. & Schwein., Conspect. Fung. Lusat.: 308 (1805); Fr., Syst. Mycol. 2(1): 141 (1822), nom. sanct. [non *Peziza vinosa* Pers. (1801), = *O. auricolor*]
≡ *Calloria vinosa* (Alb. & Schwein.) Fr., Summa Veg. Scand.: 359 (1849)
≡ *Mollisia vinosa* (Alb. & Schwein.) Gillet, Champ. Fr. Discomyc.: 125 (1882)
= *Orbilia scotica* Massee, Grevillea 22: 99 (1894)
= *Orbilia granulosa* Velen., Monogr. Discom. Bohem.: 98 (1934)
= *Orbilia pulcherrima* Velen., Monogr. Discom. Bohem.: 97, pl. 11 fig. 30 (1934)
= *Orbilia tricuspis* Velen., Monogr. Discom. Bohem.: 97, pl. 11 fig. 29 (1934)
?= *Orbilia prunorum* Velen., Monogr. Discom. Bohem.: 97 (1934)

Etymology: *vinosa*: referring to the wine-red colour of the apothecia; *scotica*: from Scotland; *granulosa*: apothecia resembling small granules; *pulcherrima*: means 'most beautiful' (after the spectacular fire-red colour); *tricuspis*: according to the associated trinacrium-like anamorph; *prunorum*: growing on *Prunus domestica*.

Typification: Germany, Oberlausitz, branch of *Quercus* etc., undated, ?J.B. Albertini (type of ***Peziza vinosa***, unlocated); Germany, Stuttgart, Wolfbusch, branch of *Fagus sylvatica*, 25.VI.2000, H.O. Baral (H.B. 6715b, RefSpec, designated here, CBS 116215, sq.: KT215266). – Great Britain, Scotland, Aboyne, branch of ?*Acer*, IX.1870, collector unknown (K(M) 36051, holotype of ***Orbilia scotica***). — Czechia, Mnichovice, between Kunice and Stráncice, branch of *Ligustrum vulgare*, VIII.1925, J. Velenovský (PRM 147400, holotype of ***O. tricuspis***). – Czechia, Mirošovice, branch of *Carpinus betulus*, X.1928, J. Velenovský (PRM 152457, lectotype of ***O. granulosa***, designated by Svrček 1954: 15). – Czechia, Hrusice, branch of *Quercus*, 27.II.1928, J. Velenovský (PRM 147776, lectotype of ***O. pulcherrima***, designated by Svrček 1954: 19). – Czechia, Mnichovice, trunk of *Prunus domestica*, 1.VII.1926, J. Velenovský (lectotype of ***O. prunorum***, illustration in Velenovský's manuscript in PRM, designated here, MBT382113).

Misapplied names: Crouan & Crouan (in sched.), as *Peziza luteorubella*; Feltgen (1899: 55), as *O. chrysocoma*.

Misinterpretation of *O. vinosa*: Bachman (1908: 57), ?= *Orbilia* sp.; Baral (in Baral & Krieglsteiner 1985: 28), = *O. aurantiorubra*; Costantin (1888), ?= *O. rosea*; Feltgen (1899: 55), = *O. luteorubella*; Fuckel (1874: 57), = *O. sarraziniana*; Jaap (1922: 15), ?= *O. luteorubella*; Persoon (1822: 303, as *Peziza*), = *O. auricolor*; Phillips (1887: 333, pl. 10 fig. 63, as *Calloria*), ?= *O. auricolor* agg.; Schweinitz (1832: 177, as *Peziza*), = *O. tenuispora* & *O. aurantiorubra*; Seaver (1911: 108), = *O. tenuispora*; Svrček (1954: 10), = *O. aprilis* (holotype); Benedict's strain (CBS 917.72), = *O.* aff. *sinensis*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.12–)0.2–0.9(–1.2) mm diam., (0.1–)0.12–0.21(–0.25) mm high (receptacle 0.09–0.12 mm), (very) pale to bright (salmon-)rose(-pink) but often also (yellowish-)orange(-red), rarely cream-ochraceous or greyish-cream, slightly to strongly translucent, round, rarely elliptical, somewhat undulating when large, very scattered to gregarious; disc slightly concave to flat, also slightly convex, margin ± distinct, 0–10 µm protruding, smooth, sometimes finely crenulate, in older apothecia sometimes immarginate; sessile or with an ill-defined, rarely abrupt broad stipe ~0.035–0.1 × 0.1–0.25 mm, superficial to slightly immersed; dry light to deep pure rose, (ochraceous-)rose-orange or orange-red.

Asci *(37–)40–65(–72) × (4.8–)5–6.5(–7)((–7.7)) {38} µm, †((30–))(33–)40–60(–65)((–70)) × (4–)4.5–5.5(–6)((–7)) {33} µm, 8-spored (very rarely 4–7-spored), spores (2–)4(–6)-seriate, ((0–))(1–)2–4((–5)) lower spores inversely oriented {30} (not or rarely slightly mixed), pars sporifera *25–28(–34) → 16–22 µm long (†25–31 µm); **apex** (†) hemispherical to slightly truncate, dome †(0.8–)1–1.5(–2) → 0.3–1 µm thick {17}, often with slight to distinct apical chamber; **base** with medium to long, thin or medium thick, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *((9.5–))(10–)11.5–18(–19)((–23)) × ((1.5–))(1.6–)1.7–2.1(–2.2)((–2.4)) µm {178}, †(9–)11–17(–18) × (1.3–)1.5–1.9(–2) µm {28}, narrowly cylindric-clavate to often fusoid-clavate, apex obtuse, sometimes rounded or subacute, base slightly to mostly medium to strongly attenuated, often ± tail-like, rarely with distinct tail *4–5 × 0.5–1 µm, straight to slightly (exceptionally medium) curved, especially near base; **SBs** *((2.5–))(3–)3.5–5.5(–6)((–7)) × (0.4–)0.5–0.8(–1)((–1.2)) {133} µm, rod-shaped (vermiform) to subulate, straight (rarely somewhat flexuous), overmature tear-shaped to ampulliform, *1.8–4 × (0.8–)1–1.3(–1.5) µm, apically narrowed to a ± wide, rarely small point. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cells *(4–)8–19 × (1.8–)2.2–3.5(–3.8) µm {9}, †11–20(–22) × (1.5–)1.8–3(–3.5) µm {4}, lower cells *((2.5–))5–12(–14) × (1.4–)1.7–2.5(–3)((–4.5)) µm {6}, †6–8.5 × 1.4–1.8 µm {1}; rarely branched at upper septum, hymenium pale to light rose. **Medullary excipulum** pale rose (or often lower part hyaline), 25–70 thick, of loose to dense textura intricata-globulosa with many inflated cells, indistinctly to sharply delimited from ectal excipulum (sometimes by a thin t. porrecta). **Ectal excipulum** hyaline to pale rose, of thin-walled or slightly gelatinized, vertically oriented t. (globulosa-) angularis-prismatica from base to mid flanks, 20–40 up to 60–100 µm thick near base, cells *(7–)10–20(–30) × (5–)8–13(–16) µm {9}; 15–30(–50) µm thick at flanks; 15–25(–30) µm near margin, of t. prismatica-porrecta oriented at a (10–)30–60(–80)° angle to the surface (cortical layer often under a lower angle than inner layer), marginal cortical cells *(5–)7–12 × (2.3–)3–4 µm {8}, †(5–)6–10 × 2.5–3.5(–4) µm {3}, **glassy processes** 0–2 µm {86}, 2–6 {21} or 5–10(–18) {16} × (2–)2.5–4(–4.5) µm, low- to high-refractive, stratified, cortical cells (including glassy processes) often converging to form minute teeth at mid flanks and margin. **Anchoring hyphae** medium to very abundant, *1.8–3 µm wide, walls 0.2–0.3(–0.5)((–1)) µm thick {9}, forming a ± dense, 5–20 µm thick t. intricata-porrecta (sometimes also at flanks), sometimes as strands. **SCBs** in paraphyses and excipular cells globose to ellipsoid, 1–3.5 µm diam., usually associated in lower parts with crystalloid SCBs {61} (1–)2–5(–6) × (0.3–)1–2.5(–3) µm, low- to high-refractive, hyaline, rarely devoid of any SCBs {6}; **LBs** in paraphyses and marginal ectal excipulum sparse, minute, hyaline. **Exudate** hyaline to light yellow-chlorinaceous, over paraphyses (0.5–)1–2(–5) µm thick, continuous though broken into rough clods, loosely attached; over margin and flanks 2–5(–8) µm thick, roughly warted, covering marginal teeth by forming radial ribs 60–70 µm long and 15–20 µm wide in surface view. — **ANAMORPH**: trinacrium-like (from ascospore isolate {7} and natural substrate {32}). **Conidiophores** *~11–23 × 2.3–3 µm, unbranched. **Conidia** Y-shaped (exceptionally tuning fork shaped), total size *(14–)23–45(–48) × (19–)25–39(–54), stipe *(9–)13–28 × 3.3–5.2 µm, 2–4(–5)-septate, arms cylindrical, not or only slightly tapering towards the rounded to obtuse end, *12–25(–30) × (3–)3.5–4.5(–5.5) µm, (1–)2–5(–6)-septate {13}, also some unbranched conidia present in pure culture: straight, *(30–)32–53(–59) × (3.6–)4–5.6 µm, 4–8(–9)-septate {4}.

Habitat: collected (0.1–)0.5–3(–16) m above the ground, corticated or decorticated, (2.5–)5–50(–65) mm thick branches, rarely up to 20 cm thick trunks, also on timber, rarely on cones, of *Abies balsamea* {1}, *Acacia heterophylla* {1}, *Acer* sp. {3/1}, *A. campestre* {2}, *A. pseudoplatanus* {3}, *Alnus* sp. {1}, *A. alnobetula* {2}, *A. glutinosa* {2}, *Amelanchier ?lamarckii* {1}, *Arbutus unedo* {2}, *Betula* sp. {3}, *B. pendula* {2}, *B. pubescens* {1}, *Buxus sempervirens* {2}, *Calicotome villosa* {1}, *Carpinus betulus* {8}, *Castanea sativa* {4}, *Ceratonia siliqua* {1}, *Chamaecytisus proliferus* {1}, *Cistus crispus* {1}, *C. ladanifer* {3/1}, *C. laurifolius* {4}, *C. monspeliensis* {3}, *C. symphytifolius* {1}, *Cornus* sp. {1}, *C. alba* {1}, *Corylus avellana* {15}, *Cotinus coggygria* {1}, *Crataegus monogyna* {2}, *Cytisus scoparius* {5}, *Erica* sp. {1}, *E. arborea* {1}, *Euphorbia atropurpurea* {1}, indet. *Fabaceae* {1}, *Fagus sylvatica* {22/2}, *F. sylvatica* subsp. *moesiaca* {1}, *Ficus carica* {1}, *Frangula alnus* {3/1}, *Fraxinus excelsior* {2}, *Gleditsia triacanthos* {1}, *Ilex aquifolium* {3}, *Juniperus communis* {1/1}, *J. oxycedrus* {1}, *Larix ?decidua* {1}, *Lavandula canariensis* {1}, *Ligustrum vulgare* {2}, *Lonicera* sp. {1}, *L. periclymenum* {1}, *L. xylosteum* {2/1}, *Malus domestica* {6}, *Olea europaea* {4}, *Periploca laevigata* {2}, *Petteria ramentacea* {1}, *Phillyrea media* {1}, *Picea abies* {10/1}, *P. ?glauca* {1}, *Pinus* sp. {6}, *P. brutia* {1}, *P. canariensis* {1}, *P. ?contorta* {1}, *P. halepensis* {3}, *P. ponderosa* {2}, *P. sylvestris* {7}, *P. uncinata* {1}, *Pistacia lentiscus* {1}, *P.* (?) *terebinthus* {1}, *Platanus orientalis* {1}, *Populus nigra* {1}, *P. tremula* {6}, *Prunus ?domestica* {2}, *P. padus* {1}, *P. spinosa* {6}, *Purshia tridentata* {1}, *Pyrus communis* {2}, *Quercus* sp. {33}, *Q. ilex* {7}, *Q. petraea* {4}, *Q. ?pubescens* {1}, *Q. pyrenaica* {1}, *Q. robur* {22}, *Q. rotundifolia* {5}, *Q. rubra* {1}, *Q. suber* {1}, *Rhamnus alaternus* {1}, *R. alpina* {1}, *R. crenulata* {1}, *Rhododendron ferrugineum* {2}, *Robinia pseudoacacia* {1}, *Rosa* sp. {11}, *R. canina* {3/1}, (?) *Rosmarinus officinalis* {1}, *Rubus fruticosus* {2/1}, *Salix* sp. {15/3}, *S. ?alba* {1}, *S.* (?)*atrocinerea* {1}, *S. caprea* {13/1}, *S. cinerea* {5}, *Sambucus racemosa* {3}, *Sonchus pinnatus* {1}, (?)*Sorbus* sp. {1}, *S. chamaemespilus* {1}, *S. torminalis* {1}, *Spartium junceum* {6}, *Syringa vulgaris* {1}, *Tamarix anglica* {1}, *T. gallica* {1}, *Tsuga ?canadensis* {1}, *Ulex europaeus* {4}, *U. parviflorus* {1}, *Ulmus* sp. {1}, *U. glabra* {1}, on 0.1–2(–4) mm deep or sometimes much deeper medium to strongly (rarely only slightly) decayed, often eroded wood {326}, more rarely bark {49} (partially detaching, on periderm {6} and bast {22}), sapwood sometimes strongly eroded or removed, often on very old, hardly recognizable *Vuilleminia* {15} (sometimes below detaching periderm), often in old wounds or empty beetle galleries, sometimes strictly on boring dust in beetle galleries, or very close to or on senescent perithecia, rarely on old *Colpoma quercinum*, substrate hardly to strongly greyed, slightly to often strongly covered by green algae. **Associated**: *Allophylaria macrospora* {1}, *Amandinea punctata* {1}, *Amphosoma atroolivaceum* {1}, *Arachnopeziza ?aurata* {1}, *Arthonia crozalsiana* {1}, *Brachysporium nigrum* {1}, *Brunnipila calyculiformis* {1}, ?*Calloria* spp. {4}, *Calycina citrina* {1}, *Candelariella lutella* {1}, *Capitotricha bicolor* {2}, *Capronia* sp. {2}, *C. ?pilosella* {1}, *C. pleiospora* {1}, *Cercophora spinosa* {1}, *Chaetosphaeria myriocarpa* {1}, '*Chlorosplenium*' *viridulum* {2}, *Ciliolarina pinicola* {2}, ?*Ciliolarina* sp. {2}, *Claussenomyces* spp. {5}, *C. olivaceus* {1}, *Cryptocoryneum condensatum* {1}, *Cryptodiscus* sp. {1}, *C. foveolaris* {21}, *C. pallidus* {1}, *C. pini* {1}, *Dacrymyces* sp. {12}, *Deltopyxis triangulispora* {1}, *Diaporthe* sp. {1}, *Diatrype undulata* {1}, *Diplolaeviopsis resinae-pini* {1}, *Durella* spp. {1/1}, *D. atrocyanea* {9/4}, *D. commutata* {2}, *D. connivens* {42/1}, *D. macrospora* {3}, *D. melanochlora* {1}, *D. suecica* {1}, *Encoelia furfuracea* {1}, *Evernia prunastri* {1}, *Exarmidium inclusum* {2}, *Exidia ?plana* {1}, *Frullania dilatata* {1}, *Helicogonium orbiliarum* (parasitic in *O. vinosa*) {7/2}, '*Helotium*' *uvidulum* {10/1}, *Hyalopeziza nectrioidea* {1}, *Hyalorbilia berberidis* {1}, *H. fusispora* {1}, *H. helicospora* {1}, *H. hergiswiliana* {1}, *H. juliae* {2}, *H. latispora* {1}, *H. orbiliicola* (parasitic on *O. vinosa*) {2}, *H. subfusispora* {11}, *Hyaloscypha minuta/intacta* {11}, *H. quercicola* {1}, *Hyphodiscus* spp. {1/2}, *H. theiodeus* {2}, *Hyphodontia* sp. {1}, *Hypoderma rubi* {1}, *Hypogymnia physodes* {3}, *Hypoxylon fuscum* {1}, *H. udum* {1}, *Hysterium acuminatum* {1}, *H. angustatum* {1}, *Hysterobrevium mori* {1}, *H. smilacis* {2}, ?*Hysteropatella* sp. {1}, *H. elliptica* {1}, *Ionomidotis fulvotingens* {2}, *Karstenia rhopaloides* {3}, *Lachnellula abietis* {1}, *L. pseudofarinacea* {1}, ?*Lasiosphaeria* sp. {1}, *Lecanora conizaeoides* {1}, *Lecidella elaeochroma* {1}, *Lecophagus ellipsoideus* {1}, *Lophiostoma* sp. {1}, *L. compressum* {2}, *Melanelia glabratula* {2}, *Mellitiosporiella* sp. {1}, *M. pulchella* {4}, *Merismodes* sp. {1}, *Minimelanolocus hughesii* {1}, *Mollisia* sp. {1}, *M. discolor* {2}, *M. ligni* {11}, *M. obscura* {1}, *M. rosae* {1},

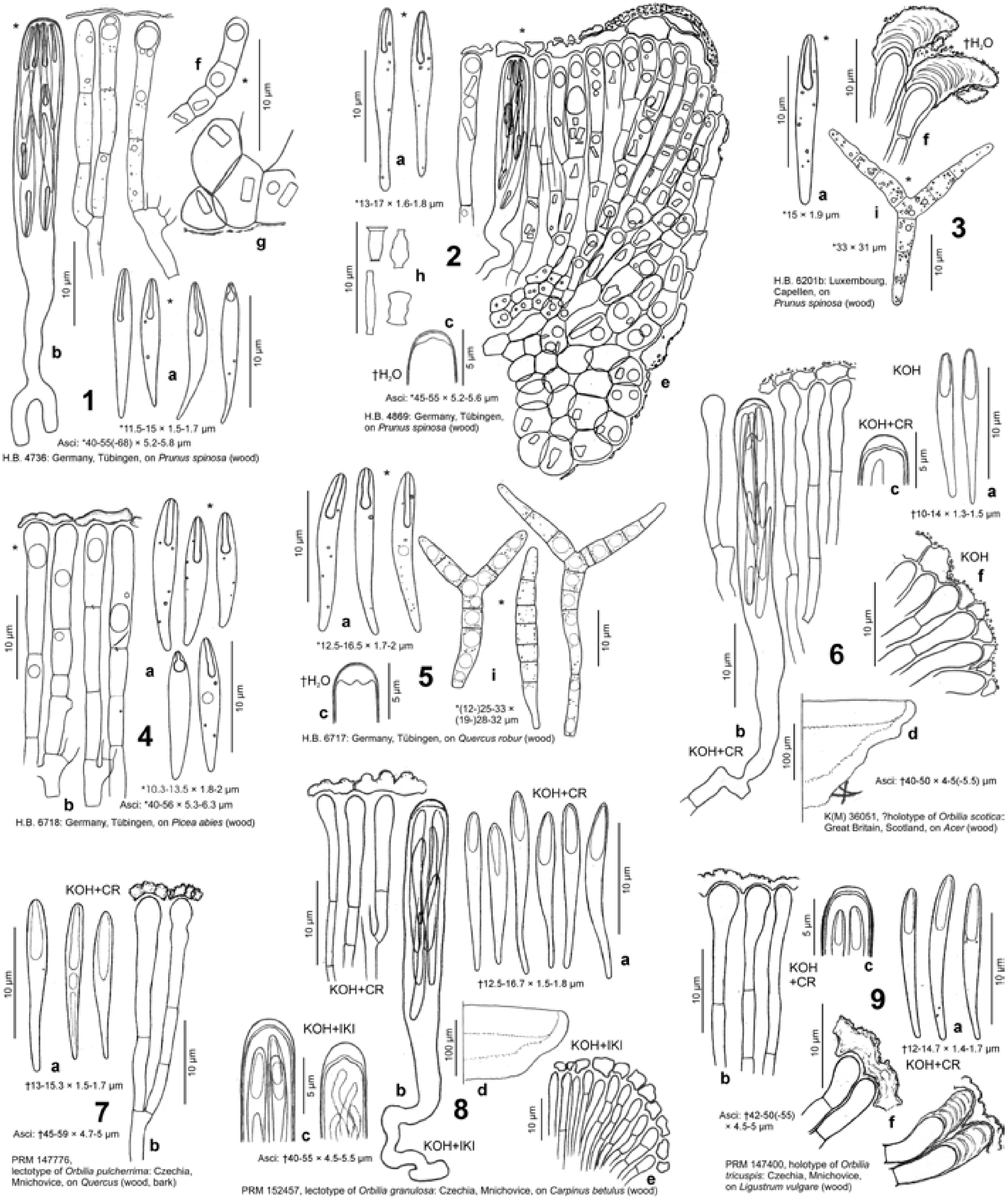


Plate 257. **1–9**: *Orbilia vinosa*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., ectal excipulum (margin and mid flanks); **f**. id., marginal cortical cells, with or without glassy processes; **g–h**. crystalloid SCBs in basal ectal excipular cells (**1g**) and at mid flanks (**2h**); **i**. conidia from substrate (**3**) and culture (**5**).

Mollisina rubi {1}, ?*Monodictys* sp. {1}, *Neodasyscypha cerina* {8}, *Odontotrema* sp. {2}, *Orbilia alpigena* {1}, *O. angiosubvinosa* {1}, *O. aprilis* {22}, *O. arachnovinosa* {2}, *O.* ?*aradi* {1}, *O. aristata* {5/1}, *O. breviaristata* {1}, *O.* ?*cejpii* {1}, *O. clavuliformis* {1}, *O. corculispora* {4}, *O. cylindrospora* {5}, *O. eucalypti* {22}, *O. euonymi* {9}, *O. filiformis* {3}, *O. flagellispora* {2}, *O. frangulae* {1}, *O. gambelii* {3}, *O. hesperidea* {3}, *O. montigena* {1}, *O. myriosphaera* {1}, *O. obtusispora* {4}, *O. olivacea* {1}, *O. ovoidea* {1}, *O. patellarioides* {2}, *O. pleiogambelii* {2}, *O. pleiomicrosoma* {3}, *O. pleistoeuonymi* {1}, *O. polyspora* {4}, *O. subaristata* {6}, *O. subclavuliformis* {2}, *O. subovoidea* {5}, *O. subsphaerospora* {2}, *O. subtrapeziformis* {1}, *O. subvinosa* {2}, *O. trapeziformis* {2}, *O. tremulae* {2/4}, *O. vibrioides*

{2}, *O. xanthoguttulata* {1}, *O. xanthostigma* {2}, *Ostropales* {1}, *Parmelia* sp. {8}, *P. sulcata* {12}, ?*Patinellaria* sp. {1}, *P. sanguinea* {1/1}, *Peniophora* sp. {2}, *Perrotia flammea* {5}, ?*Phoma* sp. {1}, *Phragmiticola* sp. {4}, *Physcia. leptalea* {1}, *P. tenella* {2}, *Pithyella frullaniae* {1}, *Polydesmia pruinosa* {1}, *Proliferodiscus pulveraceus* {4}, *Propolis farinosa* {14/3}, *P. viridis* {8}, *Protounguicularia transiens* {1}, *Pseudevernia furfuracea* {1}, *Pseudohelotium sordidulum* {1}, *Pyrenopeziza caespiticia* {1}, *Radulomyces molaris* {1}, *Resinomyces griseus* {1}, *R. kirschsteinianus* {2}, *Resupinatus applicatus* {3}, *Rhamphoria pyriformis* {1}, *Rhizodiscina lignyota* {4}, *Rhodoveronaea varioseptata* {1}, *Sarea difformis* {2}, *S. resinae* {3}, *Schizopora paradoxa* {1}, *Sclerococcum* spp. {3}, *S.* ?*epimyces* {1}, ?*Skyttea* spp. {4}, ?*Stictis* sp. {1}, *Symbiotaphrina desertorum* {1}, ?*Triblidium* sp. {1}, *Trichonectria* sp. {1}, *T. hirta* {1}, *Trichosphaerella decipiens* {1}, '*Tympanis*' *xylophila* {2/1}, *Unguiculariopsis* spp. {2}. **Desiccation tolerance**: fully viable for at least 5 months (central Europe), 13 months (Arizona), many excipular cells still alive after 12 months (central Europe), some excipular cells, ascospores and conidia after 30–32 months (mediterranean Europe). **Altitude**: 1–2405 m a.s.l. (Europe), 43–1586 m (Macaronesia), 2–2250 m (USA). **Geologie**: Cambrian & Ordovician and Silurian-Devonian-Carboniferous silt, quartz & greywacke, schist & sandstone, Permian Rotliegend, Buntsandstein, Keuper (marl & sandstone), Lower to Upper Jurassic and Cretaceous shale, lime-, clay- & marlstone, flysch, dolomite, Tertiary molasse, Quaternary sand, loess; granite, gneiss, mica schist, serpentinite, diorite, biotite-amphibolite, rhyolite, tephrite, gabbro, basalt, dolerite (diabase). **Phenology**: throughout the year (long-lived).

Phenology of *O. vinosa* (N-hemisphere)											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
17	20	26	29	31	54	30	41	37	33	17	29

Taxonomic remarks. The characteristics of *O. vinosa* are mainly those of the ascospores which are rather long and narrow, fusoid-clavate, nearly straight, mainly strongly tapered below but only slightly so above, with ± obtuse apex. At the mature stage the spores contain ± straight, rod-shaped SBs 3–6 × 0.4–1 µm. *O. aprilis* is very similar to *O. vinosa* in morphology as well as ecology, but is less frequent in montane regions and sharply differs in shorter spores (up to 9.5, rarely 10.5 µm) and SBs (1.5–2.2, rarely 2.5 µm). The mediterranean *O. hesperidea* and montane *O. montigena* and *O. alpigena* differ in distinctly wider, often also shorter spores, *O. hesperidea* also in the presence of larger, pale orange crystalloid SCBs.

Four Australian taxa match *O. vinosa* quite well in spore morphology, but differ in at least one feature: the ascus apical dome of *O. nothovinosa* is always distinctly thicker, *O. astrovinosa* has very long glassy processes that form prominent teeth, *O. helicovinosa* deviates in medium helicoid spores, and *O. pleiovinosa* in 16-spored asci.

The orosubmediterranean *O. subvinosa* (on conifer wood, mainly *Pinus*) and the montane *O. arachnovinosa* (on angiosperm wood) deviate only tentatively from *O. vinosa* in the teleomorph, showing a tendency to more intensely pigmented, mostly orange(-red) apothecia with a usually distinctly crenulate margin, also a tendency to slightly larger spores. Their main characteristic lies in the dwayaangam-like conidia, which consistently branch twice dichotomously to form 4-armed structures with two of the branches pointing downwards. *O. subulivinosa* from mesomediterranean to orotemperate southern Europe differs in longer ascospores, but the morphological limits to *O. vinosa* are not sharp.

Species of section *Helicoon* (with a hygric to semiaquatic habitat), but also those of section *Habrostictis* (with a xeric habitat), such as *O. subtrapeziformis*, *O. obtusispora*, or *O. filiformis*, may be confounded with *O. vinosa* on account of a similar spore shape and an often rose-orange colour. These species are readily distinguished by their truncate and thin-walled ascus apices and by longer and in O. *filiformis* also thinner, often more flexuous SBs.

Variation. Within the present concept of *O. vinosa*, rather great variability is observed in several features. Comparatively small apothecia of (hydrated) 0.12–0.4 mm diam. were sometimes encountered (see, e. g., Pl. 260: 4), but populations with 0.5–1.2 mm diam. also occurred, while most collections were in the range of 0.3–0.8 mm. Apothecial colour varied between pale and bright salmon-rose, but often the apothecia showed a rose-orange, yellowish-orange, or even orange-red colour (see Pls 260, 262).

The margin was generally smooth or only slightly rough, though sometimes finely crenulate, due to exudate and occasionally short glassy processes. The length of these processes turned out to be rather variable within the present concept of *O. vinosa*. In about 30 % of > 100 specimens tested for this character, glassy processes longer than 1–2 µm were noted, and these occurred on both gymno- and angiosperm substrate. The longest processes were recorded in montane specimens on *Acer* from Poland (up to 14 µm), on *Pinus* from Arizona (up to 13 µm. Pl. 259: 3), and three on *Cistus* from Spain (7–10 µm, Pl. 262: 2a). Several further samples showed a length of up to 7–9 µm, e. g., a colline sample on *Prunus* from Luxembourg (Pl. 257: 3). We have somewhat arbitrarily excluded records with processes longer than 15 µm from the description of *O. vinosa*, but mention them either here or under *O. subvinosa*.

Glassy processes may also vary within a given record. They were often only present in a part of a population or even an apothecium, e. g., in the type of *O. tricuspis* (Pl. 257: 9), or they varied in length, e. g., between 0–2 and 4–9 µm between populations on different branches (see collection on *Fagus* from Vosges, IVV: H.B. 5569). The occasional mixed occurrence of *O. vinosa* with *O. subvinosa* or *O. arachnovinosa*, which both predominantly possess glassy processes, complicates a correct identification. Besides all this, the processes are easily overlooked if shorter than about 5 µm, because they are often tightly covered by thick refractive exudate.

Considerable variation in ascus and spore dimensions was noted. Asci varied between *37–47 and 60–72 µm in length (mainly 45–60 µm) and between *4.8–5.2 and 6.5–7(–7.7) µm in width (mainly 5–6.5 µm). Ascospores ranged in length between *10–14 and 16–19 µm (mainly 12–17 µm), and in width between *1.6–1.8 and 2–2.2 µm (mainly 1.8–2 µm). Thereby, ascus length was not clearly correlated with spore length, for instance, the specimen with the longest living asci observed (*60–72 × 5–6.3 µm, H.B. 5004) showed a spore size of only *11–16.5 × 1.7–1.8(–2.2) µm. Ascus and spore size did not correlate with the geographical origin or the host. All ranges of spore length were noted, e. g., in the mediterranean region. A spore length of up to 18–19 µm was observed especially at montane and boreal (e. g., on *Acer*, IVV: H.B. 8235a) but also at orosubmediterranean sites (on *Quercus rotundifolia* and *Cistus*, Pl. 262). The longest spores in these samples closely resemble those of *O. subulivinosa* (Pl. 279), and it remains unclear where these samples actually belong. In some other collections spore length was at the lower range, e. g., on *Picea* (Pl. 257: 4). Spore bodies in mature spores varied between (2.5–)3–4 and 5–6(–

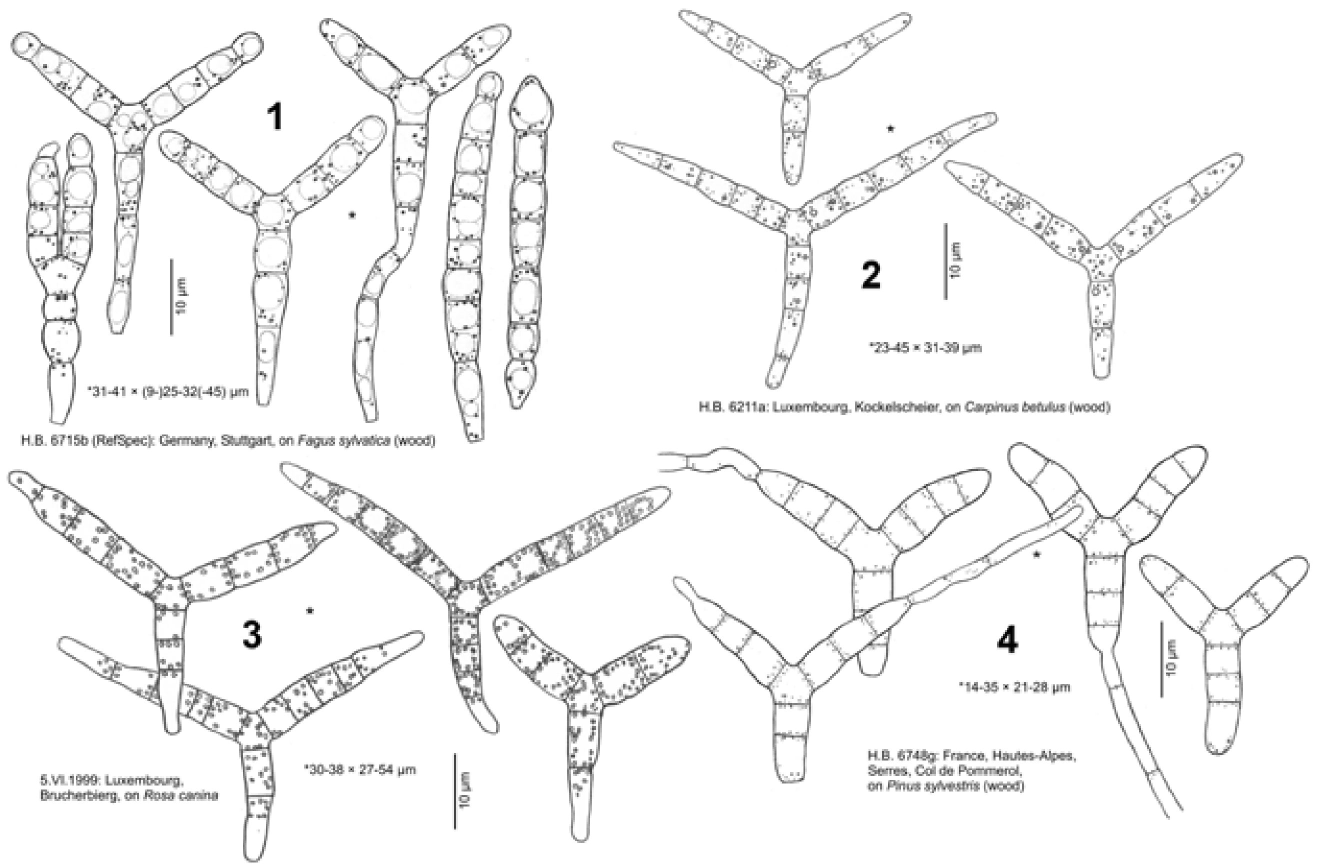


Plate 258. **1–3**: *Orbilia vinosa*; **4**: *O.* cf. *vinosa*. – Conidia from substrate (**2**, **3**) and culture (**1**, **4**).

7) µm in length (mostly 4–5.5 µm) and between 0.4–0.6 and 0.8–1(–1.2) µm in width (mostly 0.5–0.8 µm), without obvious correlation with spore size.

Crystalloid SCBs were seen in most of the collections of *O. vinosa* studied in the living state. They are comparatively small and never clearly pigmented. Frequently they occur in association with globose SCBs, but often only crystalloid SCBs were seen, and in a few specimens only globose SCBs were observed, or no SCBs at all. In a few samples the presence of these organelles varied from one apothecium to another.

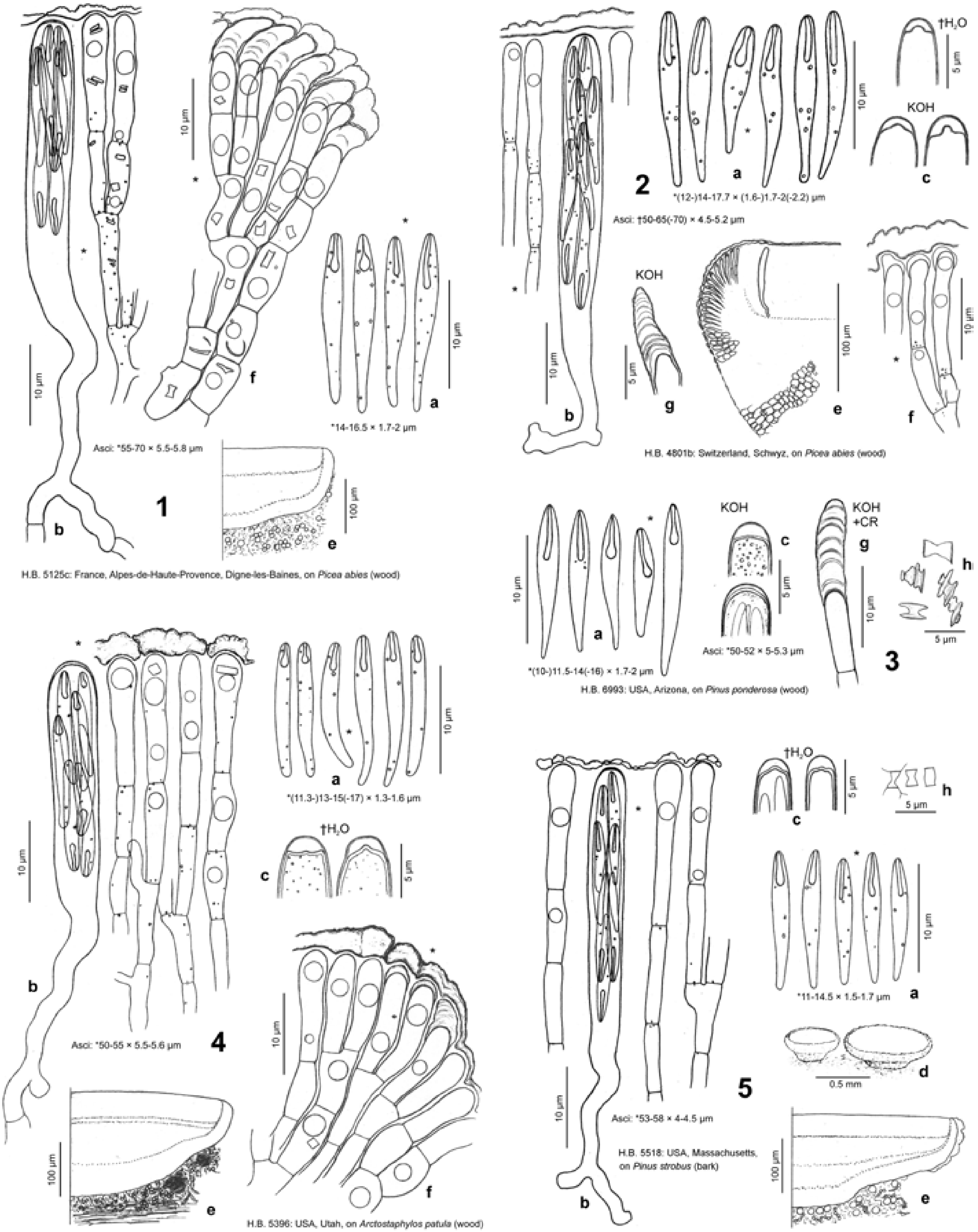
Svrček (1954: 20) mentioned conspicuous variation in the thickness of the exudate (as 'epithecium') in *O. vinosa* in correlation to the habitat. Apothecia growing on branches in the tree canopy developed a thicker 'epithecium' than those on less arid substrates. This observation was also noted by Velenovský (1934: 97) who distinguished between *O. vinosa* (on wood lying on moist ground) and *O. pulcherrima* (on sun-exposed wood of attached branches). However, such correlation could not be confirmed in the present study: in the few samples of *O. vinosa* in which the branches were lying on or sticking in moist ground (e. g., H.B. 5569, IVV), the exudate had the very same thickness as in collections on xeric branches. Svrček (l.c.) also observed great variability in exudate thickness within the lectotype of *O. pulcherrima*. Two apothecia of this material (1 on bark, 1 on wood) were examined in the present study and found to have consistently thick exudate (Pl. 257: 7b). The fact that the exudate in section *Hemiorbilia* easily detaches during preparation might be one reason for the reported variation.

Spore numbers fewer than 8 were noted in a few collections from Southern French Prealps. In two specimens (H.B. 4992a, 5142b) the spore number varied between 4, 5, 6, 7 and 8, and in one (H.B. 4987b, unillustrated, tentatively assigend to *O. subvinosa*) the asci were consistently 4- or 5-spored. The phenomenon is obviously a result of incomplete development. Size of spores and SBs in asci with reduced spore numbers was slightly larger compared to 8-spored asci in the same apothecium.

Nomenclature, **type studies and literature reports**. The epithet ***vinosa*** is adopted here in the sense of Rehm (1891: 457, p.p.) for a desiccation-tolerant lignicolous species of section *Hemiorbilia*. It traces back to Persoon (1801) who described under the name *Peziza vinosa* a caulicolous fungus. Without reference to Persoon, Albertini & Schweinitz (1805) used *P. vinosa* for a lignicolous fungus. Fries (1822: 141) adopted the name *P. vinosa* by referring to Albertini & Schweinitz, again without a clear reference to *P. vinosa* Pers. Due to this lack of citation, the true origin of the epithet *vinosa* fell into oblivion.

That Albertini & Schweinitz did not describe a new species is obvious: (1) the authors marked all of their new taxa by the addition 'NOBIS', but there is no such note for *P. vinosa*, and (2) they did not list the taxon in their 'Catalogus fungorum novorum' (Albertini & Schweinitz l.c.: XV-XVI). Fries's (1822) reference to Albertini & Schweinitz attributes the diagnosis of these authors the status of a new species. According to Art. F.3.2 (Turland et al. 2018), *P. vinosa* Alb. & Schwein. is a sanctioned species, and *P. vinosa* Pers. a homonym without priority. Therefore, later authors like Spooner (1987) correctly considered the description of Albertini & Schweinitz as the protologue of *Peziza vinosa*.

Fries (1822: 141) believed that Persoon's caulicolous fungus, which he had not personally seen, 'appears to be different' from the lignicolous fungus. Apparently because Fries knew only lignicolous collections with a resemblance to the descriptions of *P. vinosa*, he referred *P. vinosa* to Albertini



H.B. 5125c: France, Alpes-de-Haute-Provence, Digne-les-Baines, on *Picea abies* (wood)

H.B. 4801b: Switzerland, Schwyz, on *Picea abies* (wood)

H.B. 6993: USA, Arizona, on *Pinus ponderosa* (wood)

H.B. 5396: USA, Utah, on *Arctostaphylos patula* (wood)

H.B. 5518: USA, Massachusetts, on *Pinus strobus* (bark)

Plate 259. **1–3**: *Orbilia vinosa*; **4–5**: *O.* cf. *vinosa*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., marginal ectal excipulum; **g**. marginal cortical cells with glassy processes; **h**. crystalloid SCBs in ectal excipular cells (base and flanks).

& Schweinitz by reducing Persoon's taxon to a variety of their taxon. Therefore, he changed Persoon's epithet *vinosa* to *vinosella*, although Persoon was the first to publish the epithet *vinosa*. Two authentic specimens of *P. vinosa* in the Persoon Herbarium were found in the present study to belong to *O. auricolor* (see under that species, p. 1528). Because no holotype material could be located, *P. vinosa* Pers. is treated here as a possible synonym of *O. auricolor*.

Albertini & Schweinitz (1805) referred to *P. vinosa* two lignicolous, externally different, but in colour (rehydrated flesh-coloured) and consistency (gelatinous) similar forms. Both grew on wood of projecting branches of *Quercus* and other trees in spring, rarely autumn, in the vicinity of Niesky near Görlitz (Oberlausitz, eastern Germany). One (*α*, *planiuscula*: Fuchssteine; Basalthügel; Sohlander Berg, on *Taxus* etc.) had flat fruitbodies, the other more rare form (*ßß*, *subteres*: Haide) subcylindrical with slightly concave disc. The authors also stated that the gelatinous ('*tremellosa*') fruitbodies strongly swelled upon rehydration. Persoon (1822: 304) referred to these forms when stating that they are 'apparently scarcely different' from his caulicolous fungus.

According to Spooner (1987: 184), type material of *P. vinosa* 'has not been located and is unlikely to have survived'. Therefore, Spooner relied on Rehm's (1891) interpretation of *Orbilia vinosa* when redescribing the exsiccatum indicated there (Ascomyc. 17, on decorticated, rotten, hanging young twigs of *Quercus*, forest near Sugenheim, Mittelfranken, southeastern Germany) 'which is on the substrate of the type and from the same part of Europe' (the distance is over 300 km, however). Spooner's description is sufficient enough to recognize the species as interpreted in the present monograph. A duplicate of this collection in M was examined in the present study though not illustrated (asci †50–60 × 5–5.5 µm, apex hemispherical, with apical wall thickening, spores †13.5–16 × 1.7–1.8 µm, straight, tapering below, paraphyses apically uninflated, covered by 1–2 µm thick exudate). It should be noted that the label of the specimen in M bears the remark 'on hanging young twigs', whereas Spooner noted in error 'on decorticated fallen trunk'.

Spooner also believed that Svrček (1954) adopted the name *Orbilia vinosa* in the same sense, an opinion which is confirmed in the present reexamination in most cases. In our opinion, the same interpretation was shared with more or less high probability, e.g., by Ellis (NAF 1313), Karsten (1869, 1871), Nylander (1869: 56), Massee (1895: 145), Schröter (1908: 120), Velenovský (1934: 97), Nannfeldt (1936: 199), Grelet (1948a: 49), Dennis (1954: 297, 1978: 189), and Malençon & Llimona (1980: 54).

Considering the fact that the epithet *vinosa* has rather consistently been adopted in the more recent literature, we feel justified to conserve this usage rather than propose extensive name changes. Therefore, we adopt Spooner's interpretation based on Rehm (Ascomyc. 17), although Rehm's concept of *O. vinosa* was obviously heterogeneous (see below). In order to emphasize this interpretation, we here designate a collection from Germany (Stuttgart-Wolfbusch, H.B. 6715b, CBS 116215; sq.: KT215266) as **Reference Specimen** of *O. vinosa*. Its documentation includes light rose apothecia with a smooth margin, asci *(37–)44–48 × 5.2–5.4 µm, spores *13–15(–16.5) × 1.7–1.9 µm, SBs (3–)4–5 × 0.5–0.7(–1) µm, and a trinacrium-like anamorph formed in pure culture (Pl. 258: 1).

According to Spooner (1987: 186), Albertini & Schweinitz's diagnosis of *Peziza vinosa* 'is so brief, and without illustration, that there can be little confidence that this fungus [Ascomyc. 17] is that with which they [Albertini & Schweinitz] were dealing'. Schweinitz (1832: 177) reported *P. vinosa* also for the North American continent, but undated and unlocalized authentic specimens in the Schweinitz Herbarium (925-182, PH, BPI) listed under *P. vinosa* are reidentified here as *O. tenuispora* (section *Helicoon*, on wood, Pl. 562: 3). Yet, the specimens from PH contained also abundantly *O. aurantiorubra* (on bark), though on different pieces of substrate (IVV: H.B. 7726a). Undoubtedly, Schweinitz believed the two populations belonged to a single species.

Fries's (1822) description of *P. vinosa* is based on collections which he referred to the flat form of Albertini & Schweinitz. Fries described the fruitbodies as gelatinous, nearly immarginate, '1 lin.' diam. (~2 mm). He repeated the fact that they nearly disappear on drying and swell up when rehydrated. Apparently Fries's branches were collected on the ground since he replaced Albertini & Schweinitz's '*projectis*' by '*dejectis*'.

Karsten (1861: 37, 1869: 176, 1871: 101) referred to *P. vinosa* or *O. vinosa* collections from Finland on wood of *Quercus* branches. His descriptions from 1869 and 1871 quite clearly refer to an *Orbilia*, possibly *O. vinosa* s. Spooner (apothecia 0.4–0.7 mm diam., bright flesh-red or flesh-orange, asci 45–55 × 4–5 µm, spores acicular-filiform, 11–16 × 1–1.5 µm, paraphyses apically inflated).

Rehm (1891: 457) reported *O. vinosa* from rotten hanging twigs, mainly *Quercus*, more rarely *Rosa*, *Fagus* etc., from central Europe, in the Alps also on *Pinus cembra* and *Rhododendron ferrugineum*. As exsiccata he cited Rabenhorst, Fungi Eur. Exs. 1412 and Rehm, Ascomyc. 17 (both belonging to the same collection). Though the stated that spore characters (filiform-fusoid, straight, acute, 12–17 × 1.5–2 µm) and habitat (xeric twigs) fit the current concept of *O. vinosa*, Rehm described the paraphyses as 'mostly filiform, 1.5 (as 0.15) µm wide, above more or less roundish, enlarged to an ovoid, up to 4 µm wide apex'. Also Rehm's (1891: 447, I figs 1–5) illustration of *O. vinosa* (see Fig. 149) does not permit recognition of the species, except that the strongly capitate paraphyses clearly exclude *O. vinosa* and related species. We conclude that his illustration can hardly originate from Ascomyc. 17, though the substrate is said to be *Quercus* in both. The given ecology (xeric twigs) excludes a member of section *Helicoon*, given that this statement applies to all included collections.

Saccardo (1889: 622) reported quite a large number of substrates for *O. vinosa*, but without stating humidity and exposition. Based on the given diagnosis (asci 35 × 5 µm, paraphyses very slightly inflated, spores 13–14 × 0.7–1.5 µm, acicular, often slightly curved) the identity of these records remains uncertain, whereas his treatment of 'β. *O. vinosella* Pers. Myc. Eur. p. 303 (Pez.)' is a mere copy of Fries's note.

When revising Velenovský's type specimens of *Orbilia*, Svrček (1954: 23) concluded that material referred by Velenovský (1934: 97, pl. XI fig. 28) to *O. vinosa* is conspecific with five taxa described by Velenovský in the same volume. Svrček believed that his species concept of *O. vinosa* concurred with that of 'Rehm, Saccardo, and Seaver etc.'. Reexamination of Velenovský's five taxa actually indicates that 3 represent *O. vinosa* s. Spooner, whereas one belonged to a distinct species (*O. aprilis*) and one was empty. Velenovský's original manuscript drawings of several samples under the name *O. vinosa* (on *Quercus*, also *Frangula alnus*) clearly concur with the present concept of *O. vinosa*.

Beyer (1998: 192) reported in a sample on *Salix* from Kulmbach (Oberfranken, IVV: 28.II.1997) narrowly clavate, cuneate ascospores with ellipsoid to subglobose SBs, but the same sample was also examined in the present study,

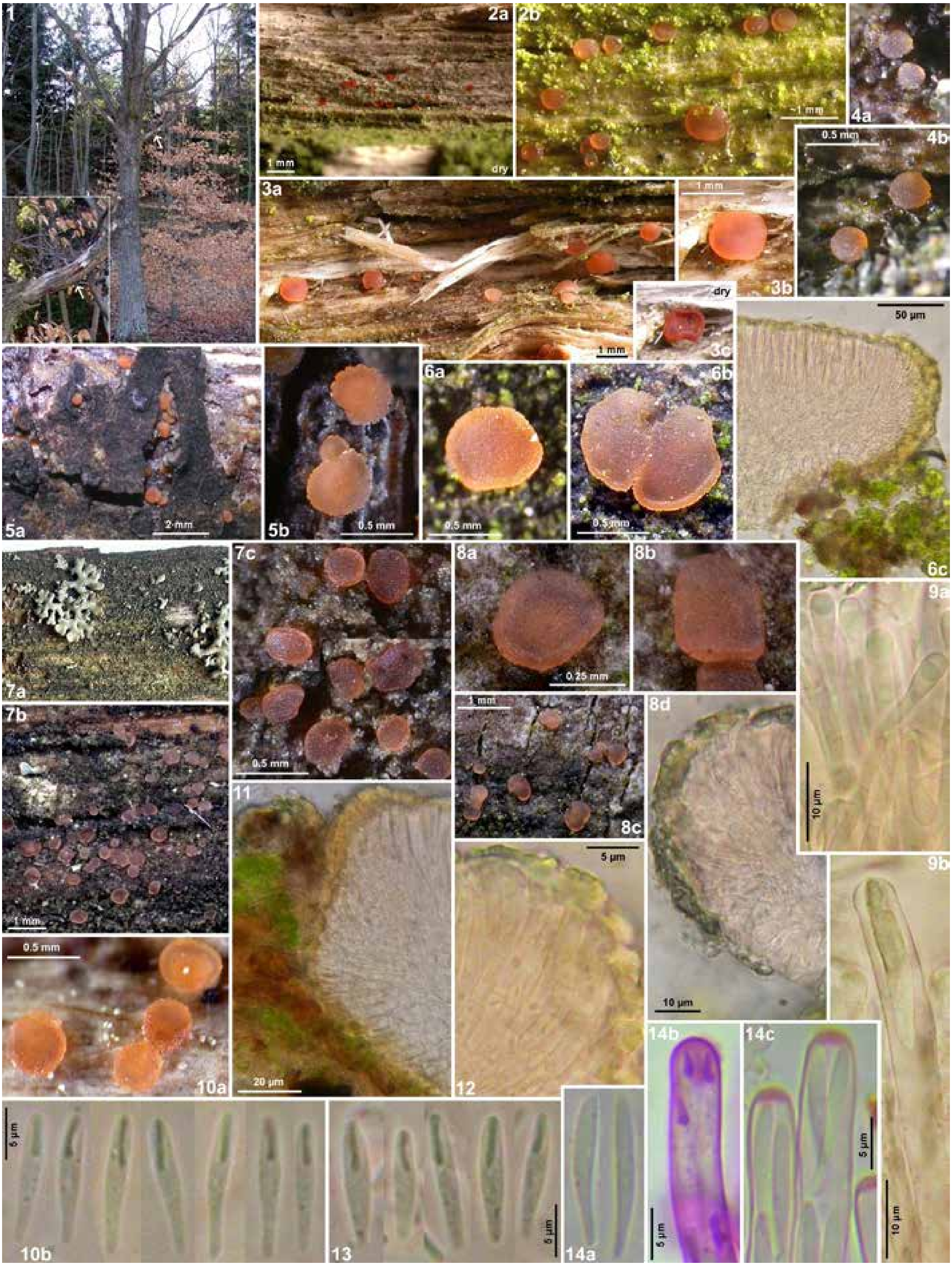


Plate 260. **1–4**, **6–14**: *Orbilia vinosa*; **5**: *O.* cf. *vinosa*. – **1a**. decorticated branch attached to standing *Quercus* tree in ~2.3 m above the ground; **2a**, **7a**. decorticated xeric branches of *Quercus robur*, with green air algae (**2**) and *Hypogymnia physodes* (**7**); **2b**, **3a–b**, **4a–b**, **5a–b**, **6a–b**, **7b–c**, **8a–c**, **10a**. rehydrated apothecia; **2a**, **3c**. dry apothecia; **6c**. apothecium in median section; **8d**, **11**, **12**. id., marginal ectal excipulum; **9a**. paraphyses; **9b**, **14b–c**. mature asci (**9b** fully turgescent); **10b**, **13**, **14a**. ascospores. – Living state (**14b** in CRB) except for **14a**, **c** (in CR_{SDS}), ascus in **14b** (CRB). – **1**: phot. P. Perz, **14a–c**: phot. I. Wagner. — **1**. P.P. 20060402: Poland, Wolany, on *Quercus*; **2a–b**. H.B. 7449a: Germany, Amberg, on *Quercus*; **3a–c**. H.B. 7451: ibid. on *Populus*; **4a–b**. H.B. 7293b: France, Nyons, on *Spartium*; **5a–b**. H.B. 5518: USA, Massachusetts, on *Pinus*. **6a–c**. H.B. 8106a: Mallorca, on *Pinus*; **7a–c**. H.B. 6717: Germany, Tübingen, on *Quercus*;

likewise in the living state, where it showed fusoid spores with subulate SBs.

Some doubts remain regarding the type material of ***O. scotica***. In the original description Massee gave the information that the taxon is based on a single specimen from Aboyne (Aberdeenshire) deposited in 'herb. Berk., Kew, under the name of *Peziza vinosa* (= *Calloria vinosa*)'. Nannfeldt (1936) discovered a specimen on a sheet of *O. vinosa* at Kew, marked in Berkeley's handwriting: '*Pez*. (*Mollisia*) – Aboyne, Sept. 1870', and assumed that this is the holotype of *O. scotica* 'though it bears no note at all in Massee's hand'.

Massee (1894a: 99, 1895: 144) described the spores as 'elliptic-oblong, ends obtuse, 4 × 1 µm' and the paraphyses 'about 1 µm thick, tips subglobose'. Later, Massee (1895) compared *O. scotica* with *O. coccinella* (s.auct.), 'differing in the narrower spores and the much smaller cells of the excipulum'. Nannfeldt discovered a few free spores in the presumed holotype which strongly deviated from those seen by Massee, being needle-shaped, 12 × 1–1.5 µm. He concluded that Massee's spore description must be erroneous, based on the experience that spores of *Orbilia* are usually difficult to see in herbarium material.

The specimen studied by Nannfeldt was reexamined here (Pl. 257: 6). It grew on unidentified, decorticated, rotten wood, possibly of *Acer*, according to the wood anatomy. Nannfeldt's opinion that *O. scotica* is a synonym of *O. vinosa* is confirmed, with a spore width at the lower end of the range. In the case the specimen was studied while it was still viable, Massee's report of small oblong spores might refer to the spore bodies which have just about that size in *O. vinosa*.

The lectotype of ***O. granulosa*** (on trunk of *Carpinus* in a shady forest in lowland Bohemia) contains ~40 mature apothecia, contrary to Svrček (1954: 15) who found only a single apothecium 0.1 mm diam. They measured rehydrated 0.12–0.35 mm diam. (protologue 0.1–0.2 mm), and are now very pale cream (fresh wine-rose, shining). Svrček's opinion that this represents *O. vinosa* is confirmed here. The margin is without glassy processes (Pl. 257: 8). The other specimen mentioned in the protologue was on a *Betula* branch from the same locality. The manuscript sketch shows apparently the lectotype and gives the spores as 16–18 µm, although the protologue says 12–16 µm.

The abundant lectotype of ***O. pulcherrima*** grew on a hanging, partially decorticated branch of *Quercus* far up in the canopy. Svrček (1954: 19) referred this taxon to synonymy with *O. vinosa*, which is confirmed here (Pl. 257: 7). The apothecia were described as igneous blood-red, 1–1.5 mm diam. (rehydrated 0.2–0.7 mm diam. and pale rose-ochraceous in present study). The margin was not examined. Velenovský considered this to be a very common taxon on xeric, sun-exposed wood of various angiosperm substrates, in contrast to *O. vinosa* which he applied to populations with pure rose apothecia on fallen, hygric angiosperm wood. The two diagnoses in Velenovský (1934) give 15–20 µm long spores, whereas his manuscript notes give them for *O. pulcherrima* as 12–16 (*Betula*) and 15–18 µm (*Quercus*), and for *O. vinosa* as 10–15, 10–16, and 15–20 µm.

The holotype of ***O. tricuspis*** grew on a decorticated branch of *Ligustrum vulgare* in lowland Bohemia. It was regarded to be a synonym of *O. vinosa* by Svrček (1954: 21), which is confirmed here (Pl. 257: 9). The rather large apothecia (1–1.5 mm diam., rehydrated 0.3–1 mm in present study) were described as lilaceous honey-coloured (lilacino-melina), but are now light dirty orange(-apricot). Short glassy processes occurred at the margin, but only at one side of the apothecium examined. For the name-giving triradiate conidia see under Anamorph.

O. prunorum was published by Velenovský (1934) based on two collections: on trunk of *Prunus domestica* (1.VII.1926), on trunkbase of *Cornus* (VII.1926), both from lowland Bohemia. In his unpublished manuscript he provided a sketch (probably from the *Prunus* specimen), from which the ascus and spore measurements in the protologue were taken. The protologue reports very small, vinaceous-yellowish apothecia (0.1 mm diam.; manuscript: 0.1–0.2 mm on *Prunus*, 0.1 mm on *Cornus*), hardly inflated paraphyses covered by thick exudate, and narrowly acicular, 12–15 µm long spores with both ends acute (on his sketch about 0.7–1 µm wide, one end slightly curved).

No material of the *Prunus* sample could be located at PRM, and in the *Cornus* sample (PRM 152416) no apothecia relating to this fungus could be found, neither by Svrček nor in the present study. There were only some overmature apothecia of what could have been *Arachnoscypha aranea* (abundant subiculum, asci with croziers, with amyloid apical rings, ascospores sometimes septate, oblong, 10 × 2.7 µm). The substrate does not have the appearance of xeric wood, so one does not expect to find *O. vinosa* here.

Velenovský separated *O. prunorum* from *O. vinosa* because of much smaller, hardly visible apothecia. Based on his diagnosis, Svrček (1954: 19) assumed conspecificity with *O. vinosa.* Velenovský's sketch could indeed refer to *O. vinosa*, but also to *O. aurantiorubra*, although the latter species is unknown to occur on these two hosts. The sketch in Velenovský's unpublished manuscript is designated here as **lectotype** of *O. prunorum* (Art. 8.1 ICN).

Misapplication. The epithet ***vinosa*** has been applied in the past also to several other, mainly desiccation-sensitive species which we assign to different sections or even subgenera. Persoon (1801) and Phillips (1887) named collections *Peziza* or *Calloria vinosa* which are assigned here to *Orbilia auricolor* (section *Arthrobotrys*). But also highly desiccation-tolerant species, such as *O. aprilis* (section *Hemiorbilia*, Svrček 1954) and *O. aurantiorubra* (section *Aurantiorubrae*, Schweinitz 1832 p.p., Baral & Krieglsteiner 1985) were misidentified as *O. vinosa*. To members of section *Helicoon* the epithet *vinosa* was attached by Schweinitz (1832 p.p.), Fuckel (1870, 1874), Costantin (1888), and Seaver (1911). Also Jaap (1922: 15) used the name *O. vinosa* for a fungus growing in a wet habitat, which was here reexamined and tentatively assigned to *O. luteorubella*. A strain from CBS (917.72, R.G. Benedict, X.1972) is found under the name *O. vinosa* in many molecular treatments; its rDNA sequence clustered in Hagedorn & Scholler's (1999) and our phylogenetic analyses near '*O. luteorubella*' (= *O.* aff. *sinensis*, series *Pseudotripoconidium*).

P.L. & H.M. Crouan (in sched., unlocalized, 15.X.1868, on *Ulmus*) figured and preserved under the name *Peziza luteorubella* a species with long-acicular spores, according to the unpublished original water colour drawing. J.P. Priou (pers. comm., unillustrated) restudied the specimen and found

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8a–d. H.B. 9194: France, Drôme, Die, on *Rosa*; **9a–b**. J.P.P. 24173: France, Morbihan, on *Ilex*; **10a–b**. H.B. 7861a: Germany, Furth im Wald, on *Fagus*; **11**. H.B. 8992: Poland, Kłodzko, on (?)*Sorbus*; **12**. H.B. 8913: Czechia, Kasperske Hory, on *Betula*; **13**. H.B. 7249c: France, Drôme, on *Pinus*; **14a–b**. 18.II.2010: Germany, Sonneberg, on *Fagus*.

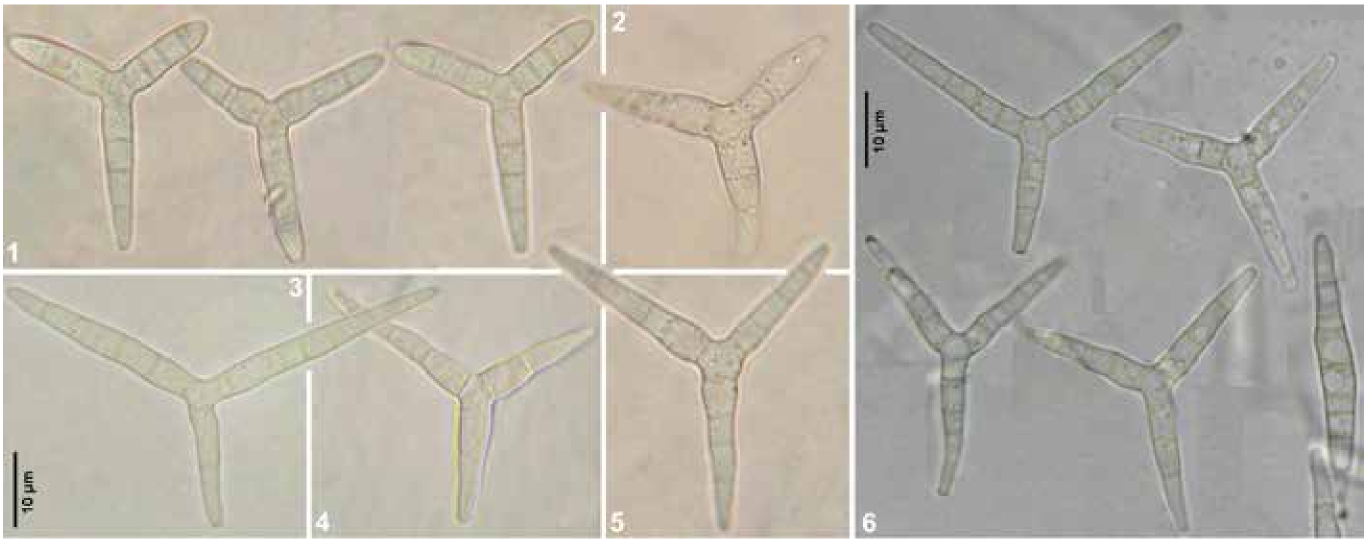


Plate 261. **1–6**: *Orbilia vinosa*. – **1–5**. conidia from substrate; **6**. conidia from pure culture. – Living state. — **1**. H.B. 8235a: Switzerland, Luzern, on *Acer*; **2**. H.B. 9084a: France, Aix-en-Provence, on *Pinus*; **3**. 3.I.2004: Luxembourg, Hesperange, on *Quercus*; **4**. H.B. 8106a: Mallorca, on *Pinus*; **5**. H.B. 8248a: Switzerland, Pilatus, on *Salix* (see p. unter arachnovinosa variation); **6**. 19.IV.2011: Luxembourg, Walferdange, on *Quercus*.

immature asci with a thick-walled, hemispherical apex which points to *O. vinosa*. Fuckel's (1870: 283, 1874: 57) very brief reports of *Calloria vinosa* refer to a fungus with capitate paraphyses, growing on various broad-leaved trees including *Ulmus campestris* (= *U. minor*). Reexamination of the *Ulmus* specimen in M (Fungi Rhenani ed. I. 2569, on bark of a branch, near Hattenheim, Mainz, Germany) suggests that Fuckel's concept of this taxon concerns *O. sarraziniana*. This collection was also studied by Rehm (1891: 455) who described the paraphyses as filiform, apically inflated to a roundish 3–5 µm wide tip, and referred it to *O. luteorubella*. Phillips (1887: 333, pl. 10 fig. 63) reported paraphyses with 'globose, pyriform or thickened apices'. Together with the spores being 'filiform-acicular' and 'straight or curved, 10–15 × 1 µm', his interpretation of *Calloria vinosa* appears to refer to a taxon of *O. auricolor* agg. Costantin (1888) provided a detailed description of samples which he referred to *O. vinosa*, but his illustration shows that they belong to section *Helicoon*, possibly to *O. rosea* (see p. 966). A specimen referred by Feltgen (1899: 55) to *O. vinosa* (on *Salix*) was found to belong to section *Helicoon* and is tentatively assigned here to *O. luteorubella*, whereas another one referred by him to *O. chrysocoma* (on *Quercus*) represents *O. vinosa*. Bachman (1908: 57) reported an interesting fungus of unknown identity under the name *O. vinosa* (from Ohio, on wood and bark), with large (1–2.5 mm) first funnel-shaped, bright red apothecia with a 1 mm long stout stipe, paraphyses with inflated, often globose apex, and acicular spores 10–14 × 1 µm.

Not included collections. Two samples on *Pinus strobus* from lowlands of Massachusetts (Pl. 259: 5, 260: 5) and New Jersey (IX.1887, J.B. Ellis, herb. Petrak, unillustrated) differ from *O. vinosa* in distinctly narrower asci (*53–58 × 3.9–4.3 µm, †40–56 × 3.5–4 µm) and a spore size at the lower end of the range (*11–14.5 × 1.5–1.7 µm, †11–14 × 1.3–1.5 µm). The glassy processes had a length of 3–20 µm. Such narrow asci and spores in combination with distinct glassy processes are quite unusual in taxa around *O. vinosa*. Another specimen of J.B. Ellis (NAF 1313, on textile) concurs in the length of glassy processes, but has wider asci (†4.7–5.5 µm) and spores (†11–14 × 1.8–2 µm). Since glassy processes longer than 15 µm were not accepted in the present circumscription of *O. vinosa*, the three records are not included in the description. Other short-spored collections on gymnosperms (e.g., Pl. 259: 3, *Pinus ponderosa*; Pl. 257: 4, *Picea abies*) differ from those on *P. strobus* in wider spores, more or less wider asci, and shorter glassy processes.

Conspecific with the above narrow-spored samples might be some on angiosperm wood. One from Massachusetts (on *Acer*, IVV: bhi-F731) has 7–15 µm long glassy processes, rather narrow spores (*11–13.6 × 1.2–1.6 um) but asci of *50–55 × 4–4.6 µm; available DNA data place it very distant from *O. vinosa*. Also a sample from Utah (on *Arctostaphylos*, Pl. 259: 4) has similar but longer spores, wider asci, and distinctly shorter SBs (2–4 µm) than typical *O. vinosa*; glassy processes are very short or absent here.

An exceptional collection of a single apothecium on a herbaceous stem (Luxembourg, Ettelbruck, *Melilotus*, 6.VII.2002, unillustrated, associated with *O. subclavuliformis* and *O. flavida*) contained only a single submature ascus. Although resembling collections of *O. vinosa* s.l. on ligneous substrate, it had rather wide asci (*60–71 × 6.5–6.7 µm) and exceptionally wide spores (*16–19.5 × 2.2–2.4 µm). The SBs were rather short (3–3.3 × 1–1.1 µm, perhaps not fully developed), the paraphyses contained crystalloid SCBs, and the margin was without glassy processes. The record is not included in either description of the *O. vinosa* aggregate, mainly because of the deviating substrate and spore width.

An Australian collection mentioned under *O. nothoaprilis* (Pls 284: 2; 285: 5) is difficult to place: it has spores and SBs intermediate in length to *O. vinosa*, but the asci are rather short.

For the not included *O. prunorum* see under Type studies.

Anamorph. *Orbilia vinosa* produces in pure culture a trinacrium-like anamorph similar to *Trinacrium tothii*, the anamorph of *O. aprilis*, but with usually distinctly longer arms (Pls 257: 3i, 5i; 258: 1–3; 261). On the natural substrate the same type of triradiate conidia was frequently observed, sometimes emerging from the excipulum of the apothecia.

Velenovský (1934: p. 97, plate XI, fig. 29) described *O. vinosa* under the name *O. tricuspis*, based on tricuspidate structures which grew out of the basal excipulum. These most probably represent the anamorph, though his schematic sketch

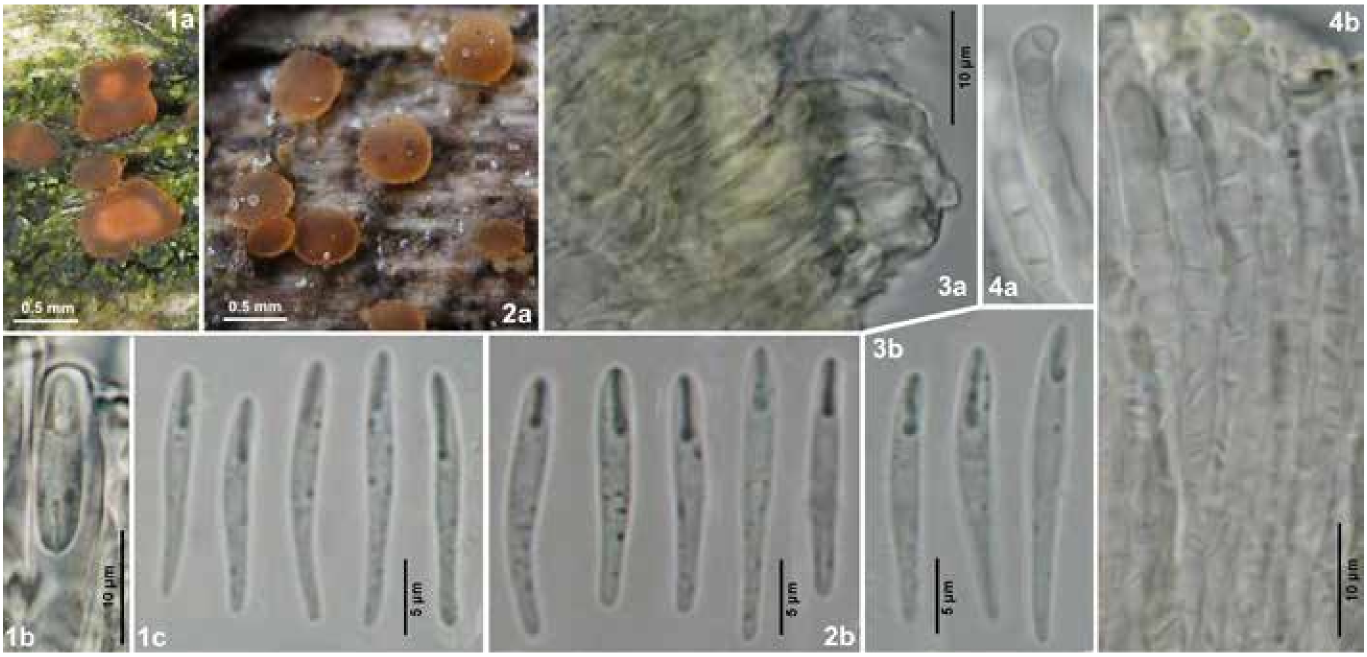


Plate 262. **1–4**: *Orbilia vinosa* (with rather long spores). – **1a**, **2a**. rehydrated apothecia; **1b**. tip of fully turgescent ascus; **1c**, **2b**, **3b**. ascospores; **3a**. marginal cortical cells with glassy processes; **4a–b**. paraphyses with crystalloid SCBs. – Living state. – **1–4**: phot. R. Tena. — **1a–c**. R.T.L. 13072201: Spain, Teruel, Sierra de Albarracín, on *Quercus*; **2a–b**. R.T.L. 11060201: ibid., on *Cistus*; **3a–b**. R.T.L. 11052601: ibid., on *Cistus*; **4a–b**. R.T.L. 11051903: ibid., on *Cistus*.

shows aseptate arms and stipes with acute ends. In the holotype these structures could not be rediscovered, neither by Svrček (1954) nor in the present examination.

In 12 collections of *O. vinosa* s.l. (including *O. arachnovinosa* and *O. angiosubvinosa*), 2–3(–4)-armed dicranidion-like conidia were detected on the natural substrate, sometimes emerging from the hymenium of some apothecia (see Pl. 137: 1d; 138: 1m). We assume that these conidia belong to a parasite which seems specific to apothecia of *O. vinosa* s.l., because it often occurred mixed with the typical conidia of the host species (trinacrium tothii-like in *O. vinosa*, dwayaangam-like in *O. arachnovinosa* and *O.* cf. *subvinosa*). We further imagine that these conidia represent the anamorph of *Hyalorbilia hergiswiliana* (see p. 433).

A pure culture gained from ascospores (H.B. 6748g, CBS 116208, Col de Pommerol, on *Pinus*, IVV: H.B. 6748f), which formed the typical trinacrium-like conidia of *O. vinosa*, was at first thought to belong to *O. subvinosa* by macroscopy and especially because of abundantly associated dwayaangam-like conidia which undoubtedly belong to *O. subvinosa*. However, its sequence placed it intermediate between *O. vinosa* and *O. subvinosa* (see below) and suggests that it belongs to a separate species. Because we saw no difference in conidial morphology, we have included it in the description of *O. vinosa*. The teleomorph was not documented and no herbarium specimen of this population was retained.

Phylogeny. *O. vinosa* clustered with *O. subvinosa*, *O. angiosubvinosa*, *O. arachnovinosa*, *O. paramontigena*, and two unnamed genotypes (H.B. 6748g, bhi-F731) in a strongly supported clade (Phyls 9, 11, S13), here called *vinosa-subvinosa* subclade. Eight sequences belonging to *O. vinosa* in the here defined sense were available (Tab. 66). They comprise mostly ITS+LSU, rarely also SSU (H.B. 6715b) or only ITS (G.M. 2011-04-19.1), and vary in the ITS region by 0–1.9%. This variation is at present remarkably correlated with the geographical origin: five sequences are from Luxembourg and vary by 0–0.7%; they differ by 1.3–1.9% from the one from Stuttgart and likewise by 1.3–1.9% from two identical sequences from southern France. Also between the latter two genotypes a distance of 1.9% is observed.

Further seven sequences belong to *O. subvinosa* and show a distance of 9.5–11% to *O. vinosa*, which strongly supports separation of *O. subvinosa* at the species level. However, the isolate with typical trinacrium-like *O. vinosa* conidia (H.B. 6748g, CBS 116208), is intermediate by showing a 10.5–11.5% ITS distance to *O. subvinosa* and 8.5–9% to *O. vinosa*. Especially in the ITS2 this strain is distinctly closer to *O. vinosa*.

A sequence of the sample from Massachusetts (on *Acer*, bhi-F731) also clustered intermediate between *O. vinosa* and *O. subvinosa*, but shows a high distance to all strains of the subclade, the minimum being 10.5% to *O.* cf. *vinosa* (H.B. 6748g).

Also in the LSU (D1–D2) *O. vinosa* and *O. subvinosa* cluster in two different subclades, with a distance of 1.1–1.3% (7–8 nt) between them (Phyl. S13). 1 nucleotide position (632) at the very 3'-end of D2 deviates in H.B. 6715b (*O. vinosa*) in having GTAAGCG**G**C as in *O. subvinosa* and the intermediate strains from Col de Pommerol (H.B. 6748g) and Boston (bhi-F731), instead of GTAAGCG**A**C as in the remaining *O. vinosa* sequences. In fact, the strain from Col de Pommerol is in the LSU surprisingly closer to O. subvinosa by showing a 0.3% distance (2 nt) but 0.8–0.9% (5–6 nt) to O. vinosa.

The S1506 intron is present in all seven sequences of O. vinosa and in that from Col de Pommerol. It varies by 0.5–2.7% among the *O. vinosa* sequences, whereas the strain from Col de Pommerol differs by 6–6.5%. The intron is absent in those four sequences of *O. subvinosa* which cover the 3'-end of SSU, and also in *O. angiosubvinosa* and the Boston strain (bhi-F731). This supports a closer relatedness between the intermediate strain from Col de Pommerol and *O. vinosa*, and between *O. subvinosa* and *O. angiosubvinosa*. For the distance to the similar *O. aprilis*, *O. nothoaprilis*, *O. crenatovinosa*, and *O. paramontigena* see under these species.

The semi-conservative Orb28s2R primer region in the LSU D2 domain upstream of the LR3 primer deviates in *O. vinosa* and *O.*

Table 66. Available sequences of the *vinosa-subvinosa* subclade together with *O. subulivinosa* and *O.* aff. *subulivinosa*. Note that *O. vinosa and O.* cf. *vinosa* with trinacrium-like anamorph possess the S1506 intron whereas *O. subvinosa* and *O. angiosubvinosa* with dwayaangam-like anamorphs lack this intron. DNA isolation from pure culture (cult. = ascospore isolate, con. isol. = conidial isolate) or from apothecia (ap.); T = holotype, RS = reference specimen.

Species	Locality	Host	Specimen number	Gene region	S1506	Isol.	Illustration	GenBank
O. vinosa^{RS}	Germany, Stuttgart	*Fagus*	H.B. 6715b, CBS 116215	SSU+ITS+LSU	+	cult.	Pl. 258: 1	KT215266
O. vinosa	Luxembourg, Walferdange	*Quercus*	G.M. 2011-04-19.1	ITS	+	cult.	IVV	KT380060
O. vinosa	Luxembourg, Koedange	*Frangula*	G.M. 2014-07-12.1	ITS+LSU	+	ap.	?	KT380090
O. vinosa	Luxembourg, Bridel	*Quercus*	G.M. 2014-02-14.1	ITS+LSU	+	cult.	IVV	KT380089
O. vinosa	Luxembourg, Kockelscheier	*Carpinus*	G.M. 2016-05-04.1	ITS+LSU	+	ap.	?	MG372377
O. vinosa	Luxembourg, Fennerholz	*Quercus*	G.M. 2017-02-09.1	ITS+LSU	+	cult.	IVV	MH221059
O. vinosa	France, Pas de la Faye	*Ficus*	G.M. 2011-09-18.1	ITS+LSU	+	ap.	IVV	KT222394
O. vinosa	France, Montélimar	*Spartium*	G.M. 2018-09-12.5	ITS+LSU	+	ap.	–	MK473402
O. cf. *vinosa*	France, Col de Pommerol	*Pinus*	H.B. 6748g, CBS 116208	SSU+ITS+LSU	+	cult.	Pl. 258: 4	KT215265
O. aff. *vinosa*	USA, Boston	*Acer*	bhi-F731	ITS+LSU	–	ap.	IVV	MH445965
O. arachnovinosa	Spain, Lago de Valle	*Erica*	H.B. 10093	ITS	+	ap.	IVV	UNITE
O. arachnovinosa	France, Pic de Bure	*Clematis*	G.M. 2015-09-15.8	ITS+LSU	+	ap.	?	MK473400
O. arachnovinosa	France, Le Bessat	*Sorbus*	G.M. 2016-08-14.5	SSU+ITS+LSU	+	ap.	?	MK473401
O. aff. *arachnovinosa*	Austria, Koralpe	*Rhododendron*	G.F. 20180360	SSU+ITS+LSU	–	ap.	IVV	MK473399
O. subvinosa	France, Moustiers-Ste.-Marie	*Pinus*	G.M. 2011-09-21.1	ITS+LSU	?	ap.	?	KT380087
O. subvinosa	France, Col du Ferrier	*Pinus*	G.M. 2009-09-24.1	ITS+LSU	–	ap.	?	MH221057
O. subvinosa	France, Col du Ferrier	*Pinus*	G.M. 2011-09-18.2	ITS+LSU	–	cult.	Pl. 265: 1	KT380088
O. subvinosa	France, Briançon	*Pinus*	G.M. 2010-09-05.1	ITS	?	con. isol.	Pl. 265: 2	KT380059
O. subvinosa	France, La Palud-sur-Verdon	*Pinus*	G.M. 2009-09-29.1	ITS+LSU	–	ap.	IVV	KT380086
O. subvinosa	France, Le Beaume	*Abies*	G.M. 2015-08-29.1	ITS+LSU	–	ap.	?	MH221058
O. subvinosa	France, Le Labouret	*Pinus*	G.M. 2015-08-30.5	SSU+ITS+LSU	–	ap.	?	MK473395
O. angiosubvinosa^{T}	Spain, Pola de Somiedo	*Corylus*	H.B. 9813a	ITS	–	ap.	Pl. 267: 3	MK493127
O. paramontigena^{T}	Spain, Ripoll	*Acer*	J.B. 658/16, H.B. 10013	SSU+ITS+LSU	+	ap.	Pl. 256: 1	MK493132
O. subulivinosa^{T}	France, Cogolin	*Erica*	H.B. 10140a	SSU+ITS+LSU	+	ap.	Pl. 279: 1	MH221056
O. aff. *subulivinosa*	Slovakia, Tatranská Javorina	*Picea*	A.P. 18/97	ITS	+	ap.	IVV	MK651741

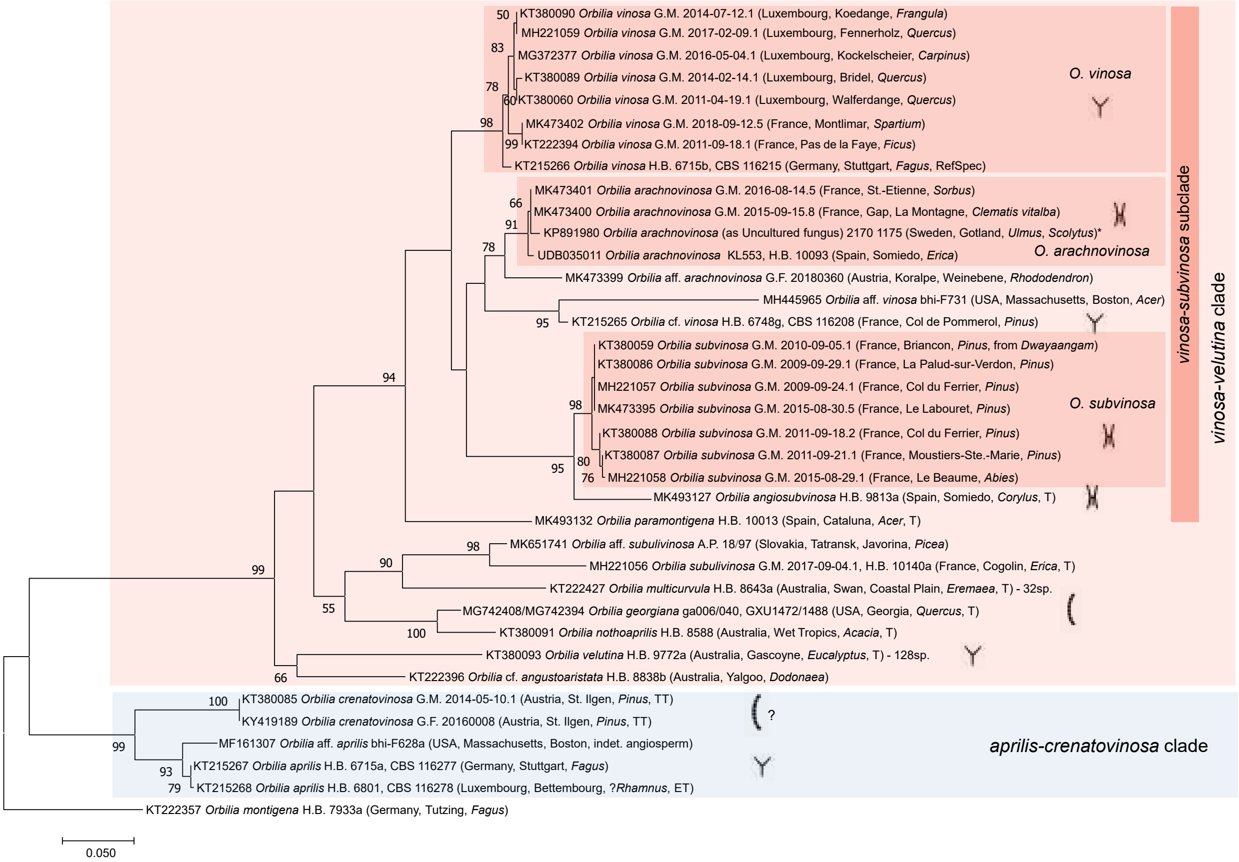
subvinosa (11 strains, including strains H.B. 6748g and bhi-F731) at 2 positions (611 and 626: GGA**C**GCTGGCTTAATGGT**C**GT) from all remaining taxa of *Orbiliomycetes* with available LSU which have GGA**T**GCTGGCTTAATGGT**T**GT, except for a few further variants (Tab. 19). The sequence of *O. multicurvula* does not cover this region.

Ecology. A total of ca. 260 specimens here referred to *O. vinosa* (including somewhat uncertain or deviating samples) have been examined by the first author and further > 120 records seen from documentations of other workers. The species grows on xeric branches (rarely trunks) of a wide variety of trees and shrubs. Decorticated areas are strongly preferred over bark (over 6:1). Also cones of *Pinus* and stems of *Rubus* are sometimes inhabited. Samples on herbaceous substrates are unknown.

The species predominantly occurs on angiosperm substrates. The most favoured host genera in our collections were *Quercus* {75}, followed by *Salix* {36}, *Fagus* {23}, *Pinus* {22}, *Rosa* {15}, *Corylus* {15}, *Prunus* {9}, *Cistus* {13}, and *Carpinus* {8}. A clearly fungicolous growth was only exceptionally noted. In a single collection its anamorph grew on the intact perithecia of an unidentified *Lasiosphaeriaceae* (H.B. 5941). Quite often the apothecia grew on very senescent, hardly recognizable basidiomata of *Vuilleminia*. Among the many fungi occurring associated with *O. vinosa*, *Durella connivens* (42 ×) is by far the most frequently noted species, followed by *Cryptdiscus foveolaris*, *O. aprilis*, *O. eucalypti*, and *Propolis farinosa*.

O. vinosa belongs to the most common xerobiotic orbiliaceous species of Europe. We met it from planar to subalpine regions, and at atlantic to continental as well as mediterranean and boreal sites. It was most often collected in cold-temperate humid central Europe, but is similarly frequent in orotemperate to orosubmediterranean zones and in warm-temperate humid or suprasub- to inframediterranean sem339ihumid regions. Only a few samples are from hemi- to supraboreal sites. Although often collected on calcareous or neutral soils, *O. vinosa* also occurs on acidic soils, e. g., on Devonian slates in the Ardennes or Buntsandstein in the Rheinland-Pfalz region, where the species diversity of *Orbilia* and other ascomycetes is comparatively poor. Mature apothecia of *O. vinosa* occur all over the year. An apparent maximum in spring and autumn is probably due to more frequent collecting activities in these seasons.

Most of our collections were made within Europe, but a few records indicate that *O. vinosa* also occurs in North America and Africa. The studied western North American collections are from cold-temperate to boreal humid ponderosa pine and Douglas fir forests of the Middle Rocky Mountains and Mogollon Rim. Other collections are from the cold-temperate humid northeast of North America. The mentioned deviating North American collections are from cold- to warm-temperate humid eastern areas, but the one on *Arctostaphylos* from a cold-temperate subhumid Douglas fir forest of the Utah Mountains. *O. vinosa* was also recorded from Tenerife (Macaronesia) in the inframediterranean lower semiarid (to semihumid) cardonal xerophytic scrubland (*Periploco laevigatae-Euphorbietum canariensis*) and in the thermomediterranean semihumid Canary pine forest (*Sideritido solutae-Pinetum canariensis cistetosum monspeliensis*), also in the north-exposed upper mesomediterranean subhumid *Pinus canariensis* forest, on substrates such as *Chamaecytisus proliferus*, *Cistus monspeliensis*, *C. symphytifolius, Euphorbia atropurpurea, Lavandula canariensis, Periploca laevigata,*



Phylogenetic analysis 11. Phylogram of *vinosa-velutina* clade inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (32 sequences, 595 positions, aligned with MUSCLE) using the K2+G model in MEGA7 (500 replicates). The tree is rooted with *O. montigena*. Asci 8-spored except when otherwise stated; RefSpec = reference specimen, T = type, ET = epitype, TT = topotype, * = without ITS1 and partial 5.8S.

Pinus canariensis, and *Rhamnus crenulata*, but never on succulents (Quijada et al. 2016). On Réunion (Mascarene Islands east of Madagascar) *O. vinosa* occurred on *Acacia* under a temperate humid (winter-dry) mountain climate.

Literature reports of *O. vinosa* are rather numerous, and the given spore size clearly excludes in all cases the similarly frequent *O. aprilis*. Yet, the often brief or even lacking descriptions do not always exclude members of other subgenera of *Orbilia*, particularly section *Helicoon*. These reports include Northern, Middle, and South America (Saccardo 1889: 622, Seaver 1951: 156), Asia (India and Sri Lanka, Saccardo l.c., Sharma 1983: 104), southeastern Australia (Beaton & Weste 1979), and New Zealand (Colenso 1887). However, the North American report by Schweinitz was found to belong to *O. tenuispora* (section *Helicoon*). From Australia we have not seen typical collections, and it is possible that the report by Beaton & Weste (1979) refers to the very similar *O. nothovinosa*, or to a member of section *Helicoon*. Hosts not reported by us are *Ailanthus*, *Broussonetia*, *Liriodendron*, *Morus*, *Vitis* (Saccardo 1889: 622), and *Pinus cembra* (Rehm 1891: 457). A report on *Clerodendron* from India (Sharma 1983: 104) is without description.

Specimens included. **GREAT BRITAIN**: **Scotland**, **Aberdeenshire**, Scottish Highlands, Grampian Mts., ~40 km WSW of Aberdeen, Aboyne, ~200 m, branch of ?*Acer*, on wood, IX.1870, collector unknown (K(M) 36051, **holotype** of *O. scotica*, H.B. 5451 ø). – **Yorkshire**, **South Yorkshire**, 3.5 km S of Barnsley, 1.3 km SW of Worsbrough, Country Park, 70 m, branch of *Salix cinerea*, on wood, 20.V.2011, H.O. Baral (ø). – 7.5 km NNW of Sheffield, 1 km WNW of Grenoside, Greno Wood, 240 m, branch of *Ilex aquifolium*, on wood, 18.V.2011, H.O. Baral (ø). – West Midlands, 17 km NNW of Birmingham, 6.7 km NNE of Walsall, Clayhanger Common, 142 m, *Quercus robur*, on wood and *Hysterobrevium mori*, 15.XI.2015, P. Thompson (P.T. 15/11/2015-2, doc. vid.). – **East Egland**, **Suffolk**, 12.5 km SSW of Southwold, 2.5 km NE of Leiston, NW of Sizewell, Kenton Hills, 4 m, branch of *Salix cinerea*, on bark, 17.VI.2004, E. Batten (E.B. 4526, K(M) 158849, doc. vid.). – ibid., 28.IV.2005, E. Batten (E.B. 4606, K(M) 158754, doc. vid.). – ibid., twigs of *Lonicera periclymenum*, on wood, 23.XII.2005, E. Batten & S.M. Francis (E.B. 4659, K(M) 159053, doc. vid.). – 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Ulex europaeus*, on wood, 10.I.2004, E. Batten (E.B. 4475, K(M) 158925, doc. vid.). – 7.3 km SW of Southwold, 2 km WNW of Dunwich, Dunwich Forest, 18 m, twig of *Quercus robur*, on wood, 11.II.2005, E. Batten (E.B. 4591, K(M) 158820, doc. vid.). – 1.5 km WSW of Dunwich, Dunwich Forest, 12 m, branch of *Q. robur*, on wood, 14.VIII.2004, E. Batten (E.B. 4551, doc. vid.). – ~1 km WSW of Dunwich, marsh near Dunwich River, 5 m, branch of *Salix*, on wood, 4.IX.2004, E. Batten (E.B. 4557, doc. vid.). – 0.7 km NW of Dunwich, 15 m, branch of *Q. robur*, on wood, 29.VIII.2004, E. Batten (E.B. 4556, K(M) 159055, doc. vid.). – 1,2 km NW of Dunwich, 18 m, twig of *Lonicera*, on wood, 7.XII.2005, S.M. Francis (E.B. 4651, doc. vid.). – **Cambridgeshire**, 8 km WNW of Peterborough, 1.5 km NE of Upton, 45 m, branch of *Ulex europaeus*, on wood, 16.IV.2017, H.O. Baral (H.B. 10057d ø). — **NORWAY**: **Nordland**, 28 km NW of Namsos, SE of Aglen, 8 m, branch of ?*Salix*, on wood, 29.VII.2010, H.O. Baral (H.B. 9401a). – **Oppland**, 20 km SE of Dovre, 3 km E of Sel, Gudbrandsdal, E of Fugleskjelle, 370 m, branch of *Betula pubescens*, on wood, 30.VII.2010, H.O. Baral (H.B. 9408a). – **Hedmark**, 8.5 km SSW of Stange, Rotlia, 200 m, branch of *Juniperus communis*, on wood, 3.VII.2016, P. Vetlesen (doc. vid.). – **Buskerud**, 18 km WSW of Hokksund, 6.5 km NW of Kongsberg, 177 m, branch of *Betula*, on wood, 21.VII.2011, S. Helleman (ø, doc. vid.). — **SWEDEN**: **Gävleborg**, 12 km SSW of Hudiksvall, 3.5 km SSW of Iggesund, NE of Njutånger, 18 m, branch of *Populus tremula*, on wood, 23.VII.2010, H.O. Baral & P. Perz (H.B. 9366a ø, anam. substr.). – **Skåne**, Kullaberg, 8.5 km NNW of Höganäs, 1 km SSE of Mölle, NW of Vattenmöllan, Möllehässle, 5 m, branch of *Rosa*, on wood, 8.VI.2006, H.O. Baral (H.B. 8204a). – Söderåsen, 6 km WNW of Röstånga, Kvärkabäckens ravine, 135 m, branch of *Ulmus glabra*, on wood, 3.VI.2006, H.O. Baral (ø). – branch of *Acer*, on wood, 3.VI.2006, H.O. Baral (ø). – branch of *Corylus avellana*, on wood, 3.VI.2006, J.G.B. Nielsen (ø). – 3.2 km NW of Röstånga, 1.2 km W of Härsnäs, Härsnäsdammen, 145 m, branch of ?*Fagus sylvatica*, on wood, 5.VI.2006, H.O. Baral (ø). — **FINLAND**: **North Karelia**, 42 km WNW of Joensuu, WNW of Outokumpu, Raivionmäki, 140 m, branch of *Prunus padus*, on wood, 30.I.2011,

M. Pennanen (ø, doc. vid.). — **RUSSIA (West)**: **Pskov**, **Loknya**, 42 km NW of Velikiye Luki, 9.5 km N of Nasva, NW of Bashovo, 140 m, twig of *Salix caprea*, on wood, 28.VII.2011, E.S. Popov (LE 247495, ESP-11-0002, doc. vid.). – **Novgorod**, **Valday**, 51 km SW of Borovichi, 16.5 km N of Valday, Krasnaja Gorka, 245 m, branch of *Quercus robur*, on wood, 22.IX.2011, E.S. Popov (LE 294567, non vid.). — **DENMARK**: **Nordjylland**, Jutland, 8 km NW of Brovst, 3 km W of Tranum, SSE of Naturcenter Fosdalen, Lien, 15 m, branch of *Quercus*, on wood, 14.V.2005, B.M. Spooner (ø). – **Sjælland**, 5.5 km NW of Sorø, SE of Bromme, Lillesø, 35 m, branch of *Corylus avellana*, on wood, 27.V.2007, H.O. Baral (ø). – 2.5 km SE of Sorø, 1.3 km NE of Frederiksberg, NNW of Kristiansminde, 45 m, branch of *Q. robur*, on wood, 28.V.2007, H.O. Baral (S). — **POLAND**: **Lower Silesia**, 10 km W of Kłodzko, 3 km N of Polanica Zdrój, Wolany, 365 m, branch of *Quercus*, on wood, 2.IV.2006, P. Perz (P.P. 20060402-2, doc. vid.). – 12 km NNW of Kłodzko, 3 km SE of Słupiec, ENE of Koszyn, 500 m, branch of *Quercus*, on wood, 3.VIII.2006, P. Perz (P.P. 20060803-1, doc. vid.). – 6 km ENE of Kłodzko, 2 km ENE of Wojciechowice, ~450 m, branch of *Quercus*, on wood, 28.XI.2006, P. Perz (P.P. 20061128-2, doc. vid.). – 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, branch of *Rosa*, on bark, 29. XII.2006, P. Perz (P.P. 20061229-2, doc. vid.). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, board of *Picea abies*, on wood, 25.IX.2009, P. Perz (H.B. 9234d ø). – 13 km SE of Bystrzyca Kłodzka, 11 km SW of Stronie Slaskie, 5 km WNW of Śnieżnick, 790 m, branch of *Salix*, on wood, 28.X.2007, P. Perz (ø, non vid.). – 18 km SSE of Bystrzyca Kłodzka, 5 km E of Miedzylesie, SW of Jodłów, 750 m, branches of *Alnus*, on wood, 13. VIII.2006, P. Perz (P.P. 20060813-1A); – ibid., branch of *Acer*, on wood (P.P. 20060813-1B). – 2 km NE of Jodłów, 820 m, branch of *Sorbus*, on wood, 15. VIII.2006, P. Perz (H.B. 8992, P.P. 200608015-3). – 11.5 km S of Bystrzyca Kłodzka, 1.2 km SE of Gniewoszów, 530 m, branch of ?*Fagus sylvatica*, on wood, 16.IV.2006, P. Perz (P.P. 20060416-2, non vid.). — **CZECHIA**: **Central Bohemia**, 8 km ESE of Beroun, 1 km NNW of Karlštejn, Dub sedmi bratři, 300 m, branch of *Salix*, on wood, 22.IX.2009, H.O. Baral & M. Chlebická (H.B. 9190a). – 23 km SE of Praha, ~2 km WNW of Mnichovice, hill between Kunice and Stráncice, ~450 m, branch of *Ligustrum vulgare*, on wood, VIII.1925, J. Velenovský (PRM 147400, **holotype** of *O. tricuspis*, H.B. 6413 ø, anam. substr.). – 3 km SSE of Mnichovice, E of Mirošovice, viaduct, 350 m, branch of *Carpinus betulus*, on wood, X.1928, J. Velenovský (H.B. 6178 ø, PRM 152457, **lectotype** of *O. granulosa*). – 3 km SE of Mnichovice, Hrusice, ~360 m, branch of *Quercus*, on bark & wood, 27.II.1928, J. Velenovský (PRM 147776, **lectotype** of *O. pulcherrima*, H.B. 6266 ø). – **South Bohemia**, 4.3 km ESE of Kasperske Hory, NE of Retenice, 905 m, branch of *Betula pendula*, on wood, 18.VIII.2008, H.O. Baral (H.B. 8913a ø). — **SLOVAKIA**: **Trnava**, 20 km NW of Trnava, 3 km WSW of Smolenice, Jahodník, 290 m, branches of *Pinus sylvestris*, on wood, 10.III.2016, A. Polhorský (A.P. 18/54,_anam. substr., doc. vid.). – **Prešov**, Carpathian Mts., Vysoké Tatry, 2 km S of Tatranská Lomnica, Stará Lesná, 803 m, branch of *Salix caprea*, on wood, 19.VIII.2019, A. Polhorský (A.P. 19/32c, non vid.). — **GERMANY**: **Brandenburg**, Cottbus, Spreewald, 4.5 km SW of Cottbus, 2.5 km NW of Kahren, W of Nutzberg, 88 m, stem of *Rubus fruticosus*, 10.IV.2004, V. Kummer (V.K.). – **Sachsen-Anhalt**, 6.5 km SE of Braunlage, WNW of Sorge, 490 m, branch of *Salix cinerea*, on wood, 20.V.2012, S. Helleman (ø, non vid.). – **Sachsen**, 2.5 km SE of Lößnitz, 1.6 km SSW of Dittersdorf, Sonntagswiese, 570 m, branch of *Betula*, on wood, 7.X.2016, B. Mühler (doc. vid.). – **Thüringen**, 3.2 km W of Sonneberg, 1.2 km W of Bettelhecken, Mürschnitzer Sack, 380 m, branch of ?*Salix*, on wood, 7.II.2009, I. Wagner (ø, doc. vid.). – ibid., twig of *Alnus glutinosa*, on wood, 14.XII.2013, I. Wagner (ø, doc. vid.). – ibid., 1.5 km W of Bettelhecken, 355 m, branch of *Fagus sylvatica*, on wood, 18.II.2010, I. Wagner (ø, doc. vid.). – ibid., 1.8 km W of Bettelhecken, 375 m, branch of *Frangula alnus*, on wood, 24.I.2013, I. Wagner (ø, doc. vid.). – 9.3 km SSE of Sonneberg, NNW of Rotheul, 345 m, branch of *Populus tremula*, on wood, 15.VII.2017, I. Wagner (ø, doc. vid.). – **Hessen**, 1.3 km E of Breitscheid, 0.8 km SW of Erdbach, Erdbachschlucht, 380 m, branch of *Prunus spinosa*, on wood, 2.V.2000, H.O. Baral (ø). – 21 km NW of Marburg, NW of Biedenkopf, Schlossberg, 350 m, branch of *Quercus*, on wood, 30.IV.2000, H.O. Baral & L.G. Krieglsteiner (ø). – **Rheinland-Pfalz**, 11 km N of Daun, E of Heyroth, 465 m, branch of *Quercus*, on wood, 7.VIII.2016, S. Helleman (doc. vid.). – 14 km SE of Pirmasens, SE of Dahn, military cemetery, 250 m, branch of *Quercus*, on wood & bark, 2.X.1994, H.O. Baral & G. Marson (H.B. 5159a). – ibid., branch of *Salix caprea*, on wood, 1.X.1994, H.O. Baral & G. Marson (ø). – 13 km SE of Pirmasens, 1 km W of Dahn, Kauert, 270 m, branch of *Fagus sylvatica*, on wood, 30.IX.1994, H.O. Baral (ø). – **Saarland**, 18 km NE of Merzig, Weiskirchen, park, 360 m, branch of *Amelanchier* ?*lamarckii*, on wood, 18.IV.2004, H.O. Baral (ø). – 15 km W of Idar-Oberstein, 7.7 km NW of Birkenfeld, NE of Thranenweier, Riedbruch, 582 m, branch of *F. sylvatica*, on wood, 16.IV.2004, S. Helleman (ø). – **Baden-Württemberg**, 12.5 km NE of Mosbach, ~5 km NE of Dallau, near Rittersbach, Elzbachtal, 275 m, branch of *Quercus*, on bark and *Colpoma quercinum*, 1.III.1997, A. Kaiser (H.B. 5726b). – 5.5 km NW of **Stuttgart**, 1.3 km S of Weilimdorf, SE of Wolfbusch, Waldfriedhof, 360 m, branch of *Fagus sylvatica*, on wood, 25.VI.2000, H.O. Baral (H.B. 6715b, **RefSpec** of *O. vinosa*, CBS 116215, anam. cult.; sq.: KT215266). – 5.3 km NW of Stuttgart, 1.5 km WNW of Feuerbach, Tannhäuserstraße, 320 m, branch of *Pyrus communis*, on wood, 16.X.1995, H.O. Baral (ø). – 3.5 km NW of Stuttgart, 1.5 km SW of Feuerbach, Heimberg, 360 m, branch of *Quercus*, on wood, 13.III.2003, H.O. Baral (ø). – 5 km WNW of Stuttgart, 1.2 km NE of Solitude, Sandkopf, Daimlerplatz, 426 m, branch of *Salix*, on wood, 18.XII.1989, H.O. Baral (H.B. 3946). – 0.3 km SE of **Tübingen**, west-end of Österberg, Wielandshöhe, 390 m, branch of *Cotinus coggygria*, on wood, 13.VII.2002, H.O. Baral (ø, anam. substr.). – 3 km SW of Tübingen, 1.3 km NNW of Weilheim, W of Ödenburg, 400 m, branch of *Carpinus betulus*, on wood, 21.XII.2003, H.O. Baral (ø, anam. substr.). – ibid., branch of *Prunus* (?) *domestica*, on wood, 21.XII.2003, H.O. Baral (ø). – 3 km NNW of Tübingen, N of Morgenstelle, Heuberg, 500 m, branch of *Salix caprea*, on wood, 5.IX.2003, H.O. Baral (ø). – E of Morgenstelle, Madenhalde, 425 m, branch of *Malus domestica*, on wood, 19.VII.1994, H.O. Baral (ø). – 4 km N of Tübingen, 1 km WSW of Bebenhausen, Goldersbach, 380 m, branch of *Prunus spinosa*, on wood, 27.VIII.1992, H.O. Baral (H.B. 4736 ø). – ibid., 20.IV.1993 (H.B. 4869 ø). – 2.6 km NW of Bebenhausen, pond W of Teufelsbrücke, 400 m, branch of *Carpinus betulus*, on wood, 17.IV.2003, H.O. Baral (ø). – ibid., S of Teufelsbrücke, 390 m, branch of *Fagus sylvatica*, on wood, 1.V.2002, H.O. Baral (ø). – 1.5 km SE of Bebenhausen, Kirnbachtal, S of Olgahain, 400 m, twig of *Lonicera xylosteum*, on wood, 4.XI.2001, H.O. Baral (H.B. 7060a). – ibid., 360 m, branch of *Ulmus*, on wood, 19.VII.1998, H.O. Baral (ø). – 8 km NW of Tübingen, 4 km N of Pfrondorf, NW of Eisenbachhain, 495 m, branch of *Quercus robur*, on wood, 17.III.1991, H.O. Baral (H.B. 4364). – 3.3 km NNE of Pfrondorf, Moosplatte, 460 m, branches of *Q. robur*, on wood, 1.VII.2000, H.O. Baral (H.B. 6717, anam. cult.). – ibid., branch of *Picea abies*, on wood (H.B. 6718, anam. substr.). – 1.8 km NNW of Pfrondorf, Zeitungseiche, 470 m, branch of *Ligustrum vulgare*, on wood, 30.I.2000, H.O. Baral (ø, anam. substr.). – 0.8 km N of Pfrondorf, Brandklinge, 410 m, branch of *Q. robur*, on wood, 3.X.2002, H.O. Baral & E. Weber (ø). – ibid., 430 m, trunk of *Malus domestica*, on bark, 9.I.2005, H.O. Baral (H.B. 7646b ø). – E of Pfrondorf, Tiefenbach, S of Einsiedlersteg, 385 m, branch of *Quercus*, on wood, 8.IV.1989, H.O. Baral (ø). – ibid., 410 m, branch of *Acer campestre*, on wood, 1.VI.1994, H.O. Baral & G.J. Krieglsteiner (ø). – ibid., branch of *Quercus robur*, on wood, 1.III.1996, H.O. Baral (ø). – ibid., 26.V.2006 (ø, anam. substr.). – ibid., branch of *Q. robur*, on bark & wood, 18. VII.1993, H.O. Baral & E. Weber (H.B. 4917). – ibid., branch of *Prunus* (?) *domestica*, on wood, 29.VI.1997, G. Marson (ø). – ibid., branch of *Populus tremula*, on wood, 11.VII.2000, H.O. Baral (ø). – 1.5 km NNE of Pfrondorf, Brand, 460 m, trunk of *Fagus sylvatica*, on wood, 30.VII.2000, H.O. Baral (ø). – 2 km SE of Pfrondorf, Hinterpfand, 370 m, branches of *Q. robur*, on wood, 10.III.2002, H.O. Baral (ø). – 0.8 km SE of Pfrondorf, Höhberg, 400 m, branch of *Salix caprea*, on wood, 27.I.2001, F. Baral-Weber (ø). – 0.5 km S of Pfrondorf, Haldenbach, 390 m, branch of *Picea abies*, on wood & bark, 8.VI.1997, H.O. Baral (ø, anam. substr.). – ibid., Mähder, branch of *Malus domestica*, on wood, 28.VII.2009, B. Liu & H.O. Baral (ø). – ibid., plank of (?)*P. abies*, on wood, no date, H.O. Baral (ø). – ibid., branch of *M. domestica*, on wood, 4.X.1994, H.O. Baral & K. Siepe (ø). – 0.9 km S of Pfrondorf, Bitzle, 350 m, branch of *Quercus robur*, on wood, 30.XI.2005, H.O. Baral (H.B. 8003a ø). – 1.3 km SW of Pfrondorf, quarry near Bitzle, 420 m, branch of *Salix caprea*, on wood, 26. III.1996, H.O. Baral (ø). – 0.3 km SW of Pfrondorf, S of Albstraße, 410 m, branch of *M. domestica*, on bark, 28.XI.1999, E. Weber & H.O. Baral (ø). – **Schwäbische Alb**, 2.5 km E of Reutlingen, 1.3 km NW of Eningen, Achalm ruin, 685 m, branch of *Acer campestre*, on wood, 25.VII.1999, H.O. Baral (ø). – 3 km SE of Urach, 1 km W of Wittlingen, Hohenwittlingen ruin, 650 m, branch of *Rosa*, on wood & bark, 16.III.2003, H.O. Baral (ø). – 6 km E of Reutlingen, 3 km ENE of Eningen, Hännersteigfels, 735 m, branch of *Quercus*, on wood, 3. III.2002, H.O. Baral (ø). – 8.5 km SSE of Reutlingen, 1.5 km SSW of Unterhausen, Gießstein, 775 m, branch of *Fagus sylvatica*, on wood, 1.IX.1999, H.O. Baral (ø). – 3.2 km SW of Urach, 1.9 km NNE of Bleichstetten, Buckenläre, 770 m, branch of *F. sylvatica*, on wood, 1.VI.1998, H.O. Baral (ø). – 3 km SE of Urach, 1 km W of Wittlingen, Hohenwittlingen farm, 680 m, branch of *Syringa vulgaris*, on wood, 16.III.2003, H.O. Baral (ø). – 3 km SW of Mössingen, 1.4 km S of Belsen, Alter Morgen, 570 m, branch of *Rosa*, on wood, 23.VI.2002, H.O. Baral (ø). – 5 km S of Gammertingen, 0.7 km E of Hermentingen, SW of Eichhalde 687 m, branch of *Salix*, on wood, 28.VI.2002, G. Marson (ø). – 16 km NE of Tuttlingen, 4 km NNW of Irndorf, Irndorfer Hardt, 870 m, branch of *Betula pendula*, on wood, 27.VI.1993, H.O. Baral (H.B. 4903a). – 14 km NNE of Ulm, ~5 km NW of Langenau, S of Lonetal, 570 m, trunk of *Picea abies*, on wood, 17.VI.1998, E. Weber (ø). – 7 km SSE of Bad Saulgau, 3 km NW of Altshausen, NW of Hirschegg, 635 m, branch of *Fagus sylvatica*, on wood, 26.VI.2005, G. Marson (ø). – **Bayern**, **Oberfranken**, 11 km NNW of Bayreuth, 3 km NW of Harsdorf, E of Fohlenhof, Trebgasttal, 333 m, branch of *Salix*, on bark, 28.II.1997, W. Beyer (ø). – 3.8 km E of Marktredwitz, S of Brand, Kleeschlag, 570 m, branch of *Acer pseudoplatanus*, on wood, 17.III.2019, M.

Map 45. Known distribution of *O. vinosa* in North America, Europe, and Tenerife (Macaronesia).

Reul (M.R. 6762, doc. vid.). – **Mittelfranken**, 40 km SE of Würzburg, ~12 km WNW of Neustadt a. d. Aisch, forest near Sugenheim, ~400 m, branch of *Quercus*, on wood, summer 1869 & 1870, H. Rehm (M, Rehm, Ascomyc. 17, Rabenhorst, Fungi Eur. Exs. 1412). – **Unterfranken**, 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz, 260 m, branch of *Rosa*, on wood & bark, 11. XI.1995, H.O. Baral & L.G. Krieglsteiner (L.K.). – **Oberpfalz**, 12 km NNE of Amberg, 1.5 km W of Hirschau, Moosweiher, 420 m, branch of *Populus tremula*, on wood, 29.XII.2003, H.O. Baral (H.B. 7451). – ibid., 1.VIII.2005 (ø). – ibid., branch of *Quercus robur*, on wood, 30.XII.2003 (H.B. 7449a, anam. substr.). – 2 km W of Hirschau, Haarbühl, 445 m, branch of *Q. robur*, on wood, 29.XII.1993, H.O. Baral (ø). – 2 km NW of Hirschau, Ziegelschlag, 450 m, branch of ?*Frangula alnus*, on wood, 11.VIII.2002, H.O. Baral (ø). – ibid., branch of *Salix caprea*, on wood, 2.VIII.2005, H.O. Baral (ø). – ibid., 460 m, branch of *Quercus*, on wood, 26.XII.2004, H.O. Baral (ø). – 1.3 km NW of Hirschau, Eschenbach, 445 m, branch of *Q. robur*, on bark and old ?*Vuilleminia*, 31.XII.1993, H.O. Baral (H.B. 5011a). – ibid., branch of *Rosa*, on bark, also on *Diaporthe* and *Diatrype stigma*, 3.VIII.1994, H.O. Baral (H.B. 5122b). – ibid., branch of *Sambucus racemosa*, on wood, 11.VIII.2002, H.O. Baral (ø). – 1.8 km WNW of Hirschau, Eschenbach, 440 m, branch of *Q. robur*, on bark & wood, 8.VIII.1993, H.O. Baral (H.B. 4929b). – 1.2 km NNW of Hirschau, Weinberg, 455 m, branch of *Salix caprea*, on wood, 27.XII.2003, H.O. Baral (ø). – ibid., 27.XII.2005 (ø). – 14.5 km NE of Amberg, 1 km W of Schnaittenbach, Hirschauer Mühlbach, E of Haidmühle, 405 m, branch of *S. cinerea*, on wood, 6.II.1992, H.O. Baral & E. Weber (ø). – 12.5 km NE of Tirschenreuth, 1.2 km S of Neualbenreuth, SE of Platzermühle, 550 m, branch of *Quercus*, on bark, 3.VIII.1995, H.O. Baral (H.B. 5312). – 15 km NE of Cham, 3.5 NW of Furth im Wald, NW of Roberthütte, 750 m, branch of *Fagus sylvatica*, on wood, 5.VIII.2005, E. Weber & H.O. Baral (H.B. 7861a ø). – 7 km NE of Regensburg, ENE of Wenzenbach-Grünthal, Spindelbach NE of Totenmannfeld, 380 m, branch of *Salix*, on wood, 31.I.1990, H.O. Baral & E. Weber (REG). – **Oberbayern**, 11 km NW of München, 1 km NE of Allach, Allacher Forst, N of Waldkolonie, 510 m, branch of *Quercus*, on wood, 11.VI.1999, L. Beenken (ø). — **SWITZERLAND**: **Nidwalden**, 8.5 km SSW of Luzern, 2 km SW of Hergiswil, Renggpass, 890 m, branch of *Acer pseudoplatanus*, on wood, 15.VIII.2006, H.O. Baral (ex H.B. 8235a, in M-0276492 [*H. hergiswiliana*], anam. substr.). – **Schwyz**, 13 km S of Einsiedeln, 4 km SW of Oberiberg, SE of Ibergeregg, Schijenloch, 1500 m, branch of *Picea abies*, on wood, 9.X.1992, G. Marson (H.B. 4801b). – **Uri**, 4 km NW of Andermatt, 2.5 km WSW of Göschenen, Steglaui, 1300 m, branch of *Alnus alnobetula*, on wood, 20.VIII.2006, H.O. Baral (H.B. 8291). – ibid., 1250 m, F. Müller (ø). – **Bern**, 10 km ESE of Frutigen, Griesalp, 1470 m, branch of *Picea abies*, on wood, 18.VII.2018, B. Senn-Irlet (B.S.I. 18/89). – **Fribourg**, 16 km NNE of Montreux, 5 km WSW of Gruyères, N of Moléson Mt., Les Joux Devant, 1270 m, twig of *P. abies*, on wood, 21.VI.2014, H. Aeberhard (ø). – **Jura**, 8 km WSW of Tramelan, 1 km SSW of Les Breuleux, Pâturage communal, 1027 m, branch of *P. abies*, on wood, 14.VI.2018, H.O. Baral (ø). – **Ticino**, 8 km WSW of Bedretto, 2022 m, twig of *Rhododendron ferrugineum*, on wood, 30.VIII.2018, J.P. Priou (J.P.P. 18048, doc. vid.). — **AUSTRIA**: **Tirol**, 9 km NW of Imst, 5.3 km ESE of Taschach, Hahntennjoch, ~1950 m, branch of *Sorbus chamaemespilus*, on wood, 20.VI.1999, L. Beenken (ø, anam. substr.). – **Kärnten**, 15 km S of Klagenfurt, 5.5 km SE of Ferlach, Waidisch, 950 m, trunk of *Fagus sylvatica*, on wood, 20.XI.2011, G. Friebes (ø, doc. vid.). – 12 km SE of Klagenfurt, NW of St. Margareten im Rosental, 565 m, branch of *Corylus avellana*, on bark, 13.X.1994, W. Jaklitsch (ø). – ibid., 550 m, branch of *F. sylvatica*, on wood, 3.XII.1994, W. Jaklitsch (H.B. 5202b). – SW of St. Margareten, NE of Sabosach, 580 m, branch of *Quercus robur*, on wood, 2.XII.1994, W. Jaklitsch (ø). – **Steiermark**, 11 km NW of Deutschlandsberg, 3 km W of Rachling, E of Rosenkogel, 1160 m, branch of *F. sylvatica*, on wood, 24.III.2012, G. Friebes (ø, doc. vid.). – 14 km SW of Hartberg, W of Herberstein, 520 m, branch of *Quercus*, on wood, 2.III.2013, G. Friebes (ø, doc. vid.). – ibid., Feistritzklamm, 380 m, branch of *Quercus*, on wood, 30.VIII.2013, G. Friebes (G.F. 20130070, anam. substr., doc. vid.). – 14 km NE of Graz, W of Rein, St. Ulrich, 540 m, branch of *F. sylvatica*, on wood & bark, 22.II.2014, G. Friebes (G.F. 20140030). – 6 km NNW of Graz, 2 km NW of Andritz, 500 m, branch of *Pinus sylvestris*, on wood, 1.IV.2013, G. Friebes (ø, doc. vid.). – 3 km NNW of Graz, NW of Reinerkogel, 440 m, branch of indet. angiosperm, on wood, 12. II.2014, G. Friebes (G.F. 20140020). – 4.5 km NNW of Gratwein, 3.5 km WSW of Unterfriesach, N of Hörgasgraben, base of Kaschlsteig, 673 m, branch of *Quercus*, on wood & bark, 9.XII.2017, G. Friebes (ø, doc. vid.). – **Burgenland**, 5.5 km WNW of Rechnitz, 1.5 km N of Althodis, Baumwipfelweg, 550 m, branch of *Quercus*, on wood, 27.II.2016, G. Friebes (G.F. 20160021, doc. vid.). — **LUXEMBOURG**: **L'Oesling**, **Vianden**, 5 km NW of Vianden, NW of Stolzembourg, Fréiboesch, 315 m, branch of *Cytisus scoparius*, on wood, 1.VI.1997, G. Marson (H.B. 5941a, anam. substr.). – **Redange**, 10.5 km W of Ettelbruck, 1.8 km NW of Grosbous, Bruch, 385 m, branch of *Salix*, on wood, 24.IV.2001, G. Marson & H.O. Baral (ø). – **Gutland**, **Diekirch**, 3.5 km E of Diekirch, 1.7 km SW of Bettendorf, Schoofsboesch, Carrières de Gilsdorf, 313 m, branch of *Rosa*, on wood & bark, 26.IV.1994, H.O. Baral (ø). – 5.5 km ENE of Diekirch, 1.5 km NE of Bettendorf, Niderbierg, 390 m, branches of *Corylus avellana*, on bark, 27.IV.1995, H.O. Baral & G. Marson (ø). – 9.5 km NE of Mersch, 2 km NW of Medernach, Seitert (central part), 330 m, branch of *Sorbus torminalis*, on wood, 24.IV.1994, H.O. Baral & G. Marson (ø). – **Echternach**, 7.5 km W of Echternach, 3.3 km SW of Berdorf, NNE of Müllerthal, Schnellert, 230 m, trunk of *Fagus sylvatica*, on wood, 7.V.1998, H.O. Baral (ø). – 4.7 km WSW of Echternach, 1.7 km N of Scheidgen, Deisterbaach, 325 m, branch of *Frangula alnus*, 1.II.2003, G. Marson (ø). – ibid., branch of *Corylus avellana* (ø). – 1.5 km E of Scheidgen, N of Michelshaff, 320 m, stem of *Rubus fruticosus*, 27.I.2007, G. Marson (ø, anam. substr.). – **Grevenmacher**, 4 km NNE of Grevenmacher, 2 km NW of Mertert, Schlaufiels, N of Schlammbaach, 220 m, branch of *Corylus avellana*, on bark, 19.III.1995, G. Marson (H.B. 5281c). – 15 km ENE of Luxembourg, 1.5 km NE of Mensdorf, Widdebierg, 380 m, branch of *Quercus*, on bark & wood, 5.III.2007, G. Marson (H.B. 8455b ø). – **Mersch**, 8 km ENE of Mersch, 1 km SW of Larochette, Manzebach, 307 m, branch of *Alnus glutinosa*, on wood, 27.IV.1994, G. Marson & H.O. Baral (ø). –

7 km ESE of Mersch, 1.2 km W of Koedange, NNE of Stuppicht, Breedschet, 405 m, branches of *Frangula alnus*, on wood, 12.VII.2014, G. Marson (G.M. 2014-07-12.1; sq.: KT380090). – **Capellen**, 4 km WNW of Capellen, 2 km E of Steinfort, Treisch, 325 m, branch of *Fagus sylvatica*, on wood, 8.V.1997, G. Marson (ø). – 2.5 km SW of Capellen, 2 km NNE of Garnich, Melzer-Schilzenheck, 315 m, branch of *Salix*, on wood, 7.V.1997, H.O. Baral, G. Marson & B. Declercq (ø). – ibid., branch of *Quercus*, on bark and old *Vuilleminia*, 6.V.1998, G. Marson (ø). – ibid., branch of *Prunus spinosa*, on wood (H.B. 6201b, anam. substr.). – 11 km NNW of Esch-sur-Alzette, 5 km NE of Pétange, Griechten, 335 m, branch of *Salix caprea*, on wood, 9.V.1999, H.O. Baral (ø). – ibid., branch of *Rosa canina*, on wood, 9.V.1999, H.O. Baral (ø). – **Luxembourg**, 5 km NW of Luxembourg, 1.3 km S of Bridel, Gebranntebësch, 355 m, branch of *Quercus rubra*, on wood, 14.II.2014, G. Marson (G.M. 2014-02-14.1, anam. cult.; sq.: KT380089). – 5.5 km NNW of Luxembourg, 1.5 km E of Bridel, Plakigebierg, 280 m, branch of *Prunus spinosa*, on wood, 1.III.1998, G. Marson (ø). – 3 km NE of Luxembourg, 1 km NE of Kirchberg, Kirchbierg, 350 m, branch of ?*Salix*, 25.VIII.1998, G. Marson (ø). – 6 km NNE of Luxembourg, 3 km E of Walferdange, Gréngewald, Stafelter, 425 m, branch of *Quercus*, on wood, 19.IV.2011, G. Marson (G.M. 2011-04-19.1, anam. cult.; sq.: KT380060). – Gréngewald, unlocalized, on wood of *Quercus*, III.1899, J. Feltgen (LUX 42533, as *O. chrysocoma*). – 8.5 km NNE of Luxembourg, 1.4 km SSE of Eisenborn, Gréngewald, SE of Judesbierg, 395 m, branch of *Fagus sylvatica*, on wood, 6.IX.2009, G. Marson (ø). – 9.5 km NE of Luxembourg, 0.8 km N of Rameldange, 378 m, branch of *Cytisus scoparius*, on wood, 12.II.2000, G. Marson (H.B. 6572). – 11 km ESE of Luxembourg, 2 km E of Oetrange, Draf, 268 m, branch of *Sambucus racemosa*, on bark & wood, 4.IX.1998, G. Marson (H.B. 6240b, anam. only). – 7 km SE of Luxembourg, 2 km ESE of Alzingen, Héid, 300 m, branch of *Carpinus betulus*, on wood, 22.VII.1993, H.O. Baral (ø). – 5 km S of Luxembourg, 1.8 km SW of Hesperange, Fennerholz, 292 m, branch of *C. betulus*, on wood, 24.II.2003, G. Marson (ø). – ibid., 295 m, branch of *Quercus*, on wood, 9.II.2017, G. Marson (G.M. 2017-02-09.1, sq.: MH221059). – 1.5 km W of Hesperange, Biersak/Géisselbierg, 290 m, branch of *Salix* ?*caprea*, on wood, 23.XII.1997, G. Marson (ø). – ibid., branch of *Quercus*, 3.I.2004, G. Marson (ø). – 5 km SSW of Luxembourg, N of Kockelscheier, Weier, 300 m, branch of *Rosa canina*, on wood, 2.XI.1997, G. Marson (ø). – branch of *Cornus alba*, on wood, 19.VIII.2010, G. Marson (ø). – NE of Kockelscheier, Laangeweier, 305 m, branches of *Salix*, on wood, 2.XI.1997, G. Marson (ø). – **Esch-sur-Alzette**, W of Kockelscheier, Houbësch, 320 m, branch of *C. betulus*, on wood, 15.VIII.1998, G. Marson (H.B. 6211a, anam. substr.). – 1.5 km SW of Kockelscheier, Conter Jans Boesch, 289 m, branch of *Carpinus betulus*, on wood, 4.V.2016, G. Marson (G.M. 2016-05-04.1, anam. cult.; sq.: MG372377). – 8.5 km SW of Luxembourg, 1.6 km WSW of Leudelange, Guedesbiirchen, 320 m, branch of *Salix* (?)*alba*, on wood, 12.I.1989, H.O. Baral & G. Marson (H.B. 3633). – ibid., branch of *Prunus spinosa*, on wood, 12.I.1989, G. Marson & H.O. Baral (H.B. 3634a). – 5.5 km E of Pétange, 2 km S of Schouweiler, Jongeboesch, 337 m, branch of *Q. robur*, on wood, 6.V.1999, H.O. Baral (ø). – 2.2 km S of Esch-sur-Alzette, 1.5 km ENE of Audun-le-Tiche, Ellergronn, 345 m, branch of *F. sylvatica*, on wood, 26.IV.2001, G. Marson (H.B. 6922d). – ibid., branch of *Salix caprea*, on bark, 26.IV.2001, H.O. Baral & G. Marson (ø). – 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, branch of *Quercus*, on wood & bark, 12.VI.1994, G. Marson (H.B. 5112). – ibid., on indet. tree, 1.V.1994, G. Marson (ø, anam. cult., H.B. 6264 [dried culture]). – ibid., branch of *Rosa canina*, on bark & wood, 5.VI.1999, G. Marson (ø, anam. substr.). – ibid., on *Cornus*, 17.VII.2001, G. Marson (ø, anam. substr.). – 1.9 km SW of Kayl, Léiffraechen, 380 m, branch of *Rosa* ?*canina*, on wood, 1.XII.1997, G. Marson (ø). – 6.5 km ESE of Esch-sur-Alzette, 1.5 km SW of Dudelange, Haard, 375 m, twig & branch of *Populus tremula*, on wood, 5.IV.2003, G. Marson (ø). – 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, branch of *Robinia pseudoacacia*, on wood, 31.X.1993, G. Marson (H.B. 4982). — **FRANCE**: **Bretagne**, **Morbihan**, 3 km S of Baud, 1.2 km W of Camors, NW of Le Petit Bois, 75 m, branch of *Ilex aquifolium*, on wood, 23.X.2004, J.P. Priou (J.P.P. 24173). – 13 km W of Herbignac, 2 km SW of Pénestin, la Poudrantais, 3 m, branch of *Ulex europaeus*, on wood, 9.XII.2005, J.P. Priou (J.P.P. 25161, non vid.). – 5.5 km SW of Guer, 2 km NE of Monteneuf, Les Pierres Droites, 140 m, branch of *Quercus petraea*, on wood, 9.VI.2003, H.O. Baral (ø, anam. substr.). – 8 km N of Carentoir, 1.7 km S of Guer, Pont de l'Oyon, 40 m, branch of *Quercus*, on wood, 18.XII.2003, J.P. Priou (J.P.P. 23135, non vid.). – 11 km W of La Gacilly, 3 km NW of St.-Martin-sur-Oust, ENE of Les Gaudines de Haut, 63 m, branch of *Castanea sativa*, on wood, 6.XII.2003, J.P. Priou (J.P.P. 23123, doc. vid.). – 5.5 km W of La Gacilly, 3.2 km NNE of Les Fougerêts, WNW of St.-André, 86 m, twig of *Ulex europaeus*, on bark, 14.XII.2003, J.P. Priou (ø, non vid.). – 1.9 km NE of La Gacilly, SW of Lieuvy, 10 m, branch of *Fraxinus excelsior*, on wood, 14.V.2010, J.P. Priou (J.P.P. 10094). – 3.3 km ENE of La Gacilly, SW of Sixt-sur-Aff, 40 m, branch of *Castanea sativa*, on wood, 10.VI.2003, H.O. Baral (ø). – 1.8 km ESE of La Gacilly, 1.4 km NNW of Cournon, Moulin de Coq, 80 m, branch of *Quercus*, on wood, 12.XII.2003, J.P. Priou (J.P.P. 23125, non vid.). – **Ille-et-Vilaine**, 8.5 km N of Redon, 2.5 km NNW of Bains-sur-Oust, la Giraudaie, 47 m, branch of *Pinus sylvestris*, on wood, 21.I.2004, J.P. Priou (J.P.P. 24027, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 13 km WSW of Nantes, NW of St.-Jean-de-Boiseau, W of La Rivière, 13 m, branch of *Cytisus scoparius*, on wood, 15.XI.2009, J.P. Priou (J.P.P. 29213, doc. vid.). – **Vendée**, 33 km NW of La Rochelle, 1.5 km WNW of La Tranche-sur-Mer, W of Savinière, 12 m, branch of *Q. ilex*, on wood, 2.VI.2003, H.O. Baral (ø). – NE of La Savinière, 4 m, branch of *Salix* (?)*atrocinerea*, on wood, 2.VI.2003, H.O. Baral (ø). – 21 km SSW of La Roche-sur-Yon, 2.3 km NNW of Avrillé, Bois de la Garde, 35 m, branch of *Castanea sativa*, on wood, 5.VI.2003, H.O. Baral (ø). – **Poitou-Charentes**, **Charente-Maritime**, 8.7 km N of St.-Jean-d'Angély, 2.3 km SSE of Lozay, Bois d'Essouvert, 90 m, branch of *Corylus avellana*, on wood, 1.I.2007, M. Hairaud (M.H. 30107, doc. vid.). – Île de Ré, 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, branch of *Tamarix anglica*, on wood, 26.IV.2006, H.O. Baral (ø). – **Deux-Sèvres**, 13.5 km N of Melle, 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 100 m, branch of *Carpinus betulus*, on wood, 17.IV.2008, S. Helleman (ø). – **Centre**, **Loiret**, Orléanais, 18 km S of Montargis, SE of Nogent-sur-Vernisson, Les Barres, 145 m, stem of *Rubus fruticosus*, 12.II.1994, A. Reynaud (H.B. 6232). – **Île-de-France**, **Yvelines**, 20 km NW of Paris, 1.8 km NW of Maisons-Laffitte, Forêt St.-Germain-en-Laye, 47 m, branch of *Fagus sylvatica*, on wood, 2.I.2004, J.P. & J.L. Priou (J.P.P. 24002, non vid.). – **Lorraine**, **Vosges**, 10 km WNW of Gérardmer, 1.8 km ESE of Rehaupal, SE of Varinfête, 630 m, branches of *Malus domestica*, on wood & bark, 7.IX.1996, H.O. Baral (ø). – 10 km NW of Gérardmer, 2.3 km SW of Granges-sur-Volonge, NW of Faing Musqué, 730 m, branch of *Sambucus racemosa*, on wood, 7.IX.1996, H.O. Baral (ø). – 2 km NW of Gérardmer, La Pépinière des Xettes, 900 m, branch of *Salix*, on wood, 7.IX.1998, H.O. Baral (ø). – 1 km NNW of Gérardmer, La Basse de la Mine, 750 m, branch of *Acer pseudoplatanus*, on wood, 7.IX.1996, G. Marson (ø). – ibid., branch of *Corylus avellana*, on wood, 8.IX.1998, H.O. Baral (ø). – 10 km SE of Gérardmer, 4 km SW of Le Hohneck, S of Lac de Blanchemer, 1200 m, branch of *Fagus sylvatica*, on wood, 9.IX.1998, F. Baral-Weber & H.O. Baral (ø). – **Alsace**, **Haut-Rhin**, 25 km W of Basel, 2 km E of Bisel, W of Rehhof, 425 m, branch of *Quercus*, on wood, 19.IX.1999, H.O. Baral (ø). – Vosges, 13 km ENE of Gérardmer, 3.5 km NE of Col de la Schlucht, Tourbière du Tanet, 1225 m, branches of *F. sylvatica*, on wood, 3.IX.1996, H.O. Baral (H.B. 5569). – **Bourgogne**, **Côte-d'Or**, 13 km SW of Dijon, 1.8 km WSW of Gevrey-Chambertin, Combe Lavaux, 350 m, branch of *Corylus avellana*, on wood, ~XI.2010, S. Bougreau, vid. J.P. Priou (ø, non vid.). – **Nièvre**, 6 km ESE of Château-Chinon-Ville, 1 km WSW of Arleuf, 605 m, branch of *Fraxinus excelsior*, on wood, 30.IV.2011, E. Weber & V. Baral (ø). – **Auvergne**, **Cantal**, 14 km ENE of Aurillac, 3.5 km ESE of Polminhac, Les Huttes, 977 m, branch of *Salix*, on wood, 31.VIII.2011, J.P. Priou (J.P.P. 11086, doc. vid.). – 12 km S of St.-Flour, 3 km ESE of Lavastrie, S of Grandval, 748 m, branch of *Quercus*, on wood, 8.IX.2009, J.P. Priou (J.P.P. 29169, non vid.). – 9 km S of St.-Flour, 1.3 km SSE of Alleuze, Bois de la Bastide, 855 m, branch of *Salix*, on wood, 8.IX.2009, J.P. Priou (J.P.P. 29176, doc. vid.). – **Haute-Loire**, 19 km SW of St.-Étienne, ~4.5 km S of Aurec-sur-Loire, ~S of La Chapelle-d'Aurec, 700 m, branch of *Pinus*, on wood, 20.IX.1993, G. Marson (H.B. 5004, anam. substr.). – **Rhône-Alpes**, **Loire**, 16 km WNW of Boën, 1.5 km S of St.-Jean-la-Vêtre, Ventuel, 880 m, branch of *Castanea sativa*, on wood & bark, 6.V.2010, N. Van Vooren (ø). – 10 km SW of Boën, 1 km SE of St.-Georges-en-Couzan, le Pont du Diable, 570 m, twig of *Lonicera xylosteum*, on wood, 5.V.2010, H.O. Baral (ø). – 19 km WSW of Roanne, 4 km WSW of Arcon, le Gué de la Chaux, 1060 m, branch of *Cytisus scoparius*, on wood, 7.V.2010, J.P. Priou (ø). – **Isère**, 19 km SW of Grenoble, 2 km SE of Villard-de-Lans, N of Les Glovettes, 1240 m, branch of *Rhamnus alpina*, on wood, 11.VIII.2009, B. Liu (H.B. 9141). – branch of *Fagus sylvatica*, on wood, 11.VIII.2009, H.O. Baral (H.B. 9128c). – **Drôme**, 19 km S of Die, 2.7 km SW of Poyols, 862 m, branch of *Rosa*, on old *Vuilleminia*, 12.VIII.2009, G. Marson (H.B. 9194 ø). – ibid., branch of *Pyrus communis*, on wood, 12.VIII.2009, H.O. Baral (H.B. 9131b). – 1 km N of Nyons, Col du Pontias, 460 m, branch of *Spartium junceum*, on wood, 11.X.2002, G. Marson (H.B. 7293b). – 17 km E of Nyons, 4.5 km S of Rémuzat, Col de Soubeyrand, 1005 m, branch of *Pinus sylvestris*, on wood, 10.X.2002, G. Marson (H.B. 7249c ø, anam. substr.). – 2 km SSE of Nyons, 550 m, on wood & bark of (?)*Rosmarinus officinalis*, 7.VIII.1999, G. Marson (ø, anam. substr.) – 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branches of *P. sylvestris*, on wood, 23.VIII.1996, G. Marson (H.B. 5626d). – 5 km SE of Montélimar, 2.3 km NW of Espeluche, 150 m, branch of *Spartium junceum*, on wood, 12.IX.2018, G. Marson (G.M. 2018-09-12.5; sq.: MK473402). – **Ardèche**, ~23.5 km NW of Aubenas, ~4.5 km ESE of St.-Cirgues-en-Montagne, ~1270 m, branch of ?*Juniperus communis*, on wood, 21.IX.1993, G. Marson (ø). – 5 km E of Vallon-Pont-d'Arc, 4 km WNW of St.-Remèze, les Mouniers, 410 m, branch of *Quercus*, on wood, bark & *Vuilleminia*, 8.X.2002, G. Marson (ø). – ibid., on twig & branch of *Ulex parviflorus*, on wood, 8.X.2002, G. Marson (ø). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 1 km NW of Gap, E of Les Coutières, Col du Festre,

1390 m, branch of *Larix ?decidua*, on wood, 23.VIII.2000, G. Marson (ø). – **Alpes-de-Haute-Provence**, 6 km NW of Manosque, NE of St.-Martin-les-Eaux, 632 m, branch of *Crataegus monogyna*, on *Vuilleminia*, 29.IX.1993, G. Marson (H.B. 5002c). – 8 km SE of St.-Julien-du-Verdon, 3 km NW of Soleilhas, Vauplane, 1595 m, branch of *Buxus sempervirens*, on wood, 16.VII.1994, G. Marson (ø). – 12 km NE of Grasse, 4 km NE of Gourdon, N of Courmes, 600 m, twig of *Fabaceae*, on wood, 19.IX.1998, D. Triebel & G. Rambold (G.R. 6258, M-0229712, deposited under *Claussenomyces* aff. *atrovirens*). – 10 km ESE of Sederon, W of Curel, 765 m, branches of *Spartium junceum*, on wood, 17.VIII.2001, G. Marson (H.B. 7024b, anam. substr.). – 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *Picea abies*, on wood, 17.VII.1994, G. Marson (H.B. 5125c ø). – **Alpes Maritimes**, 33 km ENE of Digne, 0.9 km SE of Colmars-les-Alpes, Chemin Cascade de la Lance, 1315 m, branch of *Buxus sempervirens*, on wood, 6.VI.2010, J.P. Priou (J.P.P. 10129, non vid.). – 10 km NW of Grasse, 2 km NW of St.-Vallier-de-Thiey, Pas de la Faye, 945 m, branches of *Ficus carica*, on wood, 18.IX.2011, G. Marson (G.M. 2011-09-18.1; sq.: KT222394). – 24 km N of Nizza, 1.5 km WSW of Utelle, Madone d'Utelle, 1160 m, branches of *Pinus sylvestris*, on wood, 3.X.1993, G. Marson (H.B. 5142b). – 25 km NNW of Monte Carlo, 6.5 km E of Lantosque, Col du Turini, 1640 m, branch of *Quercus*, on wood, 3.X.1993, G. Marson (ø). – **Var**, 26 km NW of Grasse, 12.5 km SE of Castellane, NNW Le Logis-du-Pin, 1035 m, branch of *Acer*, on wood, 5.X.1993, G. Marson (H.B. 4987b). – 13.3 km ENE of Hyères, 4.3 km ENE of La Londe-les-Maures, NE of vale Rose, 135 m, trunk of *Quercus suber*, on bark, 2.III.1990, C. Roux (C.R.). – **Bouches-du-Rhône**, 13 km NE of Aix-en-Provence, 5 km NE of Venelles, ~S of Meyrargues, ~300 m, branch of *Pinus*, on wood, 3.XI.2006, H. Aeberhard (H.B. 9088 ø). – ibid., 30.X.2006 (H.B. 9089 ø, anam. substr.). – ibid., twig & branch of *Pinus*, on wood & bark, (H.B. 9090a ø). – ibid., branch of *Pinus halepensis*, on wood, 31.X.2006, H. Aeberhard (H.B. 9084a). – **Vaucluse**, 14 km SE of Carpentras, 4 km SE of Venasque, 485 m, branch of *Lonicera ?xylosteum*, on wood, 9.X.2002, G. Marson (H.B. 7238d). – 18 km SE of Carpentras, 9 km NNW of Roussillon, ESE of Col de Murs, 552 m, branch of *Spartium junceum*, on wood, 9.X.2002, G. Marson (ø). – 17 km NE of Carpentras, 5.5 km E of Malaucêne, 6 km W of Mt. Ventoux summit, Les Ramayettes, 980 m, branch of *Quercus*, on wood (H.B. 4941b). – Luberon Mt., 9 km SE of Apt, 2.5 km SSE of Auribeau, Mourre Nègre, 1100 m, branches of *Corylus avellana*, on wood and old *Vuilleminia*, 28.IX.1993, G. Marson (ø). – **Languedoc-Roussillon**, **Gard**, 11 km ENE of Nîmes, near Bezouce, 70 m, branch of *Q. ilex*, on wood, 26.IX.1993, G. Marson (H.B. 4998a). – **Lozère**, 21 km NW of St.-Jean-du-Gard, WSW of Le Pompidou, ~870 m, branch of *Q. ilex*, on wood, 25.IX.1993, G. Marson (H.B. 4992a). – **Pyrénées-Orientales**, 3 km SSE of Prats-de-Mollo, Col de la Seille, 1197 m, branch of *Crataegus monogyna*, on old *Vuilleminia*, 28.IX.1999, G. Marson (ø). – **Midi-Pyrénées**, **Hautes-Pyrénées**, 44 km S of Tarbes, 15 km WNW of St.-Lary-Soulan, lac d'Aubert & d'Aumar, branch of *Pinus uncinata*, on wood, 2180 m, 27.VIII.2014, G. Moyne & R. Dougoud, vid. B. Perić (doc. vid.). – **Aquitaine**, **Pyrénées-Atlantique**, 21 km WSW of Oloron-Ste.-Marie, 6 km W of Osse-en-Aspe, Forêt de Issaux, 650 m, branch of *Corylus avellana*, on wood, 9.X.2016, H.O. Baral (ø). – ibid., branch of *Ilex aquifolium*, on wood (ø). — **ANDORRA**, 8.5 km NNW of Massana, 4 km W of El Serrat, Basses del Port de Rat, 2405 m, twig of *Rhododendron ferrugineum*, on wood, 10.VII.1996, J. Vila (A.H. 7103). — **SPAIN**: **Asturias**, 7 km NW of Tineo, SSE of Bustellán, Valle de Tablado, 512 m, branch of *Q. robur*, on wood, 5.VIII.2010, E. Rubio (E.R.D.-5183, doc. vid.). – 14 km WSW of Grado, 2.2 km ENE of Soto de los Infantes, SE of Viescas, 440 m, branch of *Q. petraea*, on bark, 5.VI.2013, W. Jaklitsch (ø). – 2.4 km N of Pola de Somiedo, 2 km S of Castro, 703 m, branch of *Q. ilex*, on wood, 7.VI.2013, H.O. Baral (ø). – 2.4 km N of Pola de Somiedo, 2 km S of Castro, 703 m, branch of *Rhamnus alaternus*, on wood, 7.VI.2013, H.O. Baral (ø). – ibid., branch of *Corylus avellana*, on wood, 7.VI.2013, H.O. Baral (H.B. 9822c). – 8.5 km ESE of Pola de Somiedo, 3.5 km ESE of Valle de Lago, 1330 m, branch of *C. avellana*, on wood, 4.VI.2013, H.O. Baral (H.B. 9794). – 6 km SE of Valle de Lago, Lago del Valle, 1560 m, branch of *Corylus avellana*, on bark, 6.VI.2017, S. Serrano (H.B. 10094 ø). – **País Vasco**, **Gipuzkoa**, 15 km ENE of San Sebastián, Irun, NW of train station, 7 m, branch of *Salix*, on wood & bark, 8.V.1996, H.O. Baral (H.B. 5458). – **Cataluña**, **Girona**, eastern Pyrenees, 26 km NE of Ripoll, 2.3 km NE of Molló, 2.6 km WSW of Col d'Ares, 1310 m, branch of *S. caprea*, on wood, 28.IX.1999, H.O. Baral (ø). – branch of *Betula*, on wood, 28.IX.1999, G. Marson (ø). – 5 km NE of Molló, Col d'Ares, 1530 m, branch of *Pinus ?contorta*, on wood, 28.IX.1999, H.O. Baral (ø). – **Aragón**, **Huesca**, 15 km N of Jaca, S of Canfranc, 1015 m, branches of *Rosa*, on wood, 13.X.2010, J.P. Priou (J.P.P. 10166, non vid.). – 12.7 km N of Jaca, NNE of Villanúa, 970 m, branches of *Rosa*, on wood, 9.X.2016, H.O. Baral (ø). – ibid., branch of *Quercus rotundifolia*, on wood (H.B. 10028b). – **Teruel**, Sierra de Albarracín, 43 km WNW of Teruel, 4 km S of Bronchales, 1.9 km NE of Noguera de Albarracín, 1595 m, branch of *Cistus laurifolius*, on wood, 26.V.2011, R. Tena (R.T.L. 11052601, doc. vid.). – 4.3 km N of Noguera de Albarracín, SW of Bronchales, 1695 m, branch of *C. laurifolius*, on wood, 19.V.2011, R. Tena (R.T.L. 11051903, doc. vid.). – ibid., 2.VI.2011 (R.T.L. 11060201, doc. vid.). – ibid., 3.IV.2013 (ø). – 49 km N of Teruel, NNE of Corbatón, 1200 m, branch of *Quercus rotundifolia*, 22.VII.2013, R. Tena (R.T.L. 13072201). – **Castilla y León**, **León**, 20 km WNW of La Robla, Mirantes de Luna, 1120 m, 20.IV.2019, E. Rubio (E.R.D. 7900, doc. vid.). – **Segovia**, Sierra de Guadarrama, 66 km ENE of Segovia, 4.8 km SE of Riofrío de Riaza, Puerto de La Quesera, 1650 m, branch of *Erica*, on wood, 26.V.1996, H.O. Baral (ø). 45 km SW of Avila, 4 km N of Cuevas del Valle, Puerto del Pico, 1348 m, branch of *Salix*, on wood, 16.VI.2017, J.P. Priou (J.P.P. 17157, doc. vid.). – **Madrid**, 30 km NW of Madrid, 1 km N of Hoyo de Manzanares, 1075 m, branch of *Cistus ladanifer*, on wood, 16.XII.2017, I. Olariaga (ø, doc. vid.). – ~14 km NNW of Madrid, El Pardo, ~650 m, branch of *Cistus ladanifer*, on wood, 5.XII.1984, G. Moreno, R. Galán & J.T. Palmer (AH 6402-2). – ibid., 3.I.1983, J. Checa (AH 6178). – **Castilla-La Mancha**, **Guadalajara**, 33 km SSE of Sigüenza, ~6 km E of Cifuentes, 1000 m, on cone of *Pinus halepensis*, 17.XII.1991, A. Raitviir (TAAM, AH 6727 slide, H.B. 5216 ø). – 18 km SW of Sigüenza, 2.5 km NE of Almadrones, 1065 m, branch of *Q. rotundifolia*, on wood, 24.IX.1999, H.O. Baral (ø, anam. substr.). – 43 km NNW of Guadalajara, 2 km NNW of Tamajón, Ermita de los Enebrales, 1040 m, branch of *Cistus ladanifer*, on wood, 14.V.1996, E. Weber (H.B. 5464b, anam. substr.). – ibid., branch of *Rosa*, on wood, 14.V.1996, H.O. Baral (H.B. 5482i). – 55 km NNW of Guadalajara, NW of Majaelrayo, Arroyo La Matilla, 1180 m, branch of *Q. pyrenaica*, on wood & bark, 14.V.1996, H.O. Baral (H.B. 5479b). – 36 km ESE of Guadalajara, SSE of Alocén, Pantano de Entrepeñas, 930 m, twig of *P. halepensis*, on wood, 25.IX.1999, H.O. Baral (ø). – **Com**. **Valenciana**, **Castellón**, 13.5 km NNW of Castellón, 3.2 km WSW of Vilafamés, Camí Costur, 400 m, branch of *P. halepensis*, on wood, 27.IX.1999, H.O. Baral (ø). – ibid., branch of indet. angiosperm, on wood & bark, 27.IX.1999, H.O. Baral (ø). – **Andalucía**, **Jaén**, 18 km SSE of Jaén, 3 km SE of El Parrizoso, 1015 m, branch of *Q. rotundifolia*, on wood, 4.X.2013, S. Tello (JA-CUSSTA 7788, doc. vid.). – 19 km NE of Quesada, 9.7 km NE of Cazorla, NNE of Arroyo frío, 770 m, twig of *Rubus fruticosus*, 7.XI.2013, M.Á. Ribes & J.F. Mateo (AH 44740, doc. vid.). – **Cádiz**, 26 km WSW of Ronda, 1 km NNW of Ubrique, W of Salto de la Mora, 455 m, twig of indet. angiosperm, on bark, 28.II.2003, F. Prieto & A. González (AH 7648b). – **Granada**, Sierra Nevada, 43 km SW of Granada, 4 km SW of Alhama de Granada, Cortijo del Navazo, 1145 m, branch of *Q. rotundifolia*, on wood, 24.II.1982, A. Ortega & R. Galán (AH 6021). – **Islas Baleares**, **Mallorca**, 15 km NNW of Palma, 4.3 km WSW of Valldemossa, 480 m, branches of *Pinus*, on wood, 26.III.2006, R. Reuter (H.B. 8106a, anam. substr.). — **PORTUGAL**: **Guarda**, 26 km SE of Guarda, 3.5 km NE of Sabugal, SW of Rendo, 820 m, branch of *Cytisus scoparius*, on wood, 1.I.2005, J.P. Priou (J.P.P. 25003/25004). – **Évora**, 13 km W of Évora, 1.3 km SW of Almendres, Cromelech dos Almendres, 400 m, branch of *Olea europaea*, on wood, 8.V.2009, J.P. Priou (J.P.P. 29084, non vid.). – **Santarém**, 10 km NNW of Santarém, 2.5 km SW of Achete, Val de Flores, SSE of Trindade, 50 m, branch of *O. europaea*, on wood, 29.XII.2004, J.P. Priou (J.P.P. 24283 ø, non vid.). — **ITALY**: **Toscana**, **Arezzo**, 24 km W of Arezzo, 7.5 km S of Montevarchi, S of San Leolino, 350 m, trunk of indet. woody plant, on bark, 30.VIII.2000, P. Döbbeler (H.B. 7271a, P.D. 7447). — **SERBIA**: **Vojvodina**, Fruška Gora, 12 km SSW of Novi Sad, 5 km SSE of Racovac, N of Zmajevac, 435 m, branch of *Carpinus betulus*, on wood, 16.XII.2019, D. Savić (doc. vid.). – 12.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, N of WWII memorial, 502 m, branch of *Quercus petraea*, on wood, 30.X.2014, D. Savić (FG-132, doc. vid.). – ibid., SW of WWII memorial, 506 m, branch of *Tamarix gallica*, on wood, 2.IV.2019, D. Savić (doc. vid.). – 15.5 km SW of Novi Sad, Orlovac, 470 m, branch of *Quercus petraea*, on wood, 19.VII.2019, D. Savić (doc. vid.). – 11 km E of Šid, 3.2 km WNW of Erdevik, Vorovo, 126 m, branch of *Gleditsia triacanthos*, on wood, 22.X.2019, D. Savić (doc. vid.). — **CROATIA**: **Split-Dalmatia**, 3.2 km ENE of Zagvozd, 11 km WSW of Imotski, podr. Brežine, 635 m, twig of *Petteria ramentacea*, on wood, 27.VII.2000, N. Matočec (CNF 2/4552, 4555, 4556, 4562, doc. vid.). – **Dubrovnik-Neretva**, **Korčula**, 9 km ESE of Vela Luka, 2 km SSE of Prigradica, Sv. Martin, 100 m, branch of *Spartium junceum*, on wood, 25.VIII.2000, N. Matočec (CNF 2/4724, anam. substr., doc. vid.). – 11.5 km W of Korčula, 2 km W of Račišće, below Samograd cave, 40 m, branch of *Olea europaea*, on bark, 4.VI.2000, H.O. Baral (CNF 2/4466). – 8 km W of Korčula, Pupnat, south-slope of Veli vrh, 400 m, branch of *Juniperus oxycedrus*, on bark, 11.VI.2000, E. Weber (ø). – 2 km WSW of Korčula, 1 km NNE of Žrnovo, 110 m, branch of *Phillyrea media*, on wood, 11.VI.2000, H.O. Baral & N. Matočec (ø). – 1.8 km NW of Žrnovo, Kočje, 190 m, branches of *Quercus ilex*, on bark, 3.VI.2000, H.O. Baral & N. Matočec (H.B. 6675, CNF 2/4462). – 1.5 km SW of Žrnovska Banja, between Kočje and Brdo, 200 m, branch of *Erica arborea*, on wood, 2.VI.2000, E. Weber (ø). – ibid., branch of *Pistacia* (?)*terebinthus*, on wood, 3.VI.2000, H.O. Baral (ø). – 2.5 km W of Korčula, Vrbovica bay, 1 m, branch of *Arbutus unedo*, on wood & bark, 2.VI.2000, H.O. Baral (ø). – ibid., branch of *Q. ilex*, on wood, 9.VI.2000 (ø). – ibid., 8 m, branch of *Ceratonia siliqua*, on wood, 6.VI.2000 (ø). – 2.5 km ESE of Korčula, Badija island, NW of Turističkosportski centar, near ruin, 50 m, branch of *Olea europaea*, on wood, 8.VI.2000, H.O. Baral (ø). – ibid., 40 m, branch of *Arbutus unedo*, on wood (ø). — **MONTENEGRO**: 51 km NNE of Podgorica, 5 km ENE of Kolašin, SE of Mušovića Rijeka, 1130 m, branch of *Fagus sylvatica* var. *moesiaca*, on wood, 5.III.2016, B. Perić (B.P. Dgf/C7D-05-03-16, doc. vid.). – 2.7 km NW of Herceg Novi, SSE of Ratiševina, 93 m, branch of *Spartium junceum*, on wood, 20. VI.2019, D. Savić (FG-1091, doc. vid.). — **GREECE**: **Peloponnese**, 17 km ESE of Pyrgos, 1 km SE of Olympia, Ancient Olympia, 30 m, branch of *Platanus orientalis*, on wood, 2.VI.2009, S. Helleman (H.B. 9099a ø). – 5.7 km SSE of Dimitsana, 2.7 km ESE of Stemnitsa, Lousios gorge, 565 m, twig of *Quercus ?pubescens*, on wood, 3.VI.2009, S. Helleman (H.B. 9100 ø). – **Rhodos**, 17 km WSW of Archangelos, 4.5 km NNW of Laerma, 185 m, branch of *Pistacia lentiscus*, on bark, 21.III.2010, V. Kummer (H.B. 9334d ø). — **TURKEY**: **Marmara**, **Balikesir**, 33.5 km N of Balikesir, 8.8 km NNE of Ilıca, Beypınar Mevkii, 485 m, branch of *Q. ilex*, on wood & bark, 15.XI.2003, T. Askun (T.A. 68a, anam. substr.). – 9 km NE of Balikesir, 2.5 km SW of Ayvatlar, Değirmen Boğazı, 135 m, branch of *Pinus brutia*, on wood, 4.II.2003, T. Askun (T.A. 53, doc. vid.). — **MOROCCO**: **Taza-Al Hoceima-Taounate**, Atlas Mts., 80 km SE of Tanger, Bab Taza, ~800 m, branch of *Cistus crispus*, on wood, 30.III.1950, M. Maire (MPU, herb. Maire Champ. Maroc 3790, as *Hyalinia rubella*). — **MACARONESIA**: **Canary Islands**, **Tenerife**, La Matanza de Acentejo, 8.5 km NE of Puerto de la Cruz, 1.5 km WNW of La Matanza de Acentejo, NW of Jagre, 43 m, branch of *Rhamnus crenulata*, on wood, 21.XI.2009, L. Quijada, E.V. Rodríguez & R. Castro (TFC Mic. 22544, non vid.). – ibid., branch of *Periploca laevigata*, on wood (TFC Mic. 22554, 22556, doc. vid.). – La Orotava, 6.7 km S of La Orotava, Escobón Cortado, 1586 m, on *Chamaecytisus proliferus*, 28.III.2013, L. & C. Quijada (TFC Mic. 24010, doc. vid.). – Santa Cruz de Tenerife, 3 km NNW of San Andrés, Hoya el Laurel, 305 m, on *Lavandula canariensis*, 5.III.2013, L. & C. Quijada (TFC Mic. 23919, non vid.). – Fasnia, 7.5 km SSW of Güímar, 1.5 km NE of Fasnia, Barranco de Herques/La Morra los Cardones, 346 m, branch of *Sonchus* (*Atalanthus*) *pinnatus*, on wood, 5.II.2010, L. Quijada, E.V. Rodríguez & R. Castro (TFC Mic. 22826, non vid.). – ibid., branch of *Cistus monspeliensis*, on wood (TFC Mic. 22828, 22840-42, non vid.). – ibid., on *Euphorbia atropurpurea* & *Periploca laevigata*. – Granadilla de Abona, 2.5 km SE of Vilaflor, La Martela, 1195 m, *Pinus canariensis*, 6.III.2012, L. & C. Quijada (TFC Mic. 23356-60, doc. vid.). – ibid., *Cistus symphytifolius*, 19.IV.2012 (TFC Mic. 23638, 23639). – ibid., *C. monspeliensis*, 19.III.2013 (TFC Mic. 23951). (For further data see Quijada et al. 2016). — **MASCARENE ISLANDS**: **Réunion**, 15.5 km E of St.-Gilles, Route du Maïdo, 2040 m, branch of *Acacia heterophylla*, on boring dust, 22.IX.2011, R. Reuter (H.B. 9722a ø). — **CANADA**: **Prince Edward Island**, 4.5 km WSW of Charlottetown, 2.7 km E of Cornwall, Ferry Rd, 29 m, branches of *Tsuga ?canadensis*, on wood, 5. XII.2018, A. Carter (anam. substr., doc. vid.). – 6.5 km S of Cornwall, Black Creek, 2 m, branch of *Abies balsamea*, on wood, 13.XI.2018, A. Carter (doc. vid.). – 16 km WSW of Charlottetown, 1.4 km ENE of Bonshaw, 4 m, branches of *Picea ?glauca*, on wood, 26.XI.2018, A. Carter (doc. vid.). — **USA**: **Wyoming**, Middle Rocky Mountains, 18.5 km N of Jackson, Grand Teton, 1960 m, branch of *Purshia tridentata*, on wood, 6.VI.1996, G. Marson (H.B. 6038c). – **Arizona**, Mogollon Rim, 36 km S of Flagstaff, 12 km E of Sedona, Fox Ranch Road Exit, 1958 m, branch of *Pinus ponderosa*, on wood, 12.VI.2000, G. Marson (H.B. 6993). – 9 km NNW of Flagstaff, San Francisco Peaks, 9 km SSW of Humphreys Peak, Rte. 180, 2250 m, branch of *P. ponderosa*, on wood, 12. VI.2000, G. Marson (H.B. 6995a, anam. substr.).

Not included. **CZECHIA**: **Central Bohemia**, Mnichovice, trunk of *Prunus domestica*, 1.VII.1926, J. Velenovský (**lectotype** of *O. prunorum*, doc. vid.). — **LUXEMBOURG**: **L'Oesling**, **Diekirch** 4.5 km SW of Diekirch, W of Ettelbruck, railway station, 197 m, stem of *Melilotus*, 6.VII.2002, G. Marson (ø). — **France**, **Drôme**, 20 km W of Serres, 4.3 km NNW of Rosans, Col de Pommerol, 1045 m, branch of *Pinus sylvestris*, on wood, 22.VIII.2000, G. Marson (H.B. 6748g ø, anam. cult., CBS 116208; sq.: KT215265). — **USA**: **Massachusetts**, 19.5 km SW of Boston, NNW of Westwood, Hale Reservation, 70 m, branch of *Pinus strobus*, on bark, 4.V.1996, D.H. Pfister (H.B. 5518). – 19.5 km SE of Boston, 2.7 km NE of Hingham, S of Rocky Neck, Weir River Road, 3 m, branch of *Acer*, in wood, 26.III.2017, L. Quijada (bhi-F731; sq.: MH445965). – **New Jersey**, ~7 km N of Vineland, Newfield, unlocalized, ~35 m, branch of *P. strobus*, on bark, IX.1887, J.B. Ellis (M, herb. Petrak, as *Ombrophila vinosa*). – ~14 km NNW of Vineland, Iona, unlocalized, ~30 m, old cotton strings, autumn 1883, collector unknown (M, herb. Ellis, NAF 1313, as '*?Peziza vinosa*'). – **Utah**, Utah Mts., Bryce Canyon, Fairview Point, 2440 m, branch of *Arctostaphylos patula*, on wood, 16.V.1995, G. Marson (H.B. 5396).

Orbilia subvinosa G. Marson, Baral & E. Weber, **sp. nov.**, MB 813559 — Pls 263–265, Map 46

Etymology: referring to the similarity with *O. vinosa*.

Typification: Spain, Teruel, branch of *Pinus sylvestris*, 26.IX.1999, G. Marson & H.O. Baral (ex H.B. 6490b, M-0281034, holotype).

Latin diagnosis: *Similis* Orbiliae vinosae *sed ascosporae paulo majores, apothecia plerumque intense aurantiaca, margine minute crenulata, conidia typo* Dwayaangam*, duplex dichotomiter ramosa differt. Habitat ad lignum putridum ramorum siccorum* Pini, *raro* Piceae, *plerumque in zona orosubmediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–0.8(–1.05) mm diam., 0.15–0.22 mm high (receptacle 0.12–0.15 mm), light to bright orange, sometimes rose-orange or rose-red, not or only slightly translucent, ± round, scattered to medium gregarious; disc slightly concave to flat, finally slightly convex, margin distinct, thin, 5–10 µm protruding, finely to distinctly crenulate, rarely ± smooth; broadly sessile, superficial, rarely immersed in cracks; dry bright to deep orange-red, with thick protruding margin. **Asci** *((45–))(50–)55–77(–88) × (5.5–)6–7 µm {7}, †(51–)60–70(–80) × (4.7–)5–6(–6.5) µm {3}, 8-spored (rarely 4–7-spored), spores *3–4-seriate, 3–4 lower spores inverted {3} (not or somewhat mixed), pars sporifera *30→ 20 µm long; **apex** (†) hemispherical, dome †0.5–0.6 or 1–1.8 → 0.3–0.4 or 0.8–1.2 µm thick {2}, with indistinct or distinct apical chamber; **base** with medium to very long, thin, flexuous stalk, T-, L- or h-shaped. **Ascospores** *(12.7–)14–20(–22) × (1.7–)1.9–2.2(–2.5) µm {10}, †14–19 × 1.8–2.2 µm {2}, cylindric-fusoid to fusoid-clavate, apex obtuse, rarely subacute, base gradually or more abruptly attenuated in a tail-like end or distinct tail *(3–)4–5(–7) × 1–1.2 µm, straight to very slightly curved near base; **SBs** *4–6(–7)((–8)) {10} × ((0.5–))(0.6–)0.7–0.9(–1) µm {8}, vermiform, often with a ± distinct basal inflation, apically

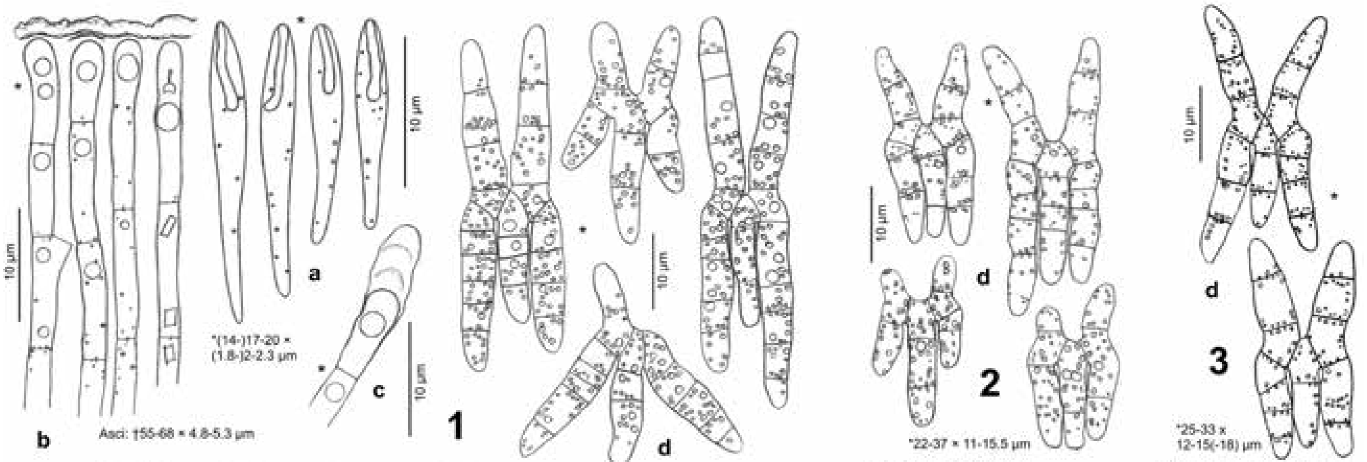


Plate 263. **1–3**. *Orbilia subvinosa*. – **a**. ascospores; **b**. paraphyses; **c**. cortical cells with glassy process; **d**. conidia (from substrate).

narrowed to a wide point or not narrowed, straight or very slightly flexuous, overmature ampulliform, (1.8–)2.5–3.5(–4.5) × 1–1.3 µm; with a few minute LBs. **Paraphyses** apically uninflated to very slightly clavate, terminal cells *6–18 × 2.2–2.8 µm {1}, †11–16 × 2–3 µm {1}, lower cells *8.5–12 × 2–2.5(–3) µm {1}, †7–14 × 1.8–2.5 µm {1}; unbranched at upper septum, hymenium pale yellow-orange, also rose. **Medullary excipulum** pale rose to orange, 50–120 µm thick, of dense (or loose in lower part) textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** subhyaline at base, pale rose to orange towards margin, of (†) not or slightly gelatinized, vertically oriented t. globulosa-angularis-prismatica from base to mid flanks, 45–60 µm thick near base, cells *(5–)6–13(–14) × (4–)5–8(–10) µm {2}; 20–35 µm thick near margin, of t. porrecta oriented at a (45–)60–90° angle to the surface, (10–)60–80° at upper margin, marginal cortical cells *6–11 × 2.5–4 µm {3}; **glassy processes** 0–3 {2} or 3–10 {7} or 10–15(–18) {3} × 3–4 µm, ± high-refractive, stratified, coherent to form small teeth. **Anchoring hyphae** abundant, †1.8–2.8 µm wide, walls 0.2 µm thick {2}. **SCBs** in paraphyses and ectal excipulum (at margin) globose, (0.8–)1.3–2.5(–2.8) µm diam., in lower part of paraphyses and in ectal excipulum at flanks and margin (also at base and in medullary excipulum) crystalloid {7}, (0.9–)1.5–2.5(–3.2) × 1–2.3 µm, very pale orange, also absent {3}; **LBs** in lower part of paraphyses and in ectal excipular cells at mid flanks and margin minute, ± sparse, pale yellowish-orange or sometimes rose-orange (carotenoids). **Exudate** over paraphyses 1–2(–3) µm thick, rough-cloddy, (very) pale yellow, loosely attached, over margin and flanks 1–5 µm thick, cloddy, hyaline or usually pale to light sulphur-yellow or chlorinaceous. — **ANAMORPH**: dwayaangam-like (from ascospore isolate {1} and natural substrate {9}). **Conidiophores** *30 × 2.8 µm, 1-septate. **Conidia** resembling clothes-pegs, total size *(20–)26–54(–60) × 10.5–12.5(–13.5) µm {8}, (13–)17–30(–36)((–55)) µm wide when arms diverging; stipe *(8.5–)10–18(–19) × (2.5–)2.8–4(–4.8) µm, (1–)2–3(–4)-septate, usually shorter than basal arms; twice dichotomously branched: 2 arms pointing upwards, 2 downwards, arms straight, not or slightly to medium tapered near the ends, *((5–))(8–)11–27((–33)) × (3–)3.3–4.5((–5.5)) µm, (0–)2–5(–7)-septate, containing some or many minute LBs, sometimes also some with 1–2 µm diam.

Habitat: collected 1–4 m above the ground, on attached (rarely broken), ± decorticated (rarely corticated with resinous wound), 11–35 mm thick branches of *Abies alba* {1}, *Pinus* sp. {3}, *P. sylvestris* {17/2}, *P. brutia* {1}, on 0.1–0.5, sometimes up to 1–2 mm deep slightly to strongly decayed wood {24} often in beetle galleries, slightly to strongly greyed, green algae sparse to abundant. **Associated**: *Amphosoma resinicola* {1}, *A. atroolivaceum* {1}, *Capronia* sp. {2}, *Ciliolarina pinicola* {1}, *Coniochaeta malacotricha* {1}, *Cryptodiscus pini* {1}, *Dacrymyces* sp. {3}, '*Helotium*' *uvidulum* {1}, *Hypogymnia physodes* {1}, *Lachnellula resinaria* {1}, *Lophium mytilinum* {1}, *Melanelia glabratula* {1}, *Melaspilea emergens* {1}, *Orbilia alpigena* {1}, *O. aristata* {1}, *O. coniferarum* {1}, *O. cylindrospora* {2}, *O. delphinus* {1}, *O. eucalypti* {2}, *O. euonymi* {1}, *O. flagellispora* {1}, *O. gambelii* {1}, *O. ?ocellata* {1}, *O. patellarioides* {11}, *O. pleiomicrosoma* {1}, *O. sphaerospora* {4}, *O. subaristata* {1}, *O. subcylindrospora* {1}, *O. subtrapeziformis* {1}, *O. trapeziformis* {1}, *O. vinosa* {2}, ?*Pragmopora* sp. {1}, *Propolis betulae* {1}, *Pseudevernia furfuracea* {1}, *Pseudohelotium sordidulum* {2}, *Resinomyces griseus* {1}, *R. kirschsteinianus* {1}, *Sarea resinae* {1}, *S. difformis* {1}. **Desiccation tolerance**: fully viable for at least 3 months, after 9 months paraphyses and immature asci still alive, after 1 year many spores still viable, conidia germinated when transferred to agar 10 months after being collected. **Altitude**: 860–1830 m a.s.l. (but 425 m in western Anatolia). **Geology**: Lower to Upper Jurassic & Cretaceous marl- & limestone, Mio- to Pliocene marl, Cenozoic silt. **Phenology**: IV, VII–X (possibly throughout the year, long-lived).

Taxonomic remarks. *Orbilia subvinosa* is segregated from *O. vinosa* and *O. arachnovinosa* mainly because of its deviating dwayaangam-like anamorph (Pls 263: 1d, 2d, 3d; 264: 1h, 3e, 4d; 265). With its usually bright orange, less translucent apothecia (due to sparse pale orange LBs in both paraphyses and excipular cells) with a crenulate margin formed by short glassy processes, the species can often already macroscopically be distinguished from *O. vinosa* which was twice found to grow in association (H.B. 5142c, 6748f). The asci and spores tend to be slightly larger: the spores are often over *2 µm wide while, in comparison, those of *O. vinosa* are usually below *2 µm.

The species was so far with certainty only found on wood of *Pinus* and once *Abies* in southern France and Spain, mainly in the orosubmediterranean humid zone. A record of the characteristic anamorph in western Anatolia (Turkey) on *Pinus brutia* is exceptional because it was made at a comparatively low altitude in the supramediterranean belt.

The very similar but angiosperm-inhabiting *O. angiosubvinosa* is described here as a separate species, because the associated conidia are slightly narrower, the spores slightly shorter and wider, and a sequence from a sample on *Corylus* distinctly deviates from sequences of typical *O. subvinosa* on coniferous substrate.

Variation. Apothecial size and colour varied somewhat among the populations, also the finely denticulate margin was not always present. Though typically light to bright orange, a distinct rose component was noted in apothecia of two collections (H.B. 5015a, 5016a). Crystalloid SCBs were usually present, but in one specimen only globose SCBs were seen (H.B. 5016a), and in the holotype they were absent in one population, while present in apothecia on a separate branch (Pl. 263: 1b). Spore length varied between 14–16 and 17–20 µm while spore width was more constant. Glassy processes were absent in a few specimens (e.g., H.B. 6729a), and varied also in length among the populations. The ascus apical dome was either around 1–1.5 µm thick or only ~0.5 µm, but more data are required to find out the predominant case.

Not included collections. Some orosubmediterranean samples on *Juniperus* and supramediterranean ones on *Abies pinsapo* might belong to *O. subvinosa* but clear evidence was lacking. Those on wood of *Abies* from three localities in the Sistema Bético of Andalucía, at first identified as *O. vinosa*, had orange-red apothecia with (2–)10–20(–25) µm long glassy processes, but conidia were not observed in any of them. The spores (†12.5–17.5 × 1.7–1.9 µm) would fit *O. vinosa*, but these samples are only assigned with hesitation to *O. subvinosa*. Three records on *Juniperus* from southern France and central Spain, with glassy processes up to 10 µm length, are also not included in the description, mainly because of the paucity of microscopic data and because conidia were not observed.

Anamorph. The characteristic dwayaangam-like conidia were observed on the natural substrate in association with apothecia of *O. subvinosa* in at least nine of our collections on *Pinus*. In 2012 we succeeded to obtain them also in pure culture from an ascospore isolate (from Grasse, Pl. 265: 1). They further developed in an isolate gained from conidia taken from the natural substrate (from Briançon, Pl. 265: 2). The same type of dwayaangam-like conidia was once observed in the submediterranean collection on *P. brutia*, but the associated apothecia belonged to *O. subaristata*, *O. pleiomicrosoma*, and *O. euonymi*.

However, in an earlier trial in 2001 to obtain the anamorph of *O. subvinosa* (from Col de Pommerol, H.B. 6748g, Pl. 258: 4), the ascospore isolate formed consistently trinacrium-like conidia typical of *O. vinosa*, although only dwayaangam-like conidia

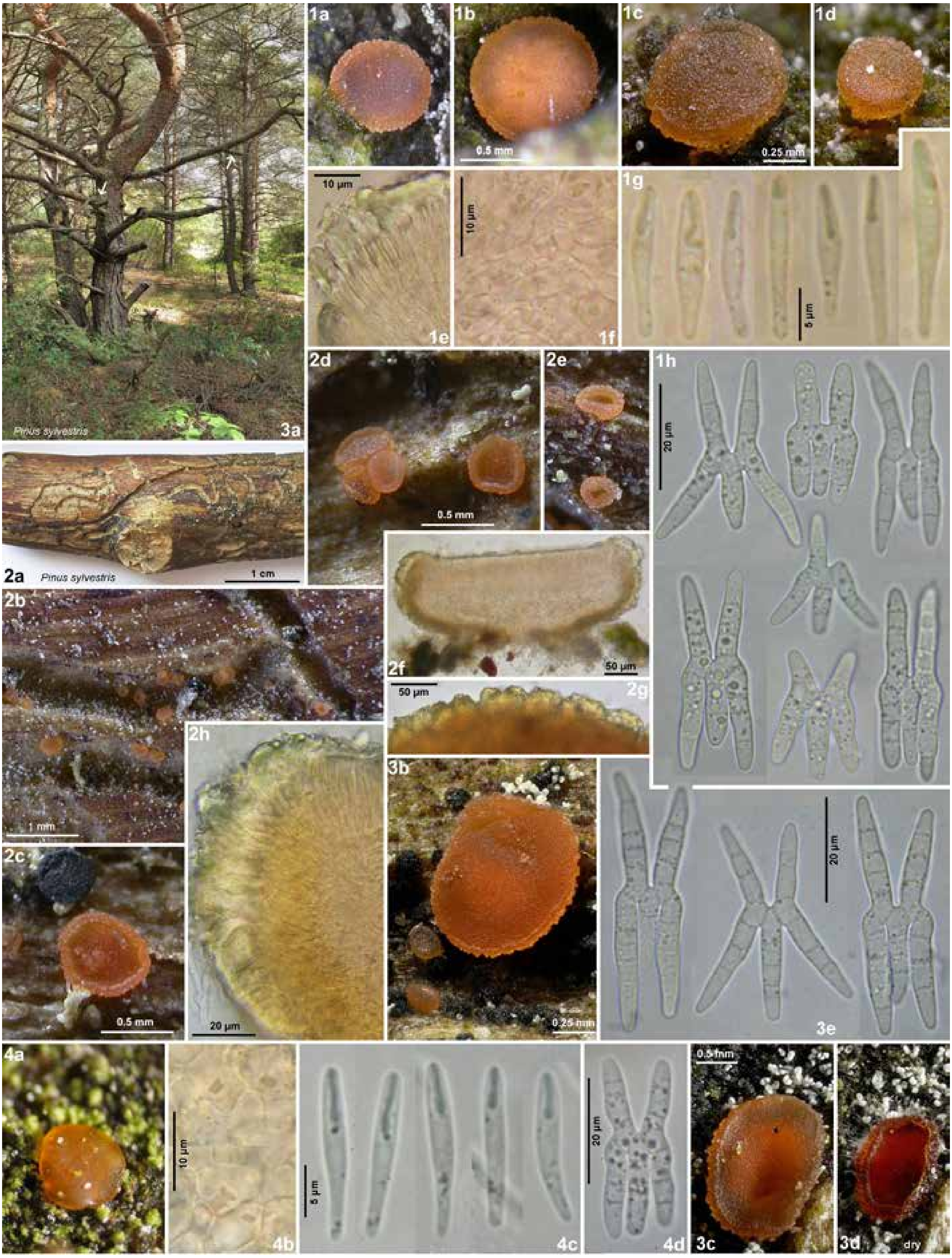


Plate 264. **1–4**: *Orbilia subvinosa*. – **1a**. orosubmediterranean *Pinus sylvestris* forest; **2a**. decorticated xeric branch of *Pinus* with old beetle galleries (rehydrated); **1a–d**, **2b–e**, **3b–c**, **4a**. rehydrated apothecia (**2c** with black apothecium of *Orbilia patellarioides*); **3d**. dry apothecium; **2f**. apothecium in median section; **1e**, **2h**. id., marginal ectal excipulum; **2g**. apothecium in top view showing marginal teeth; **1f**, **4b**. crystalloid SCBs in excipular cells of margin and flanks; **1g**, **4c**. ascospores; **1h**, **3e**, **4d**. conidia from substrate. – Living state. – **4a–d**: phot. R. Tena. — **1a–h**. H.B. 9173b: France, Mont Ventoux, on *Pinus*; **2a–h**. H.B. 6490b (holotype): Spain, Sierra de Albarracín, on *Pinus*; **3a–e**. 24.IX.2009: France, Grasse, on *Pinus*; **4a–d**. 1.IV.2012: Spain, Sierra de Javalambre, on *Pinus*.

were abundantly observed on the natural substrate (H.B. 6748f, Pl. 263: 2). Therefore, we suspected that the apothecium used for isolation belonged in the scope of *O. vinosa* rather than *O. subvinosa*. In fact, molecular data gained from this culture differ strongly from both species, but are slightly closer to *O. vinosa* (see below).

Conidia varied in total length between ~25–30 and ~35–55 µm. The arms were usually ± parallel, but sometimes they diverged and then the conidia are much wider. Also stipe length may vary between 10–13 and 13–19 µm.

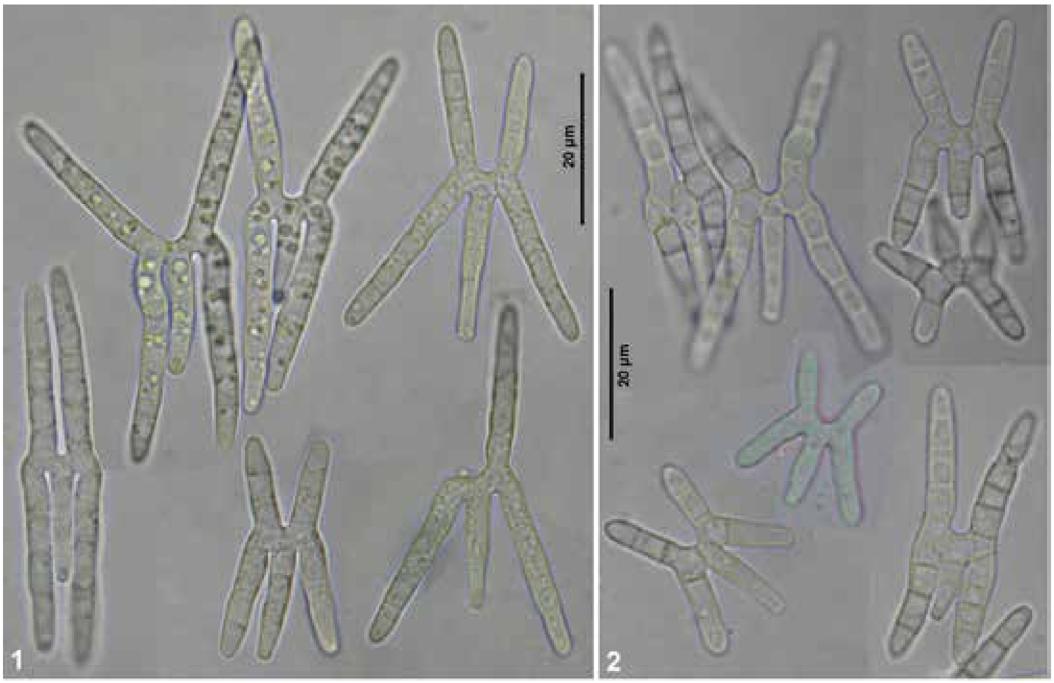


Plate 265. **1–2**: *Orbilia subvinosa*. – Conidia in pure culture (**1**. ascospore isolate, **2**. conidial isolate). – Living state. **— 1**. 18.IX.2011: France, Grasse, Col du Ferrier, on *Pinus*; **2**. 5.IX.2010: France, Briançon, Cervières, on *Pinus*.

The conidia of *O. subvinosa* resemble those of the tropical angiosperm-inhabiting *Dwayaangam yakuensis* but are certainly not conspecific (for the differences see under *O. angiosubvinosa*, p. 622).

Phylogeny. Sequences of ITS and mostly also LSU were available for seven strains of *O. subvinosa* (see Tab. 66). They differ by 0.2–1.1 % in the ITS at pos. 10 in the ITS1 and at pos. 369, 382, 406, 412, and 503 in ITS2. The six variable positions are either T or C, and in two strains 3 or all 6 positions were ambiguous (Y), which suggests that variation at these positions regularly occurs, even within a population. The seven sequences concurred at pos. 369 & 382 (4 strains T or mainly T, 3 strains C) and 406 & 412 (4 strains C or mainly C, 3 strains T). Variation at pos. 10 was only observed in the *Abies* sample (T vs. C) and at pos. 503 also in the sample from Moustiers-Ste.-Marie. No variation was observed in the two isolates from ascospores and conidia, which could mean that a single apothecium includes only 1 genotype.

To *O. angiosubvinosa* a distance of 6–7 % was found, and to *O. vinosa* 9.5–11 %. Also the intermediate sample from Col de Pommerol shows a distance of 10.5–11.5 % to *O. subvinosa*. In the LSU (D1–D2) *O. subvinosa* did not show any variation and differs from *O. vinosa* by 1.1–1.3 % (see also under *O. vinosa*, p. 609). For the phylogenetic placement see under *O. vinosa*.

Five of the seven *O. subvinosa* sequences comprise enough nucleotides of the SSU in order to verify the absence of the S1506 intron, which was also absent in the sequence of *O. angiosubvinosa* and the intermediate strain from Boston (bhi-F731), but present in all sequences of *O. vinosa*, including the intermediate strain from Col de Pommerol (Tab. 66).

Ecology. To the present knowledge, *O. subvinosa* is restricted to the altimontane to subalpine, orosubmediterranean, rarely orotemperate or suprasubmediterranean humid regions, where it was mainly found on wood of xeric branches of *Pinus*, particularly *P. sylvestris*, but also on *Abies alba*. Typical associated taxa are *O. patellarioides* and *O. sphaerospora*, which show a very similar prevalence for pine wood. However, also *O. vinosa* is not rare in these habitats, with which it was occasionally found to grow in association. The record on *Pinus brutia* was in a supramediterranean forest at 425 m altitude in western Anatolia, while all collections from Spain and France, whether included or not, derive from altitudes above 850 m.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, 20 km W of Serres, 4.3 km NNW of Rosans, Col de Pommerol, 1045 m, branches of *Pinus sylvestris*, on wood, 22.VIII.2000, G. Marson (H.B. 6748f ø, anam. substr.). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 20 km W of Serres, 4 km NNW of Rosans, Col de Pommerol, 1077 m, branch of *P. sylvestris*, on wood, 12.VIII.2009, G. Marson (H.B. 9127). – 3 km SE of Briançon, 4.3 km WNW of Cervières, 1425 m, branches of *P. sylvestris*, on wood, 5.IX.2010, G. Marson (G.M. 2010-09-05.1 ø, anam. substr., conid. isol.; sq.: KT380059). – 36 km W of Gap, W of Le Beaume, 995 m, branch of *Abies alba*, on wood, 29.VIII.2015, G. Marson (G.M. 2015-08-29.1; sq.: MH221058). – **Alpes-de-Haute-Provence**, 20.5 km NNE of Digne-les-Bains, 1.4 km NNE of Le Labouret, 1350 m, branches of *Pinus sylvestris*, on wood, 30.VIII.2015, G. Marson (G.M. 2015-08-30.5, sq.: MK473395). – 24 km S of Digne-les-Bains, 3.3 km NNW of Moustiers-Ste.-Marie, N of Canyon du Verdon, 975 m, branch of *P. sylvestris*, on wood, 6.VIII.1999, G. Marson (H.B. 6437d ø). – ibid., 21.IX.2011 (G.M. 2011-09-21.1; sq.: KT380087) – 6.5 km SE of Castellane, NW of La Bâtie, Col de Luens, 1080 m, branch of *P.* (?)*sylvestris*, on wood, 5.X.1993, G. Marson (H.B. 5015a). – 10.5 km E of St.-André-les-Alpes, 2.3 km WNW of Annot, NE of Col de l'Iscle, 1145 m, branch of *P. sylvestris*, on wood, 16.VIII.2001, G. Marson (H.B. 7061a, anam. substr.). – 27 km SE of Gap, 2.5 km NE of Montclar, Col St.-Jean, 1335 m, branch of *Pinus*, on wood, 6.X.1993, G. Marson (H.B. 5016a). – 8 km SE of St.-Julien-du-Verdon, 3 km NW of Soleilhas, Vauplane, 1595 m, branches of *Pinus*, on wood, 16.VII.1994, G. Marson (H.B. 5132b). – 8 km NW of Trigance, 3.7 km NNE of La Palud-sur-Verdon, 925 m, branch of *P. sylvestris*, on wood & boring dust, 29.IX.2009, G. Marson (G.M. 2009-09-29.1; sq.: KT380086). – **Alpes Maritimes**, 7.5 km NW of Grasse, 2 km NE of St.-Vallier-de-Thiey, Col du Ferrier, 1045 m, branch of *P. sylvestris*, on wood, 24.IX.2009, G. Marson (G.M. 2009-09-24.1, anam. substr.; sq.: MH221057). – ibid., 18.IX.2011 (G.M. 2011-09-18.2 ø, anam. cult.; sq.: KT380088). – 24 km N of Nizza, 1.5 km WSW of Utelle, Madone d'Utelle, 1160 m, branches of *P. sylvestris*, on wood, 3.X.1993, G. Marson (H.B. 5142c). – 28 km N of Monte Carlo, ~2 km NE of Col du Turini, l'Authion, ~1830 m, branch of *Pinus*, on wood, 3.X.1993, G. Marson (ø). – 19 km NNE of Grasse, 4 km NNE of Gréolières, Gréolières les Neiges, 1405 m, branch of *P. sylvestris*, on wood, 1.X.1993, G. Marson (H.B. 5001c ø, anam. substr.). – **Var**, 11 km SSE of Moustiers-Ste.-Marie, 3 km SSE of Aiguines, Grand Plan de Canjuers, 860 m, branch of *P.* (?)*sylvestris*, on wood, 5.VIII.1999, G. Marson (H.B. 6729a). – **Vaucluse**, 9.5 km NE of Bedoin, 1.5 km NW of Mt. Ventoux summit, Mt. Serein, 1385 m, branches of *P. sylvestris*, on wood, 13.VIII.2009, G. Marson, H.O. Baral

Map 46. Known distribution of *O. subvinosa* in southern Europe (yellow = not included collections from *Abies* and *Juniperus*).

& B. Liu (H.B. 9173b, anam. substr.). – 6 km W of Mt. Ventoux summit, Les Ramayettes, 980 m, branches of *P. sylvestris*, on wood, 13.VIII.1993, G. Marson (H.B. 4939, anam. substr.). — **SPAIN**: **Aragón**, **Teruel**, Sierra de Javalambre, 23 km SSE of Teruel, 1.8 km E of Camarena de la Sierra, Javalambre, 1585 m, branch of *P. sylvestris*, on wood, 1.IV.2012, R. Tena (R.T.L. 12040101, anam. substr.). – Sierra de Albarracín, 49 km W of Teruel, 5.8 km WSW of Frías de Albarracín, 1615 m, branch of *P. sylvestris*, on wood, 26.IX.1999, G. Marson & H.O. Baral (M-0281034, **holotype**; H.B. 6490b, **isotype**; anam. substr.). — **TURKEY**: **Marmara**, **Balikesir**, 50 km WSW of Balıkesir, 16.5 km SW of Ivrindi, Korucu Forest, 1.3 km ESE of Büyükılıca, Sarıpınar Mevkii, 425 m, branch of *P. brutia*, on wood, 1.XI.2002, T. Askun (T.A. 35c, H.B. 7294c ø, anam. only, doc. vid.).

Not included samples on *Juniperus communis* and *Abies pinsapo* (anamorph not observed, no molecular data). **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Var**, 26 km NW of Grasse, 12.5 km SE of Castellane, NNW Le Logis-du-Pin, 1035 m, branch of *Juniperus communis*, on wood, 5.X.1993, G. Marson (ø). – **Vaucluse**, Luberon Mt., 9 km SE of Apt, 2.5 km SSE of Auribeau, Mourre Nègre, 1100 m, branch of *J. communis*, on wood, 28.IX.1993, G. Marson (ø). — **SPAIN**: **Madrid**, Sierra de Guadarrama, 50 km NW of Madrid, 12 km NE of Cercedilla, NW of Cotos, 1860 m, branch of *J. communis* var. *saxatilis*, on wood, 5.VI.1996, H.O. Baral (ø). – **Andalucía**, **Cádiz**, 23 km W of Ronda, 4.8 km WNW of Grazalema, NNE-slope of Sierra del Pinar, 1155 m, branch of *Abies pinsapo*, on wood, 14.XI.1984, M. Honrubia (AH 6345). – 12 km SE of Ronda, Sierra de las Nieves, NE of Los Quejigales, 1300 m, branch of *A. pinsapo*, on wood, 2.IV.1982, A. Ortega, R. Galán & G. Moreno (AH 6329, 6330, 6331). – 13 km SE of Ronda, SW of La Nava, north-slope of Sierra de las Nieves, 1140 m, twigs of *A. pinsapo*, on wood, 13.VI.1984, R. Galán (AH 6332).

Orbilia angiosubvinosa Baral, R. Tena & E. Weber, **sp. nov.**, MB 825630 — Pls 266–267

Etymology: referring to the growth on angiosperms and the similarity with *O. subvinosa*.

Typification: Spain, Asturias, Pola de Somiedo, Valle de Lago, branch of *Corylus avellana*, 4.VI.2013, T. Læssøe (ex H.B. 9813a, AH 52842, sq.: MK493127, holotype).

Latin diagnosis: *Similis* Orbiliae subvinosae *sed conidia angustiores, habitat ad lignum putridum ramorum siccorum angiospermarum in zona suprasub- ad orosubmediterranea Europae meridionalis et zona oceanica Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.4–0.8 mm diam., 0.16 mm high, light to deep orange, rarely rose-orange, hardly to medium translucent, ± round, very scattered to gregarious in small groups; disc flat, margin distinct, thin or thick, 8 µm protruding, smooth to distinctly crenulate; broadly sessile, superficial; dry bright to deep orange-red, with thick protruding margin. **Asci** *(50–)55–70(–79) × (5–)6–7(–7.5) µm {2}, †40–65 × 4.6–5.5 µm {2}, 8-spored, spores *3–4-seriate, 2–4 lower spores inverted {4}, pars sporifera *25–38 µm long; **apex** (†) hemispherical, dome †0.8–1.4 → 0.7–1 µm thick {2}, with small apical chamber; **base** with short to very long, thick or thin, flexuous stalk, T- to L-shaped. **Ascospores** *((11.5–))(12.5–)14–17(–19) × (1.8–)2–2.4(–2.7)((–3)) µm {7}, narrowly fusoid (to fusoid-clavate), apex rounded to obtuse, base ± attenuated, sometimes tail-like, straight to very slightly, exceptionally strongly curved near base; **SBs** *(2.7–)3.5–5.5(–7) × 0.6–1(–1.3) µm {6}, vermiform or with a ± ellipsoid basal inflation, apically not narrowed, ± broadly attached, straight; with some small LBs. **Paraphyses** apically uninflated to very slightly clavate or lageniform, terminal cells *9.5–16 × 1.8–2.8(–3.2) µm {4}, lower cells *8–11.5 × 1.5–2.6 µm {2}; unbranched at upper septum, hymenium light orange. **Medullary excipulum** pale rose to orange, 45 µm thick, of dense textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** subhyaline at base, light orange towards margin, of (†) not or slightly gelatinized, vertically oriented t. globulosa-angularis-prismatica from base to mid flanks, 30–35 µm thick near base, cells *8–16 × 5–10(–13) µm {3}; 35 µm thick near margin, of t. porrecta oriented at a 10–50° angle to the surface, marginal cortical cells *6–15 × 2.5–3.5 µm {2}; **glassy processes** 0–1 {4} or 5–28 {3} × 2.5–3.5(–3.8) µm {2}, ± high-refractive, stratified, coherent to form indistinct to distinct teeth. **Anchoring hyphae** medium abundant, †1.5–2.7 µm wide, walls 0.2–0.3 µm thick {1}. **SCBs** in paraphyses and ectal excipulum (at margin) globose, 1–2.5 µm diam. {6}, also crystalloid {7}, in excipulum 2–4.5 × 1–1.5 µm, hyaline to pale orange; **LBs** in lower part of paraphyses and in ectal excipular cells at mid flanks and margin minute, ± scattered, light yellowish-orange (carotenoids) {1}. **Exudate** over paraphyses, margin and flanks 1–2.5 µm thick, cloddy, hyaline to pale yellow, loosely attached. — **ANAMORPH**: dwayaangam-like (presumed, from natural substrate {4}). **Conidiophores** very short, unbranched. **Conidia** resembling clothes-pegs, total size *(26–)35–52 × 10–11 µm, 12–21 µm wide when arms diverging; stipe *11–15 × 2.7–3.3(–3.7) µm, 2-septate, usually shorter than basal arms; twice dichotomously branched: two arms pointing upwards, two downwards, arms straight, not or slightly to medium tapered near the ends, *(11–)13.5–26 × 3–3.5(–3.8) µm, 2–3-septate {2}, containing many minute LBs near septa or close to wall, sometimes also with some large LBs {2}.

Habitat: collected 1–1.5 m above the ground, partially to sometimes entirely decorticated, 7–40 mm thick branches of *Corylus avellana* {2}, *Rosa* sp. {1}, *Salix* sp. {1/1}, *S. caprea* {2}, on up to 1 mm deep medium to strongly decayed wood {7}, slightly to strongly greyed, ± covered by green algae. **Associated**: *Cryptodiscus foveolaris*

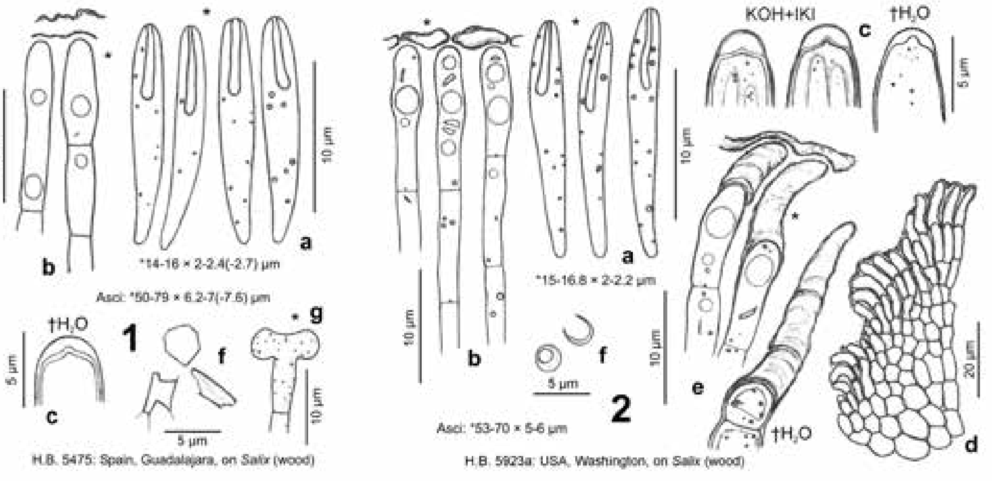


Plate 266. **1–2**: *Orbilia angiosubvinosa*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section; **e**. cortical cells with glassy process; **f**. crystalloid SCBs in excipular cells; **g**. young conidium (from substrate).

Plate 267. **1–5**: *Orbilia angiosubvinosa*. – **1a**. pond with *Salix caprea* in a *Fagus* forest; **1b–d**, **3a**, **4a**. rehydrated apothecia; **3c**. apothecium in median section; **3b**, **5**. id., marginal ectal excipulum; **1f**, **3e**. ectal excipulum with crystalloid SCBs; **1e**, **2a**, **3d**, **4b**. ascospores; **2b**, **3f**. conidia from substrate. – Living state, except for **5** (in KOH). – **1a–f**, **2a–b**, **4a–b**: phot. R. Tena. — **1a–f**. 1.VI.2013: Spain, Zaragoza, Moncayo, on *Salix*; **2a–b**. 3.VII.2011: ibid.; **3a–f**. H.B. 9813a (holotype): Spain, Asturias, Pola de Somiedo, on *Corylus*; **4**. 3.IV.2013: ibid., Teruel, on *Rosa*; **5**. H.B. 5923a: USA, Washington, on ?*Salix*.

{1}, *Deltopyxis triangulispora* {1}, *Hysterographium fraxini* {1}, *Mellitiosporiella pulchella* {1}, *Orbilia eucalypti* {1}, *O. subovoidea* {1}, *O. vinosa* {2}, *Parmelia* sp. {2}, *Physcia* sp. {1}, *Usnea* sp. {1}. **Desiccation tolerance**: fully viable for at least 2 months. **Altitude**: 1140–1548 m a.s.l. (Spain), 82 m (USA). **Geology**: Spain: slate, sand & clay, dolomite; USA: Quaternary sediment from Jurassic-Cretaceous sedimentary rock. **Phenology**: IV–VIII (possibly throughout the year, long-lived).

Taxonomic remarks. Based on the associated dwayaangam-like anamorph and the deep orange apothecia, the angiosperm-inhabiting *Orbilia angiosubvinosa* is undoubtedly closely related to the conifericolous *O. subvinosa*. Our preliminary molecular data indicate a close but distant relationship to that species. Morphologically, *O. angiosubvinosa* differs in slightly narrower conidia, also in slightly shorter and wider ascospores which resemble a bit those of *O. hesperidea*. Yet, the included SBs are longer and the crystalloid SCBs in the ectal excipulum are too small to fit *O. hesperidea*. *O. coronohesperidea* from semihumid to arid Australia mainly differs in slightly wider spores, while its anamorph is unknown.

The morphological limits in the teleomorph between *O. angiosubvinosa* and *O. vinosa* are not sharp, however, and it may well be that some collections with wider ascospores here included in *O. vinosa* belong in fact to *O. angiosubvinosa*.

Variation. The four collections from Asturias (on *Corylus*) and Zaragoza (on *Salix*) (Pl. 267) lack glassy processes, although thickened cell walls up to 1 µm were observed at the margin; therefore, the apothecia have a smooth margin. The three collections from Teruel, Guadalajara, and Washington (on *Rosa* and *Salix*) have glassy processes 5–28 µm in length (Pl. 266) which may form a crenulate margin (see also Pl. 267: 4a). Yellowish-orange LBs in paraphyses and excipular cells were only observed with certainty in the collection on *Rosa*.

Anamorph. Conidia of *O. angiosubvinosa* (Pl. 267: 2b, 3f) closely resemble those of *O. subvinosa*. However, their connection to a teleomorph was not affirmed in pure culture. Only a single dwayaangam-like conidium was seen in the specimen from Washington (IVV: H.B. 5923a), and in the sample from Guadalajara a T-shaped conidium was observed on a conidiophore emerging from the hymenium, perhaps representing a very young stage of dwayaangam-like anamorph (Pl. 266: 1g).

The similar *Dwayaangam yakuensis* (Pl. 13: a) differs from *O. subvinosa* and *O. angiosubvinosa* in conidia which never exceed 34 µm in length due to shorter arms with only (0–)1–2 septa, and in which the stipes are consistently longer than the basal arms. Therefore, we believe that this anamorph is undoubtedly not conspecific with either of these species. It was isolated from rotten angiosperm leaves in the tropics: in Japan on *Machilus thunbergii* and in Australia on *Archontophoenix alexandrae* (Matsushima 1975: 158 pl. 345, 1989: 17 fig. 517). This deviation applies also to some other records referred to *D. yakuensis*, being reported from more temperate regions: Matsushima (1981: 9 fig. 84, from bark of *Fagus crenata* in Japan), Ando & Tubaki (1984a, from rainwater from the canopy of *Quercus* spp. in Japan), and Kitz & Embree (1980, from soil and leaf mold in an oak-hickory woodland in Iowa, USA). The conidia from temperate Japan deviate from tropical *D. yakuensis* in slightly outwards curved arms, whereas those from Iowa tend to have inward curved arms. We believe that all these records are not conspecific with *O. angiosubvinosa*.

Phylogeny. A sequence of the ITS region was gained from the sample on *Corylus* from Asturias. As in *O. subvinosa* the S1506 intron is absent. *O. angiosubvinosa* clustered highly supported with *O. subvinosa* (Phyl. 11), though with a 6–7 % distance. Its distance to *O. vinosa* is 10.5–11.5 % and to the intermediate strain H.B. 6748g 11 %.

Ecology. *Orbilia angiosubvinosa* was collected in suprasub- to orosubmediterranean, (semi)humid regions of southern Europe above 1100 m altitude, repeatedly at water bodies such as ponds or streams, for instance, in a forest with *Fagus sylvatica*, *Quercus pyrenaica*, and *Betula pendula* at a pond with *Salix caprea* in the Sierra del Moncayo, or in an open vegetation along a streamlet with *Salix* and *Populus* in the northeastern part of the Sierra de Guadarrama. The holotype was found in a deciduous forest in a creek which included *Fagus sylvatica* and *Corylus avellana*. The single North American location was a deciduous lowland forest in the mild-maritime humid Pacific west at the southern end of the Coast Mountains.

Specimens included. **SPAIN**: **Asturias**, 4.1 km ESE of Pola de Somiedo, 1.2 km NE of Valle de Lago, 1165 m, branch of *Corylus avellana*, on wood, 4.VI.2013, T. Læssøe (ex H.B. 9813a, AH 52842, **holotype**, anam. substr.; sq.: MK493127). – 2.2 km SE of Pola de Somiedo, SW of Coto de Buenamadre, Hayedo de Mumián, 1155 m, branch of *C. avellana*, on wood, 2.VI.2013, T. Læssøe & J.H. Petersen (ø). – **Aragón**, **Zaragoza**, Sierra del Moncayo, 9 km SE of Ágreda, 3.8 km SW of San Martín de la Virgen de Moncayo, SW Agramonte visitor center, 1140 m, branch of *Salix caprea*, on wood, 3.VII.2011, R. Tena (ø, anam. substr., doc. vid.). – ibid., 1.VI.2013 (R.T.L. 13060101, 13060102, doc. vid.). – **Teruel**, 52 km WNW of Teruel, 2 km SW of Orihuela del Tremedal, 1548 m, branch of *Rosa*, on wood, 3.IV.2013, R. Tena (R.T.L. 03041301, doc. vid.). – **Castilla-La Mancha**, **Guadalajara**, Sierra de Guadarrama, 55 km NNW of Guadalajara, 0.7 km NW of Majaelrayo, Arroyo La Matilla, 1180 m, branch of *Salix*, on wood, 14.V.1996, H.O. Baral (H.B. 5475 ø, anam. substr.). — **USA**: **Washington**, 14 km S of Acme, 5 km S of Whatcom, railway, 82 m, branches of (?)*Salix*, on wood, 15.VIII.1997, G. Marson (H.B. 5923a, anam. substr.).

Orbilia arachnovinosa Baral & E. Weber, **sp. nov.**, MB 813560 — Pls 268–269, Map 47

?= *Orbilia rubinella* (Nyl.) P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 97 (1871)
≡ *Peziza rubinella* Nyl., Not. Sällsk. Fauna Fl. Fenn. Förh. 10: 56 (1869)
≡ *Orbilia coccinella* var. *rubinella* (Nyl.) Velen., Monogr. Discom. Bohem.: 92 (1934)

Etymology: *arachnovinosa*: named after the conidia with spider-like legs; *rubinella*: named after the ruby colour.

Typification: Germany, Miesbach, branch of *Sorbus aucuparia*, 3.VII.2005, P. Karasch (ex H.B. 7838a, M-0281049, holotype of ***O. arachnovinosa***). — Finland, Merimasku, branches of *Quercus*, XII.1858, P.A. Karsten (Karsten 3196, H-6003827, lectotype of ***O. rubinella***, designated here, MBT202705).

Latin diagnosis: *Similis* Orbiliae subvinosae *sed ramis conidiarum valde curvatis. Habitat ad lignum putridum ramorum siccorum angiospermarum in orotemperata ad boreale et orosubmediterranea Europae et Asiae.*

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated (0.2–)0.3–0.8(–1.4) mm diam., 0.15–0.3(–0.4) mm high (receptacle 0.13–0.15 mm), light to bright or deep orange-rose, yellow-orange or orange-red, rarely pure rose, not or slightly to medium translucent, round to elliptical, scattered to gregarious; disc slightly flat, finally slightly convex, margin usually distinct, 0–5 µm protruding, finely crenulate or with distinct teeth, rarely smooth; broadly sessile or often with a ± distinct, whitish to pale orange stipe 0.07–0.25 × 0.2–0.5 mm, superficial or ± immersed in cracks; dry with somewhat inrolled margin, bright to deep orange-red. **Asci** *53–80(–95) × (5.3–)6–6.5(–7) µm {5}, †(47–)50–60(–70) × 4.9–5.8 µm {2}, 8-spored, spores */†2–4-seriate, (2–)3–5 lower spores inverted {3} (not mixed), pars sporifera *24–37 µm long; **apex** (†) hemispherical, dome †1.3–1.5(–2) → 0.7–1 µm thick {3}, with apical chamber; **base** with medium to long, thin, flexuous stalk, L- shaped. **Ascospores** *(12–)15–19(–21)((–23)) × (1.7–)1.9–2.2(–2.4) µm {12}, †14–17.5(–19) × 1.8–2.1 µm {2}, (cylindric-)fusoid

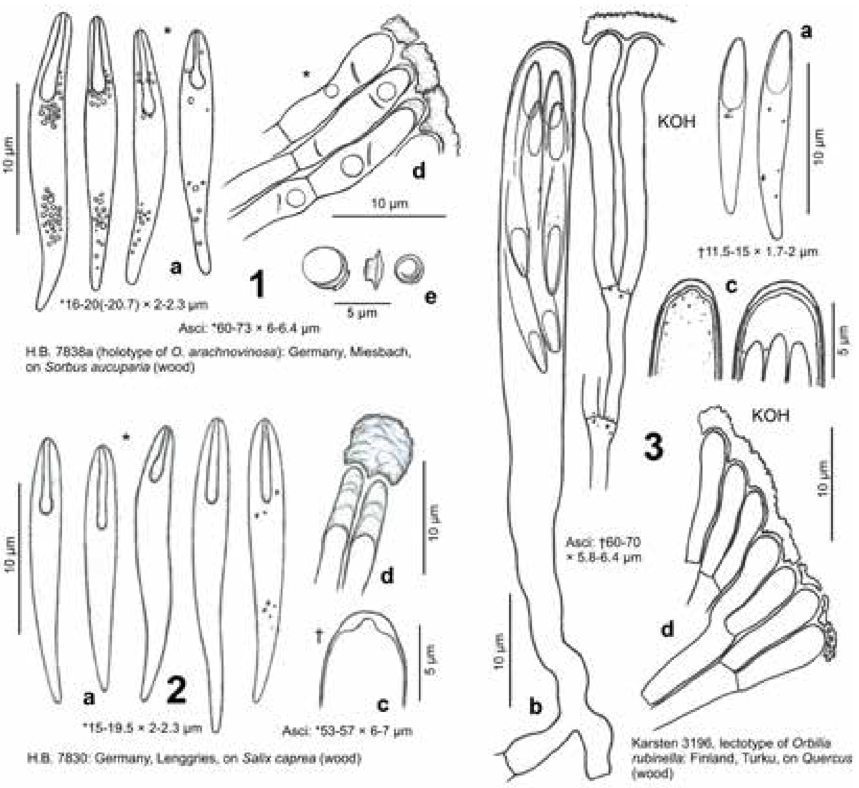


Plate 268. **1–2**: *Orbilia arachnovinosa*; **3**: *O.* cf. *arachnovinosa*. – **a**. ascospores; **b**. paraphyses and ascus; **c**. ascus apices; **d**. marginal cortical cells, with or without glassy processes; **e**. crystalloid SCBs in ectal excipular cells (base and flanks).

to fusoid-clavate, apex (rounded to) obtuse, base medium to mostly strongly attenuated, without or sometimes with a distinct tail *4–5 × 0.8–1.2 µm, straight to often distinctly bent near base, sometimes also towards apex; **SBs** *4–6(–7.5) × (0.6–)0.7–1(–1.2) µm {9}, vermiform (rod-shaped), sometimes ± inflated at the base, also subulate, apically narrowed to a small to wide point, rarely not narrowed, straight, with a few minute or also many small LBs; SBs in aged spores ampulliform, 2.5–4 × 0.9–1.3 µm {2}. **Paraphyses** apically uninflated to slightly clavate, terminal cells *11–25 × 2.3–3.5 µm {2}, †8–13.5(–22) × (1.5–)1.8–2.8 µm {1}, lower cells †7–11.5 × 1.4–1.7 µm {1}; unbranched at upper septum, hymenium pale or light rose to orange. **Medullary excipulum** hyaline to pale rose, 50–130 µm thick, of loose or dense textura intricata, with indistinctly inflated cells, medium to sharply delimited. **Ectal excipulum** hyaline to pale rose, of (†) thin-walled, ± vertically oriented textura globulosa(-prismatica) from base to mid flanks, 30–100 µm thick near base, cells *8–25 × 6–12(–20) µm {3}; 30–40(–50) µm thick near margin, of t. porrecta oriented at a 45–80° angle to the surface, marginal cortical cells *10–13 × 2.7–3.3 µm {1}; **glassy processes** 0–3 {4} or 3–10 {3} or 10–30 {9} × (2–)2.3–3.5(–4)((–5)) µm {12}, high-refractive, ± stratified, coherent, sometimes forming distinct teeth. **Anchoring hyphae** very abundant, *2–3 µm wide, walls 0.2–0.5 µm thick {1}. **SCBs** in paraphyses and ectal excipulum (near margin) absent {3} or globose {2}, 1–3 µm diam., also crystalloid {3}, hyaline to very pale orange, 1.5–6 µm diam.; **LBs** in basal part of paraphyses golden yellow to orange (carotenoids) {2}, minute or up to 1–1.5 µm diam. **Exudate** over paraphyses 0.5–2 µm thick, cloddy, hyaline, loosely attached, over margin and flanks 0.5–4 µm thick, rough, yellowish-chlorinaceous. — **ANAMORPH**: dwayaangam-like (presumed, from natural substrate {9}). **Conidiophores** unknown. **Conidia** resembling a spider or butterfly, total size *(30–)40–57(–65) × (25–)30–60(–77) {7} or *62–64 × 35–40 µm {1}; stipe *(11.5–)12.5–17(–19.5) × 3–3.7(–4.2) {7} or *25–29 × 5.2–5.4 µm {1}, 2–3-septate; twice dichotomously branched: two arms pointing upwards, two downwards, arms ± tapered, slightly to medium outwards curved, in situ *(12–)17–37(–41) × (2.5–)2.8–3.5(–4.2) {7} or *26–38 × 4.2–4.5 µm {1}, (2–)3–5(–6)-septate, containing some or many minute LBs, sometimes also larger ones with 1–1.5(–2) µm diam.

Habitat: collected 0.3–3 m above the ground, decorticated, also ± corticated, 6–50 mm thick branches, also in a wound of 25 cm thick standing trunk, of *Betula pubescens* {4}, *Clematis vitalba* {1}, *Erica arborea* {1}, *Fagus sylvatica* {3}, *Rhododendron dahuricum* {1}, *Salix* sp. {1}, *S. appendiculata* {1/1}, *S. aurita* {1}, *S. caprea* {1}, *Sorbus aucuparia* {2}, ?*Ulmus minor* {1}, on 0.2 mm deep strongly decayed wood {17}, rarely bark {2}, strongly greyed, sometimes covered by abundant green algae. **Associated**: *Cryptodiscus foveolaris* {1}, *Dacrymyces* sp. {1}, *Durella connivens* {1}, *Echinosphaeria strigosa* {1}, *Hyalorbilia helicospora* {1}, *H. juliae* {1}, *Hypogymnia physodes* {2}, *Hysteropatella elliptica* {1}, *Lecanora* sp. {1}, *Lecophagus vermicola* {1}, *Orbilia cejpii* {1}, *O. eucalypti* {1}, *O. filiformis* {1}, *O. flagellispora* {1}, *O. montigena* {1}, *O. subsphaerospora* {1}, *O. subtrapeziformis* {1}, *O. vinosa* {2}, *Parmelia sulcata* {2}, *Perrotia flammea* {1}, *Physconia distorta* {1}, *Propolis farinosa* {1}, *Sclerococcum* ?*epimyces* {1}, *Usnea* sp. {1}, pleurocarpous moss {1}. **Desiccation tolerance**: fully viable for at least 4 months. **Altitude**: 42–550 m a.s.l. (northern Europe), 1043–1845 m (central and southern Europe), 470 m (central Asia). **Geology**: Cambrian & Silurian shale, lime- & sandstone, Buntsandstein, Lower & Middle Jurassic and Cretaceous marl & limestone, dolomite, Eocene flysch, Pleistocene sand; granite, granodiorite, syenite, migmatite, dolerite, quartzite, gneiss, mica schist, phyllite, amphibolite. **Phenology**: III, VI–X (probably throughout the year, long-lived).

Taxonomic remarks. *Orbilia arachnovinosa* is separated from *O. vinosa* and *O. subvinosa* mainly because of its deviating anamorph and molecular data. Very similar to the mainly orosubmediterranean and mainly conifericolous *O. subvinosa*, the angiosperm-inhabiting, mainly boreal to orotemperate *O. arachnovinosa* tends to deviate from *O. vinosa* in apothecia with a bright orange-red colour and a finely denticulate margin, and in slightly larger ascospores, but these characteristics are too inconsistent to permit clear recognition of the species.

Variation. Apothecial colour was usually bright orange in various shades towards yellow, rose or red. In a population with mainly orange apothecia (Pl. 269: 1b–f), a few were light rose without an orange component (Pl. 269: 1g). In this collection, apart from large dwayaangam-like conidia also trinacrium-like conidia typical of *O. vinosa* were found on the substrate (Pl. 261: 5). Therefore, the light rose apothecia, though also with a crenulate margin and microscopically ± indistinguishable from the orange ones (the right spore in Pl. 269: 1i is from a rose apothecium), might belong to *O. vinosa*.

Despite the predominant orange colour, the presence of yellow-orange LBs was only noted in three collections (H.B. 7838a, 8248a, A.P. 19/31). They were perhaps present in the others too, but certainly in lower amounts. Also crystalloid SCBs were only seen in three collections (H.B. 7838a, 9408b, A.P. 19/31) while absent in others, and their presence is accordingly inconsistent. The length of the glassy processes varied among or sometimes even within the populations between ± absent (Pl.

268: 1d, 3d) and up to 30 µm long (Pl. 269: 2c); consequently the margin varied between smooth (holotype, Pl. 269: 4c–d) and ± distinctly crenulate (Pl. 269: 1c–g, 2a–b, 5b–c). Some variation was also noted in the size of asci, ascospores, and SBs.

In the collection from Norway (on *Betula*, H.B. 9408), apothecia of *O. arachnovinosa* grew intermingled with *O. vinosa* and were recognizable by their deeper colour and crenulate margin. Also Malençon & Llimona (1980: 54) drew attention to the difference in apothecial colour when comparing an supramediterranean collection on *Quercus pyrenaica* bark (with orange-red apothecia and slightly larger asci) with vinaceous apothecia in the literature.

In two collections from Scandinavia (Pl. 269: 2, 5) we were unable to detect conidia, but we have included them because of an intense apothecial colour and presence of marginal teeth in combination with an angiosperm host. Conidia were also not found in a specimen from Altay Republic (on *Rhododendron*) with bright red apothecia and spores of *17.5–20 × 2–2.3 µm, which might belong here, according to a drawing by E.S. Popov (pers. comm., IVV: 13.VIII.2008), in one from Austria (on *Fagus*), with light orange apothecia with prominent marginal teeth (G. Friebes pers. comm.), and in one from Pyrénées (on *Fagus*), in which the spores were unusually narrow (*15.5–16.5 × 1.7–1.9 µm).

Type studies. Based on comparatively large asci, a red apothecial colour, and occurrence in a hemiboreal region on angiosperm wood, it cannot be excluded that *O. rubinella* is conspecific with the present species. Unfortunately, the type sample was not searched for conidia. The spores were only seen inside the asci and here difficult to discern, and perhaps therefore, they are rather small. In any case, the SBs were visible as a transparent region of 3.8–6 × 1.2–1.4 µm (Pl. 268: 3). The apical dome was sometimes also to thicker than illustrated here. We refrained from adopting the name *O. rubinella*, e. g., because the apothecia were rather small and thin, and also the marginal ectal excipulum was comparatively thin.

The type material of *O. rubinella* in H consists of two convolutes which apparently belong to a single collection (on wood of *Quercus*, according to the wood anatomy). This was found to represent a double organism consisting of *O. vinosa* s.l. and the asci of an intrahymenial parasite, *Helicogonium orbiliarum* Baral & G. Marson (Baral 1999: 47). The protologue of *Peziza rubinella* includes elements of both the host (excipulum, paraphyses) and the parasite (asci, globose ascospores, ascoconidia). The taxon was lectotypified on the host element by Baral (l.c.) because the name *rubinella* refers to the colour of the host apothecia (flesh- to almost scarlet-red), hence became a later synonym of *O. vinosa* (s.l.). Nannfeldt (1932: 252) thought that the protologue of *P. rubinella* is erroneous as he happened to study just that part of the collection which contained asci of the *Orbilia* with narrowly fusiform ascospores, but not the globose spores reported by Nylander. Nannfeldt was in error when referring *P. rubinella* to synonymy with *Hyalinia rubella*.

When lectotypifying *P. rubinella*, Baral (1999) did not mention that two convolutes exist. In one of them (P.A. Karsten 3196, ‘ad lign querc.’) two apothecia were examined and found to contain many mature asci of *O. vinosa* s.l., though in one of the two also some immature asci of *Helicogonium* were seen. In the other convolute (labelled XII.1858, Fennia, regio Aboensis, Merimasku) three apothecia were examined and found to contain numerous parasitic asci among the paraphyses (Baral l.c., fig. 22), but no host asci. Also here the host obviously represents the same *Orbilia*. *P. rubinella* is **lectotypified** here on the convolute Karsten 3196, by excluding the sparsely observed immature parasitic asci.

Seaver’s (1951: 157) report of *O. rubinella* from North America (New Hampshire) with subglobose ascospores 2–3 µm diam. deserves reexamination. Possibly the ascospores belong to a small-spored *Orbilia*, but it could also refer to *Helicogonium orbiliarum* which was reported from Utah and Washington (USA) in apothecia of *O. vinosa* (Baral 1999).

Not included collections. In a specimen from Schwarzwald (southern Germany) and in the type of *O. rubinella* from Finland the anamorph was not observed, and in both the glassy processes were either absent or only up to 3 µm long. Since the spores were rather short (*14–16 × 2–2.3 µm in the German sample), we refrained from including them in the description.

Three orotemperate, (sub)alpine samples from Spain and Austria referred to as *O.* aff. *arachnovinosa* (on ?*Calluna*, E. Rubio, IVV: E.R.D. 6754, 7933; on *Rhododendron*, G. Friebes, IVV: 2.VI.2018) are microscopically indistinguishable from *O. subulivinosa*, but DNA data place them close to *O. arachnovinosa*, from which they deviate in distinctly narrower spores of *(14–)16–22 × 1.4–1.8(–2) µm.

Anamorph. The conidia observed in association with *O. arachnovinosa* belong to an undescribed species of the form genus *Dwayaangam* (Pl. 269: 1j, 4f, 6–7). With their outwards curved arms they resemble those of *O. junci* (?series *Vibrioides*) but are much larger due to their rather long and narrow arms with more septa. In addition, the two upper arms are always distantly inserted on very short primary arms, whereas in *O. junci* and in the similar ‘*Dwayaangam cornuta*’ as illustrated by Matsushima (1993) they touch each other more or less (Pl. 13: b–c). *D. cornuta* as described by Descals & Webster (1982) is similar but differs in much fewer septa, the arms being twice as wide, and in a tendency to higher-branched conidia. Pure cultures were not undertaken in any of the included samples of *O. arachnovinosa*, therefore, the connection of these remarkable conidia to the teleomorph could not be established with certainty.

Gönczöl & Révay (2006: fig. 19, as *D. cornuta*) illustrated a conidium which resembles the present ones even in arm width, but the arms show only 2–3-septa, also the 3-septate stipe is much longer and slightly exceeds the basal arms in length. Gönczöl & Révay observed this type of conidia in stemflow from living trees of *Fagus* and *Carpinus* collected by K. Vanký in Tübingen (southern Germany). In a sample from Loire (G.M. 2018-09-13.1) the conidia differ in their considerable length (*62–64 × 35–40 µm) and the extraordinarily long and wide stipe, also the arms are oriented more like a H than an X (IVV: 13.IX.2018). An ascospore isolate of this sample grew very slowly and finally failed to produce a mycelium.

Phylogeny. Sequences of *O. arachnovinosa* were gained from three samples: one from Asturias (on *Erica*, H.B. 10093) and two from southern France (on *Clematis*, G.M. 2015-09-15.8; on *Sorbus*, G.M. 2016-08-14.5), comprising S1506 intron+ITS, the latter two also LSU and the latter SSU. The sequence of *O.* aff. *arachnovinosa* on *Rhododendron*, comprises SSU, ITS, and LSU, and lacks the intron. No DNA data from the type of *O. arachnovinosa* were available. The characteristic conidia were only observed in one of these three samples (on *Sorbus*), and here also different types of trinacrium-like conidia occurred.

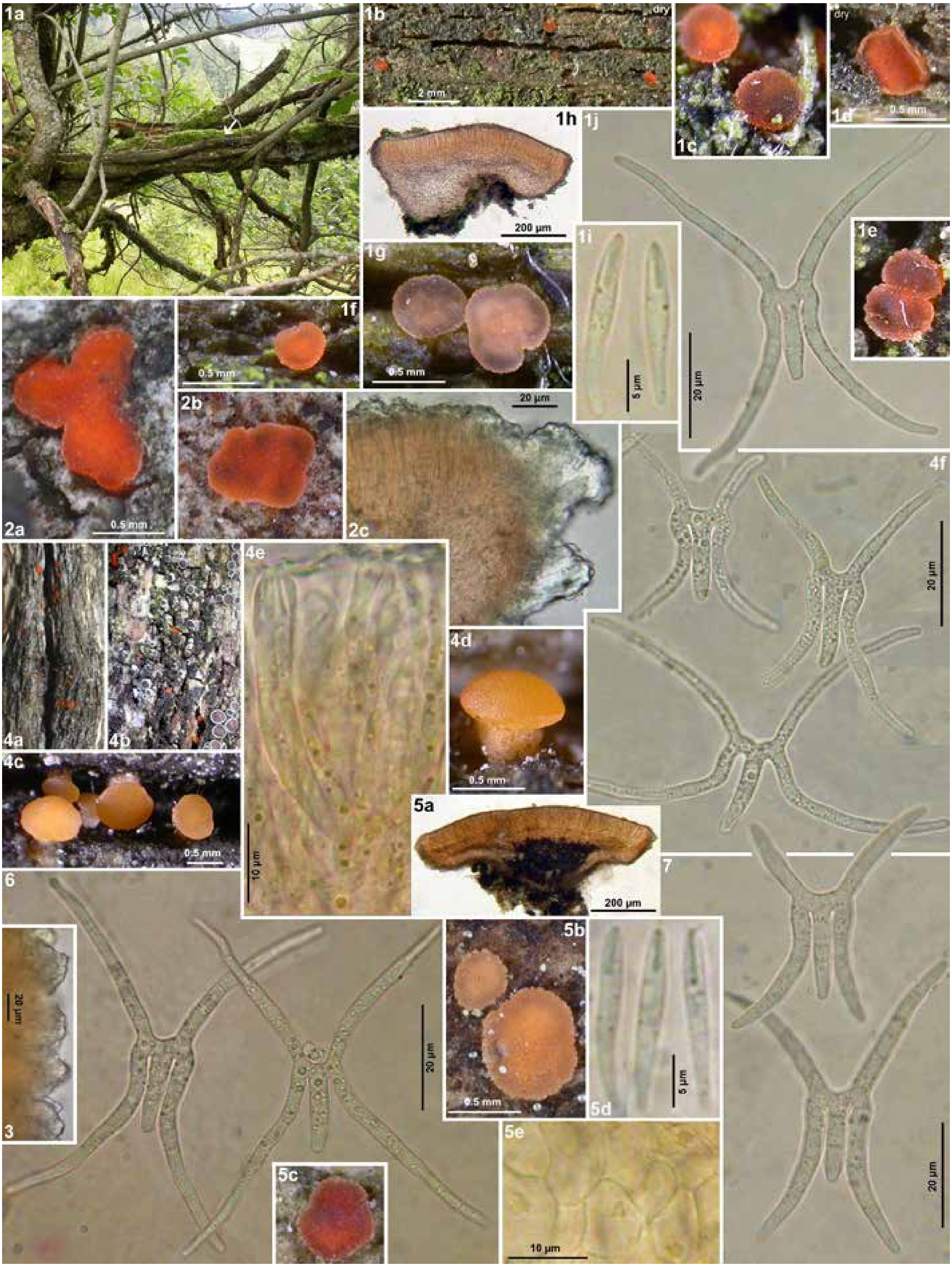


Plate 269. **1–7**: *Orbilia arachnovinosa*. – **1a**. *Salix appendiculata* in a montane pasture, dead mossy branches; **1c**, **e–g**, **2a–b**, **4a–d**, **5b–c**. fresh or rehydrated apothecia (**4b** with *Lecanora* ?*argentata*); **1b**, **d**. dry apothecia; **1h**, **5a**. apothecia in median section; **2c**. id., marginal ectal excipulum with glassy processes forming teeth; **3**. marginal teeth in top view; **5e**. crystalloid SCBs in excipular cells (lower flanks); **4e**. ascus and paraphyses (with yellow-orange LBs); **1i**, **5d**. ascospores; **1j**, **4f**, **6**, **7**. conidia from substrate. – Living state, except for **2c**, ascus in **4e** (in H_2O). — **1a–j**. H.B. 8248a: Switzerland, Luzern, on *Salix*; **2a–c**. H.B. 9360b: Sweden, Lapland, on *Betula*; **3**. H.B. 9375: ibid.; **4a–f**. H.B. 7838a (holotype): Germany, Miesbach, on *Sorbus*; **5a–e**. H.B. 9408: Norway, Gudbrandsdal, on *Betula*; **6**. H.B. 7830a: Germany, Lenggries, on *Salix*; 7. H.B. 9170b: France, Grenoble, on *Salix*.

The two strains from France have identical sequences except for 1 nt in the LSU D3 domain. They differ from the Spanish sample in the ITS1 by 1 nt, in the ITS2 by 2 nt, and in the intron by 1 nt (overlapping 403 nt). Three conspecific environmental sequences, obtained by Menkis et al. (2016) from elm bark beetles in Gotland (Sweden), comprise 5.8S+ITS2 and obviously belong to *O. arachnovinosa*. Only one of them was uploaded in GenBank (KP891980), while the other two are identical except for one of them deviating by 1 gap in the ITS2 and 1 gap in the 5'-end of LSU (A. Menkis pers. comm.). From the two above sequences these differ by 1–2 nt (1.5–2 %) and 0–1 insert in the ITS2. It is just the gap in the ITS2 that is also observed in our two strains.

O. arachnovinosa clustered in the *vinosa-subvinosa* subclade (Phyl. 11), with an ITS distance of 5 % to *O.* aff. *arachnovinosa* (not shown, mentioned under *O. subulivinosa*), 7–7.5 % to *O.* cf. *vinosa* (H.B. 6748g), 7.5–8.5 % to *O. vinosa*, and 8.5–9.5 % to *O. subvinosa*. When separately comparing ITS1 and ITS2, the distances are partly distinctly higher in the ITS2: to *O.* aff. *arachnovinosa* 7.5–8.5/5.7–6.8 %, to *O.* cf. *vinosa* 7–7.5/12.5–13.5 %, to *O. vinosa* 8–10/11–14 %, and to *O. subvinosa* 4.8–5.5/19–21 %. In the intron the distance is 6.5–8 % to *O. vinosa* and 5.5–6 % to *O.* cf. *vinosa* (H.B. 6748g), and in LSU D1–D2 only 0.5 % (3 nt deviation) to *O. subvinosa* compared to 0.8 % to *O.* cf. *vinosa*, 1.4 % to *O.* aff. *arachnovinosa* and 1.7 % to *O. vinosa*.

Ecology. *O. arachnovinosa* was recorded on ± rotten wood of xeric branches of various angiosperms. Records so far mainly derive from *Betula*, *Fagus*, and *Salix*. The species is known from a few orotemperate humid, altimontane to subalpine sites in the northern, eastern, and southern Alps, also from orotemperate to rarely orosubmediterranean Southern French Alps and Cantabrian mountains. Further records are from oroboreal Lapland and supraboreal Norway and from the orotemperate humid western Altay Mts. in central Asia. The environmental sample from cold-temperate southern Sweden (Gotland) was isolated from elm bark beetles, and the fungus probably originated from *Ulmus* bark.

Two not included collections are from montane southern Germany (Schwarzwald) and from hemiboreal southern Finland. *O.* aff. *arachnovinosa* was found in two ± alpine (orotemperate humid) European shrublands: on wood of xeric twigs and thin branches of ?*Calluna* in northern Spain and of *Rhododendron* in eastern Austria.

Map 47. Known distribution of *O. arachnovinosa* in Europe (yellow = not included collections, cyan = *O.* aff. *arachnovinosa*)

Specimens included. **NORWAY**: **Oppland**, Sel, 20 km SE of Dovre, 3 km E of Sel, Gudbrandsdal, E of Fugleskjelle, 370 m, branch of *Betula pubescens*, on wood, 30.VII.2010, H.O. Baral (H.B. 9408b). — **SWEDEN**: **Västerbotten**, Vilhelmina, 4.5 km SW of Saxnäs, Satsfjället, Pojken, 715 m, branches of *B. pubescens*, on wood & bark, 24.VII.2010, H.O. Baral (H.B. 9360b). – 0.5 km SW of Saxnäs, Fjällgarden, 550 m, trunk of *B. pubescens*, on wood, 26.VII.2010, P. Perz & H.O. Baral (H.B. 9368a, anam. substr.). – **Jämtland**, Strömsund, 57 km W of Saxnäs, E of Bjurälven, west-edge of Leipikvattnet, 475 m, branch of *B. pubescens*, on wood, 27.VII.2010, P. Perz (H.B. 9375, anam. substr.). – **Gotland**, 12.5 km S of Visby, 1.9 km N of Hogräns kyrka, 42 m, from adults of *Scolytus multistriatus* (pheromone trap, probably emerging from *Ulmus minor*), VI–VIII.2012–2014 (Menkis et al. 2016, clone 2170_1175 [921_2026 & 419_1868], mol. extr.; sq.: KP891980). — **GERMANY**: **Bayern**, **Oberbayern**, Mangfallgebirge, 16.5 km SSE of Miesbach, 2.7 km ESE of Spitzingsee, Taubenstein, 1600 m, branch of *Sorbus aucuparia*, on wood, 3.VII.2005, P. Karasch (ex H.B. 7838a, M-0281049, **holotype**, anam. substr.; MAMU 453, **isotype**). – Kocheler Berge, 6.5 km WSW of Lenggries, NW of Latschenkopfhütte, S of Vorderer Kirchstein, 1600 m, branch of *Salix caprea*, on wood, 21.VI.2005, P. Karasch & B. Fellmann (H.B. 7830a ø, anam. substr.). — **SWITZERLAND**: **Nidwalden**, 8.2 km SSW of Luzern, 3.2 km W of Hergiswil, N of Bergstation Gschwänd, 1200 m, branches of *S. appendiculata*, on wood, 18.VIII.2006, H.O. Baral (H.B. 8248a, anam. substr.). — **AUSTRIA**: **Steiermark**, 11 km NW of Deutschlandsberg, 3 km W of Rachling, E of Rosenkogel, 1150 m, branch of *Fagus sylvatica*, on wood, 24.III.2012, G. Friebes (ø, doc. vid.). — **ITALY**: **Trentino-Alto Adigo**, **Bolzano**, 3 km SSE of St. Magdalena, NNE of Seceda, 1845 m, branch of *Salix*, on wood & bark, 1.VIII.2019, A. Polhorský (A.P. 19/31, doc. vid.). — **FRANCE**: **Rhône-Alpes**, **Loire**, 12 km ESE of St.-Étienne, 2.2 km NNE of Le Bessat, 1123 m, branch of *Sorbus aucuparia*, on wood 14.VIII.2016, G. Marson (G.M. 2016-08-14.5; sq.: MK473401). – ibid., 1.9 km NNE of Le Bessat, 1145 m, branch of *S. aucuparia*, on wood, 13.IX.2018, G. Marson (G.M. 2018-09-13.1, anam. substr.). – **Isère**, Parc Naturel Regional du Vercors, 20 km SW of Grenoble, 2 km SSE of Villard-de-Lans, W of Les Glovettes, 1200 m, branch of *Salix appendiculata*, on wood, 11.VIII.2009, H.O. Baral (H.B. 9170b ø, anam. substr.). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 18.3 km WNW of Gap, 1 km NW of La Montagne, SW of Pic de Bure, 1043 m, branch of *Clematis vitalba*, on wood, 15.IX.2015, G. Marson (G.M. 2015-09-15.8; sq.: MK473400). – **Aquitaine**, **Pyrénées-Atlantique**, 23 km WSW of Oloron-Ste.-Marie, 9 km WNW of Osse-en-Aspe, Col de Labays, 1350 m, branch of *Fagus sylvatica*, on wood, 9.X.2016, H.O. Baral (H.B. 10031). — **SPAIN**: **Asturias**, 2.2 km SE of Pola de Somiedo, SW of Coto de Buenamadre, Hayedo de Mumián, 1350 m, branch of *F. sylvatica*, on wood, 3.VI.2013, J.P. Priou (H.B. 9796b ø, anam. only). – 11 km SE of Pola de Somiedo, 6 km SE of Valle de Lago, Lago de Valle, 1560 m, branch of *Erica arborea*, on wood, 6.VI.2017, H.O. Baral (ex H.B. 10093, KL553; sq.: UDB035011). – 5.8 km S of Pola de Somiedo, S of La Peral, 1297 m, branch of *Salix aurita*, on wood, 7.VI.2017, S. Helleman (H.B. 10109, anam. substr.). — **RUSSIA (East)**: **Altay**, **Turochak**, 63 km SE of Turochak, SW of Yaylyu, northern shore of Telezkoje Lake, 470 m, branch of *Rhododendron dahuricum*, on wood, 13.VIII.2008, E.S. Popov (LE 247356, doc. vid.)

O*. cf. *arachnovinosa: **FINLAND**: **Varsinais-Suomi**, 21 km W of Turku (= Abo), Merimasku, ~10 m, branches of *Quercus*, on wood, XII.1858, P.A. Karsten (Karsten 3196, H-6003827, **lectotype** of *O. rubinella*, H.B. 5221b ø). — **GERMANY**: **Baden-Württemberg**, Schwarzwald, 10 km ESE of Bühl, 7.5 km WSW of Forbach, Herrenwies, Schwarzenbach, 760 m, branch of *Salix* (?)*cinerea*, on bark, 13.VI.2005, E. Weber (ø).

O*. aff. *arachnovinosa: **AUSTRIA**: **Steiermark**, Koralpe, 16.5 km W of Deutschlandsberg, 2.2 km SSW of Weinebene, 1795 m, branch of *Rhododendron ferrugineum*, on wood, 2.VI.2018, G. Friebes (G.F. 20180360, doc. vid.; sq.: MK473399). — **SPAIN**: **Asturias**, 10 km NW of Villablino, SW of Puerto de Leitariegos, laguna del Puerto, 1690 m, twig of ?*Calluna vulgaris* (or *Vaccinium uliginosum*), on wood, 14.VII.2016, J. Linde, vid. E. Rubio (E.R.D. 6754, doc. vid.). – ibid., SW of laguna del Puerto, 1801 m, twigs of ?*C. vulgaris* (or *V. uliginosum*), on wood, 25.V.2019, J. Linde, vid. E. Rubio (E.R.D. 7933, doc. vid., sq.: MT370349).

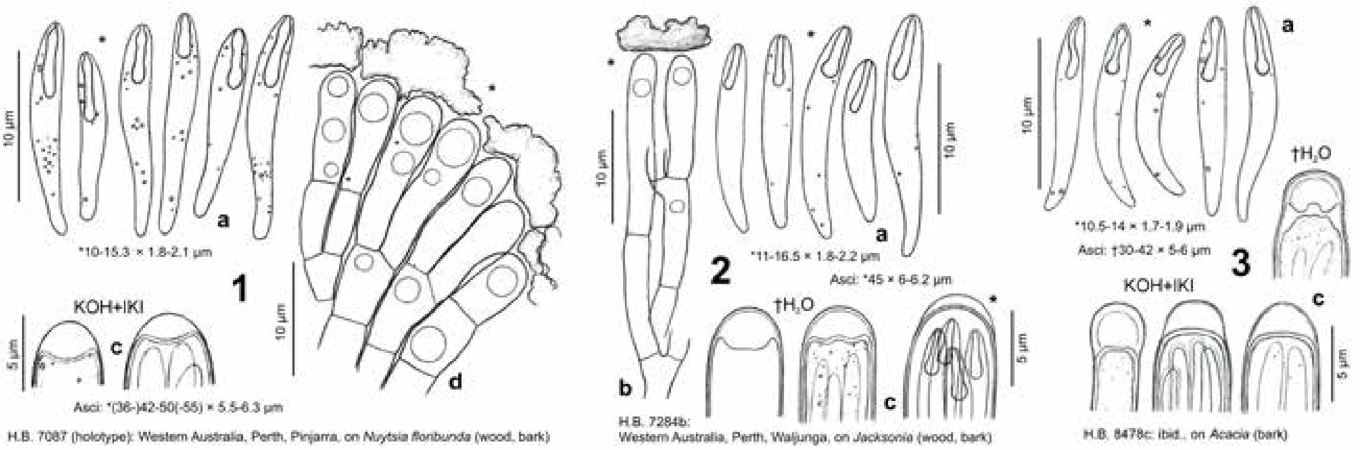


Plate 270. **1–3**: *Orbilia nothovinosa*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum (median section).

Orbilia nothovinosa Baral, **sp. nov.**, MB 813562
— Pls 270–271, Map 48

Etymology: the epithet means 'false *O. vinosa*'.

Typification: Western Australia, Mandurah, branches of *Nuytsia floribunda*, 17.XII.2001, G. Marson (ex H.B. 7087a, MEL 2389217, holotype).

Latin diagnosis: *Similis* Orbiliae vinosae *sed asci apice in statu emortuo multo magis crassitunicati, ascosporae paulo breviores. Habitat ad lignum vel corticem putridum ramulorum vel ramorum siccorum fruticum vel arborum angiospermarum* (Fabales, Myrtales), *in zona subtropica, raro temperata semi- vel (sub)humida Australiae meridio-occidentalis et orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.8(–1.1) mm diam., 0.08–0.19 mm high, pale to bright orange, orange-rose or rose, slightly to strongly translucent, round to elongate, scattered to ± gregarious, margin even to lobate; disc slightly concave to mostly flat, margin distinct, 0–10 µm protruding, smooth; sessile or with a very indistinct broad stipe 0.04–0.05 × 0.14–0.15 mm, superficial or ± immersed in clefts; dry light to bright rose- or apricot-red. **Asci** *(36–)40–50(–56) × (5.5–)5.8–6.3 µm {3}, †30–42 × (5–)5.5–6 µm {2}, 8-spored, spores *4-seriate, 3–4 lower spores inverted {3} (not mixed); **apex** (†) hemispherical, dome †(1.8–)2–2.5(–3.5) → 1–2.2 µm thick {5} (in H_2O, in KOH not thicker), sometimes with apical chamber, inner part pale reddish in IKI (dextrinoid); **base** with short to long, medium thick, flexuous stalk, L-shaped. **Ascospores** *(10–)11–15(–16.5) × (1.7–)1.8–2.1(–2.2) µm {4}, †10–14(–15) × (1.5–)1.7–2 µm {3}, narrowly cylindric-clavate to slightly fusoid-clavate, apex obtuse, sometimes rounded, base slightly to strongly attenuated, sometimes tail-like, straight to often slightly (rarely medium) curved; **SBs** 3–4.5(–5) × (0.6–)0.8–1(–1.2) µm {5}, rod-shaped to slightly ampulliform or dumbbell-shaped, apically narrowed to a small or sometimes wide point, straight (rarely somewhat flexuous), overmature *2–3.2 × 0.8–1.2(–1.5) µm. **Paraphyses** apically uninflated to slightly (rarely medium) clavate, terminal cells *9–16 × 2.3–3 µm {2}, lower cells *(5–)9–11 × 2.3–3 µm {2}; sometimes branched at upper septum. **Medullary excipulum** subhyaline to light rose or orange, 20–25 µm thick, of medium dense textura intricata with sparse or many inflated cells, indistinctly to medium sharply delimited (mainly towards margin). **Ectal excipulum** of (†) thin- to slightly thick-walled, irregularly oriented t. globulosa-angularis(-prismatica) at base and flanks, 25–80 µm thick near base, cells *6–20 × 6–12 µm {2}, †7–12 × 6–7 µm {2}; 10–25 µm thick at mid flanks and margin, at least at margin of t. prismatica-porrecta oriented at a 30–60° angle to the surface, marginal cortical cells *10–15 × 3–4 µm {1}; **glassy processes** absent {4} or present {2}, 3–4(–10) × 4–5 µm. **Anchoring hyphae** abundant, †1.5–2.5(–3.5) µm wide, walls 0.2(–0.4) µm thick {1}, forming a 5–10 µm thick layer on substrate. **SCBs** globose, in paraphyses 1.2–2 µm diam., in ectal excipulum (near margin) 2–4 µm. Yellow-orange **LBs** (carotenoids) absent or present in cells of lower part of paraphyses and in marginal excipular cells. **Exudate** over paraphyses 1.5–4 µm thick, cloddy, rough, loosely attached, subhyaline to light yellow-chlorinaceous, over margin and flanks (2–)4–6 µm thick. — **ANAMORPH**: unknown.

Habitat: collected 0.5–3 m above the ground, corticated to almost decorticated, 3–10(–50) mm thick twigs and branches of *Acacia* sp. {3}, *Eucalyptus* sp. {1}, *Jacksonia* sp. {1}, *Melaleuca* sp. {1}, *Nuytsia floribunda* {1}, on 0.2–0.5 mm deep medium to strongly decayed wood {5} and bark (periderm & bast) {5}, sometimes on inner surface of detached bark, on petioles of *Macrozamia riedlei* {1}, ± greyed, sometimes covered by abundant green algae. **Associated**: *Amandinea* sp. {1}, *Claussenomyces* sp. {2}, *Durella* sp. {1}, *D.* aff. *connivens* {1}, *Frullania* sp. {1}, *Gloniopsis* aff. *praelonga* {1}, *G. praelonga* {2}, *Orbilia acaciae* {1}, *O. albidorosea* {1}, *O. amberina* {1}, *O. australiensis* {3/1}, *O. austroobtusispora* {2}, *O. aviceps* {1}, *O. aviflagellata* {1}, *O. cejpii* {1}, *O. curvativitalbae* {1}, *O. eucalypti* {2}, *O. helicoobliqua* {1}, *O. hesperidea* {1}, *O. kingsiana* {1}, *O. macrotrapeziformis* {1}, *O. microserpens* {3}, *O. multiserpens* {1}, *O. myriofusiclava* {2}, *O. myriolilacina* {1}, *O. myrioobliqua* {4}, *O. paraobliqua* {1}, *O. pleioaustraliensis* {1}, *O. pleioaustrocylindrica* {1}, *Ostropales* {1}, *Patellaria* ?*andina* {1}, *Proliferodiscus griseoviolaceus* {1}, ?*Triblidium* sp. {1}. **Desiccation tolerance**: fully viable for at least 25 months. **Altitude**: 11–380 m a.s.l. (western Australia), 278–1073 m (eastern Australia). **Geology**: Archean, Permian, Triassic & Cretaceous sedimentary rock, Cenozoic regolith; granite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia nothovinosa* is segregated from the very similar European and North American *O. vinosa* based on the height of ascus apical dome, being distinctly above the range of *O. vinosa*, and because of slightly shorter spores on average. Comparatively large globose SCBs were noted in those specimens studied in the living state, whereas crystalloid SCBs could not be observed, though such were frequently seen in *O. vinosa*. The Australian *O. astrovinosa* has apical domes comparable to *O. vinosa*, narrower spores and SBs, and usually very long marginal teeth. *O. nothoaprilis* differs in shorter spores and much thinner apical domes, also in the presence of crystalloid SCBs.

Beaton & Weste (1979) reported *O. vinosa* from Victoria (Australia), but did not supply collection data or a description, and no Australian specimen of *O. vinosa* can be found in the Kew Herbarium (B. Spooner pers. comm.).

Variation. Macroscopically, the collections on *Nuytsia* and *Melaleuca* differ from the others in their orange colour and often somewhat larger size, but the microscopical features were comparatively consistent in all seven specimens studied. However, in the sparse, unpreserved specimen from Queensland

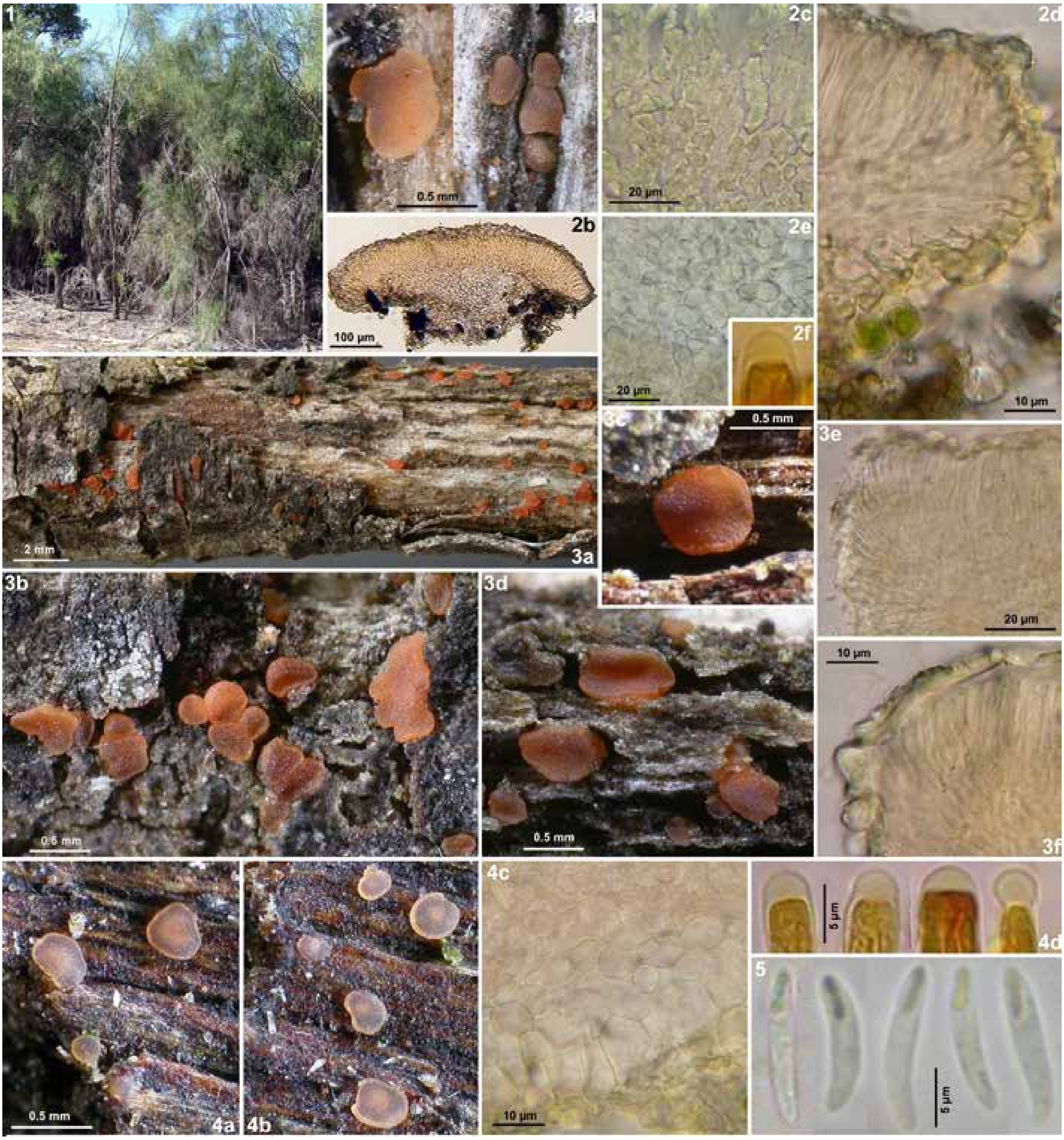


Plate 271. **1–5**: *Orbilia nothovinosa*. – **1**. semihumid Eucalypt open woodland with predominant *Jacksonia*; **2a**, **3a–d**, **4a–b**. rehydrated apothecia; **2b**. apothecium in median section; **2d**, **3e–f**. id., marginal ectal excipulum; **4c**. id., basal ectal excipulum; **2e**. id., medullary excipulum (of loose t. globulosa); **2c**. exudate on margin (external view); **2f**, **4d**. ascus apices; **5**. ascospores. – Living state: **4c**, **5**; dead state: **2c**, **e** (H_2O); **2b**, **d**, **3e–f** (in KOH); **2f**, **4d** (in IKI). — **1**. H.B. 7284b: Western Australia, Perth, on *Jacksonia*; **2a–f**. H.B. 7204r: ibid., Mt. Singleton, on *Acacia*; **3a–f**. H.B. 7087a (holotype): ibid., Perth, on *Nuytsia*; **4a–d**. H.B. 8478c: ibid., on *Acacia*; **5**. 3.IX.2006: Bindoon, on *Macrozamia*.

(on *Melaleuca*) the apical dome was only sketchily documented as about †1 µm thick, and it remains unclear whether it exceeded 2 µm in immature asci; also in that on *Macrozamia* the ascus apex was not examined. The very abundant type collection on *Nuytsia* showed the largest apothecia and, in contrast to the other samples, no associated further species of *Orbilia* could be discovered on the branches. *O. nothovinosa* varies in the glassy processes at the margin, which were found to be frequently absent, but at least in two collections present in some apothecia though rather short: in the holotype they were once seen but in all later examined apothecia they were absent, and in H.B. 7204r they were at least partly present.

Not included collections. A single apothecium on *Banksia* (2.IX.2006, unillustrated) differed in slightly shorter spores (*9.5–13.5 × 2–2.2 µm) and thinner domes (†1.5–2.2 µm). It is somewhat intermediate to *O. nothoaprilis* and, therefore, not included in either description. A similar size of spores (†8.5–12.5 × 1.8 µm) and apical domes (†1.4–1.8 µm) was noted in a sparse specimen on *Acacia*, which was only studied in the dead state (IVV: H.B. 8954c).

Map 48. Known distribution of *O. nothovinosa* in Australia (yellow = not included collections).

Ecology. *O. nothovinosa* occurs on ± rotten wood and bark of xeric twigs and branches of angiosperm trees and shrubs (*Myrtaceae*, *Fabaceae*, *Loranthaceae*) and leaves of *Cycadatae* in subtropical semihumid banksia-eucalypt woodlands (mallee) of southwestern Australia (Darling Range and Plateau) and subtropical subhumid to warm-temperate humid eucalypt open woodlands and forests in eastern and southeastern Australia (Great Dividing Range).

Specimens included. **AUSTRALIA**: **Western Australia**, Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig of *Acacia*, on wood, 24.XI.2001, G. Marson (H.B. 7204r). – Swan Coastal Plain, 15 km SE of Mandurah, SW of Pinjarra Road, NE of Sir Ross McLarty Park, 11 m, branches of *Nuytsia floribunda*, on wood & bark, 17.XII.2001, G. Marson (ex H.B. 7087a, MEL 2389217, **holotype**). – 30 km NE of Perth, 4 km N of Upper Swan, W of Walyunga, 37 m, twig & branch of *Jacksonia*, on wood & bark, 23.XI.2001, G. Marson (H.B. 7284b). – ibid., 76 m, branch of *Acacia*, on bark, 2.IX.2006, G. Marson (H.B. 8478c). – Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 272 m, leaves of *Macrozamia riedlei*, on petioles, 3.IX.2006, G. Marson (ø). – **Queensland**, Brigalow Belt South, 80 km N of Goondiwindi, 10 km S of Moonie, 278 m, branch of *Melaleuca*, on wood, 23.X.1998, G. Marson (H.B. 6823e ø). – **New South Wales**, Sydney Basin, 95 km WNW of Sydney, 11.5 km SE of Lithgow, 1.6 km SE of Mt. York, 1073 m, branch of *Eucalyptus*, on bark & wood, 26.X.1998, G. Marson (ø).

Not included. **AUSTRALIA**: **Western Australia**, Swan Valley, 30 km NE of Perth, 4 km NE of Upper Swan, W of Walyunga, 76 m, branch of *Banksia cuneata*, on wood, 2.IX.2006, G. Marson (ø). – Geraldton Sandplains, 20 km SE of Jurien Bay, 18 km NE of Cervantes, Cervantes Rd, 65 m, branch of *Acacia*, on bark, 11.XI.2007, G. Marson (H.B. 8954c ø).

Orbilia astrovinosa Baral & G. Marson, **sp. nov.**, MB 813574 — Pls 272–273

Etymology: closely related to *O. vinosa* but with long marginal teeth that resemble sun rays.

Typification: Western Australia, Cervantes, inflorescence stems of *Xanthorrhoea preissii*, 11.XII.2001, G. Marson (ex H.B. 7192a, MEL 2389219, holotype).

Latin diagnosis: *Similis* Orbiliae vinosae *sed excipulum marginale processis vitreis perlongis praeditum, dentes magnos formantibus, ascosporae paulo minores, corpusculum refringentem vermiformem ad subulatum, partim flexuosum continentes. Habitat ad corticem putridum ramorum siccorum* Proteacearum, *ad caules putridos inflorescentiae* Xanthorrhoeae, *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.55 mm diam. (0.3–0.7 mm incl. teeth), (0.1–)0.12–0.17(–0.2) mm high, pale to bright rose (also orange-ochraceous), slightly translucent, ± round, scattered; disc flat, margin distinct, 0–5 µm protruding (up to 200 µm incl. teeth), with short to usually very long whitish teeth (40–)80–140(–200) × (20–)60–120(–160) µm; broadly sessile, ± superficial; dry with bright (brick-)orange to orange-rose disc, teeth sometimes strongly incurved. **Asci** *(40–)49–55(–65) × 5.2–5.7 µm {2}, †40–47 × 4.3–4.6 {1} or 50–65 × 4.7–5.7 µm {T}, 8-spored, spores *3–4-seriate, 3–4 lower spores inverted {2} (not mixed), pars sporifera *23–30 µm long; **apex** (†) hemispherical, dome †0.8–1 → 0.5 µm {1} or 1.2–1.6 → 0.7–1 µm {T} thick, with or without minute apical chamber; **base** with short to very long, thin or thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(10.5–)12–14.5(–15.5) × (1.5–)1.6–1.8 µm {3}, †12.5–13(–15) × 1.5–1.7(–1.9) µm {2}, narrowly subcylindric-clavate to fusoid, apex (rounded to) obtuse, base medium (rarely strongly) attenuated, straight to slightly inequilateral; **SBs** *4–6 × 0.3–0.5 µm {3}, vermiform to subulate, apically narrowed to a small to wide point, straight to slightly flexuous. **Paraphyses** apically slightly to medium clavate-capitate, rarely spathulate, terminal cells *10–15(–19) × 2.3–3.5(–4.3) µm {2}, †1.8–3 µm wide {T}, lower cells *5–13 × 1.5–2.2 µm {2}; unbranched at upper septum, hymenium and subhymenium pale rose-orange. **Medullary excipulum** hyaline, 30–100 µm thick, of loose or dense textura intricata with many inflated cells, also of t. globulosa, medium sharply delimited. **Ectal excipulum** very pale orange, of (†) slightly to medium gelatinized, vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 20–50 µm thick near base, cells *10–21 × 8–14 µm {1}, †8–13 × 7–10 µm {T}; 15 µm thick near margin, inner part of t. prismatica-angularis oriented at a 70–80° angle to the surface, outer part from lower flanks up to margin of t. porrecta oriented at 20–40°, marginal cortical cells *(5–)8–13 × 2–4 µm {1}, †8–10 × 2–2.5 µm {T}; **glassy processes** 30–60 or 40–140(–200) × 2–3.3(–3.7) µm {2} (sometimes nearly absent), high-refractive, not stratified or very sparsely so, uniformly straight to distinctly inwards curved, coherent to form very compact teeth. **Anchoring hyphae** ± abundant, */†2–3.5 µm wide, walls 0.2–0.5(–1) µm thick {2}. **SCBs** in paraphyses globose (to ellipsoid), 1.3–3.3 µm diam., in marginal excipulum 1.5–2.5 µm. **Exudate** over paraphyses (0.5–)1–2 µm thick, cloddy-continuous, pale yellowish, loosely attached, over glassy processes absent. **— ANAMORPH**: unknown.

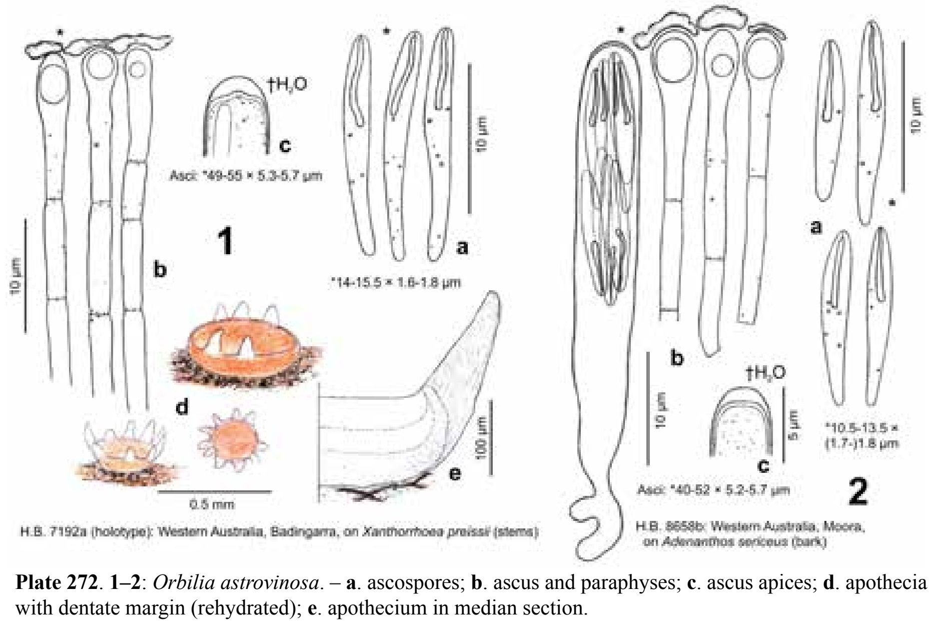


Plate 272. **1–2**: *Orbilia astrovinosa*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia with dentate margin (rehydrated); **e**. apothecium in median section.

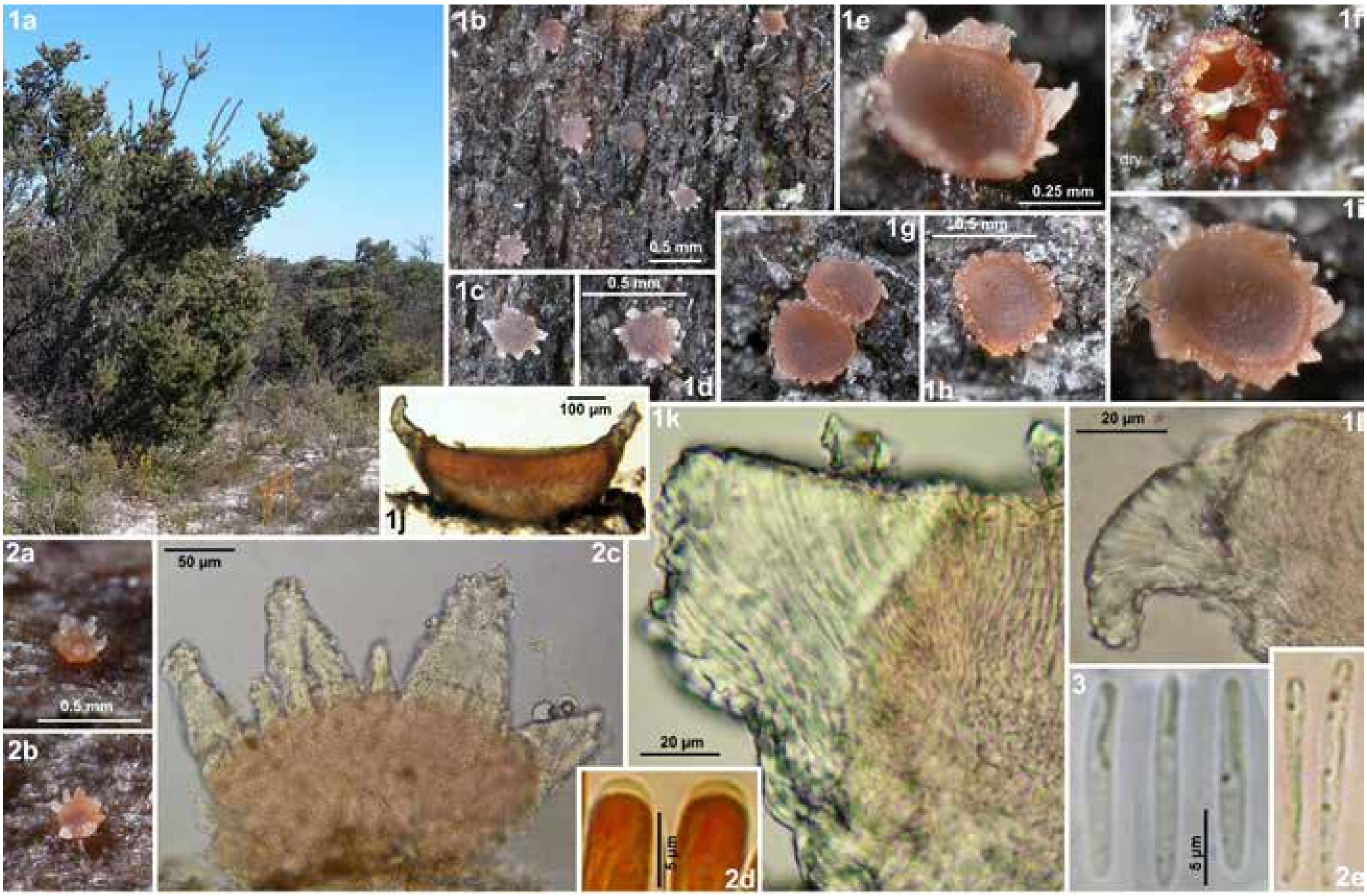


Plate 273. **1–3**: *Orbilia astrovinosa*. – **1a**. semihumid banksia-eucalypt woodland with *Adenanthos*; **1b–e**, **g–i**, **2a–b**. rehydrated apothecia; **1f**. dry apothecia; **2c**. apothecium in top view (squash mount); **1j**. apothecium in median section; **1k–l**. id., marginal ectal excipulum with teeth of conglutinated glassy processes; **2d**. ascus apices; **2e**, **3**. ascospores. – Living state, except for **2d** (in KOH+IKI), **2e** (in H_2O). — **1a–l**. H.B. 8658b: Western Australia, Moora, on *Adenanthos*; **2a–e**. H.B. 7192a (holotype): ibid., Badingarra, on *Xanthorrhoea*; **3**. 7.IX.2006: ibid., Perth, on *Banksia*.

Habitat: collected 1–2 m above the ground, corticated to decorticated, 5–21 mm thick twigs and branches of *Adenanthos sericeus* {1}, *Banksia grandis* {1}, on strongly decayed bark {2} (bast & periderm), bark partially detached, on outer surface; on woody, decorticated inflorescence stems of *Xanthorrhoea preissii* {1}, greyed, no algae. **Associated**: *Gloniopsis praelonga* {1}, *Mellitiosporiella* sp. {1}, *Orbilia austrocylindrica* {1}, *O. eucalypti* {1}. **Desiccation tolerance**: fully viable for at least 8.5 months, many mature asci still viable after 13.5 months. **Altitude**: 48–92 m a.s.l. **Geology**: Triassic to Cretaceous sedimentary rock, Cenozoic regolith (whitish sandy soil). **Phenology**: long-lived.

Taxonomic remarks. Apart from the large teeth, *O. astrovinosa* closely resembles European *O. vinosa*. Since large teeth have never been seen in European collections of *O. vinosa*, we prefer to assign the present specimens to a distinct species. A further characteristic that permits distinction from *O. vinosa* is seen in the somewhat shorter and narrower ascospores containing vermiform, slightly flexuous SBs. The triangular teeth are formed by glassy processes which all end up at about the same level by gradually decreasing in length from mid flanks to upper margin.

Variation. The rather abundant type collection mainly consists of apothecia with very short teeth or a nearly smooth margin, while only some possessed large teeth (Pl. 272: 1). However, the teeth easily break near their base, therefore, especially the older apothecia have evidently lost some or all of them. Whether those nearly smooth apothecia always have lost their large teeth is not certain. Apothecia with long teeth are predominant in the collections on bark of *Adenanthos* and *Banksia.* These differ from the type merely in slightly shorter spores.

Ecology. **–** *O. astrovinosa* was collected on wood of xeric inflorescence stems of the grass tree *Xanthorrhoea* and on bark of xeric twigs and branches of different *Proteaceae* in subtropical semihumid banksia-eucalypt open wood- and shrublands on sand dunes of southwestern Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Geraldton Sandplains, 23 km SE of Jurien Bay, 19 km NE of Cervantes, Munbinea Road, 92 m, inflorescence stem of *Xanthorrhoea preissii*, 11.XII.2001, G. Marson (ex H.B. 7192a, MEL 2389219, **holotype**). – Swan Coastal Plain, 59 km SW of Moora, 8 km NE of Cowalla, Moore River, Orange Springs Rd, 77 m, branch of *Adenanthos sericeus*, on bark, 5.IX.2006, G. Marson (H.B. 8658b). – Perth, Kings Park, 48 m, branch of *Banksia grandis*, on bark, 7.IX.2006, G. Marson (ø).

Orbilia helicovinosa Baral, **sp**. **nov**., MB 813586 — Pls 274–275

Etymology: named after the helicoid ascospores and the similarity to *O. vinosa*. **Typification**: Western Australia, Toolonga, branch of *Acacia*, 8.XI.2007, G. Marson (ex H.B. 9050b, MEL 2389278B, holotype).

Latin diagnosis: *Similis* Orbiliae vinosae *sed ascosporae distincte helicoideae in statu vivo, corpuscula refringentia breviora, apothecia hydratata roseo-lilacina. Habitat ad corticem putridum truncorum siccorum* Acaciae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.22–0.5 mm diam., 0.13–0.16 mm high, light rose- to cream-lilaceous, hardly translucent, round to somewhat lobate, scattered to subgregarious; disc flat, margin distinct, 3–10 µm protruding, smooth; sessile, slightly to strongly immersed in cracks or wood fibres; dry bright cream-orange to orange-red, slightly contracted. **Asci** *37–57 × 5.5–6.4 µm, †34–46 × 4.7–5(–5.3) µm, 8-spored, spores *8-seriate in a bundle, ~4 lower spores inverted, pars sporifera *19–23 µm long;

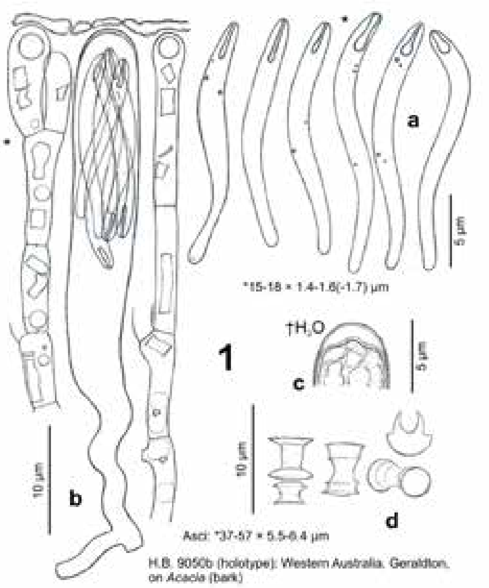


Plate 274. **1**: *Orbilia helicovinosa*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. crystalloid SCBs in ectal excipular cells.

apex (†) hemispherical, dome in KOH 1–1.4 → 0.8–1.2 µm thick, with or without small apical chamber; **base** with short to long, ± thin, flexuous stalk, L- or T-shaped. **Ascospores** *15–18 × 1.4–1.6(–1.7) µm, †(12–)14–16.5(–18) × 1.3–1.6 µm, cylindrical to narrowly subfusoid-clavate, apex obtuse to almost rounded, base not or usually slightly (rarely medium) attenuated, medium curved (helicoid, like a left-hand thread), (†) almost straight to distinctly falcate or helicoid; **SBs** *2.5–3 × 0.3–0.7 µm, vermiform to subulate or elongate tear-shaped, apically narrowed to a small or wide point, straight, overmature *1.5–2 × 1 µm. **Paraphyses** apically uninflated to slightly or medium (rarely strongly) clavate(-capitate), sometimes moniliform, terminal cells *(7–)10–16(–20) × (2–)2.5–3.8(–4.5) µm, lower cells *7–11.5 × 2–2.5(–3) µm; rarely branched at upper septum, hymenium very pale rose-lilaceous. **Medullary excipulum** hyaline to very pale rose-lilaceous, 20–40 µm thick, of dense textura intricata with many inflated cells, medium to sharply delimited. **Ectal excipulum** ± hyaline, of (†) not or slightly gelatinized, indistinctly vertically oriented t. globulosa(-prismatica) from base to mid flanks, 60–90 µm thick near base, cells *(8–)10–20(–23) × (7–)10–14(–17) µm; 20–30 µm thick near margin, inner part of t. prismatica oriented at a 60–80° angle to the surface, outer part of t. porrecta oriented at 20–40°, marginal cortical cells *6–11.5 × (2.5–)3–4(–4.5) µm; **glassy processes** absent. **Anchoring hyphae** ± abundant, *2–3.2 µm wide, walls 0.2–0.3 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.5–3.5 µm diam., and very distinct (low- to high-refractive) crystalloid SCBs, hyaline to very pale rose. **Exudate** over paraphyses 1–1.5(–2.5) µm thick, cloddy, hyaline, loosely attached, over margin and flanks 1.5–3 µm thick, rough-cloddy. — **ANAMORPH**: unknown (but see below).

Habitat: collected 0.5–1.5 m above the ground, corticated, ~5–6 cm thick trunk of *Acacia* sp., on exterior of detached, strongly decayed bark (bast), slightly to strongly greyed, no algae. **Associated**: *Orbilia anguliobliqua*, *O. angustoobliqua*, *O.* ?*atriplicis*, *O. myriella*, *O.* ?*saguarina*, ?*Triblidium* sp. **Desiccation tolerance**: fully viable for at least 18 months. **Altitude**: 190 m a.s.l. **Geology**: Cretaceous sedimentary rock (red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia helicovinosa* resembles a North American collection mentioned under *O. vinosa* (on wood of *Arctostaphylos*, Pl. 259: 4) in the narrow ascospores with short SBs; it differs in a distinctly helicoid spore shape, the abundant presence of crystalloid SCBs, and in the colour of the hydrated apothecia (rose-lilaceous).

Anamorph. Some dwayaangam-like conidia were found on the substrate in the type collection near apothecia of both *O. helicovinosa* (IVV: H.B. 9050b) and the associated *O. angustoobliqua*, resembling those of *O. subvinosa* but with longer stipes [in total */†33–42 µm high, stipe 18–24 × 4–4.5 µm, 4–5-septate, arms 6–18 × 3.5–4 µm, (1–)2–4-septate].

Ecology. *O. helicovinosa* was found on rotten xeric bark detaching from the main trunk of a ~3 m tall *Acacia* tree in a subtropical semiarid acacia open shrubland of western Australia (Yalgoo ecoregion).

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, branch of *Acacia*, on bark, 8.XI.2007, G. Marson (ex H.B. 9050b, MEL 2389278B, **holotype**).

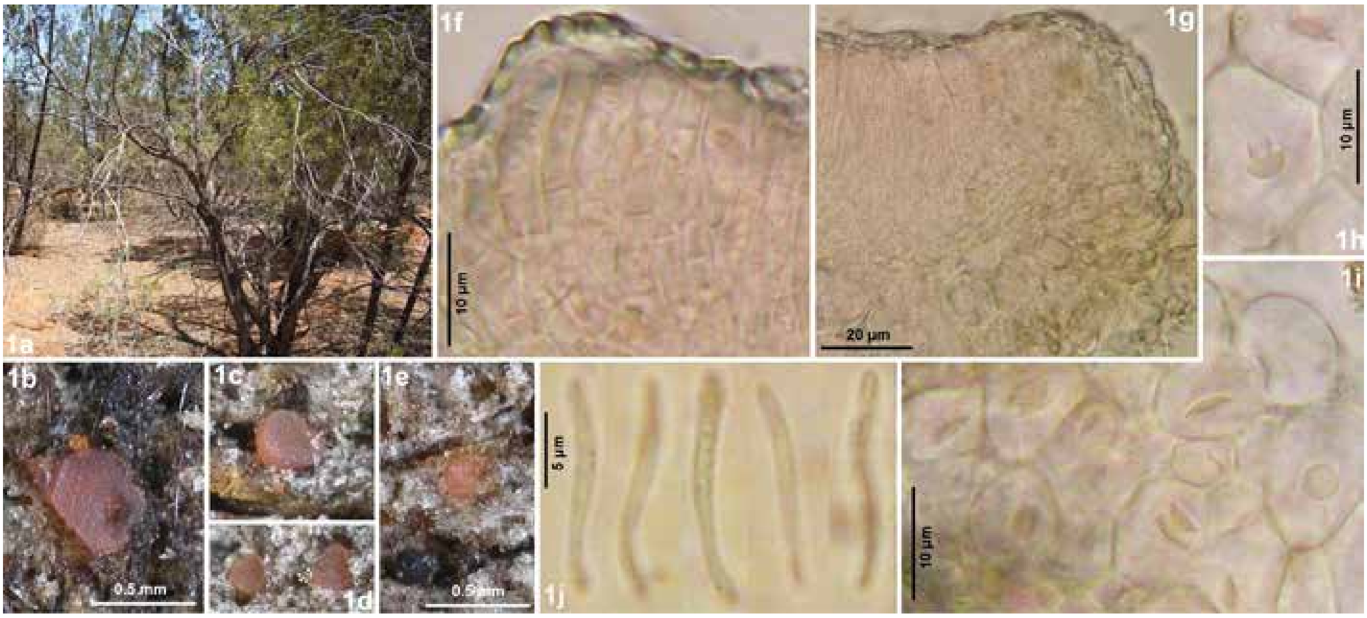


Plate 275. **1**: *Orbilia helicovinosa*. – **1a**. semiarid acacia shrubland; **1b–e**. rehydrated apothecia; **1f–g**. marginal ectal excipulum in median section; **1h–i**. crystalloid SCBs in excipular cells (mid flanks); **1j**. ascospores. – Living state, except for **1j** (in KOH). — **1a–i**. H.B. 9050b (holotype): Western Australia, Yalgoo, on *Acacia*.

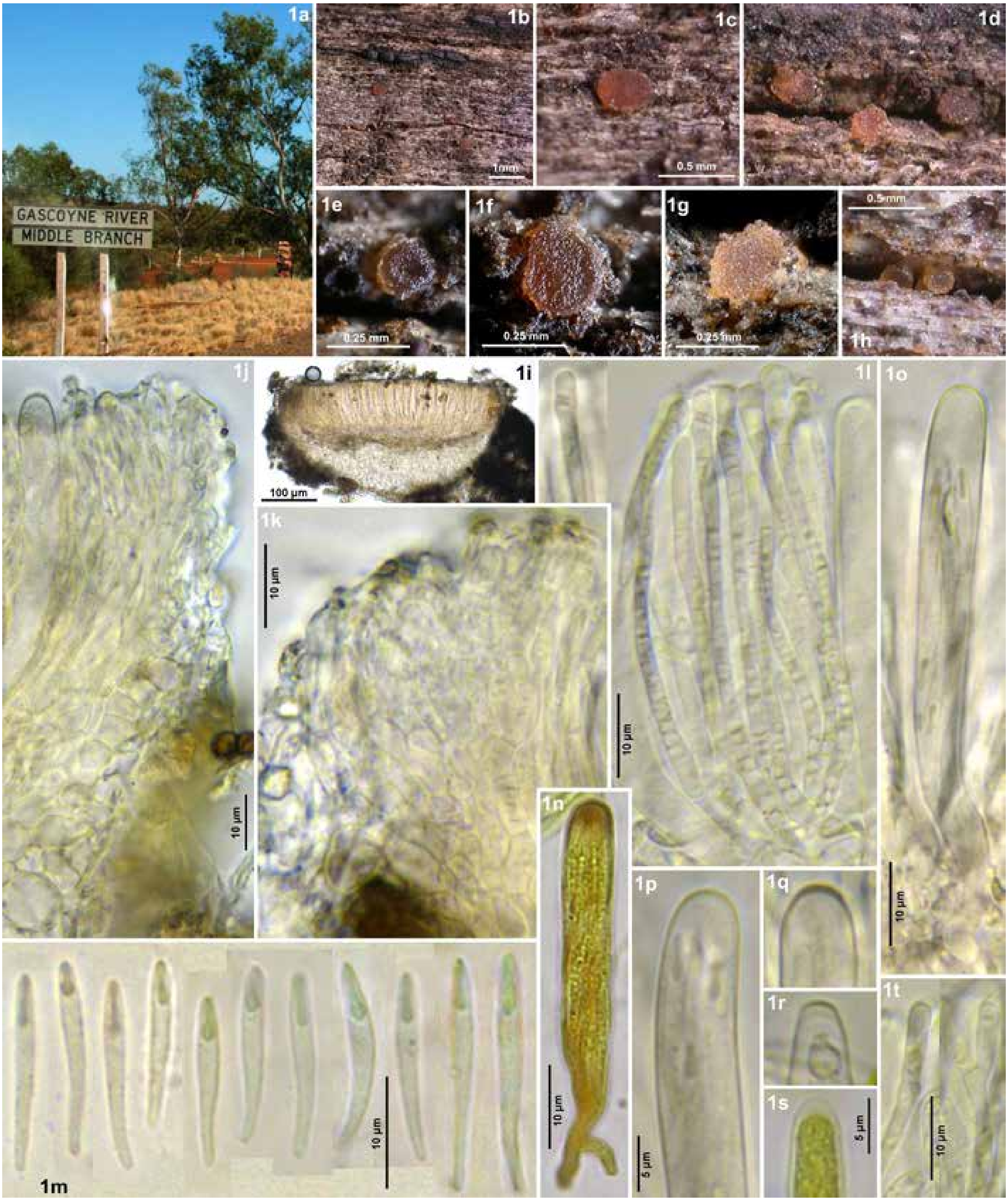


Plate 276. **1**: *Orbilia pleiovinosa*. – **1a**. bridge over Gascoyne river, arid acacia open woodland with *Eucalyptus*; **1b–h**. rehydrated apothecia; **1i**. apothecium in median section; **1j–k**. id., marginal ectal excipulum (**1k** with crystalloid SCBs); **1l**, **t**. paraphyses (with crystalloid SCBs); **1n–o**. mature asci; **1p–s**. ascus apices; **1m**. ascospores. – Living state, except for **1n**, **r–s** (**1r** in H_2O, **1n**, **s** in IKI). — **1a–t**. H.B. 9695a (holotype): Western Australia, Gascoyne, on *Acacia*.

Orbilia pleiovinosa Baral & G. Marson, **sp. nov.**, MB 813595 — Pl. 276

Etymology: named after the 16-spored asci and the similarity to *O. vinosa*.
Typification: Western Australia, Kumarina Roadhouse, branch of *Acacia cyperophylla*, 28.X.2007, G. Marson (ex H.B. 9695a, MEL 2389279B, holotype).

Latin diagnosis: *Similis* Orbiliae vinosae *sed asci 16-spori, apothecia minora. Habitat ad lignum putridum ramuli sicci* Acaciae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.17–0.36(–0.4) mm diam., 0.15–0.22 mm high, light to bright dirty orange-red, non-translucent, round, scattered or in small groups; disc flat, margin indistinct, 0–10 µm protruding, smooth or indistinctly rough to crenulated and whitish; broadly sessile, slightly immersed; dry strongly contracted and almost invisible. **Asci** *(67–)70–85(–90) × (6.2–)6.7–7.5(–8) µm, †(47–)55–65 × 5.7–6.2 µm, 16-spored, spores *~5–6-biseriate, 7–9 of lower spores inverted (mixed in middle part), pars sporifera *41–52 µm long; **apex** (†) hemispherical, dome †1.2–1.5(–1.8) → 0.7–1 µm thick, without apical chamber; **base** with short to medium long, thick, flexuous stalk, L- to h-shaped. **Ascospores** *(11.5–)13–19(–21.5) × (1.6–)1.7–2 µm, †(12–)14–17(–19) × 1.5–1.8(–2) µm, narrowly fusoid-clavate, apex obtuse to subacute, base gradually attenuated, straight to sometimes slightly curved near base; **SBs** *3–5 × 0.7–1.3 µm, rod-shaped or often dumbbell-shaped, with a narrower middle part and a ± strongly inflated globose base, apically narrowed to a wide point, straight. **Paraphyses** apically uninflated to slightly clavate-capitate or spathulate to moniliform, terminal cells *5–15(–20) × 1.8–3.5 µm, lower cells *8–14 × 1.7–2.3(–3) µm; unbranched or frequently branched at upper septum. **Medullary excipulum** pale rose-orange, 20–60 µm thick, of dense textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** subhyaline, of (†) thin-walled, irregularly or vertically oriented textura globulosa-angularis(-prismatica) from base to mid flanks, 40–80 µm thick near base, cells *(7–)10–20 × (5–)8–12(–15) µm; 15–40 µm thick near (sub) margin, of t. prismatica(-angularis) oriented at a 10–50° angle to the surface, upper margin of t. prismatica-porrecta, marginal cortical cells *5–9 × (2–)3–4(–5) µm, sometimes covered by a 10 µm thick layer of dead hyphae; **glassy processes** absent. **Anchoring hyphae** sparse to medium abundant, †2–3 µm wide, walls 0.2–0.5 µm thick, sometimes extending to the margin as a covering layer. **SCBs** in paraphyses and marginal ectal excipulum globose, 1.5–2.2 µm diam., but mainly crystalloid, hyaline to pale yellowish-rose; with or without light yellow **LBs** (carotenoids) in lower half of paraphyses. **Exudate** over paraphyses and margin 0.3–2 µm thick, ± smooth or cloddy, hyaline, loosely or firmly attached on cell each tip. **— ANAMORPH**: unknown.

Habitat: collected 2.5–3 m above the ground, decorticated, 16–20 mm thick branch *Acacia cyperophylla*, on 0.2 mm deep very decayed wood, strongly greyed, no algae. **Associated**: *Coccomycetella* spp. {2}, *Hysterobrevium mori*, *Orbilia allantoobliqua*, *O. australiensis, O. multiaustraliensis*, *O. pleioaustraliensis*, *O. ?pleiocoronohesperidea, Ostropales*. **Desiccation tolerance**: fully viable for 34 months (57 months including singular rehydration). **Altitude**: 540 m a.s.l. **Geology**: Mesoproterozoic sedimentary rock (red-brown sandstone). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleiovinosa* appears to be closely related to *O. multivinosa*, *O. helicovinosa*, and *O. vinosa*, from which it differs in 16-spored asci, from *O. helicovinosa* also in less curved ascospores. Except for *O. vinosa*, these species share also a subtropical (semi)arid habitat and comparatively small apothecia.

O. pleiovinosa grew intermingled with the very similar *O.* aff. *pleiocoronohesperidea*, which differs in shorter and particularly wider spores which are more distinctly divided into an elongated upper part and an often ± curved tail, also in shorter SBs and larger apothecia. Nine mature apothecia of *O. pleiovinosa* and five of *O.* aff. *pleiocoronohesperidea* were examined and found to be fairly consistent and sharply separated in their microfeatures.

Ecology. *O. pleiovinosa* was found on rotten wood of a decorticated xeric branch of *Acacia* in an (almost tropical) semiarid (almost arid) acacia open woodland with *Eucalyptus* in a most of the time dry riverbed in the Gascoyne ecoregion of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Acacia cyperophylla*, on wood, 28.X.2007, G. Marson (ex H.B. 9695a, MEL 2389279B, **holotype**; MEL 2389280, **isotype**).

Orbilia multivinosa Baral & G. Marson, **sp. nov.**, MB 828906 — Pl. 277

Etymology: named after the 32-spored asci and the similarity to *O. vinosa*. **Typification**: Australia, Ayers Rock, branch of *Allocasuarina decaisneana*, 12.X.1998, G. Marson (H.B. 6617j, unpreserved, holotype: illustration Pl. 73 Fig. 1).

Latin diagnosis: *Similis* Orbiliae pleiovinosae *sed asci 32-spori, ascosporae breviores. Habitat ad lignum putridum rami sicci* Allocasuarinae decaisneanae *in zona subtropica arida Australiae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated ?0.3 mm diam., light (dirty) orange-reddish, round, scattered; disc flat, margin thin, smooth; sessile. **Asci** *70–82 × 7.5–8.2 µm, 32 spored (25–28 spores counted), spores *~4–5-seriate, min. 9–10 lower spores inverted (slightly to strongly mixed), pars sporifera *55 µm long; **apex** (†) hemispherical to slightly truncate, dome †0.8–1 µm thick (immature and mature), with or without small apical chamber; **base** with short, thick, flexuous stalk, T-shaped. **Ascospores** *12–14.5 × 1.8–2 µm, narrowly fusoid-clavate, apex obtuse to subacute, base slightly to often ± strongly attenuated (sometimes tail-like), mostly slightly curved towards base; **SBs** *3–4.3 × 0.5–0.8 or 1–1.5 µm, subulate to ampulliform, apically narrowed to a small to wide point, straight. **Paraphyses** apically uninflated to medium clavate-capitate, terminal cells *5–14 × 2.5–4 µm; unbranched near apex. **Medullary excipulum** not examined. **Ectal excipulum** of textura globulosa at base and flanks, marginal cortical cells ± elongate, (†) slightly thick-walled; **glassy processes** absent. **Anchoring hyphae** no examined. **SCBs** in paraphyses and ectal excipulum crystalloid, also globose. **Exudate** over paraphyses 0.5 µm thick, granular-cloddy, ± loosely attached. **— ANAMORPH**: unknown.

Habitat: lying on ground, decorticated, 10 mm thick xeric branch of *Allocasuarina decaisneana*, on 0.1 mm deep very decayed wood, strongly greyed, no algae. **Associated**: *Orbilia macrotrapeziformis*, *O. phanosoma*, *O. pleiolentiformis*, *O. pleioobtusispora*, *O. pleiovitalbae*, *O. pluristomachia*, *O. serpentina*, *Symbiotaphrina desertorum*, *Teichosporella dura*. **Desiccation tolerance**: many mature asci still viable after 19 months. **Altitude**: 500 m a.s.l. **Geology**: Cenozoic regolith (red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia multivinosa* is characterized by 32-spored asci, while in the other features (ascospores, SBs, crystalloid SCBs) the species much resembles European *O. vinosa*. The collection contained only two apothecia which were used up during examination. *O. pleiocoronohesperidea* differs in 16-spored asci, larger spores, and glassy processes at the margin.

Since no apothecia remained and the inhabited branch fragment was not preserved, the illustration of the fungus is designated as holotype. Art. 40.5 ICN permits illustrations as

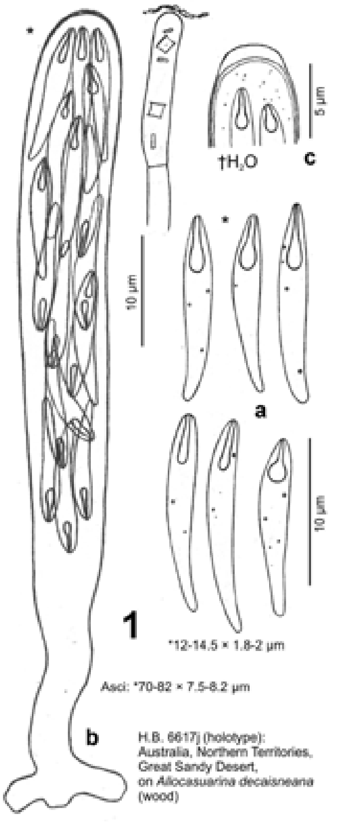


Plate 277. **1**: *Orbilia multivinosa*. – **a**. ascospores; **b**. ascus and paraphysis; **c**. dead ascus apex containing living spores.

type, if it is impossible to preserve a specimen that would show the important features. We here rely on this article, because the taxonomically relevant spore bodies (SBs) and soluble cytoplasmic bodies (SCBs) cannot be preserved by conventional methods.

Ecology. The two detected apothecia grew on rotten wood of a xeric branch of *Allocasuarina decaisneana* in a subtropical arid acacia open shrubland northeast of Ayers Rock at the southeastern end of the Great Sandy Desert of central Australia.

Specimens included. **AUSTRALIA**: **Northern Territories**, Great Sandy Desert, 11.5 km ENE of Yulara, 14 km NNE of Ayers Rock, 500 m, branch of *Allocasuarina decaisneana*, on wood, 12.X.1998, G. Marson (H.B. 6617j ø, **holotype** [illustration]).

Orbilia subulivinosa G. Marson, Baral & E. Weber, **sp. nov.**, MB 828908 — Pls 278–279

Etymology: named after the long and narrow, subulate spores.

Typification: France, Var, Cogolin, branches of *Erica arborea*, 4.IX.2017, G. Marson (ex G.M. 2017-09-04.1 & ex H.B. 10140a, M-0291757, holotype; sq.: MH221056).

Latin diagnosis: *Similis* Orbiliae vinosae *sed ascosporae longiores, excipulum et paraphyses absque corpusculis crystalloideis. Habitat ad lignum putridum ramorum siccorum* Ericae arboreae *in zona mesomediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.28–)0.33–0.8(–0.9) mm diam., 0.13–0.32 mm thick (receptacle 0.11–0.15 mm), pale to bright orange-rose, translucent, round to somewhat elongate or undulating, scattered to subgregarious, sometimes in small dense groups; disc flat, margin distinct, thin, hardly protruding, smooth to finely rough; broadly sessile or with an abrupt stipe up to 0.15 × 0.35 mm, superficial; dry light to deep brick-red, with thick protruding margin. **Asci** *~55–67 × 5.5–6.5 µm, †~53–65 × 5.2–6.2 µm, 8-spored, spores *4–8-seriate, 3–4 lower spores inverted (not mixed); apex (†) hemispherical, dome in IKI †1–1.4(–1.8) → 0.5–1 µm thick, with small apical chamber; base with short to long, ± thin, flexuous stalk, T- to L-shaped. **Ascospores** *(16–)20–22 × 1.6–1.8 µm, †17.5–22(–25) × 1.6–2 µm, narrowly subulate to acicular, apex rounded to obtuse gradually slightly to medium attenuated towards base, straight or very slightly curved in lower part; **SBs** *4.7–5.7 × 0.6–0.9 µm, narrowly subulate-vermiform, not inflated at base, straight or very slightly flexuous. **Paraphyses** apically uninflated or slightly clavate, terminal cells *8–13 × 1.8–3(–3.2) µm, lower cells *7–18 × 1.5–2.3 µm; unbranched at upper septum. **Medullary excipulum** hyaline 40–60 µm thick, of dense textura intricata with inflated cells, medium to sharply delimited. **Ectal excipulum** hyaline, of thin-walled, vertically oriented t. globulosa-prismatica from base to mid flanks, 30–100 µm thick at base, cells *(6–)8–18(–22) × 5–13 µm; 20–65 µm thick at flanks, 20–30 µm near margin, of t. prismatica-porrecta oriented at a 60–90° angle to the surface, marginal cortical cells †5–12 × 2.5–4.5 µm; **glassy processes** absent. **Anchoring hyphae** sparse, †1.5–2.7 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and ectal excipulum at base and margin sparse, globose, 1 µm diam., crystalloid SCBs absent. **Exudate** over paraphyses 0.8–1.5(–2) µm thick, cloddy, hyaline pale yellow, loosely attached, over margin and flanks 1.5–3.5(–6) µm thick, rough-cloddy, light to bright yellow. — **ANAMORPH**: unknown.

Habitat: collected 0.5–4 m above the ground, almost entirely decorticated, 11–13 mm thick branches of *Erica arborea*, on 0.1–1 mm deep very rotten wood or remnants of bark (bast), strongly greyed or sometimes blackened, green algae sparse to abundant. **Associated**: *Claussenomyces* sp. {1}, ?*Hysterobrevium smilacis* {1}, *Mollisia* sp. {1}, *Orbilia aprilis* {1}, *O. hesperidea* {1}, *Propolis viridis* {1}. **Desiccation tolerance**: excipular cells and some mature asci and ascospores viable after 6 months. **Altitude**: 380 m a.s.l. **Geology**: gneiss & mica schist. **Phenology**: IX (probably long-lived).

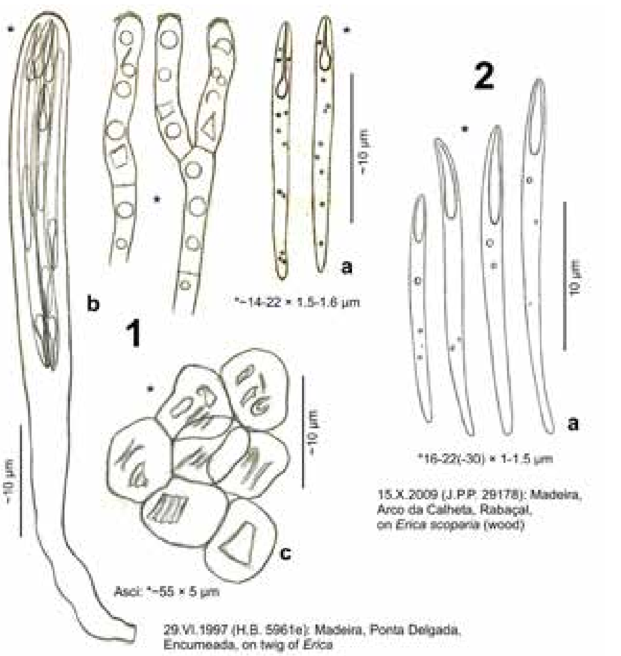


Plate 278. **1–2**: *Orbilia* cf. *subulivinosa*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ectal excipulum, with crystalloid SCBs.

Taxonomic remarks. *Orbilia subulivinosa* resembles *O. vinosa* except for its distinctly longer ascospores. It is also recognized as a species of its own based on strongly deviating DNA data. However, a morphologically similar species was not included in the description because its molecular data refer it instead in vicinity of *O. arachnovinosa* and it is thereafter here treated as *O.* aff. *arachnovinosa* (Pl. 279: 2; IVV: 2.VI.2018). Because of this genetic distance we have not included all morphologically similar collections for which no molecular data were available.

Not included collections. Most of the samples without a sequence originate from Macaronesia. Two very sparse collections on *Erica* from Madeira could not adequately be studied (Pl. 278): their acicular spores are with *(14–)16–22(–30) × 1.1–1.6 µm narrower than in *O. subulivinosa* but concur in length. Their SBs differ between the two collections (broadly subulate-vermiform vs. narrowly subulate with an abrupt tear-shaped basal inflation). The pale orange(-rose), apothecia measured 0.2–0.6 mm diam., the marginal excipulum showed 2–3 µm long marginal glassy processes, and the paraphyses contained both globose and crystalloid SCBs. Two collections on *Erica* and *Ilex* from the laurel forest in Tenerife studied by L. Quijada (IVV: TFC Mic. 23493) have similar narrow but shorter spores of *(12–)14–16(–17) × 1.3–1.5(–1.6 µm).

Various mesomediterranean collections with a comparable spore length mentioned under *O. vinosa* were not included in *O. subulivinosa* because they possess glassy processes (Pl. 262). A sample on *Picea* from Slovakia (A. Polhorský, IVV: 30.VII.2018) closely resembles *O. vinosa* (spores *14.5–19 × 1.8–2 µm); it is called *O.* aff. *subulivinosa* because its sequence clustered in a clade with *O. subulivinosa*; associated tridentaria-like conidia with mainly 4 arms support its distance to *O. vinosa* but are doubtfully connected to it.

Phylogeny. A sequence was taken from apothecia of the holotype of *O. subulivinosa*, comprising SSU, S1506 intron, ITS, and LSU. The Slovakian sample on *Picea* includes intron and ITS and two of *O.* aff. *arachnovinosa* (from Austria and Spain) ITS, one also SSU and LSU (in both the intron is absent).

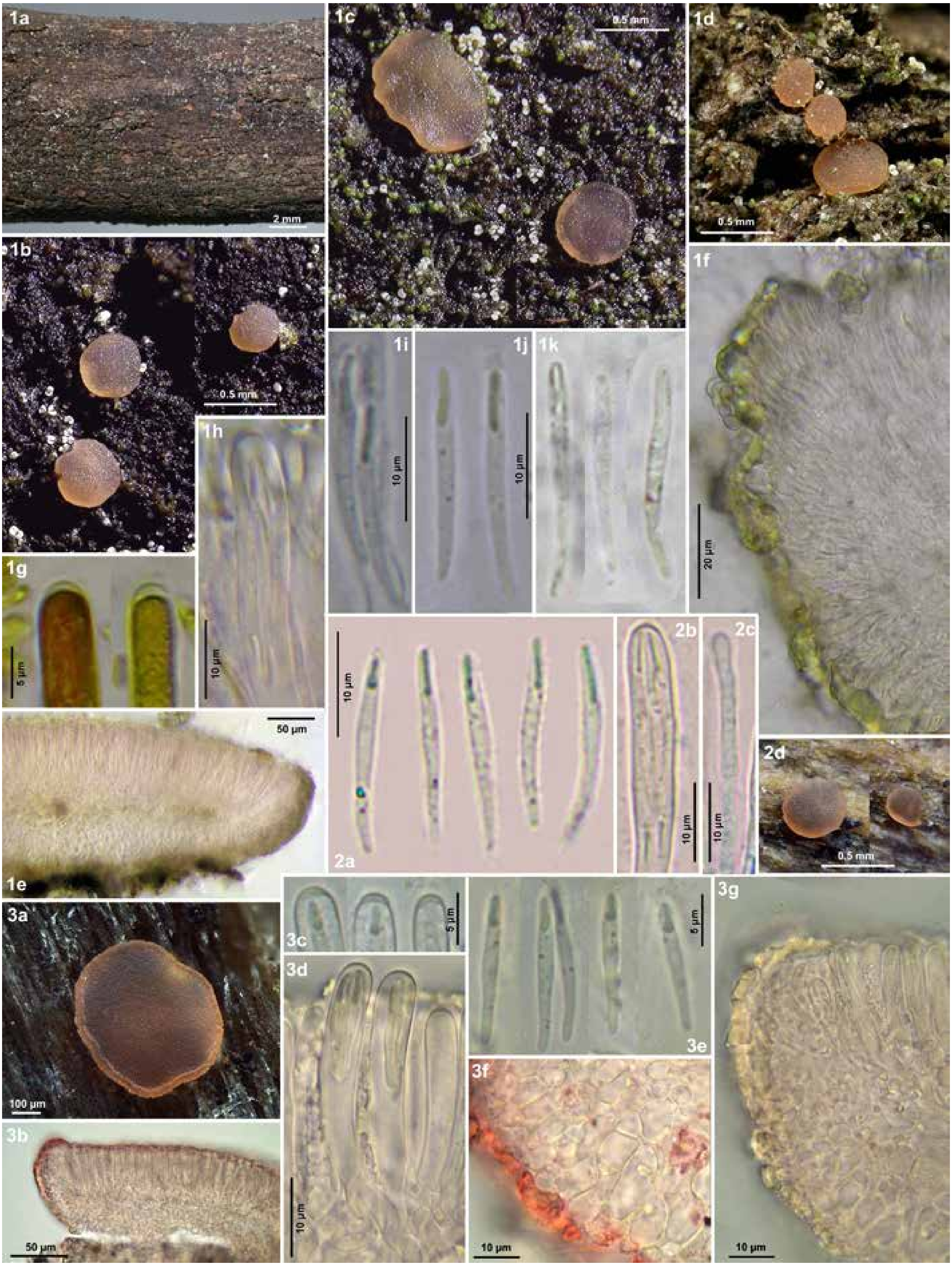


Plate 279. **1**: *Orbilia subulivinosa*; **2**: *O.* aff. *arachnovinosa*; **3**: *O.* cf. *subulivinosa*. – **1a**. ± decorticated branch of *Erica arborea* with apothecia (rehydrated); **1b–d**, **2d**, **3a**. rehydrated apothecia; **1e**, **3b**. apothecia in median section; **1f**, **3g**. id., ectal excipulum at margin; **3f**. id., at flanks; **1g**, **3c**. ascus apices; **1h**, **2b**. mature asci at normal turgescence; **3d**. mature asci at full turgescence; **2c**. paraphysis; **1i–k**, **2a**, **3e**. ascospores. – Living state (**3b** & **f** in CR), except for **1g** (in IKI), **1f**, **1k**, asci in **3c** (in H_2O). – **2**: phot. E. Rubio, **3**: phot. L. Quijada. — **1a–k**. H.B. 10140a: France, Cogolin, on *Erica*; **2a–d**. E.R.D. 6754: Spain, Villablino, on ?*Calluna* (see under *O. arachnovinosa*); **3a–g**. TFC Mic. 23493: Tenerife, on *Ilex*.

When analysing ITS, LSU, or ITS+LSU, *O. subulivinosa* clustered with medium (ITS+LSU), weak (ITS), or no support (LSU) with *O. multicurvula* (Phyls 9, 11, S13), showing an LSU D1–D2 minimum distance of 1.3 % to *O. multicurvula* and *O. nothoaprilis* (ITS 12.5–14 %). *O. vinosa* and *O. subvinosa* differ in the ITS by ~16–17 %. In the intron *O. subulivinosa* clustered with high support but high distance with *O. paramontigena* (Phyl. S13). Similarly unexplainable is the position of the Slovakian sample on *Picea*, which resembles *O. vinosa* but clustered strongly supported with the type of *O. subulivinosa* (Phyl. 11), with an ITS distance of 4.8 %.

When analysing the intron, *O. subulivinosa* clustered strongly supported with *O. paramontigena* (Phyl. S13), though with a 13.5 % distance, whereas the Slovakian *O.* aff. *subulivinosa* clustered unresolved and with high distance near the *vinosa-velutina* clade (not shown).

The two *O.* aff. *arachnovinosa* sequences are fully identical in the ITS, except for 2 gaps. They clustered in a medium supported clade with *O. arachnovinosa* when analysing ITS (not shown), to which it shows a distance of 4.5 % (ITS) and 1.4 % (LSU D1–D2). In comparison, its distance to *O. vinosa*/*O. subvinosa*/*O. subulivinosa* ranges at 8–9/9.5–10.5/17 % (ITS) and 1.7–1.9/1.3/7 % (LSU D1–D2).

Ecology. *O. subulivinosa* grew on strongly decayed wood and bark of xeric thin branches of *Erica arborea* in a mesomediterranean semihumid woodland in southeastern France. The not included collections from Macaronesia were on xeric twigs and branches of *Erica* and *Ilex* at two distant sites in the suprasubmediterranean subhumid ridge-crest laurel forest (*Ilici canariensis-Ericetum platycodonis*) on volcanic soil in Madeira, and in infra- to thermomediterranean semihumid shrublands on (trachy)basaltic flow in Tenerife. The not included sample from the High Tatras (Slovakia) was in a humid altimontane forest with *Picea abies* and *Pinus cembra* on acidic bedrock.

Specimens included. **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Var**, 10 km W of Cogolin, 5 km NW of Gorbière, SW of Capelude, 380 m, branches of *Erica arborea*, on wood & bark, 4.IX.2017, G. Marson (ex G.M. 2017-09-04.1, ex H.B. 10140a, M-0291757, **holotype**; sq.: MH221056).

Not included. **MACARONESIA**: **Madeira**, 4.5 km NNE of Arco da Calheta, SE of Rabaçal, 1305 m, branch of *Erica platycodon*, on wood, 15.X.2009, J.P. Priou (J.P.P. 29178, doc. vid.). – 8 km SSW of Ponta Delgada, 1.8 km N of Lombo do Moleiro, W of Boca da Encumeada, 990 m, twig of *Erica*, on wood (?), 29.VI.1997, R. Reuter (H.B. 5961e ø). – **Canary Islands**, **Tenerife**, Güímar, 3.5 km W of Güímar, Higueras Salvajes, 927 m, branch of *Erica arborea*, 23.III.2013, L. Quijada, I. Pérez-Vargas & J. Díaz-Armas (TFC Mic. 23976). – Los Silos, 5 km SE of Buenavista del Norte, 3.5 km SSW of Los Silos, 740 m, 4.V.2012, branch of *Ilex canariensis,* 4.V.2012, L. Quijada (TFC Mic. 23493, doc. vid.). — **SLOVAKIA**: **Prešov**, Carpathian Mts., Vysoké Tatry, 9.5 km SSW of Tatranská Javorina, Bielovodská valley, 1408 m, branch of *Picea abies*, on wood, 30.VII.2018, A. Polhorský (A.P. 18/97, doc. vid.; sq.: MK651741).

Orbilia multicurvula Baral & G. Marson, **sp. nov.**,

MB 813596 — Pls 280–281

Etymology: named after the 32-spored asci and strongly curved ascospores.

Typification: Western Australia, Cowalla, branches of *Eremaea pauciflora*, 5.IX.2006, G. Marson (ex H.B. 8643a, MEL 2389245, holotype; sq.: KT222427).

Latin diagnosis: *Apothecia rehydratata 0.25–0.75 mm diam., aurantiaca, sessilia vel subsessilia, margine valde albido-denticulata. Asci 32-spori. Ascosporae *6.8–10 × 1.3–1.6 µm, anguste subcylindrico- ad fusoideo-clavatae, apice obtusae, ad basim attenuatae, fortiter arcuatae, in statu vivo corpusculum refringens brevem, vermiformem ad subulatum, ad apicem affixum continentes. Cellulae vivae excipuli et paraphysium corpuscula globosa continentes, excipulum marginale processis vitreis longis praeditum, dentes magnos formantibus. Habitat ad corticem putridum ramorum siccorum fruticum* Eremaeae *et* Hibbertiae *etc. in zona subtropica semihumida Australiae meridio-occidentalis.*

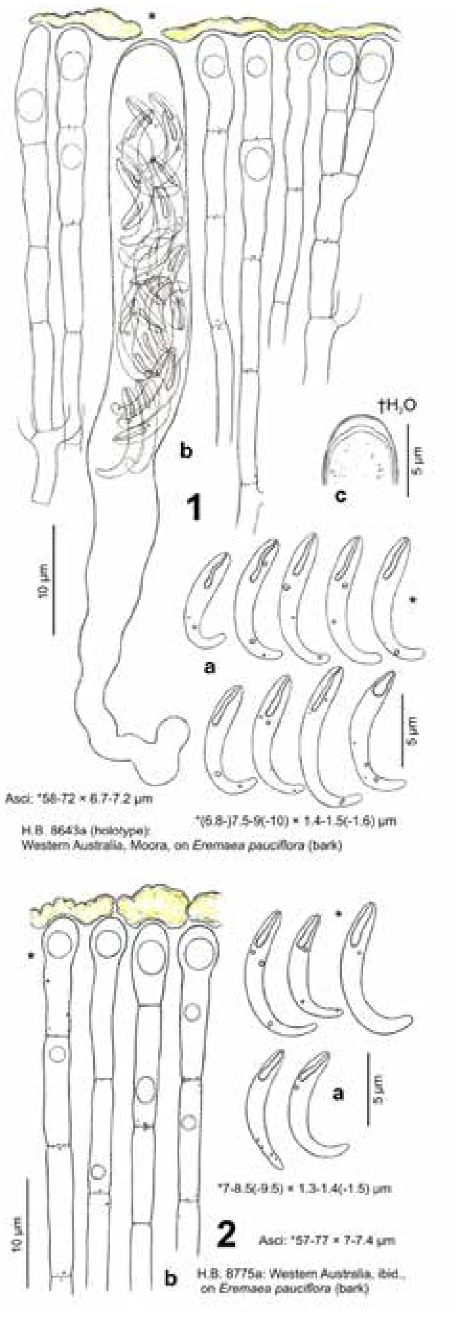


Plate 280. **1–2**: *Orbilia multicurvula*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.25–)0.3–0.5(–0.75) mm diam. [(0.2–)0.28–0.4(–0.6) mm excluding teeth], (0.11–)0.13–0.15(–0.2) mm high, (pale to) light to bright orange(-rose), slightly translucent, round (to broadly elliptical), scattered (to subgregarious); disc flat, margin thin or thick, mostly with prominent whitish teeth (30–)50–85(–100) × 30–60 µm, protruding 10–50 µm beyond disc (0–10 µm excluding glassy processes); sessile on an obconical base or distinct stipe 0.05 × 0.13 mm, ± superficial; dry bright orange-red, disc ± closed by the incurved teeth. **Asci** *57–72 × 6.7–7.4 µm {2}, †51–68 × 5.5–6.5 µm {2}, 32-spored (28–30 spores counted), spores ~4-seriate, lower spores inverted but very strongly mixed, pars sporifera *30–39 µm long; **apex** (†) hemispherical, dome †1–1.2(–1.4) → 0.8–1 µm thick {1}, with or without very indistinct apical chamber; **base** with short to long, ± thick, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *6.8–9.5(–10) × 1.3–1.5(–1.6) µm {2} (actual length ~9–12 µm), †6.8–8.5(–9.5) × (1.2–)1.3–1.5 µm {1}, narrowly

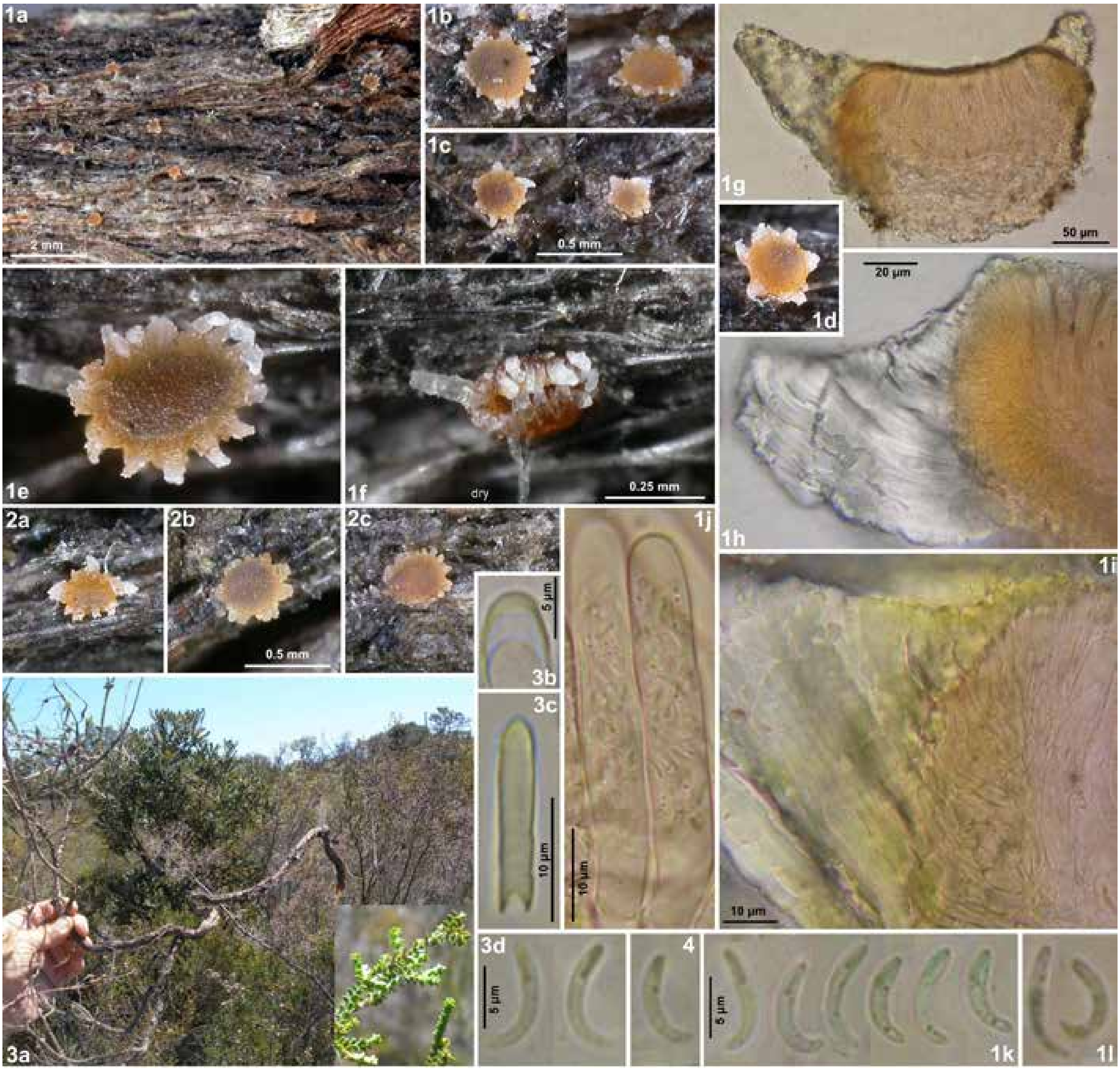


Plate 281. **1–4**: *Orbilia multicurvula*. – **3a**. semihumid banksia-eucalypt woodland with ?*Myrtaceae*; **1a–e**, **2a–c**. rehydrated apothecia; **1f**. dry apothecium; **1g**. apothecium in median section; **1h–i**. id., marginal ectal excipulum; **3c**. glassy process; **3b**. ascus apex; **1j**. mature asci; **1k–l**, **3d**, **4**. ascospores. – Living state, except for **3b**, **1l** (in H_2O). — **1a–l**. H.B. 8643a (holotype): Western Australia, Moora, on *Eremaea*; **2a–c**. H.B. 8775a: ibid., on *Eremaea*; **3a–d**. 11.XI.2007: ibid., on indet. ?*Myrtaceae*; **4**. 24.X.2007: ibid., on *Hibbertia*.

subcylindric-fusoid-clavate, apex obtuse (to subacute), base slightly to strongly attenuated, mostly very strongly curved in lower part (slightly in upper part); **SBs** *2.5–3.5 × 0.3–0.6 µm {2}, vermiform to subulate, apically narrowed to a small point, straight to slightly flexuous; in aged spores 2–3 × 0.7–1 µm, tear-shaped. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, sometimes sublageniform, terminal cells *(6–)8–15(–18) × (2–)2.5–3.2(–3.7) µm {2}, lower cells *(6–)8–12 × 1.6–2.8 µm {2}; sometimes branched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline to pale rose, (30–)50–100 µm thick, of medium dense textura intricata with many inflated cells, sharply delimited from ectal excipulum (at flanks by a thin t. porrecta), subhymenium light rose. **Ectal excipulum** hyaline, at margin pale honey-yellow to light orange, of (†) slightly gelatinized, indistinctly oriented t. angularis-globulosa from base to mid flanks, (20–)25–30 µm thick near base, cells *6–17 × 5–12 µm {1}; 15–30 → 10–20 µm thick near margin, inner part of t. prismatica-angularis oriented at a 30–40 up to 70–80° angle to the surface, outer part of t. (prismatica-) porrecta oriented at 10–20 up to 40–70°, marginal cortical cells *7–13 × 2.5–3.5 µm {2}; **glassy processes** 10–150 × (2–)2.5–3(–3.8) µm {3}, high-refractive, stratified or not, straight to slightly inwards curved, sometimes strongly hooked at the end, coherent to form compact, white or sometimes light yellow-chlorinaceous teeth. **Anchoring hyphae** medium abundant, †1.7–4 µm wide, walls (0.2–)0.3–0.8(–1.2) µm thick {1}. **SCBs** in paraphyses and ectal excipulum globose (to ellipsoid), 1.5–2.6 µm diam. **Exudate** over paraphyses 0.8–3 µm thick, cloddy-continuous, light to bright sulphur-yellow, loosely attached, over teeth absent (except for uppermost margin). **— ANAMORPH**: unknown.

Habitat: collected 0–1 m above the ground, corticated, 6–18 mm thick branches of *Eremaea pauciflora* {2}, *Hibbertia aurea* {1}, ?*Myrtaceae* {1}, on 0.3–0.5 mm deep strongly decayed bark {4} (periderm & bast), sometimes detaching, greyed, with some green algae. **Associated**: *Capronia* sp. {1}, *Durella* aff. *connivens* {1}, ?*Eutypa* sp. {1}, *Gloniopsis praelonga* {2}, *Hyalorbilia juliae* {1}, *Orbilia amberina* {1}, *O. austrocylindrica* {3}, *O. curvativitalbae* {1}, *O. eremaeae*

{1}, *O. eucalypti* {1}, *O. microserpens* {1}, *O. pleistovitalbae* {2}, *O. plurililacina* {1}, *Proliferodiscus olivaceoviridis* {2}, *Rhizodiscina lignyota* {1}. **Desiccation tolerance**: fully viable for at least 13 months. **Altitude**: 77–83 m a.s.l. **Geology**: Cretaceous sedimentary rock (whitish sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia multicurvula* is easily recognized by its strongly falcate (boomerang-shaped) ascospores, 32-spored asci, and apothecia with prominent marginal teeth, also by a sulphur-yellow colour of the exudate over the hymenium. Very similar in spore shape is *O. curvatinavajoana*, a species with 8-spored asci, tear-shaped SBs in the spores, and smooth apothecia without glassy processes.

Variation. The species appears to be quite constant in its peculiar characteristics, judging from the four known records which were, however, made within an area of only about 5 km diam. Only the length of the glassy processes varied, which did not exceed ~30 µm in the samples on *Hibbertia* and ?*Myrtaceae*.

Phylogeny. A sequence that includes SSU, ITS, and LSU (S1506 intron absent) was gained from apothecia of the holotype. In analyses of ITS+LSU, ITS, or LSU, *O. multicurvula* clustered with high support in the *vinosa*-*velutina* clade (Phyls 9, 11, S13), where it formed with *O. subulivinosa* a medium, low, or unsupported clade respectively. The ITS distance is 9% to *O.* aff. *subulivinosa* (Slovakia), 11.5% to *O. subulivinosa* (1.3% in LSU), and 13–17% to *O. vinosa*, *O. subvinosa*, and *O. nothoaprilis* (3–3.7% in LSU).

Ecology. *O. multicurvula* was found on rotten clefty bark of xeric twigs and branches of *Myrtaceae* and *Dilleniaceae* in subtropical semihumid banksia-eucalypt open wood- and shrublands of southwestern Australia. The wood core of the branches is very undecayed, and possibly the apothecia also occur on dead bark of still-living branches.

Specimens included. **AUSTRALIA**: **Western Australia**, Swan Coastal Plain, 55 km SSW of Moora, 30 km NNE of Gin Gin, Moore River, 83 m, branch of ?*Myrtaceae*, on bark, 11.XI.2007, G. Marson (G.M. 2007-11-11.1 ø). – 60 km SW of Moora, 8 km NE of Cowalla, Moore River, Orange Springs Road, 77 m, twigs & branches of *Eremaea pauciflora*, on bark, 5.IX.2006, G. Marson (ex H.B. 8643a, MEL 2389245, **holotype**; sq.: KT222427). – ibid., branches of *E. pauciflora*, on bark, 23.X.2007, G. Marson (H.B. 8775a). – 58 km SW of Moora, 10 km NE of Cowalla, Orange Springs Road, 83 m, branch of *Hibbertia aurea*, on bark, 24.X.2007, G. Marson (ø).

Orbilia velutina Baral & G. Marson, **sp. nov.**, MB 813599 — Pls 282–283

Etymology: named after the velvety exterior of the apothecia.

Typification: Western Australia, Kumarina Roadhouse, branch of *Eucalyptus*, 28.X.2007, G. Marson (ex H.B. 9772a, MEL 2389281, holotype; sq.: KT380093).

Latin diagnosis: *Apothecia rehydratata 0.2–0.75 mm diam., obscure lateritio-aurantia, sessilia, margine aspera vel distincte velutina. Asci 128-spori, apice in statu emortuo hemisphaerico, crassitunicato. Ascosporae *5.5–8 × 1.7–2.5 µm, ellipsoideo-fusoideae, rectae, corpusculum refringens cylindricum, brevem, basi leniter inflatum, ad apicem affixum continentes. Habitat ad lignum putridum rami sicci* Eucalypti *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.75 × 0.2–0.55 mm diam., 0.17–0.32 mm high, light to bright ± dirty dull orange-red, non-translucent, round (to elliptical), scattered to subgregarious; disc flat, margin usually distinct and ± thick, rough or mostly with whitish, short or sometimes long, erect or appressed hairs which protrude 30–50(–90) µm beyond disc; broadly sessile, superficial to slightly immersed; dry contracted and inconspicuous. **Asci** *(88–)108–120(–135) × (10–)11–12.5(–13) µm, †85–120 × (8.5–)9–10(–10.8) µm, 128-spored (~75–90 spores counted, ~100–130 spores evaluated from volume), in some apothecia only 64-spored (~60 spores counted), spores multiseriate, part of spores inverted (strongly mixed), pars sporifera *60–80 µm long; **apex** (†) hemispherical, dome †1.5–1.7 → 0.7–1.3 µm thick, with apical chamber, inner delimitation staining light purplish-red in $\mathrm{CR}_{\mathrm{SDS}}$; **base** with short to very long, thin or thick, straight or flexuous stalk, T, L- or h-shaped. **Ascospores** *(5.5–)6–7.5(–8)((–9)) × (1.7–)1.9–2.3(–2.5) µm, †6–7.2 × 1.7–2.1 µm, ellipsoid-fusoid (to ellipsoid-clavate), apex obtuse, base often medium to strongly attenuated, obtuse to mostly (sub)acute, straight to slightly inequilateral; **SBs** *(2–)2.5–3(–3.2) × (0.5–)0.6–0.8(–0.9) µm, elongate tear-shaped or cylindrical with a distinct small basal inflation, apically narrowed to a ± wide point, also slightly widened (dumbbell-shaped), straight. **Paraphyses** apically uninflated or slightly to medium, rarely strongly clavate-capitate or somewhat spathulate, terminal cells *8.5–20 × 2.5–4(–5) µm, sometimes ± flexuous, lower cells *(7–)9–17 × 1.7–2.8(–3.2) µm; rarely branched at apex. **Medullary excipulum** hyaline to pale yellowish-orange, 40–100 µm thick, of dense (below also loose) textura intricata with many inflated cells, sharply delimited (sometimes by an 8–15 µm thick layer of t. porrecta). **Ectal excipulum** pale rose, of (†) slightly (to medium) gelatinized, indistinctly to vertically oriented t. globulosa-angularis-prismatica, 30–80 µm thick near base, cells *(9–)11–20(–26) × (5–)8–16(–18) µm; 15–40 µm thick near margin, at mid flanks of t. globulosa-angularis or t. prismatica oriented at a 30–70° angle, cells *5–12 × 4.5–6 µm, at upper margin of t. prismatica oriented at a 10–30° angle, marginal cortical cells *6–12 × 3–5 µm, terminating in ± flexuous, septate **hairs** */†25–95 × 3–4.2 µm, wall 0.2–0.4(–1) µm thick, ± smooth, septate, individual cells 8–12 µm long; **glassy processes** absent. **Anchoring hyphae** sparse, *(1.8–)2.2–4 µm wide, walls 0.2–0.3(–0.5) µm thick. **SCBs** in paraphyses, ectal excipulum (near margin) and hairs globose, 1.5–2 µm diam., mixed with rod-shaped to angular ones, hyaline to pale yellow-orange, strongly refractive crystalloid SCBs 1–4 × 0.3–0.8 µm. **LBs** in lower half of paraphyses pale yellow (carotenoids), minute. **Exudate** over paraphyses 0.2–1 µm thick, granular-continuous, hyaline, loosely attached over ample gel, over marginal hairs as scattered low warts. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1}). **Colonies** pale to light orange. **Conidiophores** reduced. **Conidia** Y-shaped, total size *(18–)22–35(–42) × (17–)30–75(–92) µm, stipe *11.5–16(–18) × 3.5–4.6 µm, 1–2(–3)-septate, arms somewhat tapering, *(7–)20–50(–63) × (3.8–)4.2–4.7(–5.5) µm, ((1–))(2–)3–6(–7)-septate, also some unbranched conidia present: straight to slightly curved, *(28–)38–41 × 5–6.2 µm, (3–)4–6-septate {1}, both without constrictions.

Habitat: collected ~3 m above the ground, dead, decorticated, 10–18 mm thick branch of a large, fallen but living *Eucalyptus* sp., on 0.1–0.2 mm deep very decayed wood, strongly greyed, no algae. **Associated**: *Orbilia austropleiomicrosoma*, *O.* ?*multiserpens*, *O.* ?*pleioaustraliensis*. **Desiccation tolerance**: fully viable after 40 months. **Altitude**: 540 m a.s.l. **Geology**: Mesoproterozoic sedimentary rock (red-brown sand and gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia velutina* is easily recognized by its large, 128-spored asci and small, ellipsoid-fusoid ascospores containing rod-shaped SBs with a slight basal bulb, also by an apothecial margin covered with short to long, flexuous, septate hairs without glassy processes. Especially because of its hairs, *O. velutina* might occupy a rather isolated position within series *Hesperideae*. However, in spore and SB shape the species resembles *O. aprilis*.

Anamorph. The trinacrium-like conidia obtained in pure culture vary strongly in arm length. They resemble those large trinacrium-like conidia that frequently occur in series *Hemiorbilia*, but when shorter-armed they are very similar to those of *O. vinosa*.

Phylogeny. A sequence comprising S1506 intron, ITS, and LSU was gained from the holotype culture. In analyses of ITS+LSU, ITS, or LSU (Phyls 9, 11, S13), *O. velutina* clustered with high support in the *vinosa*-*velutina* clade, with a distance of

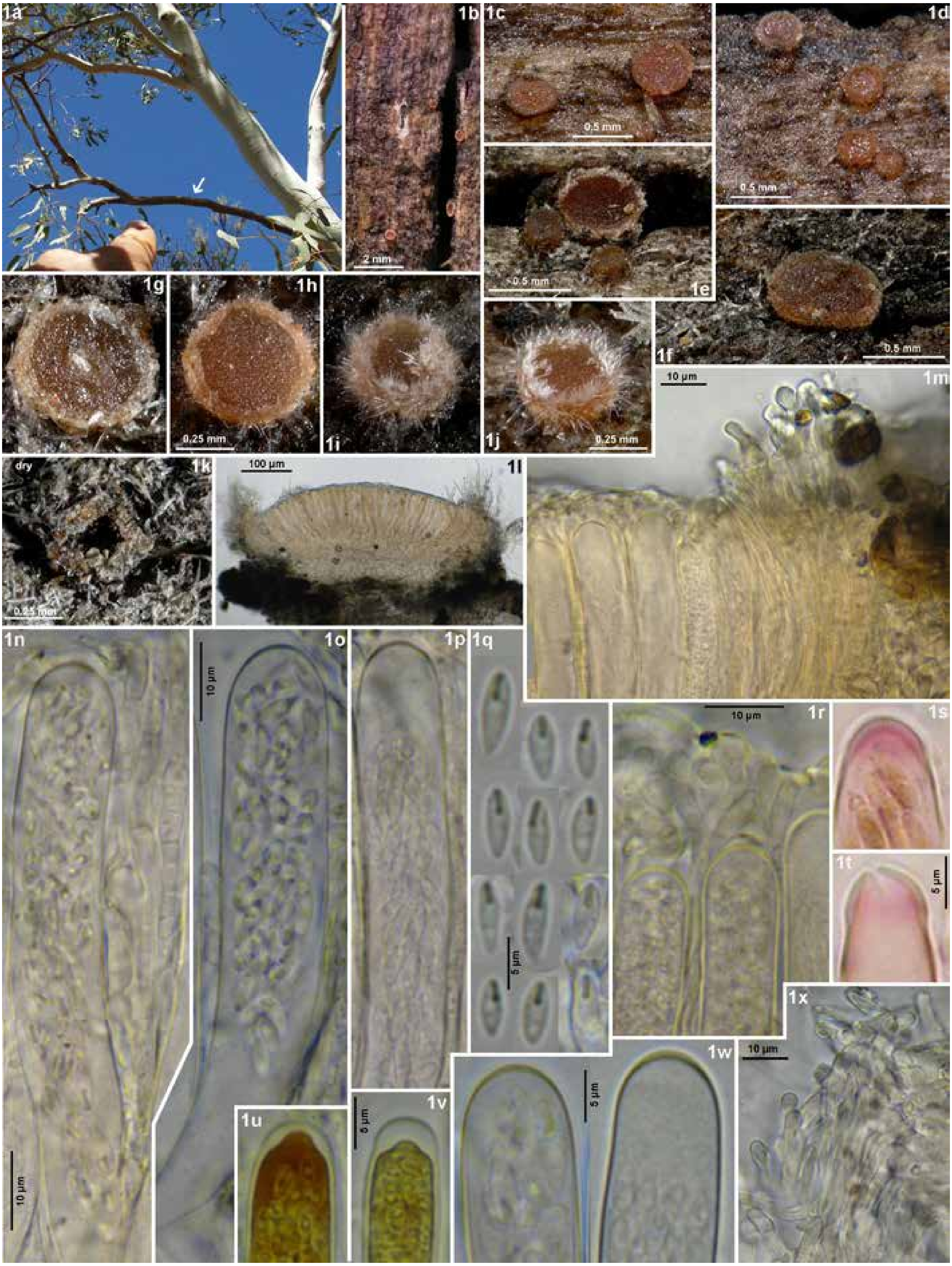


Plate 282. **1**: *Orbilia velutina*. – **1a**. 1–2 cm thick decorticated branch attached to living *Eucalyptus* tree; **1b**. surface of decorticated branch with rehydrated apothecia; **1c–j**. rehydrated apothecia; **1k**. dry apothecium; **1l**. apothecium in median section; **1m**. id., upper margin with short hairs; **1x**. ± projecting marginal hairs; **1n–o**. mature asci and paraphyses; **1p**. immature ascus; **1r**. apices of paraphyses between asci; **1.s–w**. ascus apices. – Living state, except for **1s–t** (in CR_{SDS}), **1u–v** (in KOH+IKI), **1x** (in H_2O). — **1a–w**. H.B. 9772a (holo/isotype): Western Australia, Gascoyne, on *Eucalyptus*.

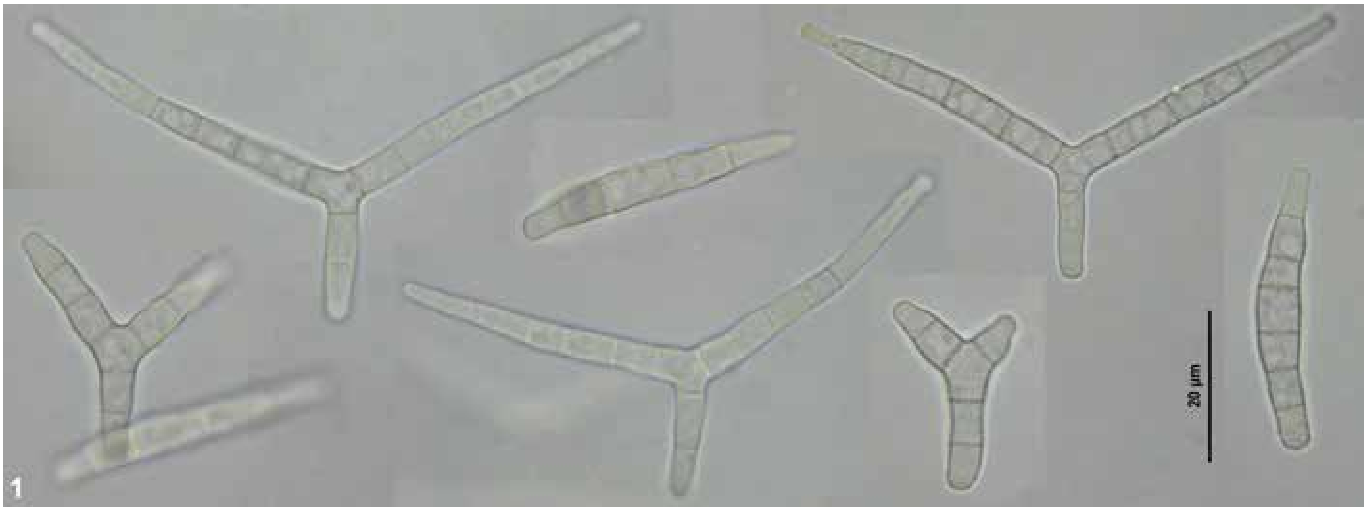


Plate 283. **1**: *Orbilia velutina*. – **1**. conidia (living state, H.B. 9772a, holotype).

11.5–20% in the ITS region to other members of the clade, the lowest percentage being to *O.* cf. *angustoaristata*, with which it formed a moderately supported clade when using ITS+LSU or LSU. Also when analysing the intron the two species clustered weakly supported together In the LSU (D1–D2) the lowest distance was 1.5% to *O.* cf. *angustoaristata*, 3% to *O. multicurvula*, and 4% to *O. vinosa*. In the intron *O. velutina* shows a distance of 7.5% to *O.* cf. *angustoaristata*, 13–14% to *O. aprilis*, and 15–16.5% to *O. vinosa*.

Ecology. *O. velutina* was found on rotten wood of a decorticated xeric branch of *Eucalyptus*, in a subtropical semiarid acacia open woodland with *Eucalyptus* in a most of the time dry riverbed in the Gascoyne ecoregion of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Eucalyptus*, on wood, 28.X.2007, G. Marson (MEL 2389281, **holotype**; H.B. 9772a, **isotype**, anam. cult.; sq.: KT380093).

Orbilia nothoaprilis Baral, **sp. nov.**, MB 813598 — Pls 284–285

Etymology: the epithet means 'false *Orbilia aprilis*'.

Typification: Australia, Queensland, Craiglie, branch of *Acacia*, 31.VIII.2006, G. Marson (ex H.B. 8588, BRI AQ799196, holotype; sq.: KT380091).

Latin diagnosis: *Similis* Orbiliae aprili *sed cellulae vivae excipuli marginalis et paraphysium corpuscula crystalloidea continentes*, *ascosporae paulo longiores*, *corpuscula refringentia longiora*, *asci apice in statu emortuo leniter crassitunicati. Habitat ad lignum putridum rami sicci* Acaciae *in zona tropica (sub)humida Australiae septentrio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.4 mm diam., 0.1 mm high (receptacle 0.08–0.09 mm), pale to light orange-rose, somewhat translucent, round (to elliptical), (very) scattered; disc flat, margin distinct, thin, 10 µm protruding, finely rough to crenulate; broadly sessile, superficial; dry light to bright orange. **Asci** *35–42 × 5.2–5.5 µm, †31–40 × 4.5–5.2 µm, 8-spored, spores *3–4-seriate, 3–5 lower spores inverted (not mixed); **apex** (†) ± hemispherical, dome in KOH 0.7–0.8 → 0.5–0.6 µm thick, with slight apical chamber; **base** with short to medium long, ± thin, flexuous stalk, L-shaped. **Ascospores** *8–11 × 1.7–1.8(–1.9) µm, †8–11 × 1.6–1.7 µm, fusoid, apex obtuse, base strongly attenuated, straight to slightly inequilateral; **SBs** *2–3 × 0.3–0.5 µm, subulate to vermiform, apically narrowed to a wide or small point, straight, overmature *1.6–1.8 × 0.6–0.8 µm. **Paraphyses** apically uninflated to slightly clavate or spathulate, terminal cells *(7–)10–13.5 × 2.2–3 µm, lower cells *(5–)7–8.5 × 1.5–2.2 µm; unbranched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline, 25 µm thick, of dense textura intricata with many inflated cells, rather sharply delimited. **Ectal excipulum** hyaline to pale rose, of (†) thin-walled, indistinctly vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 35 µm thick near base, cells *9–17 × 7–11(–14) µm; 15–20 µm thick near margin, of t. porrecta

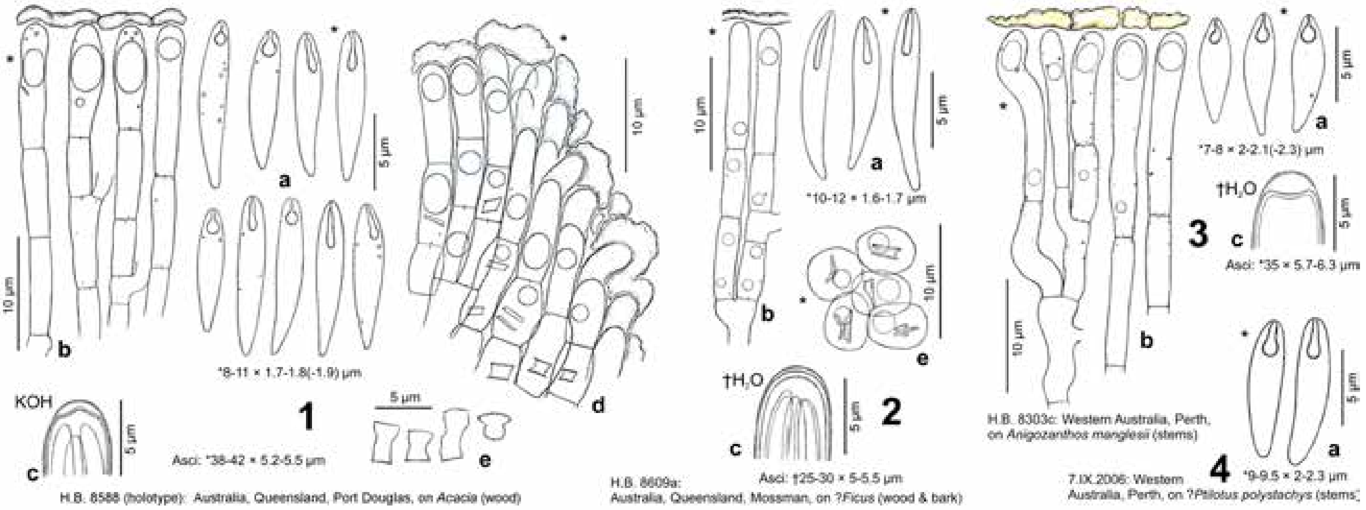


Plate 284. **1**: *Orbilia nothoaprilis*; **2**: *O.* cf. *nothoaprilis*; **3–4**: *O.* aff. *nothoaprilis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section; **e**. crystalloid SCBs in ectal excipular cells (lower and mid flanks, **2e** external view).

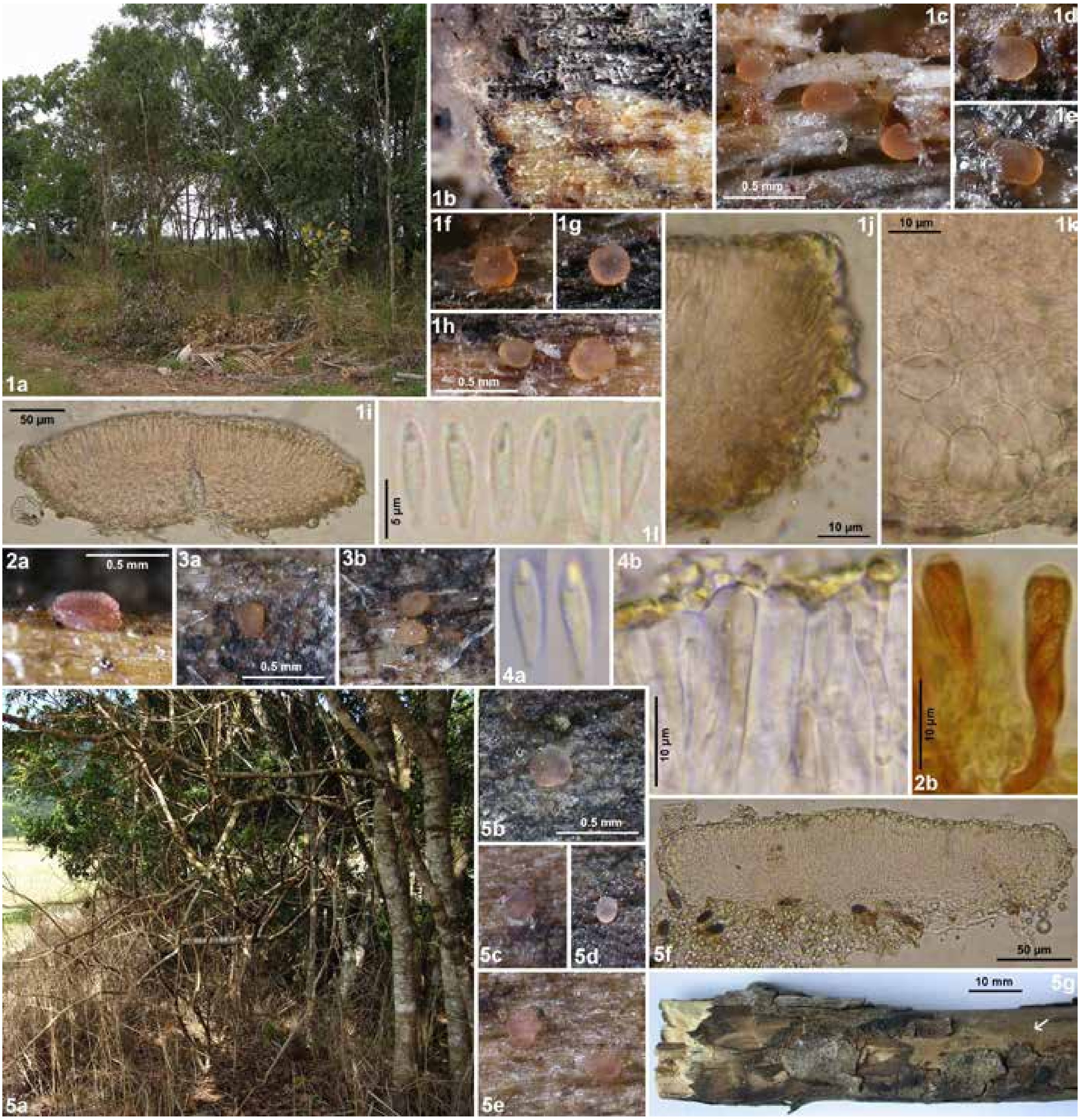


Plate 285. **1**: *Orbilia nothoaprilis*; **5**: *O.* cf. *nothoaprilis*; **2–4**: *O.* aff. *nothoaprilis*. – **1a**, **5a**. remnants of tropical humid broad-leaved forests; **5g**. dead branch of a indet. angiosperm. **1b–h**, **2a**, **3a–b**, **5b–e**. rehydrated apothecia; **1i**, **5f**. apothecia in median section; **1j**. id., marginal ectal excipulum; **1k**. id., basal ectal excipulum; **2b**, **4b**. asci and paraphyses (**2b** in IKI); **1l**, **4a**. ascospores. – Living state, except for **2b** (in KOH+IKI). — **1a–m**. H.B. 8588 (holotype): Australia, Queensland, Port Douglas, on *Acacia*; *O.* aff. *nothoaprilis*: **2a–b**. H.B. 8495: ibid., Cape Tribulation, on *Bambusa*; **3a–b**. H.B. 8303c: Western Australia, Perth, on *Anigozanthos*; **4a–b**. 7.IX.2006: ibid., on ?*Ptilotus*; **5a–g**. H.B. 8609a: Australia, Queensland, Mossman, on indet. angiosperm.

oriented at a 10–40° angle to the surface, marginal cortical cells */†6–10 × 2–2.5(–3) µm; **glassy processes** 2–5 × 2.5–3 µm, high-refractive, not stratified. **Anchoring hyphae** sparse, †1.5–2.5 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose to ellipsoid, 2–2.8 µm diam., distinct hyaline crystalloid SCBs present in ectal excipulum from base to margin, 2–4.5 × 1.7–2.8 µm. **Exudate** over paraphyses 1–1.5 µm thick, cloddy-continuous, ± loosely attached, over glassy processes 1–3 µm thick, rough-cloddy, pale yellowish-chlorinaceous. **— ANAMORPH**: unknown.

Habitat: collected 6 m above the ground, decorticated, 45 mm thick branch of *Acacia* sp., heavily perforated by ants, on 0.1 mm deep slightly to medium decayed wood in outer galleries (especially on thin walls between galleries), not or slightly greyed, with a few green algae. **Associated**: *Hypoxylon* ?*rubiginosum*, on much thinner separate branch *Hyalorbilia inflatula* (1 m above the ground). **Desiccation tolerance**: fully viable for at least 3 months, after 11 months many excipular cells and a few immature asci still alive. **Altitude**: 15 m a.s.l. **Geology**: Devonian sedimentary rock (whitish soil). **Phenology**: VIII (but rather long-lived).

Taxonomic remarks. The Australian *Orbilia nothoaprilis* is very similar to the European (and North American) *O. aprilis*, from which it differs in the presence of crystalloid SCBs in the ectal excipulum, slightly longer ascospores with distinctly longer SBs, also in slightly wider asci with thinner apical domes.

Although the taxon is so far only known from a single collection, it is described here as a separate species, based mainly on the presence of crystalloid SCBs which have never been seen in the many collections of *O. aprilis* studied in the living state.

The North American *O. georgiana* was predominantly studied in the dead state and differs from *O. nothoaprilis* only slightly in the available morphological features.

Not included collections. A lignicolous specimen from northeastern Australia (on indet. angiosperm, Pls 284: 2; 285: 5) might be conspecific with *O. nothoaprilis* on account of its very thin apical domes (†0.8 → 0.3 µm) and the presence of crystalloid SCBs. It differs in slightly longer and narrower spores, longer SBs (3–4 × 0.4–0.5 µm), shorter asci, and smaller, very thin apothecia (60 µm) and is, therefore, not included in the description. From *O. nothovinosa* this sharply differs in the thin apical domes and the presence of crystalloid SCBs.

A sparse collection from southwestern Australia (on herbaceous stem of *Anigozanthos*, Pl. 284: 3) differs from *O. nothoaprilis* in its unusual host, but also in the absence of crystalloid SCBs in paraphyses and excipulum, more fusiform spores, and a distinctly thicker apical dome (†1.5 µm). It was collected together with a similar taxon with more subcylindric-fusoid spores with obtuse ends, which grew on dicot stems (?*Ptilotus*, Pls 284: 4; 285: 4). From European *O. aprilis* both taxa differ mainly in the herbaceous substrate, the latter also in larger SBs (*2.3–2.7 × 0.6–0.9 µm). A single apothecium from northeastern Australia (on stem of *Bambusa*, Pl. 285: 2) was only studied in the dead state. It might belong to one of these taxa because of thicker ascus domes (†1.5 → 1 µm), also because of rather short asci [†20–24(–28) × 4.7–5.7 µm] and spores (†6–8.5 × 1.5–1.8 µm). We conclude that these samples on herbaceous substrates belong to 1 or more species different from *O. nothoaprilis.*

An Australian collection on *Eremaea* was only studied in the dead state (IVV: H.B. 9132a). It differs in smaller spores (†6–8 × 1.3–1.4) and sometimes strongly truncate and thin-walled ascus apices, therefore, it is not included.

Phylogeny. A sequence taken from apothecia of the isotype of *O. nothoaprilis* comprises ITS and LSU (S1506 intron absent). Surprisingly, it clustered in the highly supported *vinosa-velutina* clade (Phyls 9, 11, S13), though unresolved by showing a high distance in the ITS/LSU region: 12.5/3.7% to *O.* cf. *angustoaristata*, 13/3.7% to *O. multicurvula*, 14/3.7% to *O. velutina*, and 15–16/4.5–5% to *O. vinosa*/*O. subvinosa* (19.5/7.3% to *O. aprilis*). A sample from Georgia (USA), described as *O. georgiana* in Shao et al. 2018 based on its deviating rDNA data, clustered highly supported with *O. nothoaprilis* (for the distance see p. 643).

Ecology. *O. nothoaprilis* was found on ± rotten wood of dead, xeric branches of *Acacia* in tropical (sub)humid northeastern Australia. *O.* aff. *nothoaprilis* on *Bambusa* and bark of an indet. angiosperm (with *Carallia brachiata* close to it) are from a similar area and climate, whereas those on *Anigozanthos*, ?*Ptilotus* and *Eremaea* are from subtropical semihumid southwestern Australia.

Specimens included. **AUSTRALIA**: **Queensland**, Wet Tropics, 7 km S of Port Douglas, SSE of Craiglie, 15 m, branch of *Acacia*, on wood, 31.VIII.2006, G. Marson (ex H.B. 8588, BRI AQ799196, **holotype**; MEL 2389243, **isotype**; sq.: KT380091).

Not included. **AUSTRALIA**: **Queensland**, Wet Tropics, 43 km N of Port Douglas, Cape Tribulation, 14 m, stem of *Bambusa*, 30.VIII.2006, G. Marson (H.B. 8495). – Einasleigh Uplands, 3 km SW of Mossman, 1 km ESE of Mossman Gorge Camping, Tara Hills Road, 32 m, branch of indet. angiosperm, on wood & bark, 29.VIII.2006, G. Marson (H.B. 8609a). – **Western Australia**, Swan Coastal Plain, Perth, Kings Park, 50 m, stem of *Anigozanthos manglesii*, 7.IX.2006, G. Marson (H.B. 8303c); – ibid., stem of ?*Ptilotus polystachyus*, 7.IX.2006, G. Marson (ø). – 20 km SW of Jurien Bay, 19.5 km NE of Cervantes, Cervantes Rd, 80 m, branch of *Eremaea*, on bark, 11.XI.2007, G. Marson (H.B. 9132a ø).

Orbilia georgiana Y.Y. Shao, Baral & Bin Liu, in Shao et al., Mycol. Res. 17(11): 1228 (2018) — Pl. 286

Etymology: from the state of Georgia where the species was collected.

Typification: USA, Georgia, Albany, Chehaw Park, branch of *Quercus*, 3.IX.2015, Y.Y. Shao, P.S. Ji & H.F. Zheng (GXU 1472, holotype; ex-type culture: ga006; sq.: MG742408, MG742396).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.25–0.65(–0.8) mm in diam., 0.08 mm thick, pale to light yellow-orange or cream-reddish or orange-rose when fresh, slightly to strongly translucent, round, scattered to subgregarious; disc flat to slightly convex, translucent, margin distinct, not protruding, smooth to very finely rough; sessile on a broad base, superficial or somewhat erumpent between fibres; dry rose-red, slightly contracted. **Asci** †28–38 × 4–5 µm, 8-spored, spores †2–3-seriate, spores inversion unclear; **apex** (†) rounded to slightly truncate, dome ~0.9 µm thick, with small apical chamber; **base** with short to medium long, flexuous stalk, L- to Y-shaped. **Ascospores** *7.5–11 × 1.4–1.5 µm, †9–10.5(–11.5) × 1.3–1.6(–1.8) µm, fusoid to very slightly clavate, apex obtuse, base ± strongly attenuated, straight or sometimes slightly inequilateral; **SBs** *1.5–1.8 × 0.8 µm, elongated tear-shaped, straight. **Paraphyses** apically uninflated to slightly

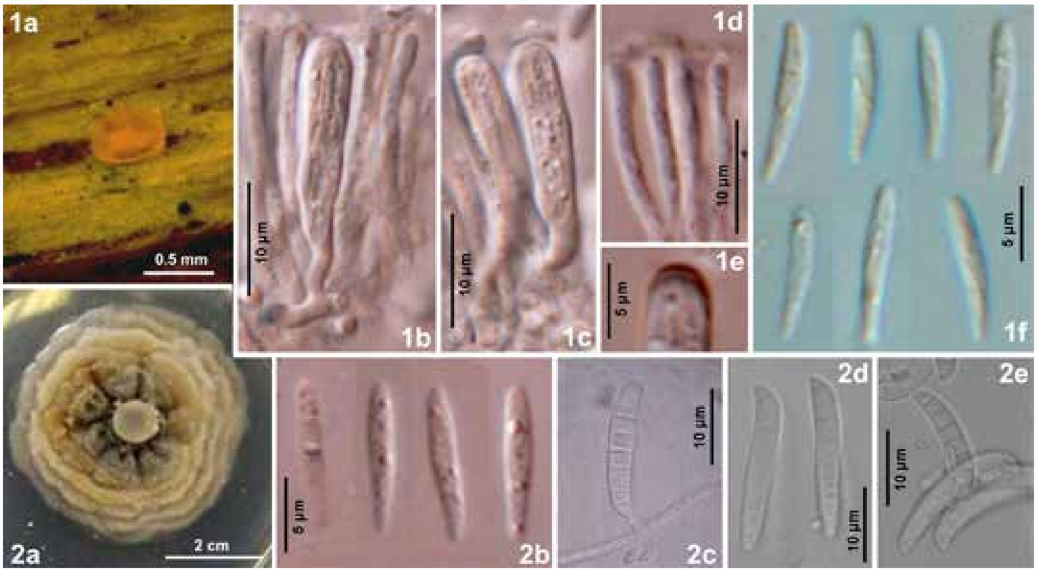


Plate 286. **1–2**: *Orbilia georgiana*. – **1a**. rehydrated apothecium; **1b–d**. asci and paraphyses; **1e**. ascus apex; **1f**, **2b**. ascospores; **2c–e**. conidia (from culture); **2a**. pure culture on PDA. – Dead state (in H_2O), except for **2c–e**. – **1–2**: phot. Y.Y. Shao. — **1a–f**. GXU 1488: USA, Georgia, Albany, on indet. angiosperm; **2a–e**. GXU 1472: ibid.

clavate-capitate, terminal cells †~11–13 × 1.5–3 µm, lower cells †1.8–2.3 µm wide; sometimes branched in middle part. **Medullary excipulum** 25 µm thick, rather sharply delimited. **Ectal excipulum** of (†) thin-walled, indistinctly vertically oriented t. angularis(-prismatica) from base to mid flanks, 25 µm thick near base, cells †6–13 × 5–9 µm; marginal cortical cells elongate, †3–6.7 µm wide; **glassy processes** not observed. **Anchoring hyphae** not examined. **SCBs** no data available. **Exudate** over paraphyses 0.3–1.5 µm thick, granular to cloddy, ± loosely attached, hyaline to pale orange-yellowish-chlorinaceous. — **ANAMORPH**: vermispora-like (from ascospore isolate {1}). **Conidiophores** integrated, sympodial, *1.5–2 × 0.8–1 µm. **Conidia** unbranched, slightly to strongly curved towards the ends, more straight in middle part, cylindrical but tapering at the ends, apex obtuse, base indistinctly truncate, *(12–)13.5–19(–22.5) × 2.5–3.2 µm, 6–7(–8) septate.

Habitat: collected on the ground, decorticated, 20–80 mm thick branches of *Acer* sp. {2}, *Quercus* sp. {2}, on decayed wood {4}, slightly to strongly greyed. **Associated**: none observed. **Desiccation tolerance**: not tested (probably tolerant). **Altitude**: 40–60 m a.s.l. **Geology**: Pennsylvanian, Eocene and Quaternary (carbonate) sedimentary rock. **Phenology**: IX (but probably long-lived).

Taxonomic remarks. The North American *Orbilia georgiana* appears to differ from the mainly European *O. aprilis* in slightly longer and narrower ascospores and from Australian *O. nothoaprilis* in narrower spores and particularly in shorter and wider SBs. Except for the spores the species was only studied in the dead state, therefore, data on the SCBs are missing.

A collection from Texas mentioned under *O. aprilis* differs from *O. georgiana* in thin-walled ascus apices and distinct glassy processes. Two collections from Massachusetts were here included in the description of *O. aprilis* although their relationship to *O. georgiana* remains uncertain.

Not included collection. One of the five samples from the type locality had distinctly smaller spores (*5.5–6.7 × 1–1.2 µm) and was, therefore, not included in the description (see also Shao et al. 2018).

Anamorph. In one of the specimens a pure culture was gained by Y.Y. Shao which produced a vermispora-like anamorph (Pl. 286: 2c–e). The conidia resemble those observed in *O. crenatovinosa*, but this species clusters in the *aprilis-crenatovinosa* clade, unlike *O. georgiana* which clusters in the *vinosa-velutina* clade. Regrettably, the anamorph of *O. nothoaprilis* is unknown.

Phylogeny. A sequence taken from pure cultures of ga006 (holotype) and ga040 comprise ITS (S1506 intron absent) and LSU D1–D3. The two ITS sequences have only in part a good signal but complement one another to permit assembling a complete (chimeric) sequence. The two LSU sequences are identical, except for 1 nt in the D1 domain. *O. georgiana* clustered in a highly supported clade with *O. nothoaprilis* when analysing ITS+LSU, ITS, or LSU, Phyls 9, 11, S13). The two species show an ITS distance of 4.5 % to each other, and 2 % in the LSU (D1–D2), or 1.3 % when including the D3 domain in which no differences were noted between the two species.

Ecology. *O. georgiana* was collected on wood of *Quercus* and *Acer* branches in the warm-temperate humid southern Appalachian Mts. and especially in the subtropical humid lowlands of Georgia (southeastern North America).

Specimens included. **USA**: **Georgia**, ~47 km WNW of Dalton, ~27 km SW of Chattanooga, Canyon State Park, 310 m, branch of *Acer* sp., on wood, 30.IX.2015, Y.Y. Shao (ga055, GXU 1497, doc. vid.). – 5 km NNE of Albany, Chehaw Park, 60 m, branch of *Quercus*, on wood, 3.IX.2015, Y.Y. Shao, P.S. Ji & H.F. Zheng (GA006, GXU 1472, **holotype**, anam. cult., doc. vid.; sq.: MG742408, MG742396). – 88 km NW of Jacksonville, ~25 km NE of Fargo, Stephen C. Foster Park, 40 m, branch of *Quercus*, on wood, 24.IX.2015, Y.Y. Shao (GA040, GXU 1488, doc. vid.; sq.: MG742394, MG742395). – ibid., branch of *Acer*, on wood, 24.IX.2015, Y.Y. Shao (ga026a, GXU 1493, doc. vid.).

Not included. **USA**: **Georgia**, 5 km NNE of Albany, Chehaw Park, 60 m, branch of indet. angiosperm, on wood, 3.IX.2015, Y.Y. Shao, P.S. Ji & H.F. Zheng (ga013, GXU 1478, doc. vid.).

Orbilia crenatovinosa Baral & Friebes, **sp. nov.**, MB 813597 — Pls 287–288

Etymology: named after the toothed margin and similarity with *O. vinosa*.
Typification: Austria, St. Ilgen, branch of *Pinus sylvestris*, 24.X.2009, G. Friebes (ex H.B. 9247, M-0276463, holotype).

Latin diagnosis: *Similis* Orbiliae vinosae *sed ascosporae paulo minores, corpuscula refringentia multo breviora, excipulum marginale processis vitreis multo longioribus praeditum. Habitat ad lignum putridum ramorum siccorum* Pini sylvestris *in zona orotemperata humida in Alpibus orientalibus Europae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.4–0.7(–0.8) mm diam., 0.15–0.2 mm high (receptacle 0.1 → 0.08 mm), light rose-orange, hardly translucent, round to angular, scattered to gregarious in small groups; disc slightly to medium concave, margin with prominent, whitish to pale cream teeth protruding 40–60 µm; sessile on a narrow or broad base, slightly to strongly immersed in furrows and biofilm; disc dry bright orange-brown, half to entirely closed. **Asci** *45–57 × 4.2–4.5 µm {2}, †(40–)45–55(–60) × 4–4.3 µm {1}, 8-spored, spores 3–4-seriate, 2–3 lower spores inverted {1} (not mixed), pars sporifera *19–26 µm long; **apex** (†) hemispherical to slightly (rarely medium) truncate, dome †0.7–1 → 0.5–0.7 µm thick {1}, apical chamber absent or indistinct; **base** with short to long, ± thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(8.7–)9.5–12(–13) × (1.3–)1.4–1.6 µm {3}, †10–12(–13) × 1.4(–1.5) µm {1}, narrowly fusoid(-clavate), apex obtuse, base slightly to often strongly attenuated, with or without an indistinct tail, straight to slightly inequilateral; **SBs** *1.8–2.2 × 0.5–0.8 µm {1}, tear-shaped, apically narrowed to a short filum. **Paraphyses** apically uninflated, rarely clavate-spathulate, terminal cells *8–21 {1} × 1.8–2.3(–2.8) µm {3}, lower cells *10–14 × 1.6–2.2(–2.5) µm {1}; unbranched at upper septum. **Medullary excipulum** pale orange, 50–80 µm thick, of dense textura intricata with many inflated cells, indistinctly to sharply delimited from ectal excipulum by a t. porrecta. **Ectal excipulum** pale orange, of (†) thin-walled to slightly gelatinized, irregularly oriented t. angularis-globulosa from base to mid flanks, 25–50 µm thick near base, cells *8–18 × 6–11(–14) µm {1}; 20–30 µm thick near margin, of t. porrecta oriented at a 10–30° angle to the surface, marginal cortical cells †10–18 × 2.3–3 µm {1}; **glassy processes** 10–40 × 2.3–3.5(–4) µm {2}, high-refractive, stratified, coherent to form distinct teeth, predominantly outwards curved.

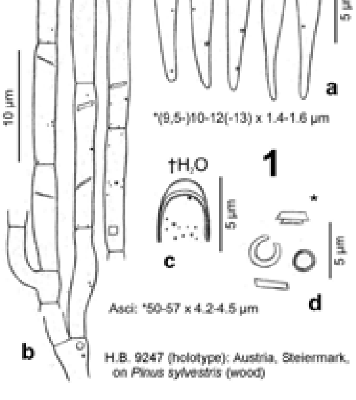


Plate 287. **1–2**: *Orbilia crenatovinosa*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex; **d**. crystalloid SCBs in ectal excipular cells at flanks.

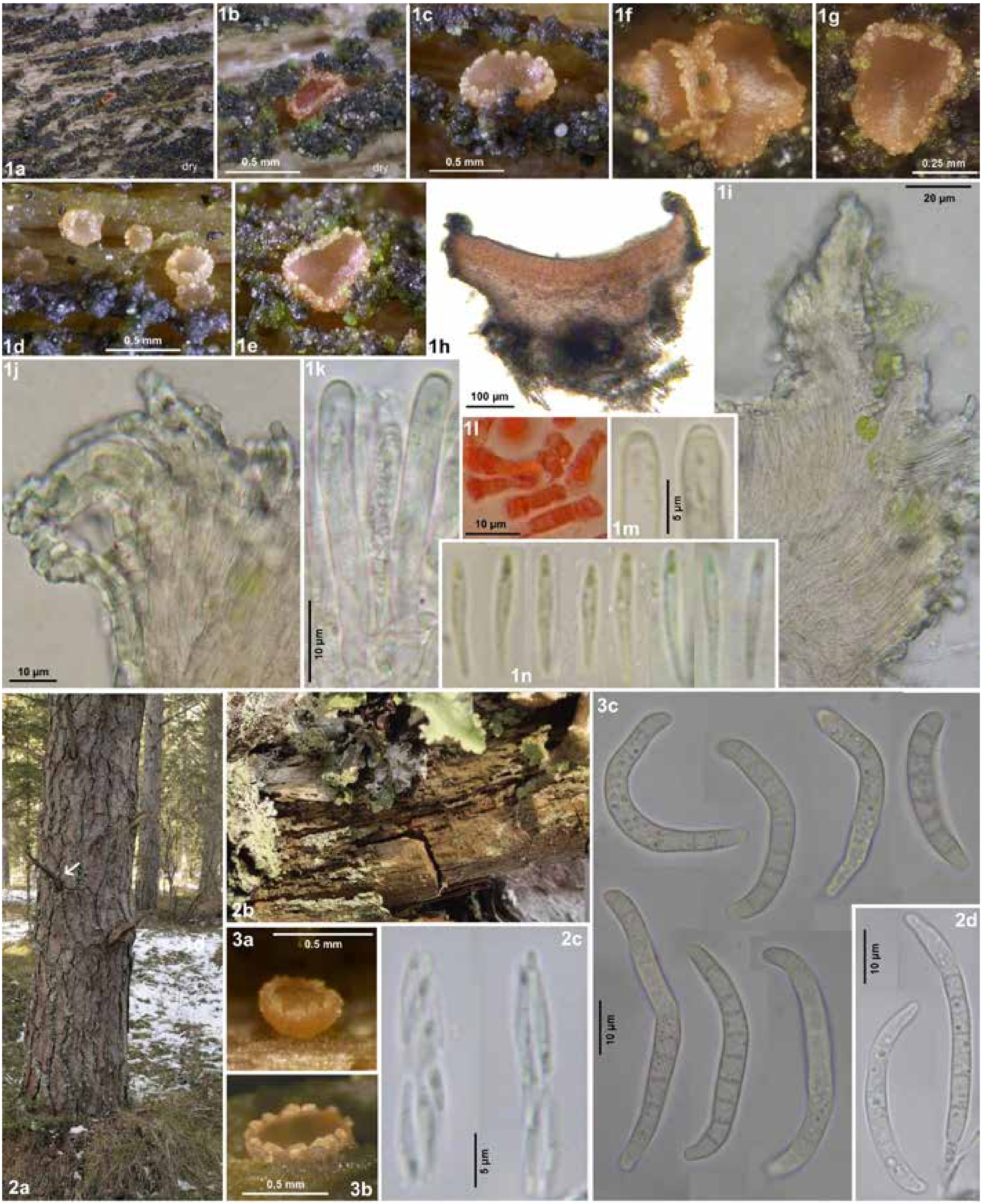


Plate 288. **1–3**: *Orbilia crenatovinosa*. – **2a**. Montane calcareous mixed forest with living trunk of *Pinus sylvestris*; **2b**. rotten xeric *Pinus* stub; **1a–b**. dry apothecia; **1c–g**, **3a–b**. rehydrated apothecia; **1h**. apothecium in median section; **1i–j**. id., marginal ectal excipulum (with glassy processes forming teeth); **1l**. glassy processes; **1k**, **m**. asci; **1n**, **2c**. ascospores (**2c** in clusters); **2d**, **3c**. conidia from substrate. – Living state, except for **1l** (in KOH+CR), asci in **1m** (in H_2O). – **1f–g**, **m–n** (left **5** spores), **2a–d**, **3a–c**: phot. G. Friebes. — **1a–n**. H.B. 9247 (holotype): Austria, Steiermark, on *Pinus*; **2a–c**. G.F. 20160008, ibid.; **3a–d**. G.M. 2014-05-10.1: ibid.

Anchoring hyphae ± abundant, †2–3 µm wide, walls 0.2–0.3(–0.5) µm thick {1}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.3–2.5 µm diam. {2}, also rod- to ring-shaped, hyaline, 1.5–3 µm diam. {2}; **Exudate** over paraphyses (0.3–)1–2(–3) µm thick, cloddy, hyaline, loosely attached, over glassy processes and elongate marginal cells 0.2–0.3 µm thick, finely granular. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {2}). **Conidiophores** not observed. **Conidia** unbranched, multiseptate, irregularly medium to strongly curved in upper and lower part or entirely, cylindrical, slightly tapering at the ends, apex obtuse, base slightly truncate, with many small LBs near septa and a few larger ones; *36–50 × 3.3–4 µm (~42–52 µm actual length), ~4–7-septate {20.II.2016}; *30–42(–57) × 4.2–4.7 µm (~33–59 actual length), 7–11-septate {10.V.2014}.

Habitat: lying close to ground or attached 1.5–2 m above the ground, partially or entirely decorticated, 12–30 mm thick branches of *Picea abies* {1}, *Pinus sylvestris* {4}, on 0.5 mm deep very decayed wood {5}, slightly to strongly greyed, with or without many green algae. **Associated**: *Mellitiosporium propolidoides* {2}, *Platismatia glauca* {1}, on separate branch *Chrysodisca peziculoides* {1}. **Desiccation tolerance**: fully viable for at least 1 week. **Altitude**: 890–950 m a.s.l. **Geology**: Mesozoic dolomite. **Phenology**: II, IV–V, X (probably throughout the year, long-lived).

Taxonomic remarks. *Orbilia crenatovinosa* is characterized by apothecia with a concave disc and distinctly dentate-crenulate margin, in combination with a spore shape similar to *O. vinosa*, and tear-shaped SBs as in *O. aprilis*. Spore length is between these two common species, and spore width somewhat below, while the glassy processes of *O. vinosa*, *O. aprilis* and the Australian *O. nothoaprilis* are never as long as in *O. crenatovinosa* and, therefore, the apothecia never so prominently dentate. The Australian *O. astrovinosa* differs in more vermiform SBs of double or triple length, and usually much longer glassy processes being inwards curved by forming more discrete teeth. *O. aprilis* and *O. astrovinosa* differ also in always lacking crystalloid SCBs.

Anamorph. More or less strongly curved phragmoconidia were observed on the natural substrate in two collections (Pl. 288: 2d, 3c). However, the two collections differ in conidial width and number of septa. Regrettably, in the culture of G.F. 20160008 no conidia developed.

Phylogeny. Sequences were gained from apothecia and an ascospore isolate of two topotypes which comprise S1506 intron, ITS, and LSU. In the intron 1 nt differs between the two strains, while the ITS and overlapping part of LSU (D1–D4) are identical, except for 3 gaps in the ITS2. In analyses of ITS and ITS+LSU, *O. crenatovinosa* clustered in a highly supported clade with *O. aprilis* (Phyls 9, 11), while in the intron and LSU only with medium support (S12, S13). To *O. aprilis* it shows a distance of 9.7 % (ITS), 3.8–4 % (LSU), and 10 % (intron), while to *O. vinosa*/*O. subvinosa* the distance is 19–22 %, 7–7.3 % and 18–19 %, respectively.

Ecology. *O. crenatovinosa* was several times found on rotten wood of xeric or semihygric branches and stubs of *Pinus* and *Picea* in montane, ± mixed forests (*Pinus sylvestris*, *Picea abies*, *Fagus sylvatica*, *Abies alba*, *Juniperus communis* etc.), see Friebes (2017: 36, fig. 27a–c, as *Orbilia* sp.). The two localities are on very calcareous soil in the subcontinental, orotemperate humid eastern Alps of central Europe. The type locality is a west-exposed slope of a valley with abundant *Cypripedium*, the other place is at the top of a crest.

Specimens included. **AUSTRIA**: **Steiermark**, 20 km NNW of Bruck an der Mur, 3 km NNW of St. Ilgen, Karlschütt, 890 m, branch of *Pinus sylvestris*, on wood, 24.X.2009, G. Friebes (ex H.B. 9247, M-0276463, **holotype**). – ibid., 10.V.2014, G. Friebes (G.M. 2014-05-10.1, anam. substr., doc. vid.; sq.: KT380085). – ibid., branches of *P. sylvestris*, on wood, 20.II.2016, G. Friebes (G.F. 20160008, anam. substr., doc. vid.; sq.: KY419189). – **Kärnten**, 15 km S of Klagenfurt, 5.5 km SE of Ferlach, Waidisch, 950 m, branch of *P. sylvestris*, on wood, 9.IV.2016, G. Friebes (G.F. 20160092, doc. vid.). – ibid., branch of *Picea abies*, on wood, 9.IV.2016, G. Friebes (G.F. 20160093, doc. vid.).

Orbilia aprilis Velen., Opera Bot. Čech. 4: 102 (1947) — Pls 289–291, Map 49

= *Trinacrium tothii* Magyar, in Magyar & Révay, Nova Hedwigia 87: 514, figs 1–57 (2008)

Etymology: *aprilis*: named after the month when the holotype was collected; *tothii*: in honour of the Hungarian mycologist Sándor Tóth.

Typification: Czechia, Mnichovice, branch of *Corylus avellana*, 28.IV.1941, J. Velenovský (PRM 152434, holotype of ***O. aprilis***); Luxembourg, Bettembourg, branch of ?*Rhamnus*, 20.X.2000, G. Marson (ex H.B. 6801, M-0291762, epitype, designated here, MBT385114, CBS 116278; sq.: KT215268). — Hungary, Tolnau, Szekszárd, *Elaeagnus angustifolia*, 12.XI.2007, D. Magyar (BP 99770, holotype of ***Trinacrium tothii***).

Misapplied names: Rehm (1891: 455, p.p. ?*O. aprilis*), as *O. luteorubella*; Svrček (1954: 9), as *O. vinosa*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.8(–1)((–1.4)) mm diam., 0.1–0.2(–0.23) mm high (receptacle 0.07–0.12 mm), (pale to) light (to bright) (orange-)rose to rose-red or rose-pink, also yellowish-ochraceous to orange, medium translucent, round, scattered to mostly ± gregarious; disc slightly concave to flat, margin ± thin, 0–15 µm protruding, smooth or mostly finely rough to crenulate; broadly sessile, sometimes with a ± distinct hidden stipe 0.02–0.09 × 0.15–0.4 mm, superficial or immersed in algal layer; dry light to bright orange-rose to apricot, slightly contracted. **Asci** *(35–)38–58(–61) × (4–)4.3–5.2(–5.5) µm {15}, †(28–)33–50(–56) × (3.5–)4–4.5(–5)((–5.8)) µm {11}, 8-spored, spores 3–4-seriate, (1–)2–4(–5) lower spores inversely oriented {27} (not or sometimes strongly mixed), pars sporifera *14–23 → 13–16 µm long; **apex** (†) hemispherical to slightly (rarely medium) truncate, dome †0.8–1.8 → 0.4–1.3 µm thick {6}, with or without apical chamber; **base** with short to very long, ± thin, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *((5.5–))(6–)6.5–9.5(–10.5) × (1.5–)1.6–2(–2.2)((–2.4)) µm {72}, †6.2–9 × (1.2–)1.4–1.7(–2) µm {4}, fusoid-clavate, rarely subcylindrical, apex rounded to obtuse, sometimes subacute, base mostly slightly to strongly attenuated (rarely tail-like), straight, sometimes slightly curved near base; **SBs** *((1.2–))1.5–2.2(–2.5)((–2.7)) × (0.3–)0.4–0.8(–0.9) µm {67}, tear-shaped, pyriform-ampulliform, or subulate to rod-shaped, apically narrowed to a small to wide point, with or without a very short filum. **Paraphyses** apically uninflated, sometimes slightly (rarely medium) clavate-capitate, exceptionally spathulate, terminal cells *(5–)7–16 × (1.7–)2–2.7(–3) µm {7}, †8–16 × 2–3 µm {T}, lower cells *(2–)4–10(–12) × 1.8–2.6 µm {5}, †5–7 × 1.7–2.2 µm {T}; never branched near apex; hymenium pale rose. **Medullary excipulum**, 30–80(–100) µm thick, of medium loose or dense textura intricata with many inflated cells, medium to sharply delimited. **Ectal excipulum** pale rose, of ± thin-walled, vertically (or irregularly) oriented t. globulosa-angularis(-prismatica) from base to submargin, 20–60(–110) µm thick near base, cells *(6–)9–20(–25) × (4–)6–13(–17) µm {9}; 10–30(–40) µm thick at flanks and margin, inner part of t. prismatica-angularis oriented at a 45–80° angle to the surface, cells *6–8 × (2–)3–5(–7) µm {2}, outer part of t. porrecta oriented at 10–40(–80)°, marginal cortical cells *6–15 × 2–4(–5) µm {8}, †6–12 × 2–3 µm {2}, **glassy processes** ± absent {8} or present {48}, (0–)1–10(–12) × (2–)2.5–3.5(–4.5) µm {23}, refractive, slightly to strongly stratified, cortical cells somewhat protruding to form 0–1-septate hairs up to 12–18 µm long, agglutinated to form small teeth (8–18 × 15–30 µm) or radial ribs at the margin. **Anchoring hyphae** sparse to medium abundant, *1.5–3 µm wide, walls 0.2–0.3 µm thick {4}, sometimes forming a dense t. intricata up to 20 µm thick. **SCBs** globose to ellipsoid {35}, in paraphyses 1.5–2.5 µm diam., in excipular cells 1–2.5 µm. **Exudate** over paraphyses (0.5–)1–2(–3) µm thick, pale yellowish-chlorinaceous, broken into clods, loosely attached; over margin and flanks (1–)2–6(–10) µm thick, coarsely rough, pale to light golden- or honey-yellow, ± firmly attached to glassy processes, also covering them as a thin layer. — **ANAMORPH**: trinacrium-like (from ascospore isolate {2} and natural substrate {17}). **Conidiophores** *~(2–)14–18 × (1.2–)1.8–2.2 µm. **Conidiogenous cells** monoblastic or sympodial. **Conidia** Y-shaped, total size *19–33 × (12.5–)15–24(–26) µm, stipe *12–21 × 4–5.2 µm, 2–4-septate, arms cylindrical with rounded to obtuse ends, not or only slightly tapered, *7–13 × (3–)3.5–

4.7 µm, 1–3(–4)-septate {7}; unbranched conidia rarely seen (both in pure culture and on natural substrate), straight, *25.5–35 × 3.3–4.8 µm, 5–7-septate {2}.

Habitat: collected (0–)1–3(–8)((–20)) m above the ground, ± corticated or often decorticated, (4–)10–65(–100) mm thick branches (rarely up to 35 cm thick trunks) of *Acer* sp. {2}, *A. campestre* {1}, *A. platanoides* {1}, *Alnus glutinosa* {3}, *Betula* sp. {1}, *B. pubescens* {1}, *Buxus sempervirens* {2}, *Calicotome villosa* {1}, *Carpinus betulus* {5}, *Castanea sativa* {10}, *Ceratonia siliqua* {1}, *Clematis vitalba* {6}, *Cornus mas* {1}, *Corylus avellana* {10}, *Crataegus* sp. {1}, *C. laevigata* {2}, *C. monogyna* {2}, *Elaeagnus angustifolia* {1}, *Erica arborea* {1}, *E. scoparia* {3}, *Fagus orientalis* {1}, *F. sylvatica* {8}, *Frangula alnus* {4}, *Ilex aquifolium* {4}, *Juglans regia* {1}, *Laburnum anagyroides* {1}, *Ligustrum vulgare* {2}, *Malus domestica* {1}, *Picea abies* {10}, *P. orientalis* {1}, *Pinus pinaster* {1}, *P. radiata* {1}, *P. sylvestris* {6}, *Pistacia lentiscus* {1}, *Populus tremula* {1}, *Prunus* sp. {1}, *P. avium* {4}, *P. domestica* {1}, *P. spinosa* {3}, *Pseudotsuga menziesii* {1}, ?*Pyrus communis* {1}, *Quercus* sp. {24}, *Q. cerris* {1}, *Q. petraea* {2}, *Q.* ?*pubescens* {1}, *Q. robur* {27/1}, *Q. rubra* {1}, *Rhamnus* sp. {1}, *R. cathartica* {1}, *Rhododendron ponticum* {1}, *Robinia pseudoacacia* {10}, *Rosaceae* {1}, *Rubus grandifolius* {1}, *Salix* sp. {7/1}, *S. caprea* {7}, *S. cinerea* × *aurita* {1}, *S. cinerea* {3/1}, *S. fragilis* {1}, *Sambucus nigra* {5}, *S. racemosa* {2}, *Sequoiadendron giganteum* {1}, *Sorbus aucuparia* {3}, *S. torminalis* {1}, *Spartium junceum* {1}, *Syringa reticulata* {1}, *S. vulgaris* {1}, *Tamarix anglica* {3}, *Taxus baccata* {1}, *Thuja occidentalis* {1}, *T. plicata* {1}, *Tilia* sp. {2}, *Ulex europaeus* {3}, *U. minor* {1}, *Ulmus* sp. {3}, on 0.1–3 mm deep (or even deeper) strongly (rarely slightly to medium) decayed wood {202}, sometimes on bark (bast) {30}, sapwood sometimes strongly eroded or removed, heartwood then either undecayed or white-rotten, sometimes in old beetle galleries or on inner surface or edges of detached bark, slightly to strongly greyed, very sparsely to often densely covered by green algae. **Associated**: *Agyrium roseum* {1}, *Amandinea punctata* {1}, *Arachnopeziza aurata* {1}, *Arthonia crozalsiana* {1}, *Capitotricha bicolor* {1}, *Capronia* sp. {1}, ?*Ceratosphaeria* sp. {1}, ?*Chaetosphaeria* sp. {1}, *C. myriocarpa* {2}, *Chalara inflatipes* {1}, ?*Ciliolarina* sp. {1}, *Coenogonium pineti* {1}, *Cryptodiscus foveolaris* {6}, *C. pallidus* {1}, *Dacrymyces* sp. {6}, ?*Durella* sp. {1}, *D. atrocyanea* {5}, *D. connivens* {19}, *Evernia prunastri* {1}, *Exarmidium inclusum* {1}, *Helicogonium orbiliarum* (parasitic in *O. aprilis*) {1}, '*Helotium*' *uvidulum* {3}, *Hyalorbilia fusispora* {1}, *H. juliae* {2}, *H. subfusispora* {3/1}, *Hyaloscypha minuta*/*intacta* {7}, *H. quercicola* {1}, *Hyphodontia* sp. {3}, *Hysterium pulicare* {2}, *Hysterobrevium smilacis* {2/1}, ?*Hysteropatella* sp. {1}, *Lecanora conizaeoides* {1}, *Minimelanolocus hughesii* {1}, *Mollisia* sp. {2}, *M. ligni* {13}, *M.* ?*melaleuca* {3}, *Nemania confluens* {2}, *Neodasyscypha cerina* {1}, *Orbilia alpigena* {1}, *O. aristata* {1}, *O. cylindrospora* {1}, *O. eucalypti* {7}, *O. euonymi* {7}, *O. hesperidea* {3}, *O. microsoma* {1}, *O. montigena* {1}, *O. pleiomicrosoma* {1}, *O. pleistoeuonymi* {3}, *O, polyspora* {1}, *O. subclavuliformis* {1}, *O. subulivinosa* {1}, *O. trapeziformis* {1}, *O.* ?*tremulae* {1}, *O. vibrioides* {1}, *O. vinosa* {22}, *Parmelia sulcata* {2}, ?*Phoma* sp. {1}, *Phragmiticola* sp. {1}, *Physcia* sp. {1}, *Polydesmia pruinosa* {1}, *Proliferodiscus pulveraceus* {3}, *Propolis farinosa* {4}, *P. viridis* {2}, *Pyrenopeziza* ?*coriariae* {1}, *Resupinatus applicatus* {3}, *Rhamphoria pyriformis* {1}, *Rhizodiscina lignyota* {1}, *Strossmayeria basitricha* {1}, *Symbiotaphrina microtheca* {1}, *Trichonectria* sp. {1}, *T. hirta* {1}, '*Tympanis*' *xylophila* {1/2}, *Unguiculariopsis* sp. {1}, crustose lichens, indet pyrenomycetes {2}. **Desiccation tolerance**: fully viable for at least 3 weeks, some mature asci still alive after 2 months, excipular cells and ascospores even after 22 months, conidia and conidiophores after 1.5 months (see also Magyar & Révay 2008). **Altitude**: 1–1083 m (northern and central Europe), 8–1400 m (southern Europe), -8–1415 m a.s.l. (eastern Europe). **Geology**: Ordovician-Devonian-Carboniferous lime-, sand-, silt- & mudstone, shale, quartz, greywacke, Permian (Rotliegend, Zechstein), Buntsandstein, Muschelkalk, Keuper-Jurassic -Cretaceous marl, clay, sand- & limestone, flysch, Tertiary molasse & limestone, Quaternary loess, moraine, till & sand; granite, migmatite, quartz diorite, porphyry, andesite, diabase, biotite-amphibole, gneiss, mica schist. **Phenology**: throughout the year (long-lived).

Phenology of *O. aprilis*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
11	11	15	31	35	26	10	23	19	15	15	18

Taxonomic remarks. *Orbilia aprilis* is characterized by rather small and narrow, fusoid-clavate ascospores with small, tear- to rod-shaped SBs. The closely related *O. vinosa*, with which *O. aprilis* might have been confused in the past, is sharply delimited by much longer spores and SBs, with (9.5–)10 µm and (3–)3.5 µm as minimum length, respectively. The measurements do not even overlap in almost all of the many collections studied. Further differences exist in the anamorph (see below). For the similar Australian *O. nothoaprilis* (p. 640) and *O. crenatovinosa* (p. 643) see there.

O. aprilis may also have been confused with species of section *Helicoon* because of a similar spore size and shape, e.g., by Rehm (1891). Section *Helicoon* differs in truncate thin-walled ascus apices, often capitate paraphyses, and a hygric to semiaquatic habitat. The European *O. luteorubella*, *O. rosea*, and *O. sarraziniana* have a similar spore size and shape as *O. aprilis* but differ in much longer, ± filiform spore bodies. Many members of section *Helicoon* have long, filiform SBs, but others from that section (*O. hoana*, *O. juruensis*, *O. yuanensis*), or *O. bannaensis* from section *Aurantiorubrae*, have rather short and thick SBs similar to *O. aprilis*.

Variation. *O. aprilis* is an easily recognizable species that shows little micromorphological variability. Ascus and spore measurements but also SB size varied to some extent among the collections [e.g., spore width between *1.5–1.7 and *1.8–1.2(–2.4) µm). Especially spore and SB length shows much less variation compared to *O. vinosa*. The short glassy processes on the cortical excipular cells, which provoke a crenulate appearance to the apothecial margin, are quite characteristic though not always present. A mediterranean collection (on *Spartium*, Pl. 291: 1) was only studied in the dead state; it deviates in a thick apothecial margin and in spores with ± distinct tails (†7–9 × 1.7–1.9 µm). However, tails were rarely also seen in some spores of other collections, e.g., Pl. 289: 8.

Type studies. The holotype of *O. aprilis* contains a corticated branch with five minute apothecia seated on very rotten, greyed, algae-covered xeric wood at the cross-cut end. The protologue says 'ad truncum sectum *Carpini betuli*', but the microanatomy of the wood clearly refers to *Corylus*. The inhabited substrate was apparently a young trunk which has been cut near the bottom some years before the apothecia developed.

Svrček (1954: 9) observed in the scanty type material only immature asci without spores. He assumed that Velenovský's report of 3–5 µm long, ellipsoid, eguttulate spores was erroneous, and that *O. aprilis* was a not fully developed *O. vinosa.* In the present examination of the largest apothecium a single nearly mature ascus with 6 visible spores (7–8 × 1.7 µm) was found. Though the ascus was apparently not fully mature, these spores appeared to have already attained their final size which would exclude *O. vinosa*. The asci showed an extraordinary width (4.5–5.5 µm), perhaps due to slight artificial flattening. Based on the mentioned ascospore size we here adopt Velenovský's taxon for this overlooked though very common and distinctive species.

In order to emphasize this interpretation, we here designate a collection from Luxembourg on *Rhamnus* (ex

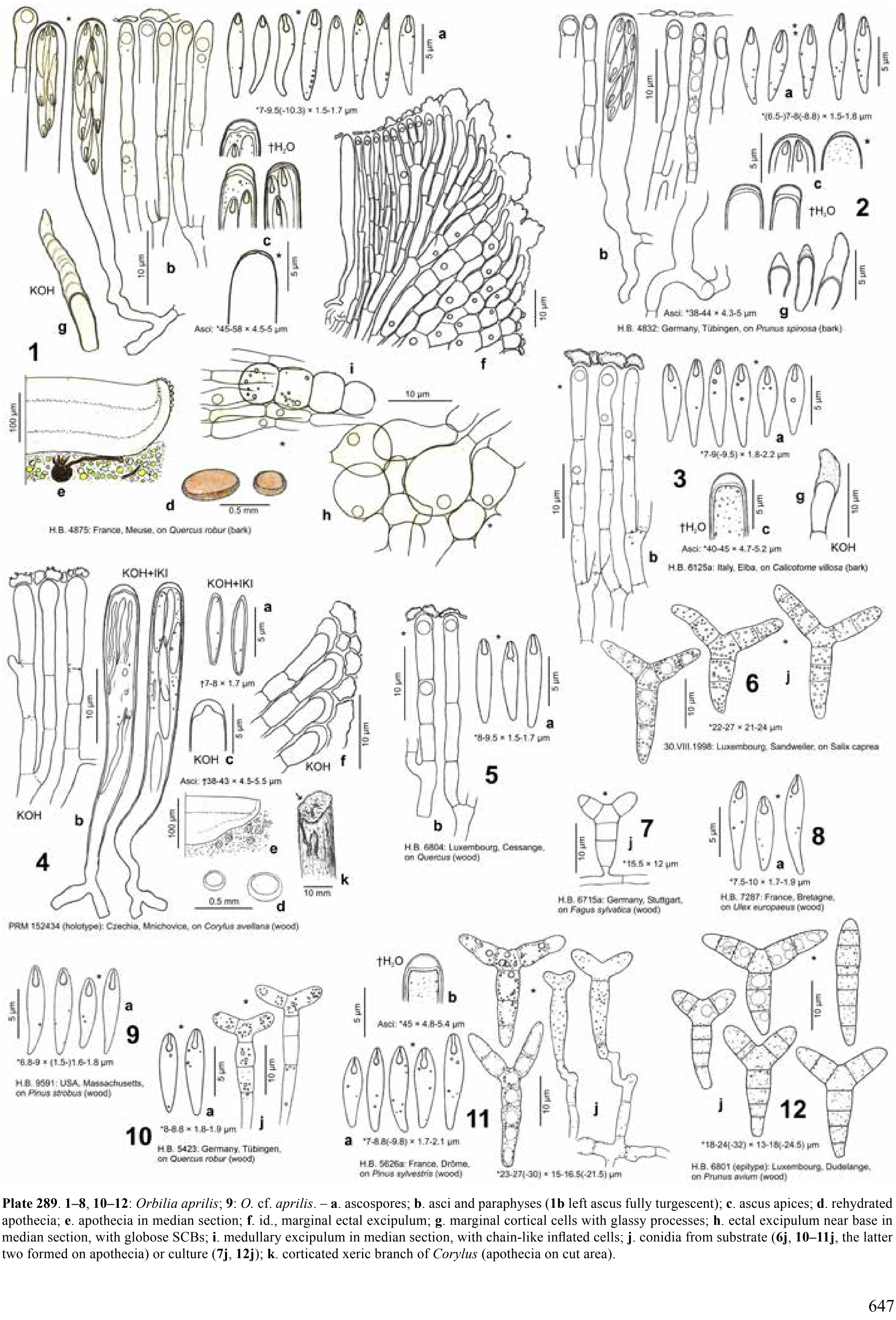


Plate 289. **1–8**, **10–12**: *Orbilia aprilis*; **9**: *O.* cf. *aprilis*. – **a**. ascospores; **b**. asci and paraphyses (**1b** left ascus fully turgescent); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., marginal ectal excipulum; **g**. marginal cortical cells with glassy processes; **h**. ectal excipulum near base in median section, with globose SCBs; **i**. medullary excipulum in median section, with chain-like inflated cells; **j**. conidia from substrate (**6j**, **10–11j**, the latter two formed on apothecia) or culture (**7j**, **12j**); **k**. corticated xeric branch of *Corylus* (apothecia on cut area).

Plate 290. **1–16**: *Orbilia aprilis*. – **1a**. rich mixed oak forest, dead xeric branch of *Quercus robur*; **1b–d**, **2a–b**, **3a**, **4**, **5a–b**, **7**, **9a–b**, **10a**. rehydrated apothecia (**10a**: with *Mollisia* sp. and empty insect eggs); **2c**, **3b**. apothecia in median section; **2d**. id., marginal ectal excipulum; **6**. margin in external view, agglutinated cortical cells; **8**. apothecium with marginal teeth in top view; **1e**, **10b**, **12a**. asci; **12b**, **14–16**. ascospores. – Living state (**1e** fully turgescent), except for asci in **10b**, **12a**, **13b** (in H_2O), **11** (in CRB), **13a** (in CR_{SDS}). – **5a–b**, **10a–b**: phot. P. Perz, **12a–b**, **13a–b**, **15**: phot. M. Bemmann. — **1a–e**. H.B. 8525: Denmark, Sjælland, on *Quercus*; **2a–d**. H.B. 8149: France, Orleans, on *Quercus*; **3a–b**. H.B. 7858a: Germany, Amberg, on *Salix*; **4**. 20.VI.2004: Germany, Tübingen, on *Juglans*;

H.B. 6801, CBS 116278; sq.: KT215268) as **epitype** of *O. aprilis* (Pl. 289: 12).

Not included collections. Two samples from Massachusetts (on *Pinus*, Pl. 289: 9; on indet angiosperm, IVV: bhi-F628a) match perfectly European *O. aprilis*. Because available sequence data of the angiosperm sample markedly differ from typical *O. aprilis* and suggest a deviating cryptic taxon (see below), we refrained from including any North American records in the description. A sample from Texas on *Quercus* (IVV: H.B. 6202) was only studied in the dead state; it deviates in a thin-walled, sometimes slightly truncate ascus apex, therefore, its resemblance with *O. aprilis* is perhaps only superficial.

Anamorph. The conidia of *O. aprilis* closely resemble those of *O. vinosa*, differing only in shorter arms and stipes with fewer septa. This anamorph concurs very well with the protologue of *Trinacrium tothii* (see Pl. 22: a), a taxon being recently described from a conidial isolate derived from colonies between layers of detaching xeric bark of *Elaeagnus angustifolia* in Hungary (Magyar & Révay 2008). Previous records were reported from stemflow samples from different tree species in Hungary (Gönczöl & Révay 2004, fig. 5; 2006, figs 49–50).

In the ex-type cultures of *T. tothii* (on CMA) apart from the Y-shaped conidia also unbranched conidia were formed, especially when permanently flooded with water. The conidia from culture were identical with those on the natural substrate, according to Magyar & Révay (l.c.). The size of the Y-shaped conidia were given as (12–)17–22(–31) × 8.7–16.7(–20) µm, with a 2.7–3.6(–5) µm wide stipe [10–20(–29) × (2.3–)2.7–4(–4.5) µm according to scale], and arms of 2.5–7.5 × (2–)2.3–2.7(–4) µm [(2.5–)4–8.5 × 2.3–3.8 µm according to scale]. This is distinctly smaller compared to our measurements of living conidia: the width of the stipe and the size of the arms overlaps only slightly. However, these measurements were made in CB_L (D. Magyar pers. comm.), which explains the smaller size to a certain degree. The phragmoconidia better fit, their smaller size in the protologue being easily be explained by the shrinking effect in CB_L.

Phylogeny. Sequences were gained from pure cultures of two samples (H.B. 6801 from Bettembourg, epitype; H.B. 6715a from Stuttgart), comprising SSU (V7–V8), S1506 intron, ITS, and LSU (D1–D2). They are of equal length (1901 nt) while a sequence from apothecia (G.M. 2017-07-30.1, Hovelange) covers S943 intron and V6 of SSU until D5 of LSU. In the SSU they are identical while 1–2 nt differ in the S1506 intron as well as in the ITS, and 0–1 nt differ in the LSU.

In spite of a strong morphological similarity, the distance between *O. aprilis* and *O. vinosa* is very high: ITS 21–22.5%, intron 18.5–19.5%, and LSU (D1–D2) 7.5% (0.3% in SSU). In phylogenetic analyses of SSU+ITS+LSU, ITS+LSU, ITS, intron, or LSU, (Phyls 7, 9–11, S12, S13), *O. aprilis* rarely clustered near *O. vinosa* (e.g., in Baral et al. 2017b) but is usually found unresolved within section *Hemiorbilia* in a clade of its own (here called *aprilis-crenatovinosa* clade). *O. aprilis* and *O. crenatovinosa* are always associated with medium or strong support (see under the latter species, p. 645). The also very similar *O. nothoaprilis* clustered in the *vinosa-velutina* clade.

From one of the North American collections from Massachusetts referable to *O. aprilis* (IVV: bhi-F628a) a sequence was gained (S1506 intron and ITS) which deviates from *O. aprilis* by 1.6–1.9% in the ITS and 3.3–3.8% in the intron, therefore, it might belong to a separate cryptic species without obvious morphological differences in the available teleomorph.

There exists an apparently confused or contaminated culture from South Africa (CBS 12521, allotype of *Metschnikowia proteae*, *Saccharomycetales*), the unofficial ITS sequence of which shows a 1.8–2% distance to *O. aprilis* (2.5% in the intron), whereas LSU sequences of the holotype culture (CBS 12522, type) in GenBank concur with those of CBS 12521 in the CBS database and cluster with *Saccharomycetales*.

Our trials to gain a sequence from the type culture of *Trinacrium tothii* failed, as it turned out to be contaminated by a *Cordycipitaceae*.

Ecology. Like *O. vinosa*, *O. aprilis* belongs to the most frequently collected species of *Orbilia* on xeric woody substrates in temperate regions of Europe. A total of 228 samples have been recorded, 153 of them examined by the first author and 79 by others. The species occurs widespread throughout atlantic, central, eastern, and southern Europe. It was also recorded in western Russia, the Caucasus mountain range, and western Anatolia. Although frequently investigated by mycologists, records from Spain and boreal parts of Scandinavia are so far wanting, and only one for Switzerland and Italy, and two for Croatia are known. Missing records in various other countries are probably only a matter of sparse collecting.

O. aprilis was mainly collected in atlantic to continental, cold- to warm-temperate humid regions of western and central Europe in thermophilous or more shady forests and shrubs. The ecological preferences are very similar to *O. vinosa*, including both calcareous and acidic geology, but *O. aprilis* appear to avoid altimontane (orotemperate) regions of central Europe. Its presence in the hemi- to thermoboreal zone is only known at present for northwestern Russia. Further records include mesosub- and mesomediterranean semihumid (more rarely orosub- to suprasubmediterranean) areas in southern Europe, the warm-continental subhumid steppic Caspian Volga floodplain, and supramediterranean semihumid western Anatolia. The few not included extra-European samples that came to our notice were from cold-temperate humid forests in northeastern North America and from a warm-temperate subhumid shrubland of *Quercus virginiana* and *Juniperus occidentalis* in the south of Northern America.

O. aprilis inhabits rotten, periodically dry wood, sometimes bark, of xeric branches of a very wide range of angiosperm but also gymnosperm trees and shrubs. The most favoured host genus in our collections was *Quercus* {57}, followed by *Salix* {21}, *Picea* (11), *Castanea* {10}, *Corylus* {10}, *Robinia* {10}, *Pinus* {8}, *Fagus* {9}, and *Prunus* {9}. The fact that *O. aprilis* could not be found in the consulted herbaria, apart from the sparse immature holotype, illustrates how seriously xeric substrate was neglected by collectors.

In concordance with the epithet, our phenological data suggest a maximum in April–June, but this is merely a result of more intense collecting activities during annual ascomycete

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5a–b. P.P. 20061211: Poland, Kłodzko, on *Betula*; **6**. H.B. 7733: Luxembourg, Berchem, on *Salix*; **7**. H.B. 8455c: Luxembourg, Mensdorf, on *Quercus*; **8**. 26.VI.2005: Germany, Ravensburg, on *Acer*; **9a–b**. H.B. 8147: France, Orleans, on *Pinus*; **10a–b**. P.P. 20061219: Poland, Kłodzko, on *Quercus*; **11**. 15.XII.2011: Germany, Sonneberg, on *Salix*; **12a–b**. 21.VIII.2010: Germany, Heidelberg, on *Robinia*; **13**. 15.I.2012: ibid., on *Acer*; **14**. H.B. 7859: Germany, Amberg, on *Betula*; **15**. 18.VII.2010: Germany, Heidelberg, on *Quercus*; **16**. H.B. 9188: Czechia, Beroun, on *Quercus*.

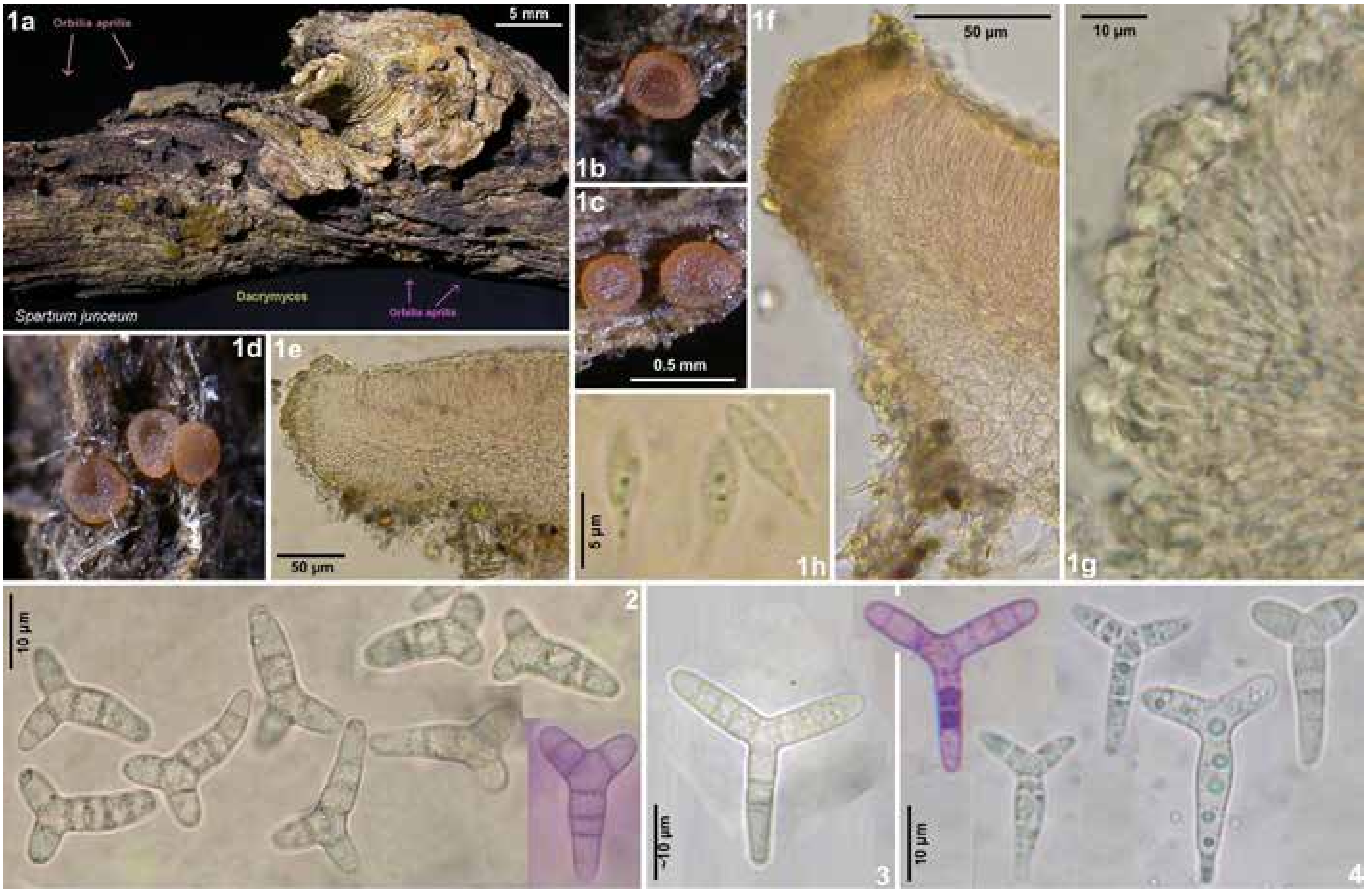


Plate 291. **1–4**: *Orbilia aprilis*. – **1a**. decorticated xeric branch of *Spartium junceum*; 1b–d. rehydrated apothecia; **1e–f**. apothecia in median section; **1f**. id., marginal ectal excipulum; **1g**. ascospores; **2**, **3**, **4**. conidia from culture (**2**) or substrate (**3–4**), partly stained by CRB. – Living state, except for **1e**, **g–h** (in KOH), **1f** (in H_2O), **4** (2 conidia and 1–2 cells in the living conidia). — **1a–g**. H.B. 6468c: France, Narbonne, on *Spartium*; **2**. H.B. 6715a: Germany, Stuttgart, on *Fagus*; **3**. 22.X.2002: Luxembourg, Waldhaff, on *Sequoiadendron*; **4**. H.B. 9237b: Poland, Kłodzko, on *Quercus*.

forays which are commonly held in spring. Indeed, mature apothecia occur all over the year and persist for several months.

Specimens included. **GREAT BRITAIN**: **Yorkshire**, **South Yorkshire**, 11 km E of Doncaster, 1.8 km SSE of Lindholme, Hatfield Moor, 1 m, branch of *Sambucus nigra*, on wood, 17.V.2011, H.O. Baral (ø). – 17 km ESE of Sheffield, 1.2 km SE of South Anston, Anston Stones Wood, 100 m, twig of *Taxus baccata*, on wood, 16.V.2011, H.O. Baral (ø). – ibid., 1.5 km SE of South Anston, 95 m, branches of *Salix*, on wood, 16.V.2011, H.O. Baral (ø). – 8 km NNW of Barnsley, 6.5 km S of Wakefield, Seckar Wood, 75 m, branch of *Salix* (?)*cinerea*, on wood, 19.V.2011, H.O. Baral (ø). – 3.5 km S of Barnsley, 1.3 km SW of Worsbrough, Worsbrough Country Park, 70 m, branch of *S. cinerea*, on wood, 20.V.2011, H.O. Baral & T. Læssøe (ø). – ibid., branch of *Crataegus laevigata*, on wood (ø). – 4 km SW of Barnsley, W of Wentworth Castle, Stainborough Park, 195 m, branch of *Rhododendron ponticum*, on wood, 15.V.2011, H.O. Baral (ø). – ibid., 185 m, branch of *Ilex aquifolium*, on wood & bark, 14.V.2011, H.O. Baral & P. Cannon (H.B. 9508a ø). – 7.5 km NNW of Sheffield, 1.3 km NW of Grenoside, Wharncliffe Wood, 260 m, branch of *Sorbus aucuparia*, on wood & bark, 18.V.2011, H. Voglmayr & H.O. Baral (ø). – ibid., 245 m, branch of *Quercus petraea*, on wood, 18.V.2011, H.O. Baral (ø). – ibid., 220 m, trunk of *Fagus sylvatica*, on bark, 18.V.2011, H.O. Baral (ø). – 1 km WNW of Grenoside, Greno Wood, 240 m, branches of *Ilex aquifolium*, on wood, 18.V.2011, H.O. Baral (H.B. 9521 ø). – **East England**, **Norfolk**, East Anglia, Broadland, Norfolk, TG 34.06, 11 km ESE of Norwich, 1.3 km SE of Brundall, Strumpshaw Fen, 4 m, branch of *Salix cinerea*, on wood, 25.IX.2004, E. Batten (E.B. 4563, K(M) 227427, doc. vid.). – **Suffolk**, 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Ulex europaeus*, on bark, 3.I.2004, S.M. Francis & E. Batten (E.B. 4471, K(M) 227401, doc. vid.). – ibid., on wood, 23.VIII.2005, E. Batten (ø, doc. vid.). – 5.7 km NNE of Leiston, Minsmere, 0.6 km NNE of Scott's Hall, 10 m, branch of *Corylus avellana*, on wood, 10.VII.2004, E. Batten (E.B. 4538, K(M) 227415, doc. vid.). – ibid., 0.2 km N of Scott's Hall, 15 m, branch of *Ulex minor*, on wood, 23.IX.2005, E. Batten (E.B. 4630, K(M) 227413, doc. vid.). – **Cambridgeshire**, 8 km WNW of Peterborough, 1.5 km NE of Upton, 45 m, branch of *Crataegus monogyna*, on wood, 16.IV.2017, H.O. Baral (ø). – 16 km NE of Cambridge, WSW of Wicken, Wicken Fen, 4 m, branch of *Rhamnus cathartica*, on wood, 21.IV.2017, H.O. Baral (ø, anam. substr.). – **Bedfordshire**, 14 km ESE of Bedford, 2.5 km SE of Sandy, Sandy Warren, 53 m, branch of *Pinus sylvestris*, on wood, 19.IV.2017, H.O. Baral (ø). – ibid., 70 m, branch of *Quercus robur*, on wood, 19.IV.2017, H.O. Baral (ø). — **NETHERLANDS**: **Flevoland**, 18 km WSW of Meppel, 1.9 km ENE of Kraggenburg, Waterloopbos, 5 m, branch of *Corylus avellana*, on wood, 13.X.2007, S. Helleman (S.H. 457, non vid.). – 6 km SW of Kampen, 9 km E of Dronten, Reve Abbert, Revebos, 9 m, branch of *Robinia pseudoacacia*, on wood, 20.III.2005, H.O. Baral (ø). – **Zeeland**, 7 km NE of Middelburg, 1.5 km E of Veere, Haringvreter island, 5 m, branch of *Ulmus*, on wood, 27.X.2010, S. Helleman (ø, non vid.). – **Noord-Brabant**, 1 km W of Boxmeer, Brestbos, 18 m, branch of *Frangula alnus*, on wood, 24.XI.2007, S. Helleman (S.H. 463, non vid.). – 10 km WSW of Boxmeer, 3.3 km WSW of Oploo, St. Anthonisbos, 30 m, trunk of *Thuja occidentalis*, on bark, 19.III.2011, S. Helleman (S.H. 692, doc. vid.). – 5 km E of Boxmeer, NE of Afferden, Quin, 18 m, branch of *Quercus*, on wood, 1.IV.2007, S. Helleman (S.H. 435, non vid.). — **SWEDEN**: **Skåne**, 3 km SE of Helsingborg, Birkagatan, 45 m, branch of *Ligustrum vulgare*, on wood & bark, 7.VI.2006, H.O. Baral (ø). — **DENMARK**, **Nordjylland**, 8 km NW of Brovst, 3 km WNW of Tranum, S of Naturcenter Fosdalen, 6 m, branch of ?*Salix*, on wood, 14.V.2005, H.O. Baral (ø). – ibid., branch of *Crataegus laevigata*, on wood, 14.V.2005, H.O. Baral & F. Baral-Weber (ø). – 24 km NNW of Aalborg, 7 km NNE of Aabybro, Store Vildmose, 6 m, branch of *Salix*, on wood, 16.V.2005, H.O. Baral (ø). – **Sjælland**, 9 km SW of København, Avedøre, Rudbølvej, 4 m, branch of *Syringa vulgaris*, on wood, 2.VI.2006, H.O. Baral (ø). – 5.5 km NW of Sorø, SE of Bromme, Lillesø, 35 m, branch of *Frangula alnus*, on wood, 27.V.2007, H.O. Baral (ø). – 2.5 km SE of Sorø, 1.3 km NE of Frederiksberg, NNW of Kristiansminde, 45 m, branch of *Quercus robur*, on wood, 28.V.2007, H.O. Baral (H.B. 8525 ø, S). – 2.7 km SE of Sorø, 1.3 km NE of Frederiksberg, Kristiansminde, 45 m, branch of *Salix aurita* × *cinerea*, on wood, 24.V.2007, H.O. Baral (ø). – 8 km NNW of Ringsted, 1 km S of Allindelille, Fredskov, 65 m, branch of *Corylus avellana*, on wood, 26.V.2007, H.O. Baral (K(M) 147739). – **Falster**, 11 km WNW of Nørre Alslev, 4 km W of Vålse, Resle Skov, 14 m, branch of *C. avellana*, on wood, 16.V.2006, J.G.B. Nielsen (J.G.B. 06-026, 06-046). — **GERMANY**: **Niedersachsen**, Harz, 3.3 km ESE of Bad Sachsa, SW of Walkenried, W of Hollenteiche, 300 m, branch of *Fagus sylvatica*, on wood,

Map 49. Known distribution of *O. aprilis* in Europe and eastern Asia (Turkey).

24.V.2012, S. Helleman (ø, non vid.). – ibid., branch of *Carpinus betulus*, on wood, 24.V.2012, S. Helleman (ø, non vid.). – NW of Walkenried, Monchwald, 295 m, trunk of *Quercus*, on wood, 23.V.2012, S. Helleman (ø, non vid.). – **Mecklenburg-Vorpommern**, 2 km NW of Rehna, Löwitzer Holz, 20 m, branch of *Quercus robur*, on wood, 26.XII.2014, T. Richter (T.R. 315/14, doc. vid.). – **Sachsen**, 15 km W of Niesky, 2.5 km WNW of Wartha, Gleinsche Heide, 164 m, branches of *Pinus sylvestris*, on wood, 21.IX.2018, H.O. Baral (ø). – 0.6 km SW of Wartha, Guttauer Teiche, 162 m, branch of *Quercus*, on wood, 20.IX.2018, H.O. Baral (H.B. 10176b ø). – ibid., branch of *Carpinus betulus*, on wood (ø). – **Thüringen**, 2.7 km NW of Sonneberg, 1.4 km N of Bettelhecken, 485 m, branch of *Picea abies*, on wood, 15.XII.2011, I. Wagner (ø, doc. vid.). – 1 km NNW of Sonneberg, Wehd, 480 m, branch of *Corylus avellana*, on wood, 8.I.2013, I. Wagner (ø, doc. vid.). ibid., branch of *Sambucus nigra*, on wood, 29.XII.2015, I. Wagner (ø, doc. vid.). – 3 km SE of Sonneberg, 1 km SE of Oberlind, Alte Ziegeleiteiche, 370 m, branch of *Salix*, on wood, 2.I.2009, P. Püwert & I. Wagner (ø, doc. vid.). – 3 km SSW of Saalfeld, 1.5 km NNE of Eyba, 552 m, branch of *Picea abies*, on wood, 10.VIII.2009, S. Helleman (ø, non vid.). – 4 km WSW of Weida, 1.9 km ENE of Rohna, WSW of Schömberg, 343 m, branch of *Quercus*, on wood, 28.VIII.2010, M. Bemmann (ø, doc. vid.). – **Hessen**, Westerwald, 1.3 km E of Breitscheid, 0.8 km SW of Erdbach, Erdbachschlucht, 380 m, branch of *Robinia pseudoacacia*, on wood, 2.V.2000, H.O. Baral (ø). – ibid., branch of *Clematis vitalba*, on wood, 2.V.2000, H.O. Baral (L.K.). – Oberes Lahntal, 21 km NW of Marburg, NW of Biedenkopf, Schlossberg, south-slope, 350 m, branch of *Robinia pseudoacacia*, on bark, 30.IV.2000, H.O. Baral & L.G. Krieglsteiner (ø). – **Rheinland-Pfalz**, Pfälzer Wald, 15 km WNW of Landau, 5 km NW of Annweiler, 1.3 km NW of Rinnthal, 208 m, branch of *Tilia*, on bark, 27.VI.2002, G. Marson (ø). – 14 km SE of Pirmasens, SE of Dahn, military cemetery, 250 m, branches of *Salix caprea*, on wood, 2.X.1994, H.O. Baral & G. Marson (ø). – **Saarland**, Hunsrück, 15 km W of Idar-Oberstein, 7.7 km NW of Birkenfeld, NE of Thranenweier, Riedbruch, 582 m, branch of *Rosaceae*, on wood, 16.IV.2004, H. Aeberhard (ø). – Saarluis, 7 km S of Merzig, NW of Eimersdorf, Heiligenkopf, 310 m, branches of *Acer campestre*, on wood, 18.IV.2004, H.O. Baral (ø). – ibid., N of Heiligenkopf, 337 m, branch of *Fagus sylvatica*, on wood & bark, 18.IV.2004, H.O. Baral (H.B. 7513a). – **Baden-Württemberg**, 6.5 km NNE of Heidelberg, 1.3 km NE of Dossenheim, 248 m, branch of *Salix cinerea*, on wood, 15.I.2012, M. Bemmann (ø, doc. vid.). – 7 km E of Heidelberg, 1.5 km SE of Ziegelhausen, Bärenbach, 150 m, branch of *Quercus*, on wood, 18.VII.2010, M. Bemmann (ø, doc. vid.). – ibid., branch of *Robinia pseudoacacia*, on wood, 21.VIII.2010, M. Bemmann (ø). – ibid., 175 m, branch of *Prunus avium*, on wood, 30.IX.2010, M. Bemmann (ø, doc. vid.). – ibid., E of Bärenbach, 163 m, branch of *Castanea sativa*, on wood, 25.VI.2011, M. Bemmann (ø, doc. vid., anam. substr.). – ibid., branch of *Quercus rubra*, on wood, 19.XI.2011, M. Bemmann (ø, doc. vid.). – 5.5 km NW of **Stuttgart**, 1.3 km S of Weilimdorf, E of Wolfbusch, cemetery, 360 m, branch of *Fagus sylvatica*, on wood, 25.VI.2000, H.O. Baral (H.B. 6715a, CBS 116277, anam. cult., anam. substr.; sq.: KT215267). – 1.8 km S of Weilimdorf, Neue Burg Dischingen, 405 m, branch of *Tilia*, on wood, 18.V.1997, H.O. Baral (ø). – 1.4 km SE of Weilimdorf, Rainweg, 350 m, branch of *Prunus spinosa*, on wood, 18.V.1997, H.O. Baral (ø). – Schönbuch, 6 km WSW of **Tübingen**, 1 km WNW of Hirschau, south of Wurmlinger Kapelle, 400 m, branch of *Prunus avium*, on wood, 3.X.2001, H.O. Baral (ø). – 0.7 km WSW of Tübingen, W of Schloss Hohentübingen, 360 m, branch of *Crataegus monogyna*, on wood, 20.X.2002, E. Weber (ø). – centre of Tübingen, Old Botanical Garden, 330 m, branches of *Syringa reticulata*, on wood, 30.VI.2003, D. Hewitt & H.O. Baral (ø). – 3 km NNW of Tübingen, N of Morgenstelle, Heuberg, 490 m, branch of *Salix caprea*, on wood, 5.IX.2003, H.O. Baral (ø). – GERMANY: Baden-Württemberg, SW of Morgenstelle, Steinenberg, 475 m, branch of *Juglans regia*, on wood, 20.VI.2004, H.O. Baral (ø). – 8 km NNW of Tübingen, 4 km NW of Bebenhausen, Steiniger Weg, 500 m, branch of *Quercus*, on wood, 1.V.2002, H.O. Baral (ø). – 3.7 km NE of Tübingen, 1.8 km W of Pfrondorf, Hägnach, 350 m, branch of *Picea abies*, on wood, 27.II.2000, H.O. Baral (ø). – ibid., branch of *Pinus sylvestris*, on wood, 26.III.2017, E. Weber (ø). – 1.5 km NW of Pfrondorf, N of Sophienpflege, 460 m, branch of *Prunus spinosa*, on bark, 23.I.1993, H.O. Baral (H.B. 4832b). – 1.7 km N of Pfrondorf, E of Zeitungseiche, 460 m, branch of *Ligustrum vulgare*, on wood, 30.I.2000, H.O. Baral (ø). – 2 km SE of Pfrondorf, Hinterpfand, 370 m, branch of *Quercus robur*, on wood, 10.III.2002, H.O. Baral (ø). – ibid., branch of *Acer*, on wood (ø). – ibid., branch of *Picea abies*, on wood, 29.I.2005, H.O. Baral (ø). – 1 km SE of Pfrondorf, Rauhalde, 380 m, branch of *Quercus*, on wood, 30.XI.2003, H.O. Baral (ø). – ibid., 345 m, branch of *Robinia pseudoacacia*, on wood, 1.II.2004, H.O. Baral (ø). – 1 km ESE of Pfrondorf, Tiefenbach, 375 m, branch of *Quercus*, on wood, 21.XI.2006, E. Weber (ø). – ibid., branch of *Alnus glutinosa*, on wood, 26.XI.2006, H.O. Baral (ø). – 0.6 km E of Pfrondorf, S of Einsiedlersteg, 385 m, trunk of *Quercus*, on bark, 17.XII.1997, H.O. Baral (ø). – ibid., 410 m, branch of *Q. robur*, on wood, 2.II.1996, H.O. Baral (H.B. 5406a). – ibid., 1.III.1996 (H.B. 5423, anam. substr.). – ibid., 28.III.1996 (H.B. 5435a). – ibid., 4.VI.1999 (ø). – ibid., 16.XII.2005 (ø). – ibid., branch of *Fagus sylvatica*, on wood, 29.VI.1997, H.O. Baral (ø). – 7.X.2007 (ø). – ibid., 26.VII.2009 (H.B. 9104 ø). – E of Einsiedlersteg, 420 m, branch of *Quercus*, on wood, 29.VI.1997, H.O. Baral & G. Marson (ø). – ibid., Stangenhölzlesklinge, 430 m, branch of *Sambucus nigra*, on wood, 26.XI.2005, H.O. Baral (ø). – **Schwäbische Alb**, 8 km W of Münsingen, 1.5 km N of Gomadingen, Eichach, 765 m, branch of *Quercus robur*, on wood, 25.II.1994, H.O. Baral (ø). – 3 km SE of Urach, 1 km W of Wittlingen, Gehöft Hohenwittlingen, 680 m, branch of *Prunus domestica*, on wood, 16.III.2003, F. Baral-Weber & H.O. Baral (ø). – **Oberschwaben**, 7 km SSE of Bad Saulgau, 3 km NW of Altshausen, NW of Hirschegg, 635 m, branch of *Acer*, on wood, 26.VI.2005, G. Marson (ø). – ibid., branch of *Quercus*, on wood, 26.VI.2005, G. Marson (ø). – **Bayern**, **Unterfranken**, Spessart, 35 km NW of Würzburg, Gemünden/Main, S of Scherenburg, 185 m, branch of *Quercus robur*, on wood, 15.II.2004, H.O. Baral (ø). – 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz, 260 m, branches of *Robinia pseudoacacia*, on wood, 11.XI.1995, H.O. Baral & L.G. Krieglsteiner (H.B. 5369, Krieglsteiner 1999: 272, as 10.XI., *Orbilia* sp. 2). – 8.5 km NW of Würzburg, 2.5 km NW of Güntersleben, Edelmannswald, 320 m, branch of *Corylus avellana*, on wood, 4.III.1995, L.G. Krieglsteiner (L.K.). – **Oberpfalz**, Oberpfälzisches Hügelland, 12 km NNE of Amberg, 1.5 km W of Hirschau, W of Moosweiher, 420 m, branch of *Betula pubescens*, on wood, 3.VIII.2005, H.O. Baral (H.B. 7859 ø). – ibid., Moosweiher, 415 m, branch of *Quercus robur*, on wood, 30.XII.2003, H.O. Baral (H.B. 7449b ø). – 2 km NW of Hirschau, Ziegelschlag, 450 m, branch of *Salix caprea*, on wood, 2.VIII.2005, H.O. Baral (H.B. 7858a). – 1.3 km NW of Hirschau, Eschenbach, 445 m, branch of *Pinus sylvestris*, on wood, 11.VIII.2002, H.O. Baral (H.B. 7190, anam. substr.). – ibid., branch of *Quercus* (?)*robur*, on wood, 30.VII.1995, H.O. Baral (H.B. 5310a). – ibid., Eschenbach-Teiche, 440 m, branch of *Quercus robur*, on bark, 8.VIII.1993, H.O. Baral (H.B. 4930). – Oberpfälzer Wald, 16 km NE of Cham, 1.5 km NW of Furth im Wald, E of Schloss Voithenberg, 520 m, branch of *Salix caprea*, on wood, 5.VIII.2005, H.O. Baral (ø). – **Oberbayern**, Starnberger See, 9 km S of Feldafing, 1 km ESE of Bernried, 600 m, branch of *Quercus*, on wood, 10.XI.2012, P. Karasch, vid. B. Fellmann (ø, doc. vid.). – 11 km NW of München, 1 km NE of Allach, Allacher Forst, Waldkolonie, 505 m, branch of *Quercus*, on wood, 11.VI.1999, L. Beenken (H.B. 6392). – Fünfseenland, 8 km NW of Tutzing, 3.5 km S of Andechs, Goaslweide, 720 m, branch of *Q. robur*, on wood, 4.I.2003, P. Karasch (H.B. 7263). – 6 km NNW of Bad Reichenhall, 1.2 km WSW of Aufham, Bichlweg, 680 m, branch of *Picea abies*, on wood, 13.VIII.2018, H.O. Baral (ø). – ibid., branch of *Salix*, on wood, E. Weber, vid. H.O. Baral (H.B. 10172 ø). – 2.8 km SW of Aufham, Steineralm, 1083 m, branch of *Picea abies*, on wood, 12.VIII.2018, H.O. Baral (H.B. 10170c ø). –– **SWITZERLAND**: **Uri**, Urner Alpen, 22 km ESE of Luzern, 1.2 km S of Seelisberg, SW of Treib, 455 m, branch of *Salix*, on wood, 18.VIII.2006, H.O. Baral (H.B. 8246, anam. substr.). –– **AUSTRIA**: **Wien**, 7.5 km NW of Wien, 2 km NW of Grinzing, Cobenzl, 400 m, branch of *Prunus avium*, on wood, 11.II.1995, W. Jaklitsch (ø). – **Steiermark**, 3 km NNW of Graz, NW of Reinerkogel, 440 m, branch of *Quercus*, on bark, 17.III.2013, G. Friebes (G.F. 20130037, doc. vid.). – 17 km NNW of Graz, 1.7 km W of Semriach, Römergrab, 865 m, branch of *Clematis vitalba*, on wood, 26.IX.2013, G. Friebes (G.F. 20130165, doc. vid.). – 4.5 km NNW of Gratwein, 3.5 km WSW of Unterfriesach, N of Hörgasgraben, base of Kaschlsteig, 673 m, branch of *Picea abies*, on wood, 9.XII.2017, G. Friebes (GJO 88899, doc. vid.). – **Kärnten**, 13 km SE of Klagenfurt, ENE of St. Margareten im Rosental, 575 m, branch of *Alnus glutinosa*, on bark & wood, 21.XII.1994, W. Jaklitsch (ø). –– **LUXEMBOURG**: **L'Oesling**, **Diekirch**, 7.5 km N of Ettelbruck, SE of Lipperscheid, Gringlee, 330 m, trunk of *Quercus*, on wood, 6.VI.1993, G.

Marson (H.B. 4898). – 3.3 km NNW of Diekirch, 2.2 km W of Tomm, NE of Fridhaff, Hooldaer, 365 m, branch of *Salix*, on wood, 23.IV.1995, H.O. Baral (ø). – **Gutland**, **Diekirch**, 3.5 km E of Diekirch, 1.7 km SW of Bettendorf, Schoofsboesch, Carrières de Gilsdorf, 313 m, branch of *Salix caprea*, on wood, 26.IV.1994, G. Marson & H.O. Baral (ø). – ibid., branch of *Clematis vitalba*, on bark (H.B. 5064). – ibid., branch of *C. vitalba*, on wood, 8.VII.2001, G. Marson (G.M.). – **Mersch**, **Luxembourg Plateau**, 8 km NW of Mersch, 1.6 km E of Schrondweiler, Bakes, 305 m, branch of *Robinia pseudoacacia*, on wood, 6. XI.1993, G. Marson (ø). – 8 km NE of Mersch, E of Nommern, W of Këngerboesch, 403 m, branch of *Sorbus aucuparia*, on wood, 23.IV.1994, H.O. Baral (ø). – 9.5 km NE of Mersch, 2 km NW of Medernach, Seitert, 330 m, branch of *Quercus robur*, on wood, 24.IV.1994, H.O. Baral & G. Marson (ø). – ibid., branch of *R. pseudoacacia*, on wood, 24.IV.1994, G. Marson & H.O. Baral (ø). – **Redange**, 5.5 km SSE of Redange, SSE of Hovelange, Haard, 355 m, branches of *Frangula alnus*, on wood, 30.VII.2017, G. Marson (G.M. 2017-07-30.1; sq.: MK493153). – **Echternach**, Petite Suisse, 4.7 km WSW of Echternach, 1.7 km N of Scheidgen, Deisterbaach, 325 m, branch of *Frangula alnus*, 1.II.2003, G. Marson (ø). – Luxembourg Plateau, 18.5 km NE of Luxembourg, NW of Graulinster, Marscherwald, 400 m, trunk of *Fagus sylvatica*, on bark, 9. VI.2004, G. Marson (ø). – **Grevenmacher**, 12 km ESE of Mersch, 1 km NE of Junglinster, Bichel, 340 m, branch of *Sambucus racemosa*, on wood, 8.V.2001, G. Marson (ø). – 15 km ENE of Luxembourg, 1.5 km NE of Mensdorf, Widdebierg, 380 m, branch of *Quercus*, on wood, 5.III.2007, G. Marson (H.B. 8455c ø). – Valée de Moselle, 8 km NW of Grevenmacher, 2.2 km WNW of Biwer, Breinert, 270 m, branch of *Sorbus torminalis*, on wood, 27.II.2000, G. Marson (ø). – 3.5 km N of Grevenmacher, 1.7 km ENE of Manternach, Valley of Syre, WNW of Fielsmillen, 185 m, branch of *Acer platanoides*, on wood, 16. XI.1993, G. Marson (H.B. 5005b). – 1.8 km NW of Mertert, Schlammbaach, 180 m, branch of *Sorbus aucuparia*, on wood, 24.IV.1995, G. Marson (ø). – **Remich**, Valée de Moselle, 13 km SE of Luxembourg, 1.8 km SSW of Filsdorf, Filsdorfergrund, 255 m, branch of *Robinia pseudoacacia*, on wood, 5.X.1997, G. Marson (H.B. 5921). – **Luxembourg**, Luxembourg Plateau, 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, branch of *Quercus*, on wood, 7.X.2000, G. Marson (H.B. 6804 ø). – 5.5 km NNW of Luxembourg, 1.5 km E of Bridel, Plakigebierg, 280 m, branch of *Sambucus nigra*, on wood, 1.III.1998, G. Marson (H.B. 6072b). – ibid., 260 m, branches of *Sambucus nigra*, on wood & bark, 3.VI.2004, G. Marson (ø, anam. substr.). – ibid., branch of *Picea abies*, on wood, 3.VI.2004, G. Marson (ø). – 5 km S of Luxembourg, 1.5 km W of Hesperange, Biersak/Géisselbierg, 290 m, branch of *Corylus avellana*, on wood, 2.II.2000, G. Marson (ø). – 6 km NE of Luxembourg, SE of Waldhaff, Gréngewald, Arboretum, 410 m, branches of *Sequoiadendron giganteum*, on wood & bark, 22.XII.2002, G. Marson (ø, anam. substr.). – ibid., branch of *Pseudotsuga menziesii*, on wood, 20.VIII.2009, G. Marson (ø). – 10.5 km NE of Luxembourg, 1.2 km W of Ernster, Wuurzelwis, 350 m, branch of *Fagus sylvatica*, on wood, 22.X.2000, G. Marson (ø, anam. substr.). – ibid., trunk of *F. sylvatica*, on bark, 12.IX.2004, G. Marson (ø). – 7.5 km E of Luxembourg, 1.2 km ENE of Sandweiler, Neimillen, 305 m, branch of *Salix caprea*, 30.VIII.1998, G. Marson (ø, anam. substr.). – 11 km ESE of Luxembourg, 2 km E of Oetrange, Draf, 268 m, branch of *Sambucus racemosa*, on bark & wood, 4.IX.1998, G. Marson (H.B. 6240a). – **Esch-sur-Alzette**, **Terres rouges**, 9 km WNW of Esch-sur-Alzette, 2 km W of Differdange, Tillebierg, 412 m, branch of *Corylus avellana*, on wood, 5.V.1999, H.O. Baral (ø). – ibid., branch of *Clematis vitalba*, on wood, 5.V.1999, H.O. Baral (ø). – 5.5 km E of Pétange, 2 km S of Schouweiler, Héierchen, Jongeboesch, 337 m, branch of *Quercus robur*, on wood, 6.V.1999, H.O. Baral (ø). – 2.3 km SSE of Dudelange, Gënzebierg, ~387 m, branch of *C. vitalba*, on wood, 14.IV.2002, G. Marson (ø). – 2 km NNE of Dudelange, 1.5 km S of Bettembourg, train station, 275 m, branch of *Rhamnus*, on wood, 20.X.2000, G. Marson (ex H.B. 6801, M-0291762, **epitype**, CBS 116278, anam. cult.; sq.: KT215268). – 7 km S of Luxembourg, 1.5 km NW of Berchem, Angelsbierg (SE of Kockelscheier), 295 m, trunks of *Thuja plicata*, on bark & wood, 19.III.2005, G. Marson (H.B. 7733). — **FRANCE**: **Bretagne**, **Morbihan**, 3 km S of Baud, 1.2 km W of Camors, Etang du Petit Bois, 75 m, branch of *Ilex aquifolium*, on wood, 23.X.2004, J.P. Priou (J.P.P. 24171, non vid.). – 21 km SE of Vannes, 2.3 km E of Ambon, Kerlann, 13 m, branch of *Erica scoparia*, on wood, 13.XII.2009, J.P. Priou (J.P.P. 29240, non vid.). – 12 km S of Auray, 1.5 km SW of Locmariaquer, SE of St.-Pierre Lopérec, Breneguy, 2 m, branch of *Tamarix anglica*, on wood, 29.XII.2003, J.P. Priou & A. Delannoy (J.P.P. 23154, non vid.). – ibid., 14.XI.2004, J.P. Priou (J.P.P. 24239, doc. vid.). – 9.5 km SE of Malestroit, 2.7 km WNW of St.-Martin-sur-Oust, Beauvais, 8 m, branch of *Pinus radiata*, on wood, 14.I.2004, J.P. Priou (J.P.P. 24024, non vid.). – 8 km N of Carentoir, 1.7 km S of Guer, Pont de l'Oyon, 40 m, branch of *Quercus*, on wood, 18.XII.2003, J.P. Priou (ø, non vid.). – 11 km W of La Gacilly, 3 km NW of St.-Martin-sur-Oust, ENE of Les Gaudines de Haut, 63 m, branches of *Castanea sativa*, on wood, 6.XII.2003, J.P. Priou (J.P.P. 23122, 23119, doc. vid.). – 0.5 km WSW of La Gacilly, Rue du Menhir, Menhir la Roche Piquée, 30 m, branch of *C. sativa*, on wood, 7.VI.2003, H.O. Baral (ø). – 1 km WNW of La Gacilly, rue de Picardie (= Gazo) (Le Quellec), 38 m, branch of *Ulex europaeus*, on wood, 27.I.2003, J.P. Priou (H.B. 7287 ø, J.P.P. 2308). – ibid., La Glouzie, 45 m, branch of *C. sativa*, on wood, 11.VI.2003, J.P. Priou (ø). – 1.3 km SE of La Gacilly, 1.6 km NW of Cournon, Château de la Ville Janvier, 37 m, branch of *C. sativa*, on wood, 7.VI.2003, H.O. Baral (ø). – 1.8 km ESE of La Gacilly, 1.4 km NNW of Cournon, 350 m N of Le Brossay, Moulin de Coq, 80 m, branch of *Quercus*, on wood, ~12.XII.2003, J.P. Priou (J.P.P. 23127, non vid.). – **Ille-et-Vilaine**, 0.5 km E of La Gacilly, SE of Ville Neuve, 35 m, branch of *C. sativa*, on wood, 10.VI.2003, H.O. Baral (ø). – 10 km SW of Rennes, 2.2 km NNW of Bruz, Bois de Cicé, 31 m, branch of *Populus tremula*, on wood, 15.X.2004, J.P. Priou (J.P.P. 24161, non vid.). – **Pays-de-la-Loire**, **Vendée**, 21 km SSW of La Roche-sur-Yon, 2.3 km NNW of Avrillé, Bois de la Garde, 35 m, branch of *Ilex aquifolium*, on wood, 5.VI.2003, H.O. Baral (ø). – **Poitou-Charentes**, **Charente-Maritime**, Île de Ré, 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, branch of *Pinus pinaster*, on wood, 26.IV.2006, H.O. Baral (ø). – ibid., branch of *Tamarix anglica*, on wood (ø). – **Deux-Sèvres**, 13.5 km N of Melle, 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 100 m, branch of *Castanea sativa*, on wood, 17.IV.2008, S. Helleman (H.B. 8818 ø). – 1.8 km S of Fonfreroux, Forêt de L'Hermitain, 180 m, branch of *C. sativa*, on wood, 27.IV.2006, H.O. Baral, G. Marson & F. Valade (H.B. 8182 ø). – ibid., branch of *C. sativa*, on wood, 27.IV.2006, (ø). – **Aquitaine**, **Gironde**, 12 km SW of Royan, 1.5 km NE of Soulac-sur-Mer, Tourterelles, 20 m, twig of *Erica scoparia*, 19.XI.2011, J.P. Priou (J.P.P. 11209, non vid.). – 6 km SSW of Soulac-sur-Mer, Arrière dune, 12 m, twig of *E. scoparia*, on wood, 20.XI.2011, J.P. Priou (J.P.P. 11208, doc. vid.). – **Midi-Pyrénées**, **Ariège**, 16.5 km ENE of St.-Girons, NE of Castelnau-Durban, les Mouns, 450 m, branch of *Robinia pseudoacacia*, on wood, 26.X.2011, J.P. Priou (H.B. 9621b ø, J.P.P. 11160). – **Centre**, **Eure-et-Loire**, 23 km NNW of Orleans, 1.3 km NE of Poupry, Le Aire Héron Cendré, 125 m, branch of *Ulmus*, on wood, 12.IV.2008, S. Helleman & H.O. Baral (ø). – **Loiret**, 28 km E of Orleans, 6.7 km NE of Châteauneuf-sur-Loire, la Charbonnières, 128 m, branch of *Quercus robur*, on wood, 29.IV.2006, G. Marson & H.O. Baral (H.B. 8149). – 9 km NE of Châteauneuf-sur-Loire, les Six Routes, 132 m, branch of *Pinus sylvestris*, on wood, 29.IV.2006, H.O. Baral (H.B. 8147 ø). – **Loir-et-Cher**, 40 km NE of Tours, 1.5 km WNW of Herbault, Aire de la Chatière, 123 m, branch of *Carpinus betulus*, on wood, 22.IV.2006, H.O. Baral (ø, anam. substr.). – ibid., branch of *Prunus avium*, on wood (ø). – **Île-de-France**, **Yvelines**, 20 km NW of Paris, 2.8 km NW of Maisons-Laffitte, SE of Pavillon de la Muette, 50 m, branch of *P. spinosa*, on wood, 2.I.2004, J.P. Priou (J.P.P. 24004, non vid.). – **Essonne**, 36 km SW of Paris, 1.2 km NW of Angervilliers, forêt d'Angervilliers, 135 m, branch of *Carpinus betulus*, on wood, 1.V.2008, F. Valade (doc. vid.). – **Lorraine**, **Meuse**, Lorraine, 6 km E of St.-Dizier, 1 km NE of Ancerville, 205 m, branch of *Quercus robur*, on bark, 10.V.1993, H.O. Baral (H.B. 4875). **Bourgogne**, **Côte-d'Or**, 13 km SW of Dijon, 1.8 km WSW of Gevrey-Chambertin, Combe Lavaux, 350 m, branch of *Buxus sempervirens*, on bark & wood, 13.IV.2008, A. Gardiennet (H.B. 8828 ø). – **Rhône-Alpes**, **Drôme**, 48 km SW of Grenoble, 8.3 km N of Die, 2.5 km SW of Col de Rousset, 1250 m, branch of *Laburnum anagyroides*, on wood, 22. VIII.2000, G. Marson (H.B. 7158c, ø). – 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branch of *Pinus sylvestris*, on wood, 23.VIII.1996, G. Marson (H.B. 5626a, anam. substr.). – **Provence-Alpes-Côte d'Azur**, **Var**, 10 km W of Cogolin, 5 km NW of Gorbière, SW of Capelude, 380 m, branch of *Erica arborea*, on wood, 4.IX.2017, G. Marson (G.M. 2017-09-04.6, H.B. 10140b, anam. substr.). – **Alpes Maritimes**, 33 km ENE of Digne-les-Bains, 0.7 km E of Colmars-les-Alpes, 5 km W of Col des Champs, 1400 m, branch of *Buxus sempervirens*, on wood, 9.VI.2010, J.P. Priou (J.P.P. 10143 ø, non vid.). – **Languedoc-Roussillon**, **Gard**, 10 km WNW of St.-Jean-du-Gard, 2.3 km N of Saumane, 500 m, branch of *Castanea sativa*, on wood, 25.IX.1993, G. Marson (H.B. 4995a). – **Aude**, 15 km SSW of Narbonne, 3.7 km NNW of Sigean, Reserve africaine, 9 m, branch of *Spartium junceum*, on wood, 21.IX.1999, H.O. Baral (H.B. 6468c). — **ITALY**: **Toscana**, **Livorno**, Isola d'Elba, 4.5 km WNW of Portoferraio, Capo d'Enfola, 40 m, branch of *Calicotome villosa*, on bark, 23.IV.1998, D. Triebel & G. Rambold G.R. 6229 (M-0229702, H.B. 6125a ø). — **POLAND**: **Greater Poland**, 9 km WSW of Śrem, 2 km ENE of Rąbiń, Uroszysko Rąbiń, 103 m, branch of *Quercus*, 25.VIII.2007, A. Kujawa & P. Perz (P.P. 20070825-4-Kuja, doc. vid., anam. substr.). – **Lower Silesia**, 5 km SE of Kudowa Zdrój, W of Lewin Kłodzki, 437 m, branch of *Crataegus*, 10.III.2006, P. Perz (ø, doc. vid.). – 12 km NNW of Kłodzko, 3 km SE of Słupiec, ENE of Koszyn, 500 m, branch of *Quercus*, on wood, 3.VIII.2006, P. Perz (P.P. 20060803-2, doc. vid.). – ibid., branch of *Betula*, on bark, 11.XII.2006, P. Perz (P.P. 20061211-2, doc. vid.). – 3.3 km ENE of Kłodzko, S of Wojciechowice, hotel Kukulka, 420 m, branch of *Quercus*, on wood, 19.XII.2006, P. Perz (P.P. 20061219-3, doc. vid., anam. substr.). – 12 km SE of Kłodzko, S of Skrzynka, 430 m, on wood of *Malus domestica*, 6.XII.2006, P. Perz (P.P. 20061206-1, doc. vid., anam. substr.). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, branch of *Corylus avellana*, on wood, 16.IV.2006, P. Perz (P.P. 20060416-1, doc. vid.). – ibid., branch of *Q. robur*, on wood, 27.XII.2009,

A. Perz (H.B. 9237b, P.P. 20091227-2b). — **CZECHIA**: **Central Bohemia**, 6.3 km ESE of Beroun, 2.8 km NW of Karlštejn, Velká hora, 380 m, branch of *Cornus mas*, on wood, 22.IX.2009, H.O. Baral (H.B. 9187a). – ibid., branch of *Q. pubescens*, on wood, 22.IX.2009, H.O. Baral (H.B. 9188 ø, PRM). – 8 km ESE of Beroun, 1 km NNW of Karlštejn, Dub sedmi bratři, 300 m, branch of *Salix*, on wood, 22.IX.2009, H.O. Baral & M. Chlebická (H.B. 9190b). – ~1.5 km ENE of Mnichovice, Myšlín, 400 m, branch of *Corylus avellana*, on wood, 28.IV.1941, J. Velenovský (PRM 152434, **holotype** of *O. aprilis*, as *Carpinus*, H.B. 6053 ø). — **SLOVAKIA**: **Banská Bystrica**, 8.8 km S of Banská Štiavnica, 2.8 km NNW of Prenčov, 436 m, branch of ?*Pyrus communis*, on wood, 27.IV.2018, A. Polhorský (A.P. 18/42, doc. vid.). – **Bratislava**, 10.5 km WNW of Bratislava, 1.1 km N of Devín, Sandberg, 285 m, branch of *Ulmus*, on wood, 15.VI. 2018, A. Polhorský (A.P. 18/58, doc. vid.). – 10 km SE of Bratislava, 4.8 km S of Podunajské Biskupice, Topol'ové hony, 130 m, log of *Quercus*, on wood, 1.VI.2019, A. Polhorský (ø, non vid.). — **HUNGARY**, **Budapest**, Danube-Ipoly National Park, 42 km NNW of Budapest, 5 km NNE of Szob, 2 km E of Márianosztra, 260 m, branch of *Quercus cerris*, on wood, 15.X.1999, L. Beenken (H.B. 6512a). – **Tolna**, 10 km SSW of Tolna, Szekszárd, centre of town, 92 m, *Elaeagnus angustifolia*, on bark, 12.XI.2007, D. Magyar (BP 99770, **holotype** of *Trinacrium tothii*, conid. isol., culture T51, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 17 km SW of Novi Sad, 6.5 km WSW of Beočin, Testera, 165 m, branch of *Alnus glutinosa*, on bark, 28.II.2014, D. Savić (FG-355, doc. vid.). – 12.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, SW of WWII memorial, 506 m, branch of *Prunus*, on bark, 21.II.2019, D. Savić (FG-1003, doc. vid.). – 15.5 km SW of Novi Sad, Orlovac, 470 m, branch of *Quercus petraea*, on wood, 19.VII.2019, D. Savić (doc. vid.). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 2.5 km W of Korčula, NW of Žrnovska Banja, N of Vrbovica, 8 m, branch of *Ceratonia siliqua*, on wood, 6.VI.2000, H.O. Baral (ø). – ibid., branch of *Pistacia lentiscus*, on wood, 16.VIII.2000, N. Matočec (CNF 2/4605, doc. vid.). — **TURKEY**: **Marmara**, **Balıkesir**, 28 km N of Balıkesir, 1.2 km W of Hisaralan, 250 m, branch of *Fagus orientalis*, on bark, 15.XI.2003, T. Askun (T.A. 67, anam. substr., doc. vid.). — **RUSSIA (West)**: **Novgorod**, **Valday**, 51 km SW of Borovichi, 16.5 km N of Valday, Krasnaja Gorka, 245 m, branch of *Quercus robur*, on wood, 22.IX.2011, E.S. Popov (LE 247100, non vid.). – 12 km WSW of Valday, 4.5 km W of Seredeya, Poddubye, 225 m, branch of *Q. robur*, on wood, 22.IX.2011, E.S. Popov (LE 247949, non vid.). – ibid., twig of *Picea abies*, on wood, 22.IX.2011, E.S. Popov (LE 247946, non vid.). – **Cholm**, 11.5 km SSE of Cholm, SE of Balutino, 72 m, branch of *Q. robur*, on wood, 5.V.2011, E.S. Popov (LE 247945, non vid.). – **Pskov**, **Loknya**, 52 km NW of Velikiye Luki, 18 km NE of Pustoschka, Ivantsevo, 205 m, twig of *Salix fragilis*, on wood, 13.VIII.2011, E.S. Popov (LE 247498, ESP-11-0047, non vid.). – ibid., branch of *Q. robur*, on wood, 24. VII.2011, E.S. Popov (ø, doc. vid.). – 42 km NW of Velikiye Luki, 9.5 km N of Nasva, NW of Bashovo, 140 m, twig of *S. caprea*, on wood, 28.VII.2011, E.S. Popov (LE 247571, ESP-11-0010, non vid.). – ibid., 4 km W of Samolukovo, 160 m, branch of *Q. robur*, on wood, 20.VII.2011, E.S. Popov (ø, doc. vid.). – **Bryansk**, **Suzemka**, Bryanskiy Les, 95 km SSW of Bryansk, 14 km SSE of Trubchevsk, WNW of Chukhrai, Nerussa River, 141 m, trunk of *Q. robur*, on wood, 22.X.2012, E.S. Popov (LE 274939, doc. vid.). – **Volgograd**, **Svetly Yar**, Volga-Akhtuba floodplain, 35 km SE of Volgograd, 12 km NE of Svetly Yar, SE of Utinoye lake, -8 m, twig of *Q. robur*, on wood, 21.IX.2012, E.S. Popov (LE 248352, doc. vid.). – **Karachayevo-Cherkesiya**, Caucasus Mts., 95 km SSW of Tscherkessk, 6 km SSW of Teberda, 1415 m, twig of *Picea orientalis*, on wood, 19.VIII.2012, E.S. Popov (LE 247948, non vid.).

Not included. **USA**: **Massachusetts**, 30 km WNW of Boston, 4.5 km SSW of West Concord, Maynard-Sudbury, 61 m, twig of *Pinus strobus*, on wood, 8.VIII.2011, U. Graf (H.B. 9591). – 16 km SE of Boston, 3.5 km NNE of Hingham, Slate Island, 2 m, branch of indet. angiosperm, on wood, 21.III.2017, A.C. Dirks & L.A. Kappler, vid. L. Quijada (bhi-F628a; sq.: MF161307). – **Texas**, Oaks and Prairies, 65 km W of Austin, ~2 km WSW of Johnson City, 378 m, branch of *Quercus virginiana*, on wood, 18.VI.1996, G. Marson (H.B. 6202).

Orbilia myriofusiclava Baral & G. Marson, **sp. nov.**, MB 813533 — Pls 292–293, Map 50

Etymology: referring to the 64-spored asci and the fusoid-clavate spores.

Typification: Western Australia, Northampton, branches of *Acacia*, 9.XII.2001, G. Marson (ex H.B. 7237a, MEL 2389232, holotype; CBS 116224; sq.: KT215274).

Latin diagnosis: *Apothecia rehydratata 0.3–1.3 mm diam., vivide aurantiaca, sessilia vel substipitata, margine subaspera vel minute crenulata. Asci 64-spori, apice in statu emortuo hemisphaerico, crassitunicato. Ascosporae *5–10.5 × 2–2.7 µm, fusoideo-clavatae, apice obtusae ad acutae, basi plerumque valde attenuatae, leniter ad valde curvatae, corpusculum refringens pyriformem, ad apicem affixum continentes. Cellulae vivae excipuli marginalis et paraphysium corpuscula crystalloidea hyalina vel pallide aurantiaca, et globosa continentes. Habitat ad corticem leniter vel valde putridum ramorum* Acaciae *et* Jacksoniae *in zona subtropica semihumida ad arida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1(–1.3) mm diam., 0.15–0.25(–0.45) mm high, light to bright (sometimes dirty) orange, non-translucent, round to irregularly elongate, scattered to densely gregarious in ± small groups; disc slightly concave to flat, margin distinct, thin, 5–30 µm protruding, ± smooth to finely rough or crenulate; broadly sessile, sometimes with a broad stipe up to 0.2 × 0.5 mm, superficial if on inner surface of bark, often partially to completely immersed in clefts of outer surface; dry ± closed (sometimes hysterioid), bright to deep orange-red or rose-carmine. **Asci** *((71–))(80–)85–110(–120) {4} × (7.5–)8–9(–10) µm {5}, †(73–)80–98(–108) × (6.7–)7–8(–8.5) µm {3}, 64-spored (46–52 spores counted), spores *4–5-seriate, many spores inverted (strongly mixed), pars sporifera *60–75 µm long; **apex** (†) hemispherical to very slightly truncate, dome †0.8–1.2 → 0.5–0.8 µm thick {3, in H_2O or KOH}, with distinct apical chamber; **base** with short, flexuous stalk, T-, L- or h-shaped. **Ascospores** *(5–)6–8.5(–10.5) × (2–)2.2–2.5(–2.7) µm {5}, †(6–)7–8(–9) × 2–2.6(–2.8) µm {2}, fusoid-clavate, apex rounded to obtuse or usually subacute to acute, base mostly strongly attenuated (often tail-like), slightly to very strongly curved, especially near base; **SBs** apically attached to spore wall, *(1.8–)2–2.8(–3) × 0.8–1.3 µm {3}, pear-shaped, apically narrowed to a small to wide point. **Paraphyses** apically uninflated or mostly slightly to medium clavate(-capitate), sometimes sublageniform, terminal cells *8.5–25 × (2.3–)3–4.5(–5) µm {3}, projecting 5–25 µm beyond dead asci, lower cells *8.5–23 × 1.8–3 µm {2} (towards upper septum sometimes up to 4.5 µm wide); sometimes or rather frequently branched near apex, hymenium pale orange-rose. **Medullary excipulum** hyaline to pale orange, 25–45(–60) µm thick, of medium loose or dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a parallel 10 µm thick layer of t. porrecta. **Ectal excipulum** hyaline to pale orange-rose, of (†) thin-walled to slightly gelatinized, indistinctly to vertically oriented t. angularis(-prismatica) from base to submargin, 25–100(–270) µm thick near base, cells *(5–)10–20(–28) × (6–)8–14(–20) µm {4}, †6–11 × 6–9 µm {1}; 15–30 µm thick near margin, upper part of t. prismatica-porrecta oriented at a 20–50° angle to the surface, marginal cortical cells *7–17 × 3–5(–6) µm {4}, cylindric-clavate; **glassy processes** absent. **Anchoring hyphae** sparse to quite abundant, †1.5–2.5 µm wide, walls 0.2–0.4 µm thick {3}. Globose **SCBs** in paraphyses (1.8–3 µm diam) and marginal ectal excipulum (2.5–4 µm), crystalloid SCBs in upper part of paraphyses and from basal to marginal ectal excipulum {4}, hyaline to light yellow-orange. Light yellow-orange **LBs** 0.2–1 µm diam. (carotenoids) abundant in ectal excipulum (especially towards margin) and paraphyses (except for apex). **Exudate** over paraphyses (0.5–)1–4(–6) µm thick, coarsely continuous to cloddy, hyaline to pale yellowish, loosely attached; over margin and flanks (0.5–)1–5(–15) µm thick, cloddy, light yellow (to ochre-orange). — **ANAMORPH**: vermispora-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** absent. **Conidiogenous cells** integrated, with short pegs *1.5–3 × 2.2–2.5 µm. **Conidia** unbranched, curved in upper part, rarely straight, narrowly fusoid, tapering especially at the tip, truncate at the base, *(26–)31–42 × (3.7–)4–4.5(–4.8) µm, (3–)6–8-septate {1}.

Habitat: collected ~0.2–2.5 m above the ground, corticated, 8–50 mm thick branches of *Acacia* sp. {6}, *Jacksonia* sp. {2}, on mostly slightly to entirely detached, slightly to strongly decayed bark {8}, on periderm or bast (especially on outer surface in cracks of periderm, also often on inner surface), slightly to strongly greyed, green algae very sparse to abundant. **Associated**: *Baggea* sp. {1}, *Caloplaca* sp. {2}, *Claussenomyces* sp. {3}, *Durella* sp. {1}, *D.* aff. *connivens* {1}, *Gloniopsis praelonga* {3}, *Hyalorbilia* ?*erythrostigma* {1}, *Hypoxylon* sp. {1}, ?*Hysteropatella* sp. {1}, *Muellerella lichenicola* {1}, *Orbilia albidorosea* {1}, *O. anguliobliqua* {1}, *O. australiensis* {5}, *O. commarosa* {2}, *O. curvativitalbae* {2}, *O. curvatiobliqua*

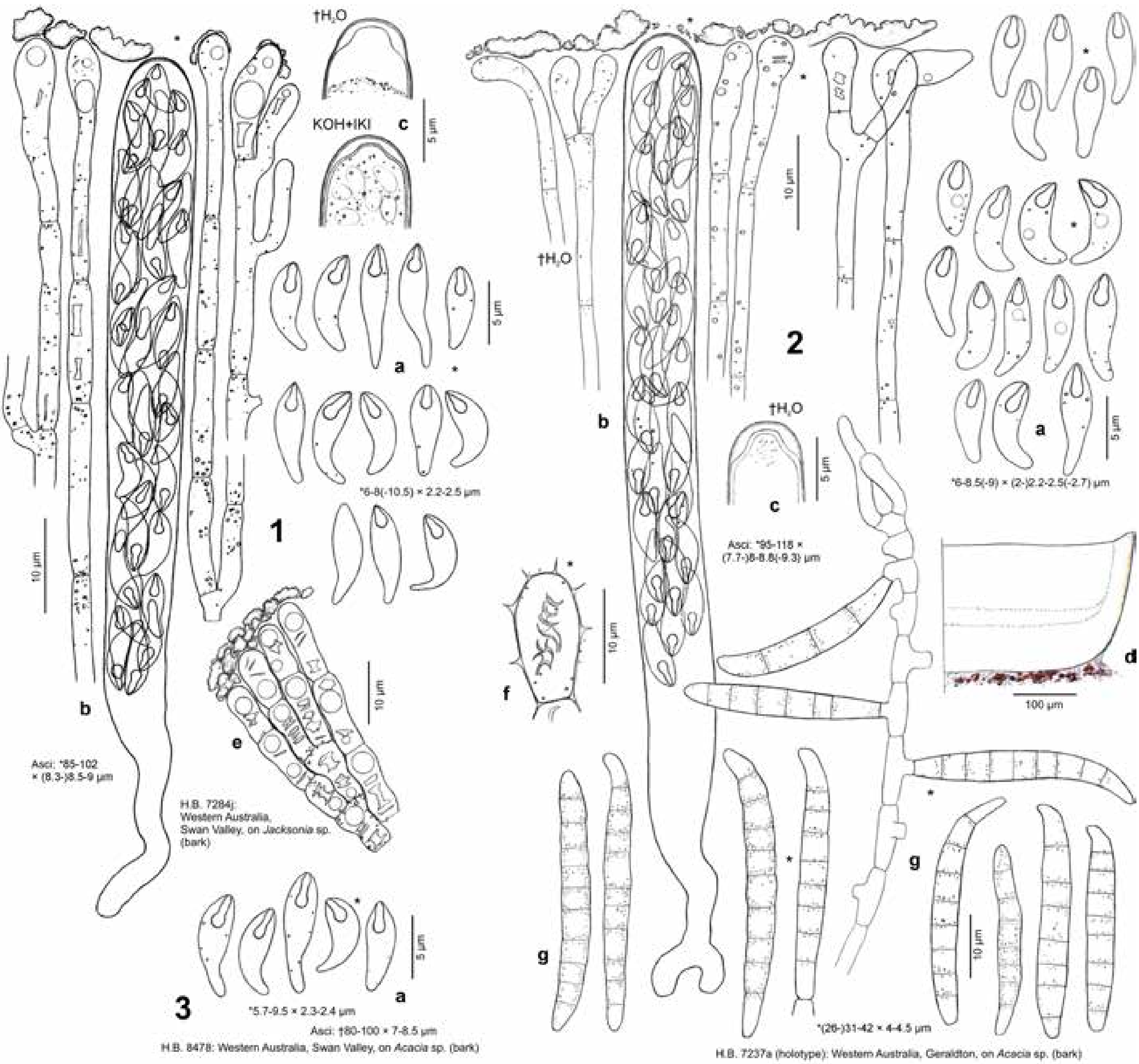


Plate 292. **1–3**: *Orbilia myriofusiclava*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum; **f**. ectal excipular cell at flanks containing crystalloid SCBs; **g**. conidia and integrated conidiogenous cells from culture.

{1}, *O. eucalypti* {4/1}, *O. helicoobliqua* {1}, *O. hesperidea* {1}, *O. kingsiana* {1}, *O. macrotrapeziformis* {2}, *O. microserpens* {2}, *O. ?multiserpens* {1}, *O. myrioeuonymi* {1}, *O. myriolilacina* {1}, *O. myriomuscula* {1}, *O. myrionanosoma* {1}, *O. myrioobliqua* {5}, *O. myriopseudoregalis* {1}, *O. nothovinosa* {2}, *O. paraobliqua* {1}, *O. pleioaustraliensis* {2}, *O. pleioquaestiformis* {1}, *O. ?pleioserpens* {1}, *O. pluristomachia* {1}, *O. ?serpentina* {1}, *O. wannerooensis* {1}, *Patellaria atrata* {1}, *Schizoxylon* sp. {1}, ?*Triblidium* sp. {1}, indet. coelomycete {1}. **Desiccation tolerance**: many mature asci still viable after 12 months, some still after 14.5 months. **Altitude**: 37–278 m a.s.l. **Geology**: Archean and Cretaceous sedimentary rock, Cenozoic regolith (whitish sand); granite, granitic gneiss. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia myriofusiclava* is characterized by 64-spored asci and fusoid-clavate, often strongly curved ascospores. The species resembles *O. cryptogena*, from which it differs in smaller spores with usually acute apices, and in the presence of crystalloid SCBs. Two species of series *Hesperideae*, *O. palmicola* and *O. multiaustraliensis*, differ in 32-spored asci and in having wider and scarcely curved spores. For the similar *O. myriohesperidea* see Pl. 247.

Variation. *O. myriofusiclava* seems to be a rather constant species. Remarkable variation was only observed in the spore apices, which varied between rounded-obtuse and subacute-acute: more or less acute spore apices were seen in most of the collections examined, but in some of them spores with rounded to obtuse apices also occurred. In the holotype, one apothecium showed only spores with rounded to obtuse apices (Pl. 292: 2a, above 5 spores), and also in the sparse collection H.B. 7215d only rounded spore apices were seen (dead state, see IVV). The living asci varied between 71–83 and 100–120 µm in length (within H.B. 8745e), and between 8–8.3 and 8.5–10 µm in width (between different collections). Extraordinarily small apothecia were noted in H.B. 7215d (0.15–0.17 mm diam).

Anamorph. The anamorph obtained in pure culture resembles *Vermispora spermatophaga* in conidial morphology. However,

Plate 293. **1–6**: *Orbilia myriofusiclava*. – **3a**. semihumid Eucalypt open forest (Jarrah Forest); **2a–b**. ± corticated xeric branches of *Acacia*; **1a–c**, **2a**, **d**, **3b**, **5a–c**, **6a**. rehydrated apothecia; **2c**. dry apothecia; **3c**, **5d**. apothecia in median section; **5e**. id., marginal ectal excipulum; **5f–h**, **6c**. crystalloid SCBs in ectal excipular cells; **2f–g**, **3d–e**. ascus apices; **2i**, **4a**. asci; **2j**, **h**, **4b**, **6b**. ascospores. – Living state, except for **2f–g** (in H$_2$O), **3d–e**, **4a** (in KOH+IKI), **4b** (in KOH). — **1a–c**. H.B. 7237a (holotype): Western Australia, Northampton, on *Acacia*; **2a–j**. H.B. 8923b: Moora, on *Acacia*; **3a–e**. H.B. 8478d: Swan Valley, on *Acacia*; **4a–b**. H.B. 7215d: Carnarvon, on *Acacia*; **5a–h**. H.B. 8611d: Swan Valley, on *Jacksonia*; **6a–c**. H.B. 8745e: Swan Coastal Plain, on *Acacia*.

Map 50. Known distribution of *O. myriofusiclava* in (south) western Australia.

in *V. spermatophaga* the conidiophores are 35–75 µm long whereas in *O. myriofusiclava* they are strongly reduced pegs of 1.5–3 µm length. Consistently phragmosporous (unbranched) conidia are quite exceptional in section *Hemiorbilia*, being otherwise only seen in the neighbourhood of *O. crenatovinosa* and possibly representing its anamorph.

Phylogeny. Sequences from three collections of *O. myriofusiclava* were gained: from pure culture of the holotype (SSU+ITS+LSU) and from apothecia of H.B. 8923b and G.M. 2007-10-26 (ITS). In all of them the S1506 intron is absent at the 3'-end of SSU. The three strains are identical except for 1 nt differing in the ITS2 region of the holotype.

In our analyses, *O. myriofusiclava* clustered with medium (ITS+LSU) or no support (ITS, LSU) with *O. adenocarpi*, *O. concoloris*, and *O. sarothamni* in a subclade of the *cryptogena-sarothamni* clade (Phyls 9–10, S13). In the ITS region *O. adenocarpi* and *O. sarothamni* show a distance of ~ 15–17 % to *O. myriofusiclava* (1.3 % and 2.8 % in the LSU, respectively), and also *O. octocorculispora*, *O. corculispora*, and *O. cyptogena* differ by 17–18.5 % from that species (2.8–3.2 % in the LSU). The ITS1 of *O. myriofusiclava* is distinctly longer than in other sequences of section *Hemiorbilia* with which it partly badly aligns, while this is not the case in the ITS2.

Ecology. *O. myriofusiclava* was collected on ± rotten bark of xeric branches of different *Fabales*. It is known from several sites in western and southwestern Australia not far from the coastline, where it occurs in subtropical semiarid to arid open acacia shrublands or semihumid open eucalypt woodlands (mallee) or open forests (jarrah forest), e.g., with *Acacia*, *Jacksonia* and *Nuytsia floribunda*.

Specimens included. **AUSTRALIA**: **Western Australia**, Carnarvon, 183 km SSE of Carnarvon, 10 km W of Overlander Roadhouse, 12 km NE of Hamelin Pool, Denham-Hamelin Road, 67 m, branch of *Acacia*, on bark, 7.XII.2001, G. Marson (H.B. 7215d ø). – Geraldton Sandplains, 60 km N of Geraldton, 12 km N of Northampton, 278 m, branches of *Acacia*, on bark, 9.XII.2001, G. Marson (ex H.B. 7237a, MEL 2389232, **holotype**, CBS 116224, anam. cult., anam. substr.; sq.: KT215274). – Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig of *Acacia*, on bark, 24.XI.2001, G. Marson (G.M. 2001-11-24.1, non vid.). – ibid., 26.X.2007 (G.M. 2007-10-26.1, H.B. 8883l ø; sq.: MK473436). – Swan Coastal Plain, 150 km N of Perth, 13 km WNW of Moora, Dandaragan Road, 235 m, branch of *Acacia*, on bark, 24.X.2007, G. Marson (H.B. 8923b ø; sq.: KT380062). – 30 km NNW of Perth, 1 km NW of Kinross, Tamala Park, 38 m, branch of *Acacia*, on bark, 23.X.2007, G. Marson (H.B. 8745e). – Jarrah Forest, 30 km NE of Perth, 4 km N of Upper Swan, W of Walyunga, 37 m, branches of *Jacksonia*, on bark, 23.XI.2001, G. Marson (H.B. 7284j). – ibid., 76 m, branch of *Acacia*, on bark, 2.IX.2006, G. Marson (H.B. 8478d). – ibid., branch of *Jacksonia*, on bark, 2.IX.2006, G. Marson (H.B. 8611f).

Orbilia corculispora Baral & G. Marson, in Karasch et al., Österr. Z. Pilzk. 14: 285 (2005) — Pls 294–295, Map 51

Etymology: referring to the heart-shaped ascospores.
Typification: France, Séderon, branches of *Spartium junceum*, 17.VIII.2001, G. Marson (ex H.B. 7039a, M-0140892, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.7(–0.8) × 0.25–0.5 mm, 0.14–0.24(–0.32) mm high (receptacle 0.14–0.18 mm), pale to bright (brick-)orange(-red) to (orange-)rose, rarely whitish, round to ± elliptical, scattered to (sub)gregarious in smaller or larger groups; disc slightly concave then flat, margin distinct, rising 0–25 µm above disc, smooth or distinctly scurfy, exterior finely whitish-powdered; sessile or with broad obconical stipe-like base, slightly to strongly erumpent from cracks or immersed in biofilm, rarely nearly superficial; dry light to bright orange-ochre. **Asci** *(60–)65–95 × (6.5–)7–9(–9.6) µm {7}, †55–80(–94)((–120)) × (5.7–)6–7.3(–7.7) µm {4}, 16-spored (rarely only 12), spores 1(–2)-seriate, with SBs ± laterally oriented but also up- or downwards, pars sporifera *38–70 → 26–37 µm long; **apex** (†) hemispherical, dome †0.8–1.5 → 0.8–1 µm thick {5}, with distinct apical chamber; **base** with short to medium long stalk, L-, Y- or h-shaped. **Ascospores** *(5–)6–8(–9.5) × 3–4.2(–4.5) µm {13}, †5.3–7 × 3–3.5 µm {2}, medium to strongly heart- or kidney-shaped, with a lateral, either distinct and subacute, or indistinct and obtuse protrusion, sometimes subglobose to ellipsoid or only slightly inequilateral to kidney-shaped, *(4–)4.5–6(–7) × (3.5–)3.8–4.5(–5) µm {5}; both ends rounded; **SBs** attached at the lateral protrusion (in ellipsoid spores also at subapical to apical end), *(2–)2.5–3.5(–4.5) × (0.8–)1.2–1.7(–2) µm {8}, broadly tear- to pear-shaped, terminally narrowed to a small point, sometimes with a very short filum; germinating spores with 1 eccentrical septum, multiguttulate. **Paraphyses** apically uninflated to medium clavate-capitate (rarely spathulate), terminal cells *6–15 × (1.5–)2–3(–4) µm {6}, lower cells *7–13 × (1.2–)1.5–2(–2.5) µm {4}; rarely or frequently branched near apex. **Medullary excipulum** hyaline to very pale orange, 25–50 µm thick, of medium dense textura intricata with many inflated cells, indistinctly to medium sharply delimited. **Ectal excipulum** hyaline, near margin partly pale orange, of thin-walled, vertically oriented t. (globulosa-)angularis(-prismatica) from base to margin, (40–)60–100(–200) µm thick near base, cells from base to mid flanks *(6–)9–17(–26) × (6–)8–12(–17) µm {5}; 20–35 µm thick at flanks and margin, outer part of margin of ± thick t. prismatica oriented at a 20–80° angle to the surface, marginal cortical cells *5–11 × (2.5–)3–4.5(–5.5) µm {6}, †2.7–4 µm wide {2}, **glassy processes** absent. **SCBs** in paraphyses and marginal excipulum globose (in excipulum 1.8–2.5 µm wide), also crystalloid {14}, hyaline or pale to light orange, in excipulum 3–8(–13) × 2–5.5 µm, in basal excipulum smaller, hyaline. **Exudate** over paraphyses 1–4 µm thick, ± hyaline, clod-shaped, loosely attached; over excipulum ~(0.5–)1.5–3(–6) µm thick, large-cloddy, hyaline to light golden yellow. **Anchoring hyphae** sparse, *2–3.5 µm wide, walls 0.2–0.3 µm thick {3}. — **ANAMORPH**: trinacrium-like (from ascospore isolate {2} and natural substrate {3}). **Conidiophores** ~30–40 × 2.2–3.5 µm, simple, straight {1}. **Conidia** 2-armed (T-shaped), total size *29–55 × 24–46 µm, stipe *22–41.5 × 4–5.5 µm, (2–)3–5(–7)-septate, arms tapering, bent out- or downwards, *12–29 × 2.5–4.3(–5) µm (in situ, actual length ~12.5–30 µm), 2–3-septate {2}.

Habitat: collected 0–8 m above the ground, ± corticated, 3–25 mm thick twigs and branches of *Acacia* sp. {2}, *Anagyris foetida* {1}, *Chamaecytisus proliferus* {2}, *Cistus monspeliensis* {1}, *Cytisus scoparius* {1}, *Geijera parviflora* {1}, *Laburnum anagyroides* {1}, *Magnolia denudata* {1}, *Olea europaea* {1}, *Spartium junceum* {6}, *Syringa vulgaris* {1}, *Tipuana tipu* {1}, *Ulex europaeus* {24}, *U. parviflorus* {1}, *U. minor* {1}, ?*Vachellia* sp. {1}, *V. farnesiana* {2}, on slightly to strongly decayed bark {41} (on periderm {6} and bast {10}), rarely wood {8}, sometimes in cracks or cross-fissures of periderm, sometimes on inner surface of detached bark, medium to strongly greyed, green algae very sparse to abundant, sometimes close to or on pyrenomycetes (e.g., *Diaporthe eres* {4}). **Further associated**:

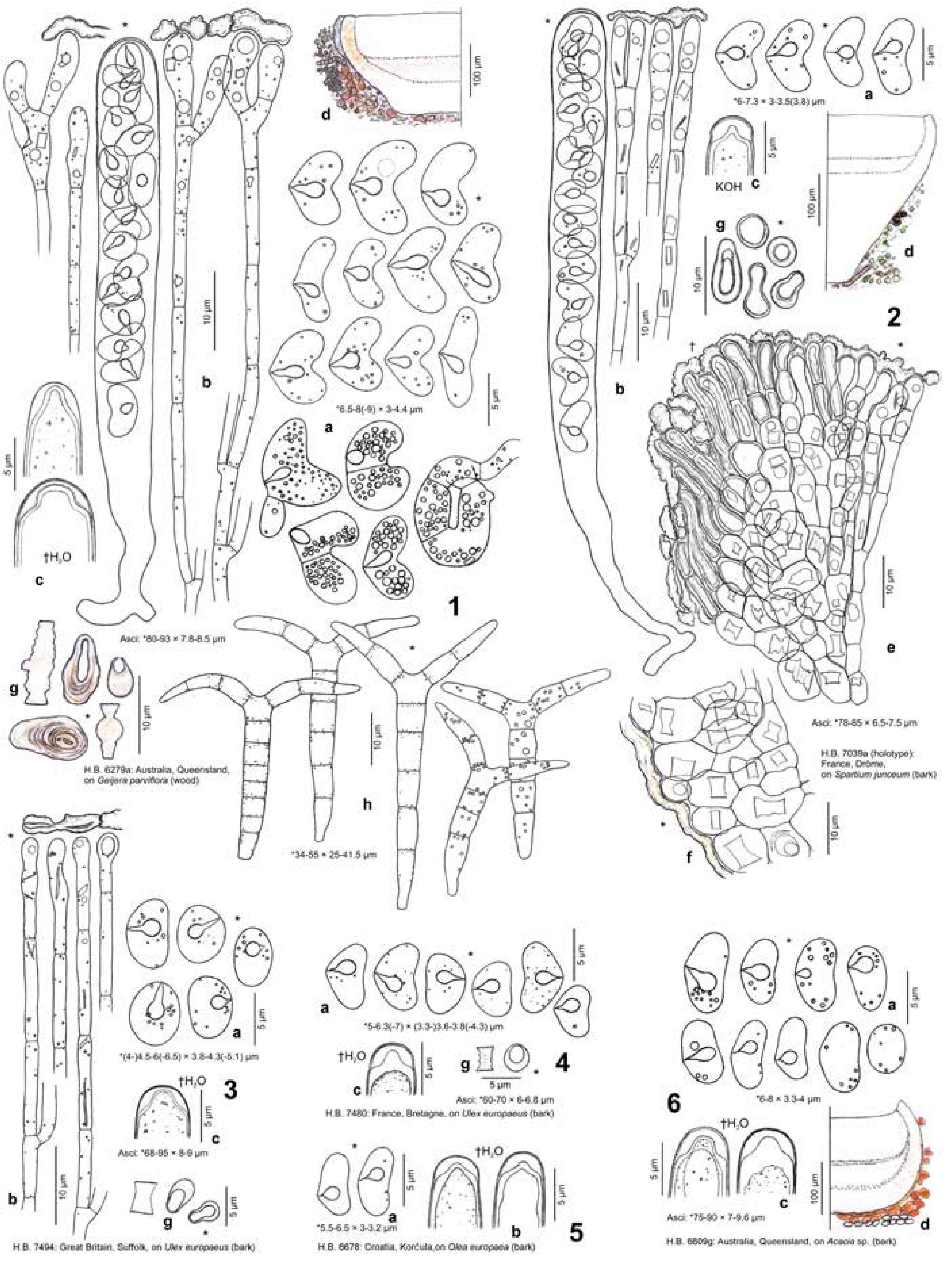


Plate 294. **1–6**: *Orbilia corculispora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. id., mid flanks; **g**. crystalloid SCBs in ectal excipular cells; **h**. conidia from culture (left) and substrate (2 right).

Bionectria ralfsii {1}, *Caloplaca* sp. {1}, *Claussenomyces* sp. {2}, *Coniochaeta ?alkalivirens* {1}, *Durella ?atrocyanea* {1}, *Echinosphaeria* sp. {1}, *Exidia glandulosa* {1}, *Gloniopsis praelonga* {1}, ?*Herpotrichia* sp. {1}, *Hyalorbilia ?erythrostigma* {2}, *H. subfusispora* {1}, *Hysterobrevium mori* {1}, *Ionomidotis fulvotingens* {1}, *Lecanora* sp. {1}, *Lecidella* sp. {1}, *Melanomma seminudum* {1}, *Nectriaceae* {1}, *Orbilia acaciae* {1}, *O. aurantiorubra* {2}, *O. breviaristata* {2}, *O. ?cejpii* {1}, *O. coronohesperidea* {1}, *O. eucalypti* {4}, *O. farnesianae* {2}, *O. gambelii* {3}, *O. geijerae* {1}, *O. macrocarpa* {1}, *O. montigena* {1}, *O. ?multivirgula* {1}, *O. myriella* {1/1}, *O. myriomuscula* {1}, *O. octocercocarpi* {2}, *O. octoserpentina* {1}, *O. pleioaustraliensis* {1}, *O. pleiomicrosoma* {1}, *O. pleioungulata* {1}, *O. polyspora* {1}, *O. ?pseudeuphorbiae* {1}, *O. serpentina* {1}, *O. subclavuliformis* {3}, *O. vinosa* {4}, *Patellaria* '*andina*' {2}, *P. atrata* {1}, *Patellariopsis dennisii* {1}, *Physcia* sp. {1}, *Propolis ?farinosa* {1}, *Pseudolachnea hispidula* {1}, *Psiloglonium lineare* {1}, *Ramalina* sp. {1}, *Rhizodiscina* sp. {1}, *Rhytidhysteron* sp. {1}, *Schizoxylon* sp. {1}, *Sclerococcum* sp. {1}, ?*Skyttea* sp. {1}, ?*Stictis* sp. {3}, *Thyronectria* sp. {1}, *Unguiculariopsis* spp. {2}, *U. ilicincola* {1}, *U. rehmii* {1}, *Xanthoria* sp. {1}. **Desiccation tolerance**: fully viable for at least 17.5 months. **Altitude**: 1–1106 m a.s.l. **Geology**: Proterozoic, Cambrian, Ordovician, Silurian & Permian clayey silt, quartzitic wacke & schist etc., Cretaceous & Tertiary clayey sand-, marl- & limestone, Pleistocene sand & till; granite, migmatite, basalt. **Phenology**: throughout the year (long-lived).

Phenology of *O. corculispora* in Europe											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
11	3	2	0	0	3	0	1	4	5	10	3

Taxonomic remarks. Typical *O. corculispora* is easily recognized by its heart-shaped ascospores containing a large tear-shaped spore body inserted in the ± acute end of the heart, and 16-spored asci. The reniform spores of *O. cryptogena* resemble somewhat those of *O. corculispora*, but the spore body is here consistently attached to one of the spore ends.

Shape of apical dome and spore body indicate relationship of *O. corculispora* near species such as *O. cryptogena* or *O. arizonensis*. The lateral insertion of the spore body is probably an apomorphy that developed from an ancestor with terminal insertion. This view is supported by the below-mentioned variant of *O. corculispora* with ellipsoid to kidney-shaped spores (see also Fig. 65).

Variation. The collections from Europe well correspond to those from Macaronesia, Australia, southeastern Asia, and southeastern Africa. However, great variability in spore shape was noted. In the more mediterranean material (Australia, Asia, Macaronesia, southern Europe) the ascospores are distinctly heart-shaped, with a more or less pronounced lateral protrusion. In the more temperate, atlantic collections the spores tend to be kidney-shaped, and especially in Great Britain nearly ellipsoid or even subglobose in almost every collection studied. However, kidney-shaped spores occurred in some of these British records (E.B. 4660: mainly kidney-shaped, H.B. 8045: both ellipsoid and kidney-shaped), and also the African sample and one of the Australian samples also showed some or many kidney-shaped to sometimes nearly ellipsoid spores. In those northwestern European collections all intermediate spore types from subglobose to strongly kidney-shaped were observed, even within a single apothecium.

Anamorph. Trinacrium-like conidia grew in pure culture of a Chinese (Ren et al. 2014b who also observed conidiophores) and an Australian sample (Pl. 294: 1h). The two arms of the conidia are mostly distinctly bent downwards, similar as in the type of *Trinacrium incurvum*, which has slightly smaller conidia. *Amphosoma resinicola*, *Hyalorbilia erythrostigma*/*H. orbiliicola* (with *T. ?angamosense*), and particularly *O. spermoides* have similar conidia, but all these species are phylogenetically not closely related to each other, while DNA data of *T. incurvum* were unavailable.

Phylogeny. Sequences were available from pure culture of an eastern Australian sample on *Geijera* and from apothecia of three French samples on the type substrate *Spartium* from the type locality and 27–80 km remote from it. All comprise SSU, ITS, and LSU, but the S1506 intron is present in the Australian sample and absent in the French ones. The latter are identical in the ITS region except for 1 nt in the 5.8S in the sample from Montelimar, whereas the former differs by 3% (15–16 nt, 2 gap). In the SSU V8–V9 all four sequences are identical, and in the LSU D1–D2 the Australian sample differs by 1.1% (7 nt) from the three identical French ones.

Our phylogenetic analyses of different regions of rDNA support a close relationship between *O. corculispora*, *O. octocorculispora*, and *O. cryptogena*, with which it formed a medium (ITS+LSU) or weakly (ITS, LSU) supported subclade within the *cryptogena-sarothamni* clade (Phyls 9, 10, S13). The lowest distance in the ITS region within the clade is 10–10.5% to *O. cryptogena* (LSU 2.8–3.5%) and 11–12% to *O. octocorculispora* (LSU 3.5–4.5%). The S1506 intron shows a high distance to other members of section *Hemiorbilia*, with a minimum of 20% to *O. octocorculispora* and *O. crenatovinosa*. An unavailable ITS+LSU sequence from the culture of the Chinese collection (Ren et al. 2014b) shows a distance of 3% (ITS) or 1.7% (LSU D1–D2) to the Australian sequence and 4% or 1.9% to that from France (B. Liu pers. comm.).

Ecology. *O. corculispora* inhabits slightly to strongly decayed bark (rarely wood) of xeric twigs and branches of predominantly *Fabales*. *Ulex* is probably overrepresented in the above host listing because gorse-rich areas of atlantic, meso- to supratemperate humid western Europe were often visited by J.P. Priou in France (Bretagne) and E. Batten & S. Francis in England (Suffolk). In central Europe the species was once recorded in a thermophilous forest strip at the cold-temperate humid lac Léman. In southern Europe (Aquitaine, Provence, Dalmatia) it occurred in suprasub- to mesomediterranean semihumid shrublands (maquis), and in Macaronesia in the thermomediterranean semihumid zone of La Palma on *Chamaecytisus proliferus* (tagasaste) planted there as fodder crop (Karasch et al. 2005), and in Tenerife on *Cistus* and *Chamaecytisus* in the Canary pine forest (*Sideritido solutae-Pinetum canariensis cistetosum monspeliensis*). In eastern and northeastern Australia *O. corculispora* was found at the northern Great Dividing Range in subtropical semiarid to tropical subhumid open eucalypt woodlands, while records from western Australia were made in subtropical (almost tropical) arid open acacia wood- and shrublands (mulga) at the southern border of the Pilbara desert. The site in southeastern Africa is a subtropical humid (winter-dry) savannah-like shrubland with *Acacia*, and that in southeastern Asia a planted tree in a park at a subtropical humid (winter-dry) monsoon-influenced climate.

Specimens included. **GREAT BRITAIN**: **East England**, **Suffolk**, 12 km WSW of Lowestoft, NE of Beccles, Beccles Common, 5 m, branch of *Ulex europaeus*, on bark, 15.VI.2005, E. Batten (E.B. 4612, K(M) 145645, doc. vid.). – 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *U. europaeus*, on bark, 3.II.2004, S.M. Francis & E. Batten (E.B. 4478 ø, H.B. 7476b ø, doc. vid.). – ibid., branch of *U. europaeus*, on bark and pyrenomycete, 3.III.2004, S.M. Francis & E. Batten (E.B. 4495, K(M) 227397, E.B. 4496, K(M) 145644, H.B. 7494). – ibid., branch of *U. europaeus*, on bark,

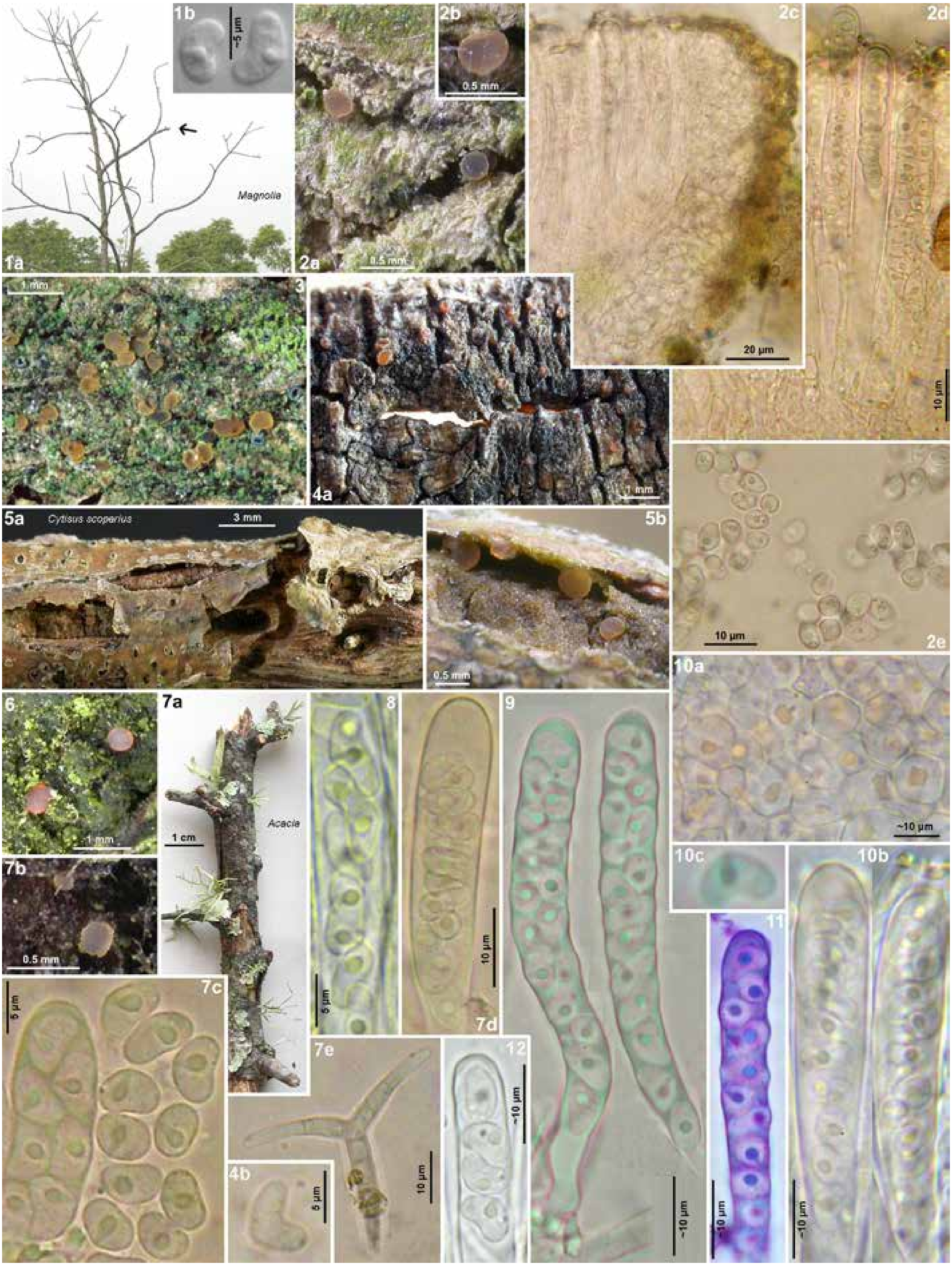


Plate 295. **1–12**: *Orbilia corculispora*. – **1a**. dead *Magnolia* tree on university campus; **7a**. dead corticated branch of *Acacia* with lichens; **2a–b**, **3**, **4a**, **5a–b**, **6**, **7b**. rehydrated apothecia; **2c**. marginal ectal excipulum in median section; **10a**. excipular cells with crystalloid SCBs; **2d**, **7c–d**, **8**, **9**, **10b**, **11**, **12**. asci with ascospores; **2e**. clusters of freshly ejected ascospores; **1b**, **4b**, **7c**, **10c**. ascospores; **7e**. conidium from substrate. – Living state, except for **4b** (in KOH), asci in **7c**, **8**, **9**, **11** (in CRB), **12**. – **1**: phot. B. Liu (**1b** DIC); **9**, **11**: phot. J.P. Priou; **12**: phot. L. Beenken. — **1**. 1.XI.2009: China, Guangxi, on *Magnolia*; **2a–e**. H.B. 8045: Great Britain, Suffolk, on *Ulex*; **3**. H.B. 7039a (holotype): France, Drôme, on *Spartium*; **4a–b**. H.B. 6279a: Australia, Queensland, on *Geijera*; **5a–b**. H.B. 8379b: Great Britain, Suffolk, on *Cytisus*; **6**. H.B. 7494: ibid., on *Ulex*; **7a–e**. H.B. 8087a: South Africa, Nelspruit, on *?Vachellia*; **8**. H.B. 8997g: Western Australia, Carnarvon, on *Vachellia*; **9**. J.P.P. 23133: France, Morbihan, on *Ulex*; **10a–b**. H.B. 7317a: France, Ardèche, on *Ulex*; **11**. J.P.P. 23138: France, Morbihan, on *Ulex*; **12**. 26.II.2011: Switzerland, Waadt, on *Laburnum*.

Map 51. Known distribution of *O. corculispora* in Macaronesia, Europe, and Australia.

20.IX.2004, E. Batten (E.B. 4561, K(M) 227400, doc. vid.). – ibid., S.M. Francis, 15.I.2005 (E.B. 4578 ø, K(M) 227398, doc. vid.). – ibid., 10.I.2006, E. Batten & S.M. Francis (E.B. 4662 ø, K(M) 227399, H.B. 8045a). – ibid., branch of *Cytisus scoparius*, on wood, 30.XI.2006, S.M. Francis (H.B. 8379b). – 5.5 km SW of Southwold, 1.5 km NNW of Dunwich, Dunwich Forest 20 m, branch of *Ulex minor*, on bark, 2.I.2006, E. Batten (E.B. 4660, K(M) 145647, doc. vid.). — **FRANCE**: **Nord-Pas-de-Calais**, **Nord**, 8 km WSW of Dunkerque, 2 km WSW of Grande-Synthe, La Ferme des Jésuites, 0 m, 24.X.2016, twig & branch of *Ulex europaeus*, on bark, J.P. Priou (J.P.P. 16262, doc. vid.). – **Bretagne**, **Finistère**, 6 km ESE of Quimperlé, WSW of Rédené, Rosbigot, 40 m, twig og *Ulex*, on bark, 11.XI.2013, P.Y. Courio (J.P.P. 13129, doc. vid.). **– Ille-et-Vilaine**, 11.5 km WSW of Bruz, 3.3 km ESE of Baulon, Landes blanches, 64 m, branch of *U. europaeus*, on bark, 22.II.2008, J.P. Priou (J.P.P. 28030 ø, non vid.). – 5.3 km NE of Pipriac, NE of Courbouton, 38 m, branch of *U. europaeus*, on bark, 27.XI.2007, J.P. Priou (J.P.P. 27132 ø, doc. vid.). – 14.5 km NE of Redon, 1.6 km WSW of St.-Just, Cojoux rivulet, 37 m, branch of *U. europaeus*, on *Diaporthe eres*, 16.XI.2006, J.P. Priou (J.P.P. 26193, non vid.). – **Morbihan**, 9.5 km SE of Malestroit, 2.7 km WNW of St.-Martin-sur-Oust, Beauvais, 8 m, branch of *Cytisus scoparius*, on bark, 15.I.2010, J.P. Priou (J.P.P. 10001, non vid.). – 8 km N of Carentoir, 1.7 km SSW of Guer, Pont de l'Oyon, 37 m, branch of *Ulex europaeus*, on bark, 18.XII.2003, J.P. Priou (J.P.P. 23138, doc. vid.). – 1 km N of La Gacilly, Yves Rocher, 27 m, branch of *Tipuana tipu*, on bark, 19.VI.2016, J.P. Priou (J.P.P. 16166, doc. vid.). – La Gacilly, centre ville, Hotel de France, 20 m, branch of *Syringa vulgaris*, on bark, 14.I.2012, J.P. Priou (J.P.P. 12019, doc. vid.). – 1 km WNW of La Gacilly, La Glouzie, 45 m, twig of *Ulex europaeus*, on bark, 6.I.2004, J.P. Priou (J.P.P. 24007, non vid.). – 0.3 km W of La Glouzie, Buhan, 57 m, branch of *U. europaeus*, on wood & bark and *Diaporthe eres*, 23.I.2004, J.P. Priou (J.P.P. 24035, non vid.). – 2.5 km NW of La Gacilly, ENE of La ville Orion, SW of L'hôtel Séro, 33 m, twig of *U. europaeus*, on bark and *D. eres*, 23.I.2004, J.P. Priou (J.P.P. 24038, H.B. 7480). – ibid., 0.8 km WNW of Le Tay, La Villouët, 32 m, branch of *U. europaeus*, on bark & wood, 23.I.2004, J.P. Priou (J.P.P. 24037, non vid.). – 4.5 km WSW of La Gacilly, 2.2 km NE of Les Fougerêts, E of La Ville Macé, 57 m, twig of *Cytisus scoparius*, 8.XI.2005, J.P. Priou (J.P.P. 25144, non vid.). – 3.2 km NNE of Les Fougerêts, 1.4 km WNW of St.-André, 86 m, twig of *Ulex europaeus*, on bark, 14.XII.2003, J.P. Priou (J.P.P. 23133, doc. vid.). – 1.2 km N of Les Fougerêts, S of La ville Basse, La Rochonaie, 52 m, branch of *U. europaeus*, on bark, 17.X.2004, J.P. Priou (J.P.P. 24162, doc. vid.). – 8 km WNW of La Gacilly, S of St.-Nicolas-du-Tertre, Etang près La Croix, 47 m, branch of *Cytisus scoparius*, 25.XII.2003, J.P. Priou (J.P.P. 23144, non vid.). – 9 km WNW of Redon, 2 km E of St.-Jacut-les-Pins, Moulin de Calléon, 20 m, branch of *Ulex europaeus*, on bark, 24.I.2005, J.P. Priou (J.P.P. 25014, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 2.4 km SSE of St.-Dolay, 1 km ENE of La Couarde, le Forsdoff, 50 m, branch of *U. europaeus*, on wood, 9.XI.2010, J.P. Priou (J.P.P. 10195, non vid.). – 20 km NW of St.-Nazaire, 2.3 km SW of Herbignac, E of La Cour aux Cerfs, 30 m, branch of *U. europaeus*, on wood, 9.XI.2010, J.P. Priou (J.P.P. 10196, doc. vid.). – 3 km ESE of Piriac-sur-Mer, 0.5 km E of St.-Sébastien, 20 m, branch of *U. europaeus*, on wood, 10.XI.2007, J.P. Priou (J.P.P. 27124, non vid.). – 2.3 km NE of Mesquer, l'Île de Rostu, 2 m, branch of *U. europaeus*, on bark, 11.XI.2008, C. Lechat, vid. J.P. Priou (J.P.P. 28218, non vid.). – **Aquitaine**, **Landes**, Cap-Breton, 11 m, branch of *U. europaeus*, on bark, 4.I.2008, J.P. Priou (J.P.P. 28006, doc. vid.). – **Rhône-Alpes**, **Ardèche**, 5 km E of Vallon-Pont-d'Arc, 4 km WNW of St.-Remèze, les Mouniers, 410 m, branches of *U. parviflorus*, on bark, 8.X.2002, G. Marson (H.B. 7317a ø). – **Drôme**, 1 km N of Nyons, Col du Pontias, 460 m, branch of *Spartium junceum*, on bark, 11.X.2002, G. Marson (ø). – 5 km SE of Montélimar, 2.3 km NW of Espeluche, 150 m, branch of *S. junceum*, on bark, 13.X.2016, G. Marson (G.M. 2016-10-13.6; sq.: MK473423). – ibid., 12.IX.2018, G. Marson (G.M. 2018-09-12.1). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 15 km WSW of Serres, 4.8 km ENE of Rosans, Col du Palluel, 800 m, branches of *S. junceum*, on bark (and wood), 12.IX.2018, G. Marson (G.M. 2018-09-12.6; sq.: MK473425). – **Alpes-de-Haute-Provence**, 10 km ESE of Séderon, W of Curel, 765 m, branch of *S. junceum*, on bark, 17.VIII.2001, G. Marson (ex H.B. 7039a, M-0140892, **holotype**). – ibid., branches of *S. junceum*, on bark, 20.IX.2019, G. Marson (G.M. 2019-09-20.4, **topotype**, sq.: MN907100). — **SWITZERLAND**: **Waadt**, Lac Léman, 3 km ESE of Lausanne, E of Pully, 420 m, branch of *Laburnum anagyroides*, on bark and old *Eutypella* ?*scoparia*, 26.II.2011, L. Beenken (ZT, doc. vid.). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 11 km W of Korčula, 1.5 km W of Račišće, S of Zaglavak hill, 50 m, branch of *Olea europaea*, on bark, 4.VI.2000, H.O. Baral (H.B. 6678 ø). — **GREECE**: **South Aegean**, **Rhodos**, 17 km WNW of Archangelos, 1 km SSE of Salakos, NNE of Profitis Ilias, 495 m, branch of *Anagyris foetida*, on bark, 20.III.2010, V. Kummer (H.B. 9353d ø). — **MACARONESIA**: **Canary Islands**, **La Palma**, La Caldera, 2.5 km E of El Paso, Centro Visitantes, 845 m, branch of *Chamaecytisus proliferus*, on bark, 15.I.2005, P. Karasch (H.B. 7664d ø). – **Tenerife**, Granadilla de Abona, 2.5 km SE of Vilaflor, La Martela, 1195 m, on *Cistus monspeliensis*, 21.III.2012, L. & C. Quijada (TFC Mic. 23361, doc. vid.). – ibid., on *Chamaecytisus proliferus*, 19.IV.2012, L. & C. Quijada (TFC Mic. 23635, 23637, doc. vid.). — **SOUTH AFRICA**: **Mpumalanga**, Drakensberg Mts., 12 km SSE of Mbombela (Nelspruit), NE of Umhloti Lodge, 1106 m, branch of ?*Vachellia*, on bark, 16.II.2006, V. Kummer (H.B. 8087a ø, anam. substr.). — **CHINA**: **Guangxi**, **Nanning**, 7 km E of Nanning, University campus of Guangxi, 80 m, branch of *Magnolia denudata*, on bark, 1.XI.2009, B. Liu (B.L. 1043, doc. vid.). – **Fangchenggang**, 28 km SSE of Shangsi, S of Nianban, Shiwandashan, ~400 m, twig of indet. angiosperm, 4.VIII.2012, Y.L. Ren (B.L. 1501, anam. cult., doc. vid.; sq.: ined.). — **AUSTRALIA**: **Western Australia**, Carnarvon, 117 km NNE of Carnarvon, 7 km SSE of Minilya Roadhouse, Barrabiddy Creek, 13 m, twig of *Vachellia farnesiana*, on bark & wood, 6.XII.2001, G. Marson (H.B. 8590b ø, anam. substr.). – ibid., branch of *V. farnesiana*, on bark, 6.XI.2007, G. Marson (H.B. 8997g ø). – Gascoyne, south-border of Collier Range, 175 km NE of Meekatharra, 41 km SW of Kumarina Roadhouse, 560 m, branch of *Acacia*, on bark, 26.XI.2001, G. Marson (H.B. 8697e). – **Queensland**, Brigalow Belt South, 138 km SSW of Rockhampton, 11 km SW of Banana, 136 m, branch of *Geijera parviflora*, on bark, 22.X.1998, G. Marson (H.B. 6279a, CBS 116231, anam. cult., anam. substr. [descalsia-like]; sq.: KT215273). – Desert Uplands, 29 km E of Hughenden, 13 km W of Prairie, 390 m, twig of *Acacia*, on bark, 16.X.1998, G. Marson (H.B. 6609g ø).

Orbilia octocorculispora R. Tena, Baral & E. Weber, **sp. nov.**, MB 813534 — Pl. 296

Etymology: referring to the 8-spored asci and resemblance to *O. corculispora*.
Typification: Spain, Valencia, Serra, branch of *Gleditsia triacanthos*, 23.III.2014, R. Tena (M-0276541, holotype; KT222382).

Latin diagnosis: Orbiliae corculisporae *similis, sed asci octospori, ascosporae plus minusve triangulares, corpuscula crystalloidea absentia. Habitat ad lignum vel corticem putridum ramorum siccorum* Fabacearum *vel* Pini *in zona mediterranea semihumida Europae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.65 mm diam., 0.19–0.21 mm high, bright orange to brick- or carmine-red, round (to broadly elliptical), scattered to subgregarious in small groups;

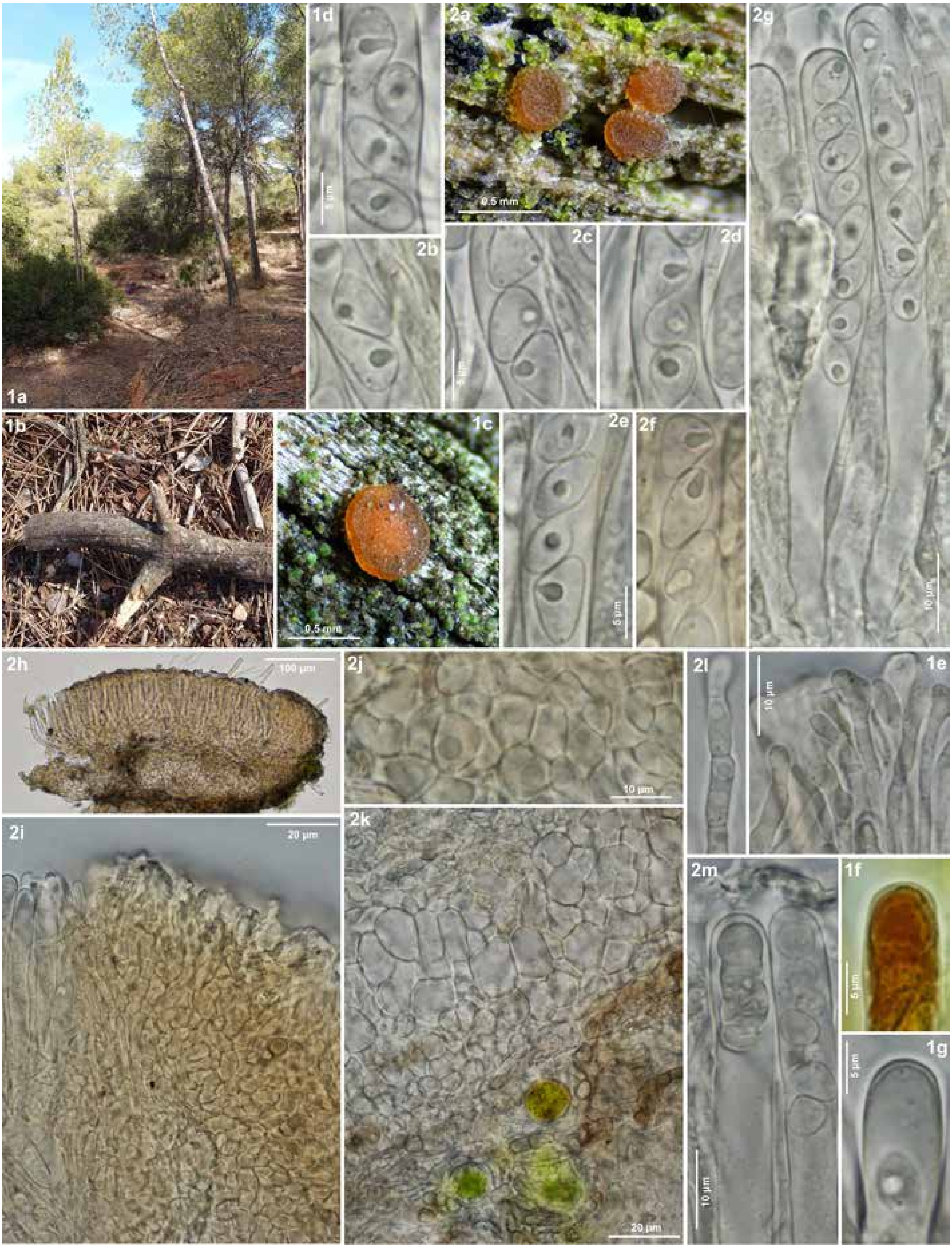


Plate 296. **1–2**: *Orbilia octocorculispora*. – **1a**. type locality with thermomediterranean open pine woodland; **1b**. decorticated xeric branch of *Pinus* in situ; **1c**, **2a**. rehydrated apothecia; **2h**. apothecium in median section; **2g**, m. mature asci with ascospores (normal turgescence in **2g** and **2m** right; full turgescence in **2m** left); **2i**. marginal ectal excipulum in median section; **2k**. id., at lower flanks; **2j**. globose SCBs at mid flanks; **1e**, **2l**. paraphyses; **1d**, **2b–f**. ascospores inside living asci; **1f–g**. ascus apices. – Living state, except for asci in **1f–g** (**1f** in IKI). — **1a–g**. phot. R. Tena, R.T.L. 14012601: Spain, Valencia, on *Pinus*; **2a–m**. phot. R. Tena, R.T.L. 14032301 (holotype): ibid., on *Gleditsia*.

disc flat, margin thick, rising 0–10 µm above disc, slightly rough; broadly sessile, ± erumpent from fibres and biofilm; dry cupulate, bright brick-red. **Asci** *~(56–)75–85(–115) × 7–8.2(–9) µm {2}, †~6.5–7.5 µm wide {1}, 8-spored, spores 1-seriate, or 2-seriate above, with SBs ± laterally oriented, rarely the upper upwards and/or the lower downwards, pars sporifera *30–43 → 17–21 µm long; **apex** (†) hemispherical to slightly truncate, dome †0.4–0.7 → 0.4–0.5 µm thick {2}, also subapically thickened; **base** with short to long, thick stalk, ± L- to Y-shaped. **Ascospores** *(6–)7–9(–10.5) × 4.2–5.5 × 4–4.5(–4.8) µm {3}, triangular, 1 side obtusely conical, opposite side ± straight; **SBs** attached at the conical side, *(2.5–)2.8–3.6(–4) × (1.2–)1.4–1.6(–1.7) µm {2}, tear- to pear-shaped, terminally narrowed to a small or sometimes rather wide point. **Paraphyses** apically slightly to medium clavate-capitate, terminal cells *(4–)6–13(–16) × (2.5–)3–4(–4.8) µm {2}, lower cells *7–17 × 1.6–2.5(–3) µm {2}; sometimes branched near apex. **Medullary excipulum** pale orange, 30 µm thick, of dense, small-celled textura angularis-intricata, medium sharply delimited. **Ectal excipulum** very pale orange, of thin-walled († slightly gelatinized), indistinctly oriented t. angularis from base to submargin, 45–60 up to 90–100 µm thick near base, cells from base to mid flanks *(8–)12–18(–22) × (7–)8–12.5 µm {2}; 25–35 µm thick at flanks and margin, outer part of margin of t. prismatica oriented at a ~50–80° angle to the surface, marginal cortical cells *~6–10 × 2.5–3.5 µm {1}, sometimes forming dead, thick-walled, protruding hyphoid elements, **glassy processes** absent. **SCBs** in paraphyses and marginal excipulum globose, hyaline, in paraphyses 1.4–2.4 µm wide, in ectal excipulum 1.8–3.3 µm {2}. Minute hyaline **LBs** very scattered in paraphyses and excipulum. **Exudate** over paraphyses and marginal excipulum 0.5–1 µm thick, hyaline, clod-shaped, loosely attached; pale yellowish-orange extracellular granules very scattered between paraphyses and cells of medullary excipulum. **Anchoring hyphae** sparse, *~1.7–3.5 µm wide, walls 0.2 µm thick {1}. **— ANAMORPH**: unknown.

Habitat: collected 0–2 m above the ground, decorticated, 6–18 mm thick twigs and branches of *Gleditsia triacanthos* {1}, *Pinus halepensis* {1}, *Ulex* sp. {1}, on 0.3–0.5 mm deep very decayed wood {2} and bark {1}, rather strongly greyed and with sparse or often abundant green algae. **Associated**: *Lophiostoma ?quadrinucleatum* {1}, *Orbilia microserpens* {1}, *Caloplaca* sp. and other crustose lichens {1}. **Desiccation tolerance**: fully viable after 14 months. **Altitude**: 185–430 m a.s.l. **Geology**: Tertiary clay & gypsum, Quaternary limestone, sandstone, marl & clay. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia octocorculispora* was collected and studied from the type locality by R. Tena (pers. comm., Pl. 296), and from a third sample by J.P. Priou (pers. comm., IVV: 16.V.2015). The above description is almost exclusively based on Tena's numerous photos. The species resembles *O. corculispora* in spore shape and lateral attachment of SBs, though the spores never show an indentation at the opposite side as in typical *O. corculispora*. The main difference lies in the 8-spored asci, but also in the complete absence of crystalloid SCBs in paraphyses and excipular cells. Spore shape is also reminiscent of *O. triangulispora* and *O. aviceps*, but these species differ in long glassy processes, the latter also in spores with a basal tail.

Variation. The two collections from the type locality closely concur in spite of the different hosts, and no morphological differences worth mentioning were found. The attachment of the SBs varies within an apothecia on both hosts between a narrow and rather broad point. The sparse collection studied by J.P. Priou also concurs with them except for a spore length at the lower end of the range [*6–6.5 × 4–5 µm, holotype: *(6–)7–9(–9.5) × 4.2–5.5 µm].

Phylogeny. A sequence taken from the holotype comprises S1506 intron, ITS, and LSU. In the ITS region the lowest distance is 11 % to *O. corculispora*, followed by 12.5 % to *O. cryptogena* and min. 16 % to *O. spermoides* and other taxa, whereas in the LSU (D1–D2) the lowest distance is 2.7 % to *O. cryptogena* and 3 % to *O. adenocarpi* (3.5 % to *O. corculispora*). In the intron the distance to other species, including *O. corculispora*, is consistently min. 20 %. For the phylogenetic placement see under *O. corculispora* (p. 658).

Ecology. *O. octocorculispora* was collected on rotten wood of xeric branches of *Pinus* and *Gleditsia* at the type locality, a thermomediterranean semihumid open pine woodland near a hospital in southeastern Spain. The branch of *Pinus* was lying on the ground when collected, but it has been cut perhaps not long ago by local people in order to prevent fires. The third collection was on bark of *Ulex* not far from this place in a mesomediterranean maquis and consisted of only one apothecium.

Specimens included. **SPAIN**: **Com**. **Valenciana**, **Valencia**, 22 km NNW of Valencia, 5.2 km SW of Serra, Porta Çoeli, 500 m SE of Hospital Doctor Moliner, 185 m, branch of *Pinus halepensis*, on wood, 26.I.2014, R. Tena (R.T.L. 14012601, doc. vid.). – ibid., 100 m ENE of Hospital, 203 m, branch of *Gleditsia triacanthos*, on wood, 23.III.2014, R. Tena (ex R.T.L. 14032301, M-0276541, **holotype**, doc. vid.; sq.: KT222382). – 65 km WSW of Valencia, 7.5 km N of Jalance, 3 km NNW of Cofrentes, 430 m, branch of *Ulex*, on bark, 16.V.2015, J.P. Priou (ø, doc. vid.).

Orbilia cryptogena Baral & G. Marson, sp. nov., MB 813538 — Pls 297–298, Map 52

Etymology: named after the apothecia being deeply immersed in the substrate and almost invisible when dry.

Typification: USA, Arizona, New River, branch of *Larrea tridentata*, 19.VI.2003, G. Marson (ex H.B. 7397a, M-0276464, holotype; CBS 140819; sq.: KT215272, MH878189).

Latin diagnosis: *Apothecia rehydratata 0.25–0.6 mm diam., vivide aurantiorubra, sessilia, margine sublaevi, erumpentia, in statu sicco retracta. Asci 32-spori. Ascosporae *8–16 × 3–4.5 µm, valde curvatae (botuliformes), apice rotundatae vel obtusae, basi saepe leniter attenuatae, in statu vivo corpusculum refringens magnum, lacrimiformem, ad apicem affixum continentes. Cellulae vivae paraphysium corpuscula globosa minuta continentes. Habitat ad lignum putridum ramorum siccorum* Larreae tridentatae *in zona subtropica semiarida ad arida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.5(–0.6)((–0.8)) × 0.2–0.3(–0.4) mm diam., 0.14–0.23 mm high, light to bright (dirty) orange(-brick-red), round or often (narrowly) elliptical, subgregarious in smaller or larger groups; disc flat, margin distinct, 0–10 µm rising above disc, ± smooth; broadly sessile or with indistinct obconical base, slightly to nearly completely immersed between fibres; dry strongly retracted and immersed in substrate, deep orange-red, elongate apothecia becoming slit-like. **Asci** *(83–)90–110(–130) × (10.5–)12–13.5(–16) µm {5}, †(73–)80–100(–120) × (10.5–)11–13(–15.5) {4}, 32-spored (rarely very few asci 16-spored), spores *3–4-seriate, about half of spores inversely oriented (strongly mixed), pars sporifera *65–80(–90) µm long, †52–66 µm; **apex** (†) hemispherical to slightly truncate, dome †0.7–1.7 → 0.3–0.8(–1.2) µm thick {5}, rarely with small apical chamber; **base** with or without short to long, thin or thick, ± flexuous stalk, L- or Y-shaped, with short legs. **Ascospores** *(8–)9.5–13(–16)((–17.5)) × (3–)3.5–4.5((–5.5)) µm {5}, †9–11.5(–13) × (2.5–)2.8–4(–4.3) µm {4}, ± subcylindrical, apex rounded to obtuse, base not or often slightly attenuated, slightly to (very) strongly curved [mainly in lower part (L-shaped), also reniform to cashew-shaped]; **SBs** apically attached to spore wall, *2.5–3.5(–4.2) × (1–)1.2–1.6(–1.8) µm {3}, tear- to pear-shaped, apically narrowed to a ± small point, overmature *2–2.5 × 1.7–1.9 µm; with a few minute LBs. **Paraphyses** apically uninflated to medium clavate-capitate, sometimes sublageniform, terminal cells *(4.5–)8–15(–17) × 2.5–3.5(–4) µm {1}, †5–18 × 1.8–3(–4) µm {3}, lower cells *8–20 × 1.8–2.5 µm {1}, †(8–)12–16 × (1–)1.4–1.8(–3) µm {1}; rather frequently branched near apex {6}, often flexuous. **Medullary excipulum** pale rose, 10–50 µm thick, of dense horizontally oriented textura intricata with many inflated cells, sharply delimited.

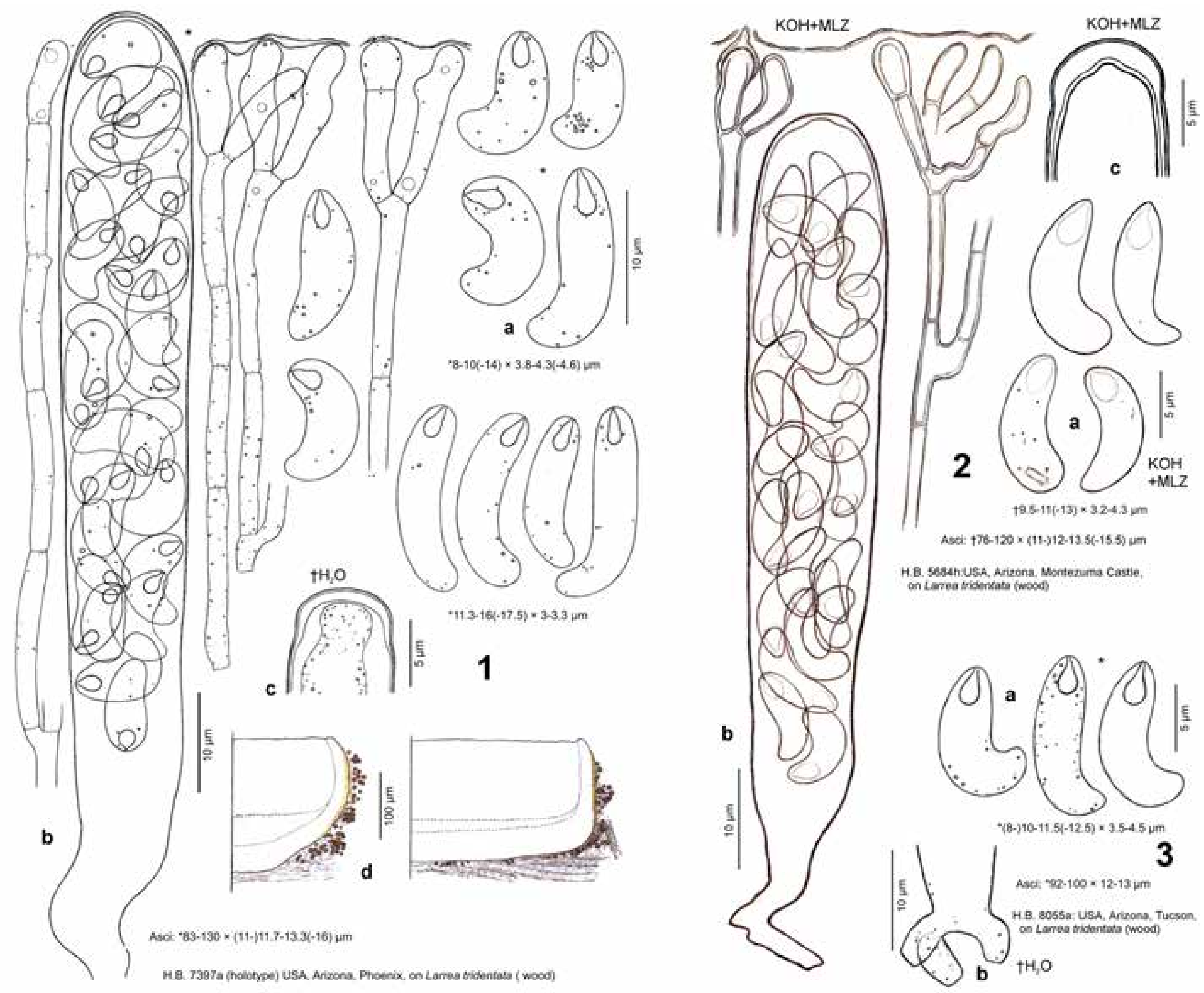


Plate 297. **1–3**: *Orbilia cryptogena*. – **a**. ascospores; **b**. asci and paraphyses (**3b** ascus base); **c**. ascus apices; **d**. apothecia in median section.

Ectal excipulum pale rose, outer layer light to bright golden- or honey-yellow (especially at mid flanks), of (†) not or slightly gelatinized, vertically or indistinctly oriented t. angularis(-prismatica) from base to mid flanks, 25–50 µm thick near base, cells *8–16(–20) × 6–11 µm {1}, †6–12 × (4–)5–8(–10) µm {3}; 15–20 µm thick near margin, of t. prismatica-porrecta oriented at a 10–45° angle to the surface, marginal cortical cells †5–12 × 3–5 µm {2}; **glassy processes** absent. **Anchoring hyphae** medium abundant, †1.8–3 µm wide, walls †0.2–0.4(–0.8) µm thick {3}, sometimes covering mid flanks and margin as a t. porrecta-intricata 10–20 µm thick. **SCBs** in terminal cells of paraphyses globose, 0.5–1.3 µm diam. **Exudate** over paraphyses 0.2–0.5(–1) µm thick, ± continuous or as scattered granules, loosely attached; over excipulum as very scattered granules. — **ANAMORPH**: unknown (an ascospore isolate did not produce conidia and finally died off, therefore it could not be deposited in a culture collection).

Habitat: collected 0.2–2.5 m above the ground, decorticated, 6–14 mm thick branches of *Larrea tridentata* {6}, on 0.2–0.5 mm deep medium to very decayed wood {6}, strongly greyed, no algae. **Associated**: *Carestiella schizoxyloides* {1/1}, *Coniochaeta* sp. {1}, *Hysterobrevium mori* {1}, *Melaspilea emergens* {1}, ?*Muellerella* sp. {1}, *Odontotremataceae* sp. {1}, *Orbilia arizonensis* {1}, *O.* ?*breviclava* {1}, *O. calyptrata* {2}, *O. lacrimispora* {1}, *O. macrodelphinus* {1}, *O. multicercocarpi* {1}, *O. multigambelii* {1}, *O. multiurosperma* {3}, *O.* ?*navajoana* {1}, *O. pluristomachia* {3}, *O. sedonensis* {1}, *O. sonorensis* {1}, *O.* ?*vitalbae* {1}, *Patellaria atrata* {1}, *Symbiotaphrina larreae* {2}. **Desiccation tolerance**: fully tolerant for at least 11 months, after 32 months still many spores viable. **Altitude**: 500–1030 m a.s.l. **Geology**: Neogene sand- & limestone, silt, clay; granite, diorite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia cryptogena* is characterized by 32-spored asci and medium to strongly curved, ± cashew-shaped, comparatively large ascospores with tear-shaped spore bodies in the apex. For the closely related *O. subcryptogena* (p. 665) and *O. myriofusiclava* (p. 653) see there.

Variation. Some variation is observed in spore size and curvature, but such also occurs within a population. Typically the apothecia are elongate when rehydrated and turn slit-like when dry, but some are ± round and remain so when dry and contracted.

Phylogeny. A sequence from pure culture of the holotype of *O. cryptogena* comprises SSU, ITS, and LSU (the S1506 intron is absent). Phylogenetic analyses support a relationship to *O. corculispora* and *O. octocorculispora* (see there, Phyls 9–10, S13), the distances being 10/2.8% and 12.5/ 2.7% in the ITS/ LSU region, respectively.

Ecology. *O. cryptogena* appears to be restricted to ± rotten wood of xeric branches of *Larrea tridentata* (creosotebush). It was collected in the southwest of Northern America in the deserts

Plate 298. **1–4**: *Orbilia cryptogena*. – **1a**. *Larrea tridentata* in dry riverbed of subtropical arid Sonoran Desert; **2a–b**, **3**, **4a–b**, **e**. rehydrated apothecia (**4e** with *Symbiotaphrina desertorum*); **2b**, **d**, **4c**. dry apothecia; **4g**. apothecium in median section; **4f**. id., marginal ectal excipulum; **2f**, **4i**. mature asci and paraphyses; **2e**, **3b**. ascus apices; **1b**, **2g**, **4h**. ascospores. – Living state: ascospores in **1b**, **4h–i**; dead state: **2g**, **4f–g** (in KOH), **2e–f**, **3b** (in KOH+IKI). — **1a–b**. H.B. 7397a (holotype): USA, Arizona, Phoenix, on *Larrea*; **2a–g**. H.B. 5684h: ibid., Montezuma Castle, on *Larrea*; **3a–b**. H.B. 5658a: ibid., Wickenburg, on *Larrea*; **4a–i**. H.B. 8055a: ibid., Tucson, on *Larrea*.

Map 52. Known distribution of *O. cryptogena* in North America.

of Mojave (Death valley) and Sonora, and in the Verde Valley adjacent to Mogollon Rim. The climate is warm-temperate to often subtropical, semiarid to arid and the vegetation includes the Sonoran paloverde-mixed cacti desert scrub, and the Sonoran and Mojave creosotebush desert scrub.

Specimens included. **USA**: **Nevada**, Mojave Desert, 6 km SW of Beatty, 2.6 km SSE of Rhyolite, E of Death Valley, S of Ladd Mt., 1030 m, branches of *Larrea tridentata*, on wood, 2.V.1995, G. Marson (H.B. 5660a). – **Arizona**, Sonoran Desert, 68 km SSW of Flagstaff, 5.5 km NNE of Camp Verde, Montezuma Castle, 975 m, branch of *L. tridentata*, on wood, 8.V.1995, G. Marson (H.B. 5684h). – 200 km NW of Phoenix, Wikieup, ~600 m, branches of *L. tridentata*, on wood, 3.V.1995, G. Marson (H.B. 9573b). – 82 km NW of Phoenix, ~1.5 km SE of Wickenburg, 615 m, branches of *L. tridentata*, on wood, 4.V.1995, G. Marson (H.B. 5658a). – 32 km NNW of Phoenix, 13 km SW of New River, SE of Lake Pleasant, 500 m, branch of *L. tridentata*, on wood, 19.VI.2003, G. Marson (ex H.B. 7397a, M-0276464, **holotype**, CBS 140819; sq.: KT215272, MH878189). – 23 km WNW of Tucson, 6 km SE of Picture Rocks, Saguaro, 882 m, branches of *L. tridentata*, on wood, 30.V.2003, G. Marson (H.B. 8055a).

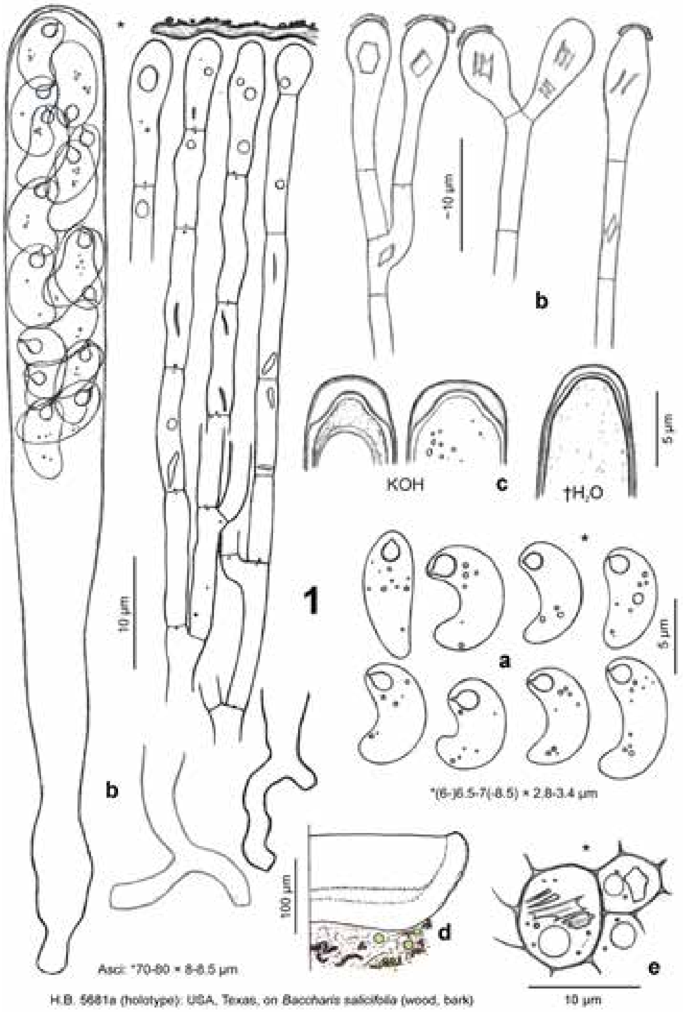


Plate 299. **1**: *Orbilia subcryptogena*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. ectal excipular cells at flanks (containing globose and crystalloid SCBs).

Orbilia subcryptogena Baral & G. Marson, **sp. nov.**, MB 813539 — Pls 299–300

Etymology: closely related to *O. cryptogena.*

Typification: USA, Texas, Hempstead, branch of *Baccharis salicifolia*, 19.VI.1996, G. Marson (ex H.B. 5681a, M-0276593, holotype).

Latin diagnosis: *Differt ab* Orbilia cryptogena *ascis 16-sporis, ascosporis minoribus, corpusculum refringens subglobosum continentibus, cellulis vivis excipuli et paraphysium corpuscula crystalloidea pallide aurantiaca continentibus. Habitat ad lignum vel corticem putridum ramorum siccorum* Baccharidis salicifoliae *in zona subtropica subhumida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.55 mm diam., 0.13–0.23 mm high, deep orange-apricot, round to broadly elliptical, scattered; disc slightly concave to flat, margin thick, rising ~10 µm above disc, ± smooth; broadly sessile, ± erumpent, young completely immersed, mature ± half so or nearly superficial; dry dirty orange-red, somewhat retracted but not deeply sunken. **Asci** *67–82 × (6.8–)7.6–8.5 µm, †70–83(–90) × 6.5–7.8 µm, 16-spored, spores 2–3-seriate, min. ~4 spores inversely oriented (strongly mixed), pars sporifera *49 µm long (†40–50 µm); **apex** (†) hemispherical to slightly (conico-)truncate, dome †1–1.3 → 0.5–1 thick, with broad apical chamber; **base** with short to long, thick stalk, Y-, T- to h-shaped. **Ascospores** *(6–)6.5–8(–8.5) × 2.8–3.6 µm, †5–7 × 2.6–3.2 µm, reniform to cashew-shaped, apex rounded to obtuse, base not or slightly tapered, slightly to mostly medium to very strongly curved; **SBs** apically attached to spore wall, *1.3–2 × 1–1.5 µm, broadly tear-shaped to globose, apically narrowed to a small point, with some minute and larger LBs. **Paraphyses** apically uninflated or slightly to medium clavate-capitate, rarely sublageniform, terminal cells *4.5–13 × 2.2–4(–4.5) µm, lower cells *(6–)8–13 × 1.5–2.5 µm; sometimes branched at upper septum. **Medullary excipulum** pale orange, 20–40 µm thick, of dense textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** hyaline, mid flanks and margin light orange-rose, of (†) slightly to medium gelatinized, vertically oriented t. angularis(-prismatica) from base to margin, 30–80 µm thick near base, cells *10–15 × 8–12 µm, †7–13 × 5–8 µm; 25–40 µm thick at flanks and margin, at margin oriented at a 30–50° angle to the surface, upper margin or outer hyaline layer of t. porrecta oriented at 20°, marginal cortical cells *10–14 × 2.5–3.2 µm, thin-walled, **glassy processes** absent. **Anchoring hyphae** very abundant, †1.7–2.5 µm wide, walls 0.2(–0.3) µm thick, forming a dense 40–70 µm thick, distinctly gelatinized t. intricata. **SCBs** in paraphyses and marginal excipulum globose, 1–1.5 vs. 2–2.8 µm diam., and light orange-rose crystalloid SCBs (in excipular cells 2.5–5 µm diam). **Exudate** over paraphyses (0.5–)1–3(–4) µm thick, continuous, warted, loosely attached; over margin 1–5 µm thick. **— ANAMORPH**: unknown.

Habitat: collected 0.2–1 m above the ground, partially decorticated, 10–12 mm thick branches of *Baccharis salicifolia*, on 0.3 mm deep strongly decayed wood and bark (bast), greyed, with some green algae. **Associated**: *Haematomma* sp., *Hysterobrevium smilacis*, *Lecanora* sp., *Orbilia brachychitonis*, *Parmelia* sp., other crustose and foliose lichens. **Desiccation tolerance**: immature asci still alive after 6.5 months. **Altitude**: 70 m a.s.l. **Geology**: Miocene-Oligocene clay and mud, Quaternary fluviatile sediments. **Phenology**: long-lived.

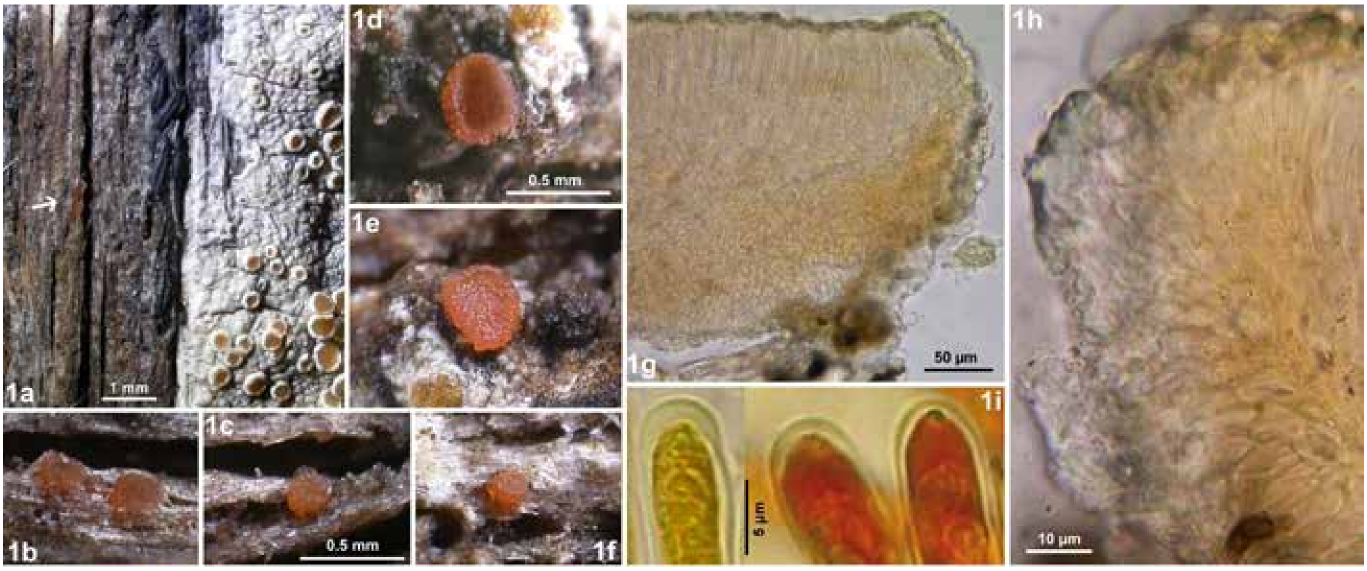


Plate 300. **1**: *Orbilia subcryptogena*. – **1a**. sector of partially decorticated xeric branch of *Baccharis salicifolia*, with *Lecanora* sp. (on bark) and *Hysterobrevium smilacis*; **1b–f**. rehydrated apothecia; **1g**. apothecium in median section; **1h**. id., marginal ectal excipulum; **1i**. ascus apices. – Dead state (**1g–h** in KOH, **1i** in KOH+IKI). — **1a–i**. H.B. 5681a (holotype): USA, Texas, on *Baccharis*.

Taxonomic remarks. *Orbilia subcryptogena* differs from *O. cryptogena* in 16-spored asci, distinctly smaller ascospores, presence of crystalloid SCBs, finally in growing on *Baccharis* instead of *Larrea*. *O. subcryptogena* also resembles *O. vibrioides* of series *Vibrioides* which differs in 8-spored asci, smaller spores, and absence of crystalloid SCBs. The somewhat variable 16-spored *O. corculispora* differs in laterally attached SBs, but may be confused in the dead state if the spores are kidney-shaped.

Ecology. *O. subcryptogena* was found on rotten wood and bark of xeric branches of *Baccharis salicifolia* in a subtropical subhumid woodland at a dry rivulet in the Coastal Prairies of the south of Northern America.

Specimens included. **USA**: **Texas**, Coastal Prairies, 100 km WNW of Houston, 13 km WNW of Hempstead, W of bridge over Brazos river, 70 m, branch of *Baccharis salicifolia*, on wood & bark, 19.VI.1996, G. Marson (ex H.B. 5681a, M-0276593, **holotype**).

Orbilia myriomuscula Baral & G. Marson, **sp. nov.**, MB 813540 — Pls 301–302, Map 53

Etymology: named after the spores resembling little mice.

Typification: Western Australia, Kumarina Roadhouse, branch of *Acacia*, 26.XI.2001, G. Marson (ex H.B. 8697c, MEL 2389248, holotype).

Latin diagnosis: *Apothecia rehydratata 0.22–0.75 mm diam.*, *vivide aurantiaca*, *sessilia*, *erumpentia*, *margine subaspera. Asci 64-spori. Ascosporae *5.7–8 × 3–3.6 µm*, *lunatae*, *apice obtusae*, *basi in caudam *2–6 × 0.3–0.5 µm*, *lateraliter projectam vel apicem versus curvatam extensae*, *corpusculum refringens globosum ad lacrimiformem*, *ad apicem cuspide brevi affixum continentes. Cellulae vivae excipuli marginalis et paraphysium corpuscula crystalloidea pallide aurantiaca, et globosa continentes. Habitat ad corticem, raro lignum putridum ramorum siccorum* Acaciae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.22–0.75 × 0.2–0.4 mm diam., 0.16–0.3 mm high, light to bright orange, non-translucent, round to often ± angular or elongate, scattered to densely gregarious in small groups; disc slightly concave to flat, margin distinct, thick, 0–15 µm protruding, smooth to slightly rough; broadly sessile, ± erumpent between fibres (slightly to strongly immersed). **Asci** *92–120 × 10–11.5 µm {3}, †110–120 × 9.5–11 µm {1}, 64-spored

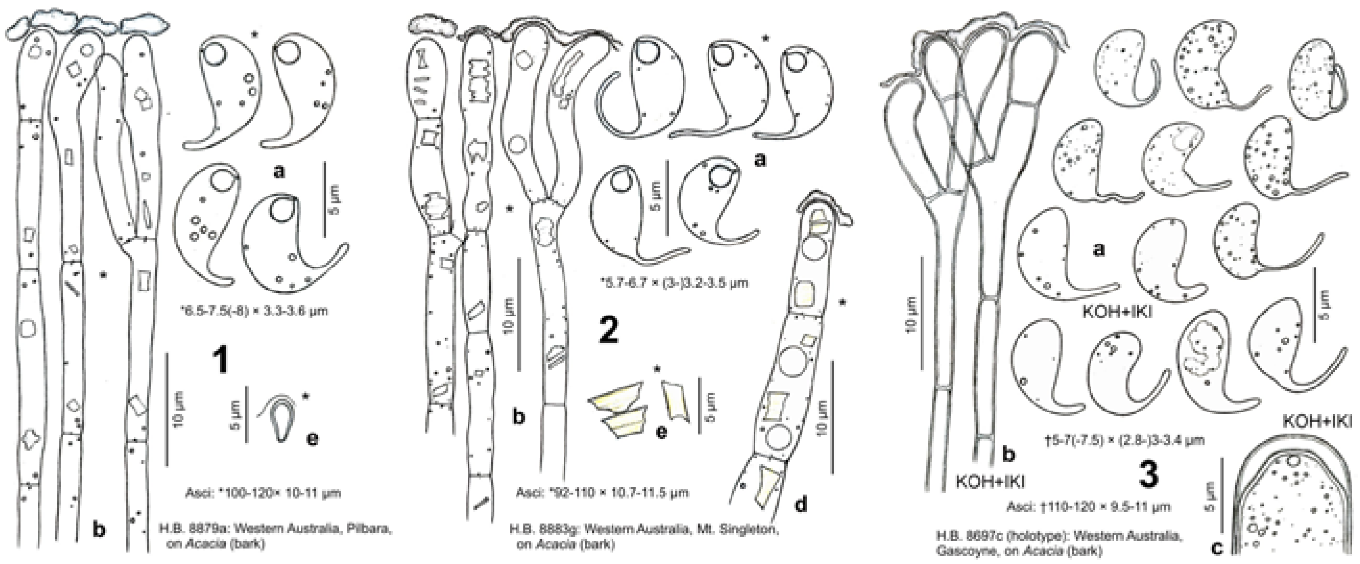


Plate 301. **1–3**: *Orbilia myriomuscula*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex; **d**. marginal cortical cells containing SCBs; **e**. crystalloid SCBs.

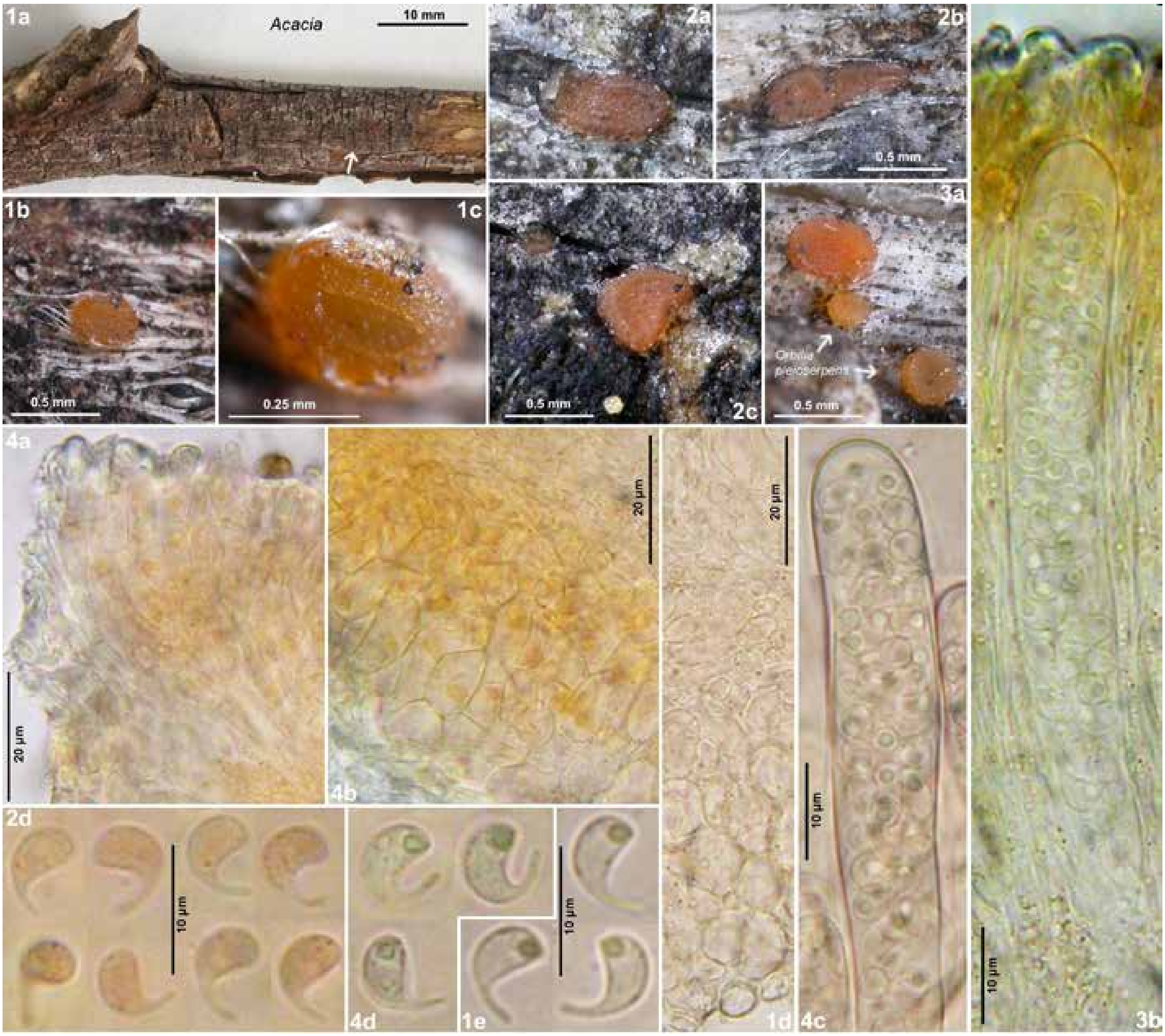


Plate 302. **1–4**: *Orbilia myriomuscula*. – **1a**. dead corticated xeric branch of *Acacia*; **1b–c**, **2a–c**, **3a**. rehydrated apothecia; **4a**. marginal ectal excipulum in median section (cells containing yellow-orange crystalloid SCBs); **1d**, **4b**. id., at base and flanks; **3b**, **4c**. mature asci (and paraphyses); **1e**, **2d**, **4d**. ascospores. – Living state, except for **2d** (in KOH+CR). — **1a–e**. H.B. 8879a: Western Australia, Pilbara, on *Acacia*; **2a–d**. H.B. 8697c (holotype): Gascoyne, on *Acacia*; **3a–b**. H.B. 8940b: Pilbara, on *Acacia*; **4a–d**. H.B. 8883h: Mt. Singleton, on *Acacia*.

(60–62 spores counted), spores (*) 4–5-seriate, orientation irregular, pars sporifera *65–80 µm long (†65–88 µm); **apex** (†) hemispherical to very slightly truncate, dome †0.8–1.3 → 0.4(–0.8) µm thick {3}, with broad, indistinct apical chamber; **base** with short to long, thin or thick, ± flexuous stalk, L- or Y-shaped. **Ascospores** *(5.7–)6.3–7(–8) × (3–)3.3–3.6 µm {2} in situ (actual length ~9–10 µm), †5–7(–7.5) × (2.8–)3–3.4 µm {1}, with ellipsoid head and a distinct, gradually to abruptly attenuated tail *(2–)2.5–4(–6) × 0.3–0.5 µm, †(2–)3–4(–5) × 0.25–0.4(–0.7) µm, head slightly to medium curved (lunate, especially in dead state), apex obtuse (to subacute), tail straight to strongly curved, end projecting at a ~90–150(–250)° angle to the ventral side of the head; **SBs** apically to subapically attached to spore wall, 1.8–2 × 1.2–1.6 µm {2}, globose to broadly tear-shaped or ampulliform, apically narrowed to a small point. **Paraphyses** apically (not or) slightly (rarely medium) clavate, rarely sublageniform, terminal cells *7–21 × 2.5–3.5 µm {2}, †5–15 × 2.5–4 µm {1}, lower cells *9–20 × 1.6–3(–3.5) µm {2}, †10–17 × 1.5–2 µm {1}; sometimes or frequently branched near apex. **Medullary excipulum** subhyaline, 20–50 µm thick, of dense textura intricata with many inflated cells, medium to sharply delimited. **Ectal excipulum** (very) pale yellowish-orange-rose, of (†) slightly gelatinized, vertically oriented t. angularis-prismatica at base, 25–90 µm thick, cells *7–16(–20) × 5–10(–12) µm {3}, †6–13 × 5–9 µm {1}, sometimes containing very pale yellowish **LBs** (carotenoids) 0.2–1.5 µm diam.; 25–40 µm thick at flanks, of. t. angularis(-prismatica), 30–50 µm thick near margin, of t. prismatica-porrecta oriented at a 0–30(–50)° angle to the surface, marginal cells *6–14 × 3–5 µm {2}, sometimes terminated in hyaline appressed hyphae with †10–12 × 2.5–3(–4) µm large cells; **glassy processes** absent. **Anchoring hyphae** abundant, †2–3(–4) µm wide, walls 0.2(–0.3) µm thick {2}. **SCBs** in paraphyses angular, low-refractive, 1–1.7 × 0.7–1.5 µm, in ectal excipulum crystalloid to keyhole-shaped, light yellow-orange, 2–5 × 1.5–3 µm, here also globose, 2–3 µm diam. **Exudate** over paraphyses and margin (0.3–)1–1.5(–2) µm thick, cloddy(-continuous), hyaline, loosely to firmly attached. — **ANAMORPH**: unknown.

Habitat: collected 0.5–3 m above the ground, corticated, 5–15 mm thick branches of *Acacia* sp. {5}, on medium decayed bark {4} (bast, on or in cracks of periderm, or on small periderm-free areas), rarely wood {1}, strongly greyed, no algae. **Associated**: *Amandinea* sp. {1}, *Caloplaca* sp. {1}, *Orbilia anguliobliqua* {1}, *O. australiensis* {1}, *O. corculispora* {1}, *O. curvatiobliqua* {1}, *O. helicoobliqua* {1}, *O. hesperidea* {1}, *O. macrocarpa* {1}, *O. ?mirabilis* {1}, *O. ?multivirgula*

Map 53. Known distribution of *O. myriomuscula* in southwestern Australia.

{1}, *O. myriella* {1}, *O. myrioaustraliensis* {1}, *O. myriofusiclava* {1}, *O. myriolilacina* {1}, *O. myrionanosoma* {1}, *O. myrioobliqua* {1}, *O. paraobliqua* {1}, *O. phanosoma* {2}, *O. pleioaustraliensis* {1}, *O. pleioserpens* {2}, *O. pleioungulata* {1}, *O. ?pseudeuphorbiae* {1}, *Ostropales* {1}, *Rhizodiscina* sp. {1}, ?*Triblidium* sp. {1}. **Desiccation tolerance**: asci and ascospores viable even after 38 months. **Altitude**: 379–690 m a.s.l. **Geology**: Precambrian sedimentary rock (ochre to red-brown sand and gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia myriomuscula* is very remarkable on account of its ascospore tails projecting laterally or even upwards, due to a strong curvature of the spores at the base, in combination with 64-spored asci. The closest relative appears to be *O. myriofusiclava*, which differs in narrower spores with more tapered apices and thicker, much less differentiated tails which are rarely strongly curved. The North American *O. cryptogena* differs in 32-spored asci and much longer spores without tails

Variation. Within a population, considerable variation is noted in the spore tails: they vary in length, thickness, and curvature, as well as between gradually and abruptly attenuated at their insertion. For the other features, *O. myriomuscula* seems to be a very constant species, judging from the few available records.

Ecology. The four rather sparse collections of *O. myriomuscula* were made on bark (rarely wood) of xeric branches of *Acacia* sp. in subtropical semiarid open acacia wood- and shrublands (mulga) inside and south of the Pilbara desert and in the Avon Wheatbelt of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Pilbara, 49 km NW of Newman, northern border of Ophthalmia Range, 690 m, branch of *Acacia*, on bark, 28.X.2007, G. Marson (ex H.B. 8940b, mixture in MEL 2389267 [type of *O. pleioserpens*]; H.B. 8879a). – Gascoyne, south-border of Collier Range, 175 km NE of Meekatharra, 41 km SW of Kumarina Roadhouse, 560 m, branch of *Acacia*, on bark, 26.XI.2001, G. Marson (ex H.B. 8697c, MEL 2389248, **holotype**). - 62 km SSW of Kumarina Roadhouse, 16 km NW Plutonic Gold Mine, 540 m, branch of *Acacia*, on bark, 28.X.2007, G. Marson (ø). – Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, branch of *Acacia*, on bark, 26.X.2007, G. Marson (H.B. 8883h ø).

Orbilia sarothamni Baral, **sp. nov.**, MB 813543 — Pls 303–304

Etymology: named according to the host of the holotype, *Sarothamnus scoparius*, the former name for *Cytisus scoparius*.

Typification: France, Bellecombe, twig of *Cytisus scoparius*, 10.X.2002, G. Marson (ex H.B. 7251c, M-0276583, holotype).

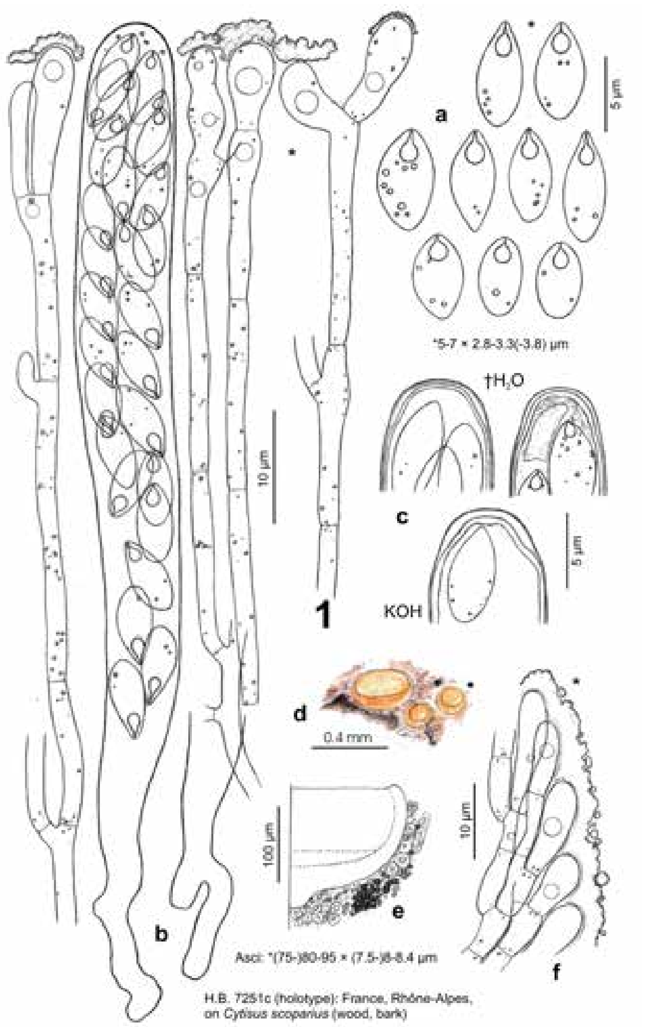


Plate 303. **1**: *Orbilia sarothamni*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., marginal ectal excipulum.

Latin diagnosis: *Similis* Orbiliae palmicolae *sed ascosporae lacrimiformes, corpuscula refringentia tenuiter affixa, cellulae vivae excipuli et paraphysium absque corpusculis crystalloideis. Habitat ad corticem putridum ramulis* Cytisi *et* Erinaceae *in zona supra(sub)mediterranea Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.35 mm diam., 0.12–0.16 mm high, light orange, somewhat translucent, round, scattered or gregarious in small groups; disc slightly concave to flat, margin distinct, 0–10 µm protruding, smooth; broadly sessile or with a peg-like base, superficial, sometimes immersed in biofilm; dry bright orange-red. **Asci** *(75–)80–95 × (7.5–)8–8.4 {T} or (72–)79–93(–107) × 6.5–8 µm {1}, †(60–)72–95 × 6.5–7.6 µm {T}, 32-spored (28–31 spores counted), spores *4-seriate, lower spores inverted (strongly mixed), pars sporifera *(50–)55–65(–78) µm long; **apex** (†) hemispherical to very slightly truncate, dome †0.4–0.8 {T} or 0.8–1 µm thick {1}, with indistinct or distinct apical chamber; **base** with short, thick, flexuous stalk, L- or h-shaped. **Ascospores** *5–7 × 2.8–3.3(–3.8) {T} or *7–8(–8.5) × (2–)2.3–3 µm {1}, ellipsoid to mostly fusoid to fusiform (often ± tear-shaped), rarely ovoid or amygdaliform, apex (obtuse to) subacute to acute (rarely acuminate), base mostly rounded to obtuse, sometimes (sub)acute, ± straight; **SBs** *1.8–2.3 × 1–1.2 {T} or 2–2.6 × 0.9–1.1 µm {1}, tear-shaped or ± globose, apically narrowed to a very short filum. **Paraphyses** apically slightly to medium clavate-capitate, terminal cells *(7–)10–20(–26) × (2–)3–4 µm {2}, lower cells *10–18 × 1.5–2.2(–2.7) µm {2}; frequently branched at upper septum, hymenium pale orange. **Medullary excipulum** hyaline, 20–30 µm thick, of medium dense textura intricata with many inflated cells, very sharply delimited. **Ectal excipulum** pale orange, of (*) thin-walled, (†) distinctly gelatinized, vertically oriented t. angularis(-globulosa)

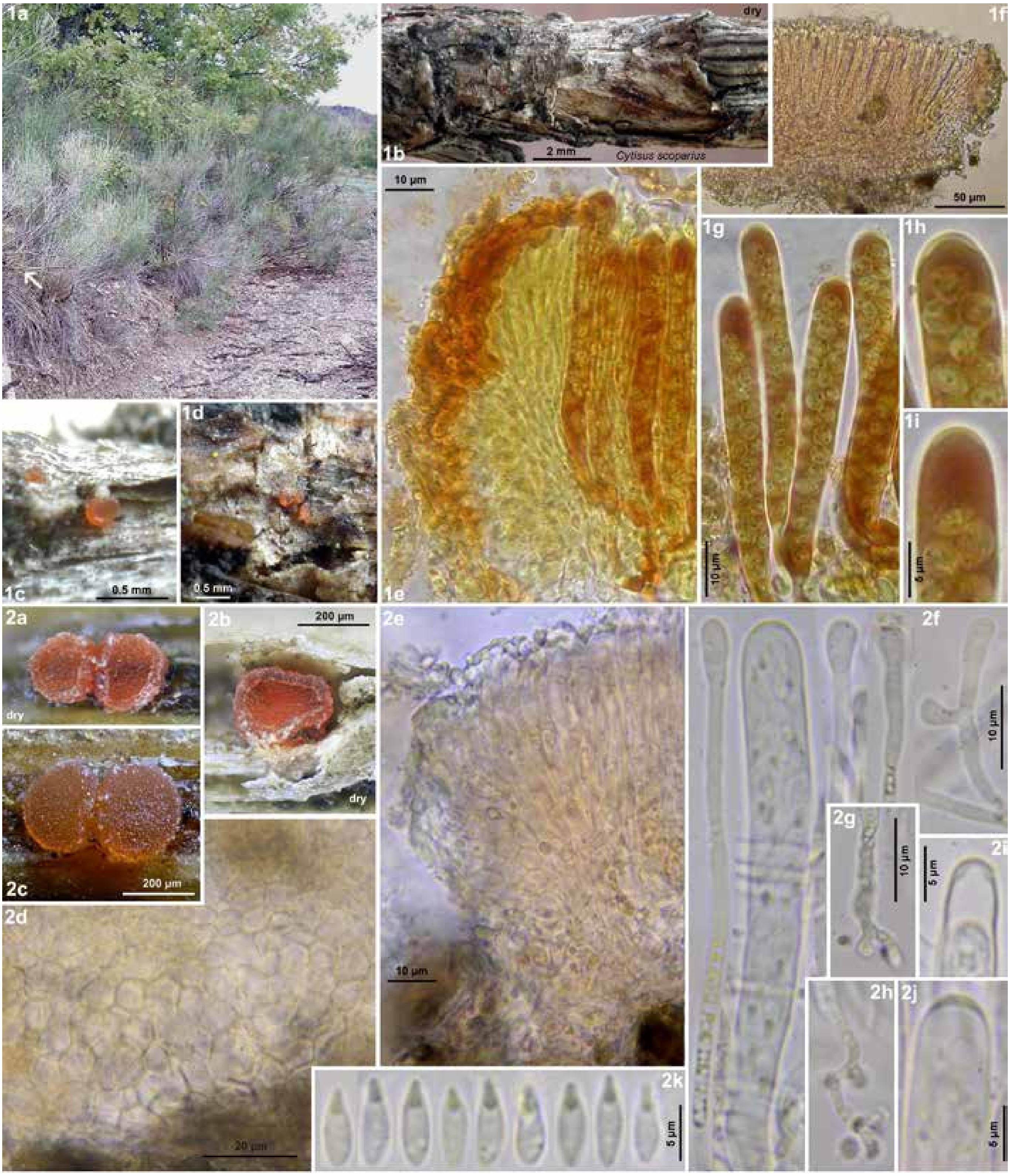


Plate 304. **1–2**: *Orbilia sarothamni*. – **1a**. suprasubmediterranean mixed forest with *Quercus*, *Cytisus scoparius* in foreground; **1b**. dead corticated xeric branch of *C. scoparius*; **1c–d**, **2c**. rehydrated apothecia; **2a–b**. dry apothecia; **1f**. apothecium in median section; **1e**, **2e**. id., marginal ectal excipulum; **2d**. basal ectal excipulum; **1g**. mature asci; **2f**. mature ascus and paraphyses; **2g–h**. furcate ascus bases; **1h–i**, **2i–j**. ascus apices. – Living state: **2d–f**, **2j–k**; dead state: **1f** in KOH; **1e**, **g–i** in KOH+IKI; **2i** in H_2O. — **1a–i**. H.B. 7251c (holotype): France, Rhône-Alpes, on *Cytisus*; **2a–k**. 19.IV.2014: Spain, Andalucía, on *Erinacea*.

from base to mid flanks, 25–40 µm thick near base, cells *7–16 × 6–13 µm {T}, common walls 0.5–1.5 µm thick; 15–25 µm thick at mid flanks, 15–20 µm near margin, of t. prismatica-porrecta oriented at a 10–30(–40)° angle to the surface, marginal cortical cells *8–16 × 3–4.3 µm {T}, †2.5–3.5 µm wide {T}, thin-walled (walls †0.2 µm thick); **glassy processes** absent {2}. **Anchoring hyphae** very sparse, †2–3 µm wide, walls 0.2–0.3(–0.4) µm thick {T}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.5–2.5 µm diam. {2}; with minute pale orange **LBs** (carotenoids) especially near septa. **Exudate** over paraphyses 1–2 µm thick, cloddy-bizarre, hyaline, rather loosely attached; over margin and flanks 1–4 µm thick, pale chlorinaceous. — **ANAMORPH**: unknown.

Habitat: collected 0.1–1 m above the ground, ± corticated, 1–6 mm thick twigs of *Cytisus scoparius* {T}, *Erinacea anthyllis* {1}, on strongly decayed bark {2} (periderm & bast), also sometimes in beetle galleries on wood {T}, slightly to medium greyed, with some or many green algae. **Associated**: *Caloplaca* sp. {1}, *Claussenomyces* sp. {1}, *Orbilia gambelii* {1}, *O. pleiogambelii* {1}, *O. polyspora* {1}, *O. subclavuliformis* {1}. **Desiccation tolerance**: fully viable for at least 6 weeks, some spores still alive after 2 years. **Altitude**: 880–1690 m a.s.l. **Geology**: Cretaceous marl & gravel, dolomite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia sarothamni* is characterized by 32-spored asci and ± tear-shaped to fusoid ascospores. It resembles the Australian *O. palmicola*, from which it differs in the absence of crystalloid SCBs, more acute spore apices, never tail-like spore bases, and a narrower attachment of the SBs. *O. sarothamni* also resembles *O. polyspora* (section *Ovoideae*), which differs in narrower, ellipsoid ascospores with rounded apices and smaller SBs, in the total absence of an apical dome, finally in the presence of thick-walled hair-like marginal hyphae.

Variation. The sample on *Erinacea* differs from the holotype in longer and narrower spores and SBs, narrower asci, and in apically less narrowed SBs. Whether these differences represent variation of a single species as assumed here remains uncertain, until further collections are available.

Phylogeny. A sequence taken from pure culture of the Spanish paratype comprises S1506 intron, ITS, and LSU. *O. sarothamni* clustered with strong or medium support (ITS+LSU, ITS) in a subclade of the *cryptogena-sarothamni* clade, together with *O. adenocarpi* and *O. concoloris* with an ITS distance of 9.3 %, to which *O. myriofusiclava* is associated with medium support and a 16 % distance (Phyls 9, S13). The undocumented Australian collection on *Acacia aneura* with 8-spored asci (G.M. 2007-11-02.1; ITS, S1506 intron absent) clustered with a 9.2 % ITS distance strongly supported with *O. sarothamni* (Phyl. 10).

Ecology. *O. sarothamni* was found on rotten bark and wood of xeric twigs of *Cytisus* and *Erinacea* shrubs (*Faboideae*) in a thermophilous (south-exposed) suprasubmediterranean semihumid shrubland with *Juniperus*, *Sorbus*, *Acer*, *Quercus*, and different members of *Fabaceae* in the Southern French Prealps, and in a supramediterranean (semihumid) dwarf shrub vegetation of max. 30 cm height on limestone rock in the Sistema Bético of southern Europe. In the paratype the inhabited twig was only 1 mm thick.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Drôme**, 16.3 km E of Nyons, 1.5 km NNW of Bellecombe, 1 km SW of Col de Soubeyrand, 880 m, twig of *Cytisus scoparius*, on bark & wood, 10.X.2002, G. Marson (ex H.B. 7251c, M-0276583, **holotype**). — **SPAIN**: **Andalucía**, **Jaén**, Sierra de La Pandera, 15 km S of Jaén, 5 km NNE of Valdepeñas de Jaén, 1690 m, twig of *Erinacea anthyllis*, on bark, 19.IV.2014, S. Tello (H.B. 9880; sq.: KT380083).

Orbilia myrioauris Baral & G. Marson, sp. nov.,
MB 813535 — Pls 305–306

Etymology: named after the 64-spored asci and the somewhat ear-shaped ascospores.

Typification: Western Australia, Hamelin Pool, twig of *Acacia*, 6.XI.2007, G. Marson (ex H.B. 8727b, MEL 2389251, holotype).

Latin diagnosis: *Apothecia rehydratata 0.18–0.32 mm diam., lateritio-rubra, sessilia, margine subtiliter aspera. Asci 64-spori. Ascosporae *6.8–11.5 × 2.2–3 µm, cylindrico-clavatae, apice obtusae, ad basim leniter vel valde curvatae, in statu vivo corpusculum refringens globosum, ad tunicam lateralem vel interdum (sub)apicalem cuspide brevi affixum continentes. Cellulae vivae excipuli marginalis et paraphysium corpuscula globosa et crystalloidea continentes. Habitat ad corticem putridum ramuli sicci* Acaciae *in zona subtropica arida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.18–0.32 mm diam., 0.15 mm high (receptacle 0.11 mm), light brick-red(-orange), somewhat translucent, round, scattered; disc flat, margin distinct, thin or thick, 0–10 µm protruding, finely rough; broadly sessile, with hidden stipe-like base 0.05 × 0.1 mm, partially to entirely immersed in biofilm; dry ± invisible. **Asci** *(67–)75–109 × (10–)10.5–12 µm {2} → 13.5 µm wide, †58–76 × 8.5–10.7 µm {1}, 64-spored (~60 spores counted), spores *multiseriate, lower spores inverted (strongly mixed), pars sporifera *48–63 → 46 µm long; **apex** (†) hemispherical to medium truncate, dome †1–1.5 → 0.8–1 µm thick {1}, with broad apical chamber; **base** with (very) short, thick stalk, Y- to h-shaped. **Ascospores** *(6.8–)7.5–9.5(–11.5) × (2.2–)2.4–2.8(–3) µm {2}, cylindric-clavate, both ends rounded to obtuse, base not or usually slightly attenuated (almost homopolar), very slightly to rather strongly curved (entirely or near base); **SBs** laterally attached at the convex side at or somewhat below the middle of the spore, rarely ± subapically, *1.5–2 × 1.1–1.3(–1.5) µm {2}, broadly tear-shaped to ampulliform or subglobose, apically narrowed to a small or rather wide point. **Paraphyses** apically uninflated to slightly (rarely strongly) clavate, terminal cells *(6–)7.5–11.5 × 2.3–3.5 µm {1}, lower cells *(8–)10–19(–23) × 1.6–2.5(–3.3) µm {1}; sometimes branched at upper septum. **Medullary excipulum** hyaline, 25 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** subhyaline near base, pale rose at margin, of (†) thin-walled to slightly gelatinized, vertically oriented t. angularis-prismatica at base, 45 µm thick, cells *7–12 × 5–8 µm {1}, t. angularis at flanks, 15–20 µm thick near margin, submargin of t. prismatica-angularis oriented at a 10–20° angle to the surface, cells *8–12 × 4–6 µm {1}, upper margin of t. porrecta oriented at 10°, marginal cortical cells */†6–12.5 × 3–7 µm {1}; **glassy processes** absent. **Anchoring hyphae** sparse, †1.7–2.3 µm wide, walls 0.2–0.3 µm thick {1}. **SCBs** globose, in paraphyses 1–2 µm diam., in marginal ectal excipulum 2–3.5 µm; also crystalloid SCBs frequent in paraphyses and ectal excipulum (margin and flanks), hyaline to pale orange. **Exudate** over paraphyses (0.5–)1–2 µm thick, cloddy, hyaline, ± loosely attached, over margin and flanks 0.3–2(–5) µm thick. **— ANAMORPH**: unknown.

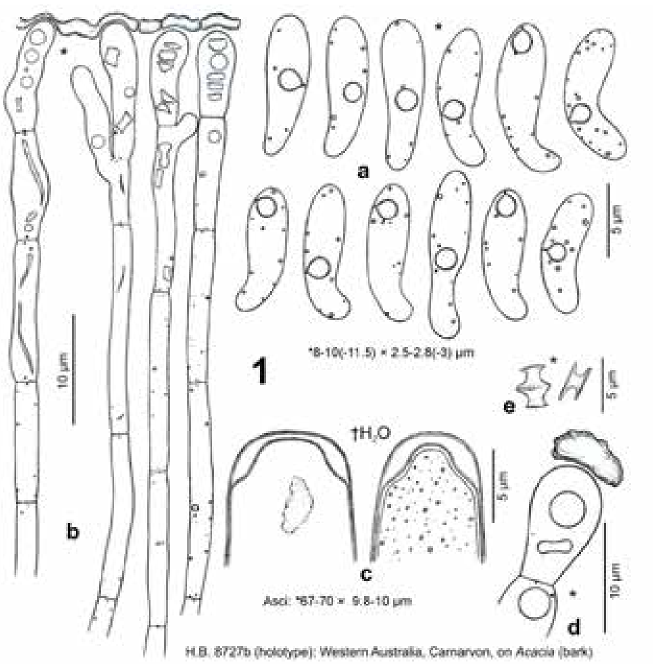


Plate 305. **1**: *Orbilia myrioauris*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal cells of ectal excipulum, tipped by exudate; **e**. crystalloid SCBs in ectal excipular cells (flanks and margin).

Habitat: collected 0.5–2 m above the ground, corticated, 4–6 mm thick twigs and thicker branches of *Acacia* sp. {2}, on strongly decayed bark (bast) {2}, in cross-clefts of periderm, strongly greyed, with some green algae. **Associated**: *Coccomycetella* sp. {1}, *Hyalorbilia ?erythrostigma* {1}, *Hysterobrevium mori* {1}, *Orbilia commarosa* {1}, *O. curvatimyriella* {1}, *O. microserpens* {1}, *O. multigambelii* {1}, *O. myriella* {1}, *O. ?myrionamibica* {1}, *O. pleioaustraliensis* {1}, *O.*

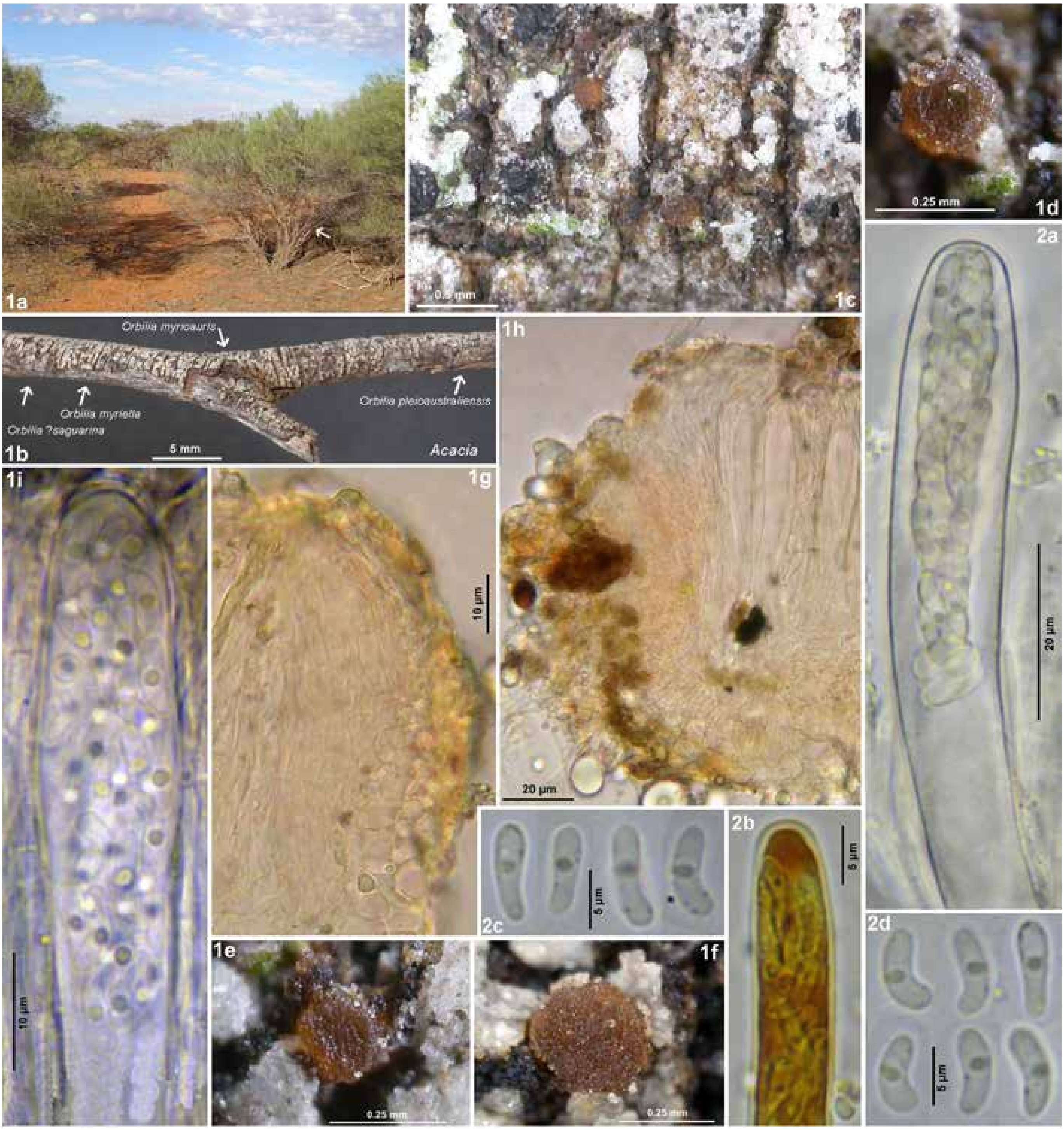


Plate 306. **1–2**: *Orbilia myrioauris*. – **1a**. semiarid acacia shrubland; **1b**. dead corticated xeric branch of *Acacia*; **1c–f**. rehydrated apothecia; **1g–h**. marginal ectal excipulum in median section; **1i**, **2a**. asci with ascospores (**2a** fully turgescent); **2b**. ascus apex. **2c–d**. ascospores. – Living state, except for **2b** (in IKI). — **1a–i**. H.B. 8727b (holotype): Western Australia, Carnarvon, on *Acacia*; **2**. 4.XI.2007: ibid., Pilbara, on *Acacia*.

pleistoobliqua {1}, *O. ?saguarina* {1}, *Ostropales* {1}, *Tryblidaria* sp. {1}. **Desiccation tolerance**: fully viable for 40 months. **Altitude**: 67–300 m a.s.l. **Geology**: Cretaceous sedimentary rock, Cenozoic regolith (red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. In addition to its 64-spored asci, *O. myrioauris* is easily recognized in the living state by cylindric-clavate ascospores which are more or less curved towards their base, and particularly by the subglobose to ampulliform spore body at the convex side of the spore, often a bit below the middle. However, because of their approximate homopolarity the upper spore end is not always clearly recognizable. In a few spores of an ascus the SBs were attached at the spore apex or close to it, but this peculiarity was seen only in the holotype. The lateral attachment of SBs in *O. myrioauris* somewhat resembles the situation in the 16-spored *O. corculispora*.

Ecology. The very sparse and scattered apothecia of *O. myrioauris* occurred on rotten bark of thin xeric branches of *Acacia* in subtropical semiarid to almost tropical arid acacia open shrublands (at the latter site in a tussock grassland with *Livistona alfredii*) in dry riverbeds of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Pilbara, 96 km S of Roebourne, 42 km SSW of Python Pool, SW Millstream-Chichester, Road crossing the Fortescue River, 300 m, branch of *Acacia*, on bark, 4.XI.2007, G. Marson (ø). – Carnarvon, 183 km SSE of Carnarvon, 10 km

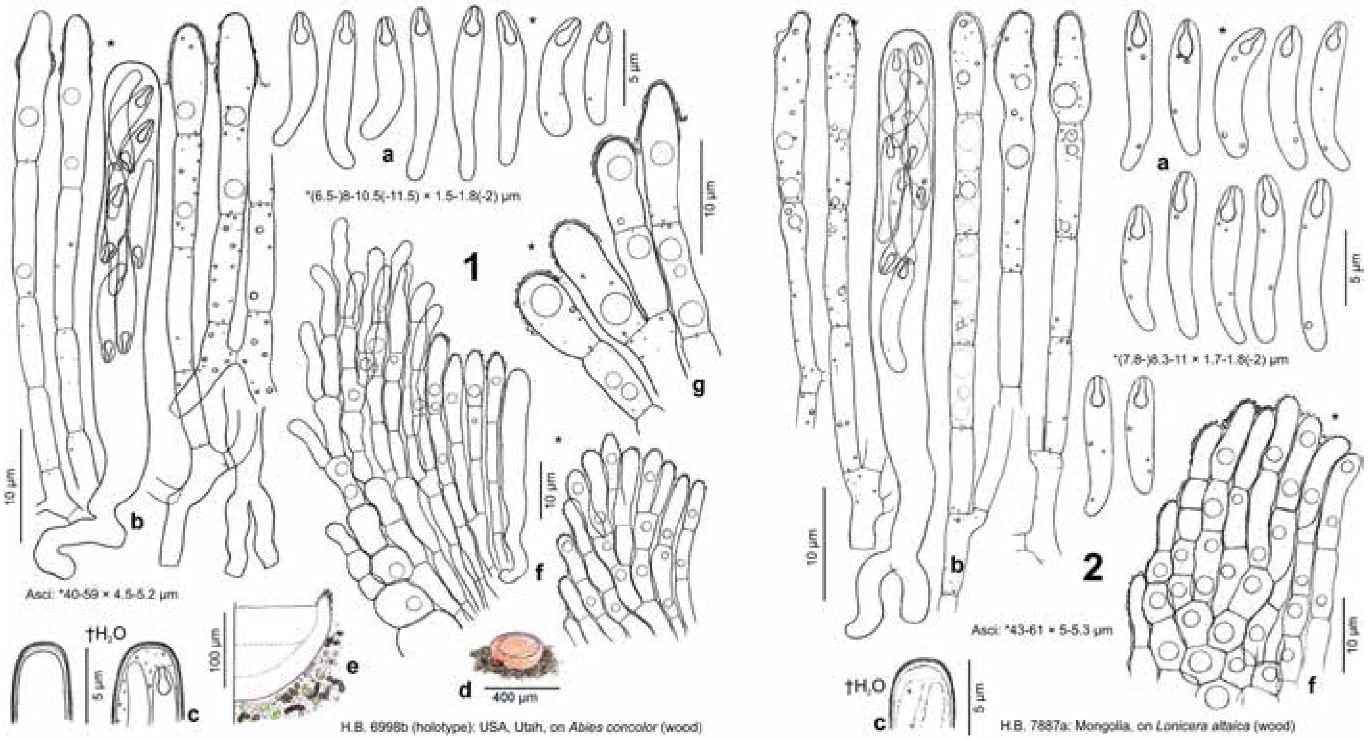


Plate 307. **1–2**: *Orbilia concoloris*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium (rehydrated); **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. id., cortical cells with thin exudate.

W of Overlander Roadhouse, 12 km NE of Hamelin Pool, Denham-Hamelin Road, 67 m, twigs of *Acacia*, on bark, 6.XI.2007, G. Marson (ex H.B. 8727b, MEL 2389251, **holotype**).

Orbilia concoloris Baral & G. Marson, **sp. nov.**, MB 813758 — Pls 307–309

Etymology: named after the host plant in the holotype, *Abies concolor*.
Typification: USA, Utah, Panguitch, branch of *Abies concolor*, 20.VI.2000, G. Marson (ex H.B. 6998b, M-0276460, holotype).

Latin diagnosis: *Apothecia rehydratata 0.18–0.7 mm diam., roseo-aurantiaca, sessilia, suberumpentia, margine glabro vel saepe subtiliter crenulato. Ascosporae *6.5–11.5 × 1.5–2 µm, subcylindricae, apice rotundatae vel obtusae, basi non vel leniter attenuatae, leniter vel modice curvatae, in statu vivo corpusculum refringens ampulliformem continentes. Paraphyses ad apicem leniter inflatae, spathulatae ad lageniformes. Margo excipuli subpilosa, absque processis vitreis. Habitat ad lignum putridum ramorum siccorum* Abietis *vel* Lonicerae *in zona boreali ad temperata humida ad subhumida continentali Americae septentrionalis et Asiae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.18–)0.25–0.6(–0.7) mm diam., 0.11–0.21 mm high (receptacle 0.1–0.13 mm), light to bright rose to rose-orange, semitranslucent, round (to elliptical), very scattered to subgregarious; disc medium concave to flat, margin 5–40 µm protruding, smooth to often finely pubescent or crenulate; sessile on an obconical base, or with obconical stipe 0.06 × 0.15 mm, slightly erumpent from wood fibres. **Asci** *40–61 × 4.5–5.3 µm {2}, †39–56 × 4.2–4.7 µm {1}, 8-spored, spores *2–3-seriate, (2–)3–4 lower spores inverted (often strongly mixed) {3}, pars sporifera *23–30 µm long; **apex** (†) slightly to medium truncate (never indented or laterally inflated), hemispherical in profile view, thin-walled {3}; **base** with or without short to medium long, ± thick, flexuous stalk, L- to Y-shaped. **Ascospores** *(6.5–)8–11.5(–12.3) × (1.5–)1.6–2 µm {3}, subcylindric(-clavate), rarely fusoid-clavate, apex rounded to obtuse, base not or often slightly narrowed, sometimes in a thick tail-like end, slightly to medium curved or geniculate, especially near base; **SBs** *1.5–2.7 × 0.7–1 µm {3}, ampulliform, rarely tear-shaped, apically narrowed to a wide or narrow point. **Paraphyses** apically slightly (to medium) spathulate to lageniform, terminal cells *(6.5–)9–19(–23) × 2.5–3.3(–3.6) µm {3}, exceeding the living asci by 0–5 µm, the dead asci by 3–7 µm, lower cells *8–13(–17) × 1.8–2.8 µm {2} (5–9 µm long near base); never branched at upper septum. **Medullary excipulum** pale rose-orange, 20–80 µm thick, of dense or loose textura intricata with many inflated cells, indistinctly or sharply delimited. **Ectal excipulum** very pale rose, of thin-walled († slightly gelatinized), irregularly vertically oriented t. globulosa-angularis from base to submargin, 20–100 µm thick near base, cells *7–21 × 6–12(–15) µm {3}; 15–20 µm thick near margin, uppermost margin of t. prismatica-porrecta oriented at a 10–30° angle to the surface, marginal cortical cells *7–13(–19) {3} × 2.5–4.5 {1} or 5–6 {1} µm, often terminating as free short **hairs** (7–20 µm long) or conglutinate to form small teeth; **glassy processes** absent. **Anchoring hyphae** ± sparse to medium abundant, */†2–4 µm wide, walls 0.2–0.7(–1) µm thick {3}. **SCBs** globose, in paraphyses 1–2 µm diam.; in marginal excipulum 1.5–3.2 µm diam. **Exudate** 0.1–0.2(–0.4) µm thick, ± firmly attached, over paraphyses covering apex and lateral sides; over margin more granular. **— ANAMORPH**: vermispora-like (presumed, from natural substrate {1}). **Conidiophores** not observed. A single **conidium** found, curved at the ends, straight in middle part, *42.5 × 5 µm, 11-septate.

Habitat: collected 0.2–3 m above the ground, decorticated, 5–22 mm thick twigs and branches of *Abies concolor* {1}, *Lonicera altaica* {1}, *L. microphylla* {1}, on 0.2–0.5 mm deep strongly decayed wood {3}, at edge of longitudinal cleft, or in old beetle galleries, strongly greyed, with many green algae. **Associated**: *Amandinea* sp. {1}, *Claussenomyces* sp. {1}, *Durella atrocyanea* {1/1}, *Glyphium corrugatum* {1}, *Lachnellula* sp. {1}, *Lecanora* sp. {1}, *Orbilia basiflexa* {1}, *O. delphinus* {2}, *O. euonymi* {1}, *O. maeandrina* {1}, *O. phanosoma* {1}, *O. pileosoma* {1}, *Parmelia* sp. {1}, *Stenocybe* sp. {1}, ?*Teichospora* sp. {1}. **Desiccation tolerance**: fully viable for at least 17 months. **Altitude**: 2095–2778 m a.s.l. **Geology**: USA: Upper Cretaceous calcareous sandstone; Mongolia: Paleozoic sediment. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia concoloris* is characterized by medium-sized, subcylindrical, basally ± geniculate ascospores having rounded to obtuse apices with ± ampulliform SBs, only slightly tapered bases, the absence of an ascus apical wall thickening, apically spathulate to lageniform, though hardly

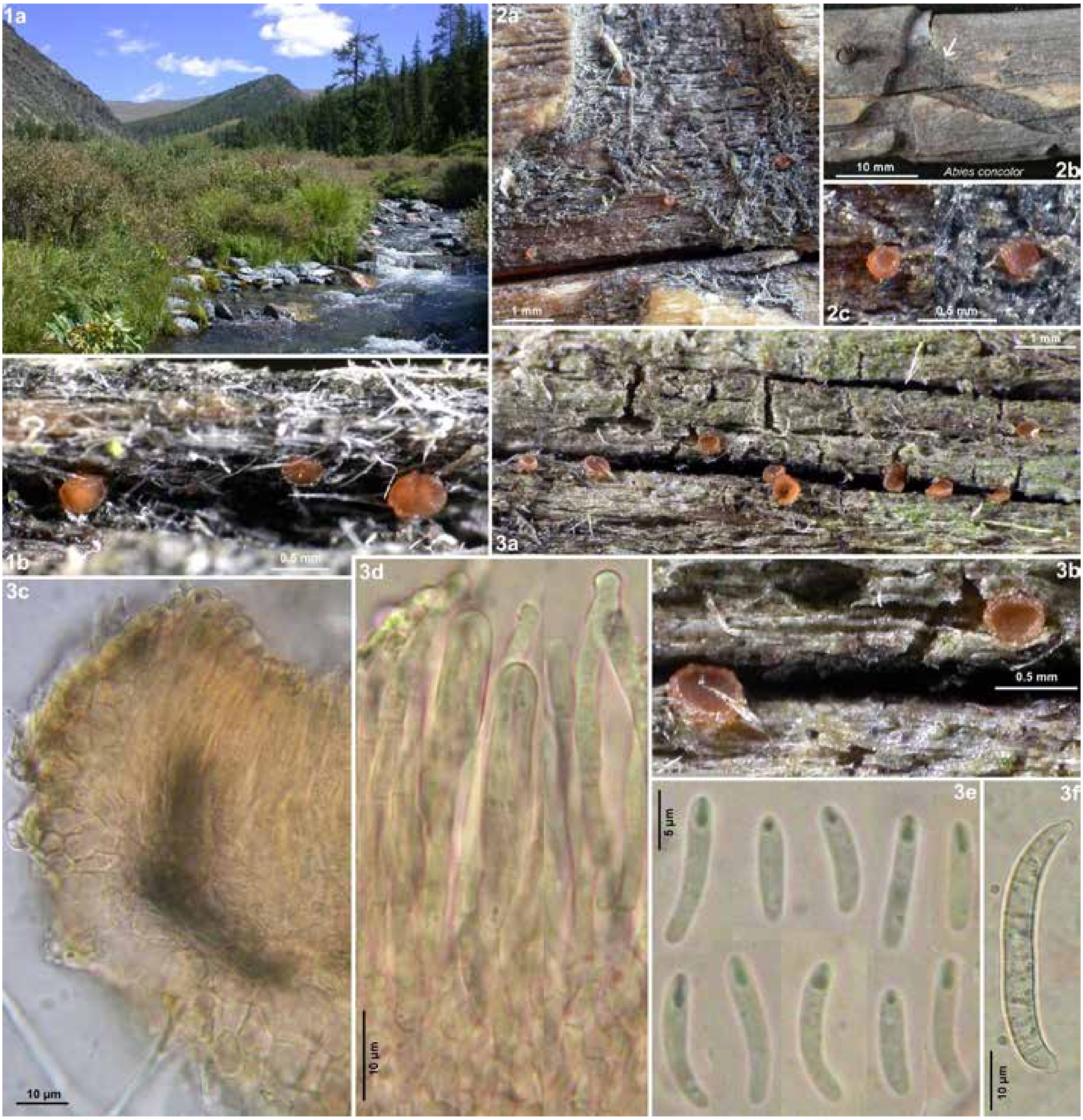


Plate 308. **1–3**: *Orbilia concoloris*. – **1a**. mountainous humid taiga with *Larix sibirica*, *Picea obovata*; **1c**. xeric decorticated branch with beetle gallery; **1b**, **2a**, **c**, **3a–b**. rehydrated apothecia; **3d**. apothecium in median section (margin and flanks); **3d**. asci and paraphyses; **3e**. ascospores; **3f**. conidium from substrate. – Living state. – **1a**: phot. P. Karasch. — **1a–b**. H.B. 7887a: Mongolia, Altay Mts., on *Lonicera altaica*; **2a–c**. H.B. 6998b (holotype): USA, Utah, on *Abies*; **3a–f**. H.B. 7897a: Mongolia, Altay Mts., on *Lonicera microphylla*.

inflated paraphyses with a thin cap-like exudate that covers their apices also laterally, and hair-like marginal cells without glassy processes. The spores resemble those of *O. denticulata* (series *Regales* of section *Aurantiorubrae*), which differs, e.g., in smaller SBs, more strongly inflated paraphysis apices with thick exudate caps, and in having glassy processes forming small to large teeth at the margin.

In spore morphology *O. concoloris* s.l. resembles also a North American specimen on *Larrea* with 16-spored asci and crystalloid SCBs mentioned under *O. pleionavajoana* (H.B. 5687g).

Unusual within series *Hesperideae* are the paraphyses and hair-like elements of *O. concoloris* with their thin layer of exudate, and particularly the thin-walled ascus apex. Placement in series *Hesperideae* is supported by ascospore and SB morphology, and particularly by the presence of an apical thickening in the very similar sample from Poland.

Variation. The Mongolian samples have longer SBs (2–2.7 µm) and very slightly larger spores, but otherwise well concur with the North American type specimen (SBs 1.5–2.2 µm). In all three collections the SBs vary in their apical attachment between narrowly and rather broadly attached.

Not included collection. On a coniferous fence in southern Poland a single apothecium was observed, which closely resembles *O. concoloris* in the spathulate paraphyses with a

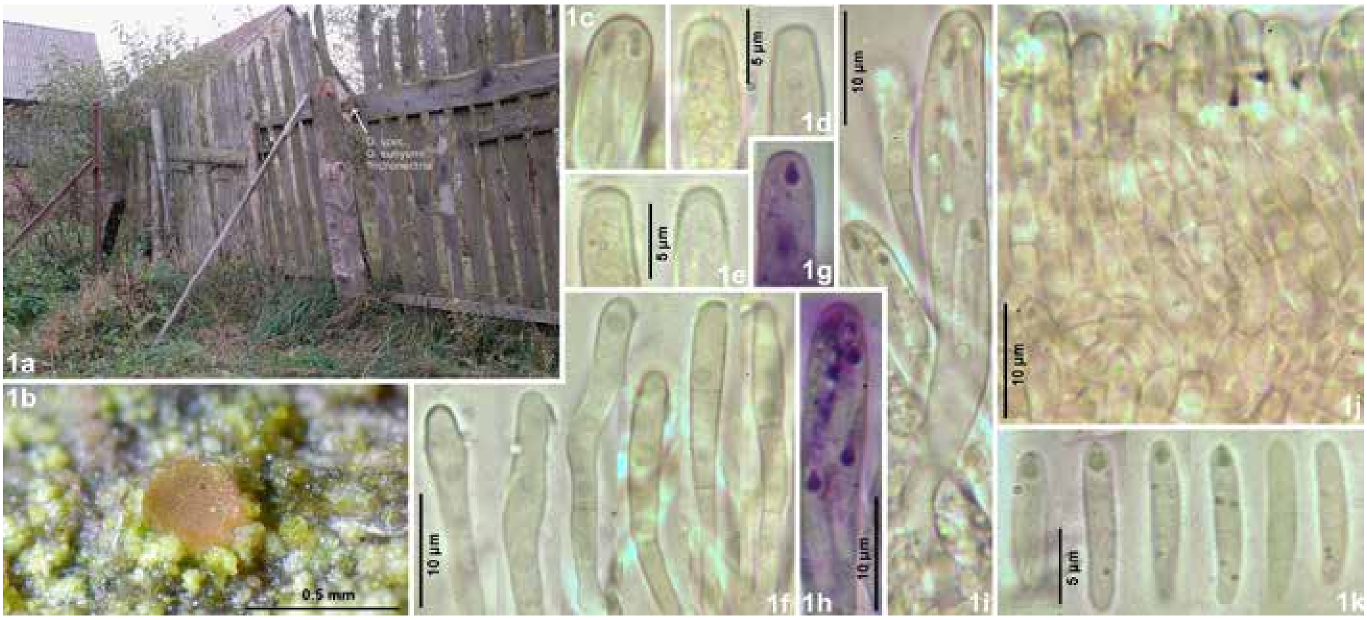


Plate 309. **1**: *Orbilia* aff. *concoloris*. – **1a**. old *Picea* fence; **1b**. rehydrated apothecium; **1c–e**, **g–h**. ascus apices; **1f**, **i**. asci and paraphyses; **1j**. marginal ectal excipulum (external view); **1k**. ascospores. – Living state, except for **1d–e** (in KOH); asci in **1g–h** (in CRB); 2 right spores in **1k** (in H_2O). — **1a–k**: phot. P. Perz, H.B. 9234b: Poland, Kłodzko, on *Picea*.

thin exudate and in the spores (*9–11.2 × 1.7–2 µm) and SBs (1.4–2 × 0.7–0.9 µm). It merely differs in a distinct ascus apical thickening of 0.7 µm and never distinctly curved spores (Pl. 309).

Phylogeny. From apothecia of one of the Mongolian specimens an ITS sequence was gained, in which the S1506 intron is absent. *O. concoloris* was first thought to belong to series *Regales* of section *Aurantiorubrae*. However, the species clustered unresolved when analysing a dataset restricted to that section by showing a distance of 20–21 % to members of series *Regales*, whereas in phylogenetic analyses of section *Hemiorbilia* (Phyls 9–10) it clustered with high (ITS+LSU) or medium (ITS) support in a subclade of the *cryptogena*-*sarothamni* clade, together with *O. adenocarpi* and *O. sarothamni*, with an ITS distance of 8.3 % and 9.3 %, respectively. Indeed, BLAST search for *O. concoloris* in GenBank yielded these two species of series *Hesperideae* as closest match, besides various other members of section *Hemiorbilia*. *O. concoloris* is indeed very different from series *Regales* in both the ITS1 and ITS2 region.

Ecology. *O. concoloris* was found on rotten wood of xeric twigs and branches of both gymno- and angiosperms. In western North America it occurred on *Abies* in the boreal humid Douglas fir mixed conifer forest at the southern end of the Utah Mountains, and in central Asia on *Lonicera* in an orotemperate (sub)humid (winter-dry), subalpine, continental, north-exposed mountain taiga (with *Larix sibirica* and *Picea obovata*) and adjacent south-exposed shrub vegetation (with *Spiraea alpina*, *Ribes nigrum*, *Juniperus sabina*). The not included collection from Poland was on a standing *Picea* fence on calcareous (Cretaceous) clay soil in temperate humid central Europe.

Specimens included. **USA**: **Utah**, Utah Mts., Bryce Canyon, 42 km SSE of Panguitch, Rainbow Point, 2778 m, branch of *Abies concolor*, on wood, 20.VI.2000, G. Marson (M-0276460, **holotype**; **isotype** in H.B. 6998b). — **MONGOLIA**: **Bayan Ölgii**, Sagsai, Altay Mts., S-part of Tavan Bogd, 25 km SE of Dayan lake, 8 km NE of Chinese border, Songino Gol river valley, 2100 m, twig & branch of *Lonicera altaica*, on wood, 15.VIII.2005, P. Karasch (H.B. 7887a). – ibid., 2095 m, branch of *L. microphylla*, on wood, 16.VIII.2005, P. Karasch (H.B. 7897a, anam. substr.; sq.: KT222352).

Not included. **POLAND**: **Lower Silesia**, 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, board of *Picea abies*, on wood, 25.IX.2009, P. Perz (H.B. 9234b ø, doc. vid.).

Orbilia adenocarpi Baral, Quijada & Beltrán-Tej., in Quijada et al., Nova Hedwigia 96: 239 (2012) — Pls 310–311, Map 54

Etymology: named after the substrate of the type, *Adenocarpus viscosus*.
Typification: Macaronesia, Tenerife, El Portillo, branch of *Adenocarpus viscosus*, 25.III.2009, L. Quijada, E.V. Rodríguez & R. Castro (ex H.B. 9056, TFC Mic. 21741, holotype; sq.: KT222366).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.25–0.7(–0.9) mm diam., (0.12–)0.15–0.23(–0.3) mm high, light orange to rose(-orange), not or slightly translucent, round, scattered to subgregarious; disc flat (to slightly convex), margin distinct, ± thick, 5–10 µm protruding, smooth to very finely rough; broadly sessile or on a narrowed base, superficial or somewhat erumpent between fibres; dry slightly contracted, deep orange. **Asci** *(61–)71–108(–116) × (5.3–)5.8–7(–7.6) µm {2}, †(55–)65–90(–110) × 5–6(–6.3) µm {2} (up to 6.8 µm if flattened), 8-spored, spores *~4-seriate, 3–5(–7) lower spores inverted {3} (often strongly mixed), pars sporifera *(34–)38–48(–55) µm long; **apex** (†) hemispherical (to slightly truncate), dome †0.8–1.3 → 0.5–0.7 µm thick {2}, with distinct apical chamber; **base** with short to long, thin or thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(13.2–)18–27(–30) × ((1.7–))(2–)2.2–2.7(–3) µm {3}, †(13.7–)16–22(–24) × 2–2.5 µm {1} (up to 2.7–3.3 µm if flattened), fusoid to mostly fusoid-clavate, apex obtuse to subacute, base medium to mostly strongly attenuated in a tail or tail-like end *(3–)5–8(–10) × 0.9–1.2 µm, straight or slightly flexuous, sometimes slightly curved near base; **SBs** *(2.5–)3–3.5(–3.8) × (0.8–)1–1.2(–1.3) µm {2}, †3–3.5 × 0.8–1.2 µm {1}, elongate tear-shaped to subulate, apically narrowed to a narrow point, straight. **Paraphyses** apically uninflated or often slightly (to medium) clavate(-capitate), terminal cells *(8–)12–25 × (2–)2.5–3.2(–4) µm {3}, †2–2.5(–3.8) µm wide {1}, lower cells *10–18.5 × 1.7–2.3(–3) µm {2}; unbranched at upper septum. **Medullary excipulum** 40–60 µm thick, of dense textura intricata with many slightly inflated cells, indistinctly to sharply delimited from ectal excipulum by a ± distinct t. porrecta. **Ectal excipulum** of (†) not or slightly gelatinized, vertically oriented t. angularis(-prismatica) from base to mid flanks, 25–50 µm thick near base, cells *9–15(–19) × 6–9(–10) µm {1}, †4–8 µm wide; 20–30 µm thick near margin, of t. porrecta oriented at a 20–

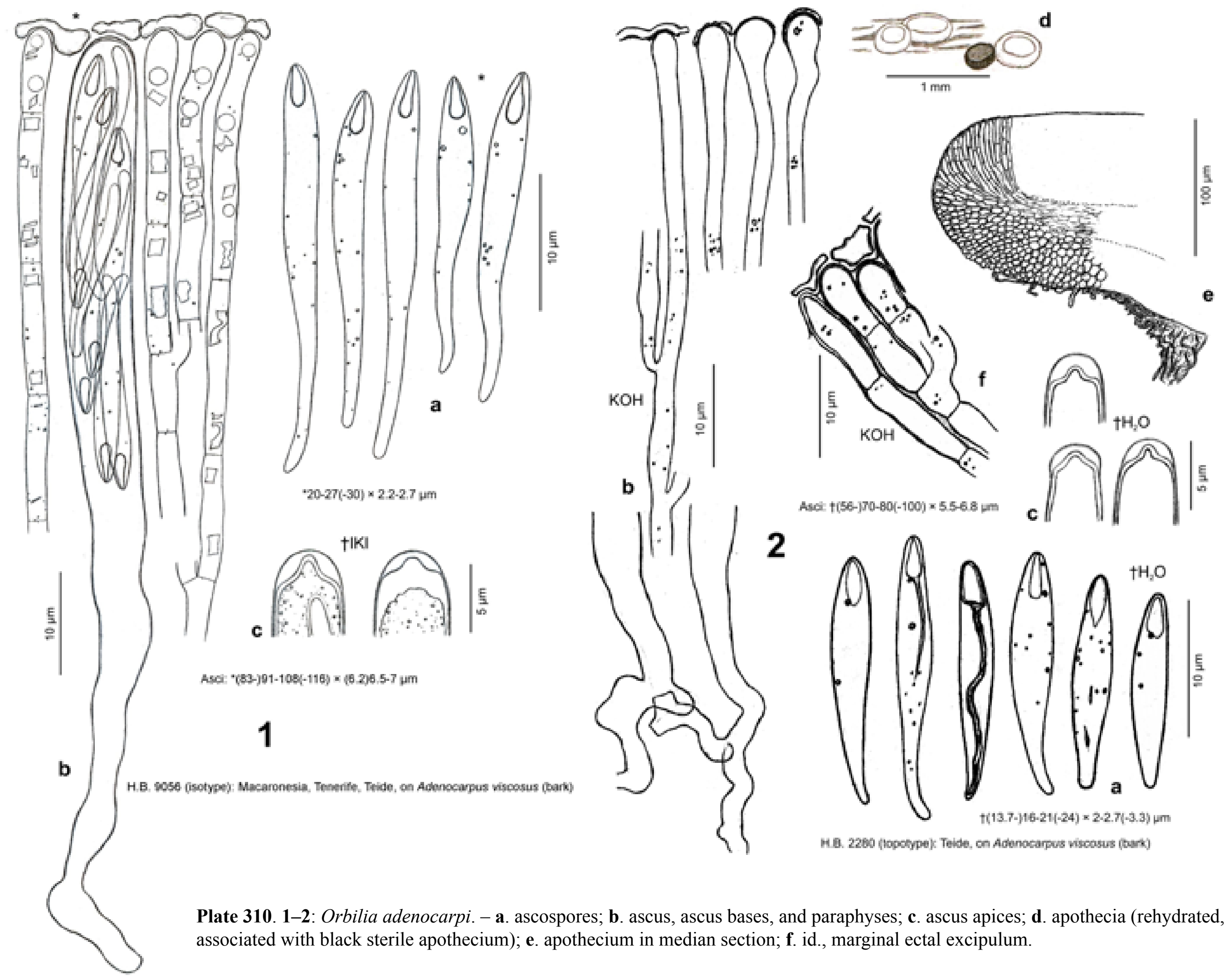


Plate 310. **1–2**: *Orbilia adenocarpi*. – **a**. ascospores; **b**. ascus, ascus bases, and paraphyses; **c**. ascus apices; **d**. apothecia (rehydrated, associated with black sterile apothecium); **e**. apothecium in median section; **f**. id., marginal ectal excipulum.

45° angle to the surface, marginal cortical cells *8–13 × 3–4.5 µm {3}, 7–10 × 2–3 µm {1}; **glassy processes** absent, at submargin sometimes with scattered, straight to flexuous, thick-walled, protruding hair-like hyphae 10–25 × 3–5 µm {2}. **Anchoring hyphae** abundant, */†2–3 µm wide, walls 0.2(–0.3) µm thick {2}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.2–2 µm diam., mixed with many hyaline crystalloid ones of 1.2–3.5 × 0.3–1.7 µm. **Exudate** hyaline to very pale yellowish, over paraphyses (0.5–)1–2(–3) µm thick, (granular-)cloddy, ± firmly attached, over margin and flanks 1–3(–5) µm thick, cloddy. **— ANAMORPH**: unknown.

Habitat: lying on dry ground or still attached but close to the ground, corticated, 10–30 mm thick dead or living branches and stumps of *Adenocarpus viscosus* subsp. *viscosus* {10}, on medium to very decayed bark {10} (on uneven periderm), hardly to strongly greyed, algae absent or very sparse. **Associated**: *Coniochaeta* sp. {1}, *Helotiales* {1}, *Orbilia pleiogambelii* {1}, *Peniophora* sp. {1}, *Teichosporella dura* {1}. **Desiccation tolerance**: fully viable for at least 8 weeks. **Altitude**: [1300–1450] 1920–2660 m a.s.l. **Geology**: trachyte, phonolite, basalt. **Phenology**: X–XII, II–VI (probably throughout the year, long-lived).

Taxonomic remarks. *Orbilia adenocarpi* differs from *O. vinosa* in distinctly longer and wider ascospores, shorter and wider SBs with a narrower attachment, and distinctly larger asci. It also resembles the North American *O. navajoana* (series *Hesperideae*), from which it differs in the presence of crystalloid SCBs, also in longer and narrower spores with longer SBs. *O. hesperidea* corresponds to *O. adenocarpi* in many respects, including SB size and shape, but likewise differs in distinctly shorter spores.

Variation. Ascospore length varies strongly within populations, but also between them. In the first and some later records spores longer than 24 µm could not be found, while in the holotype some attained 30 µm because of a rather long tail. The above description is mainly based on the two here studied specimens (isotype and H.B. 2280), while not all data from other samples studied by L. Quijada were available.

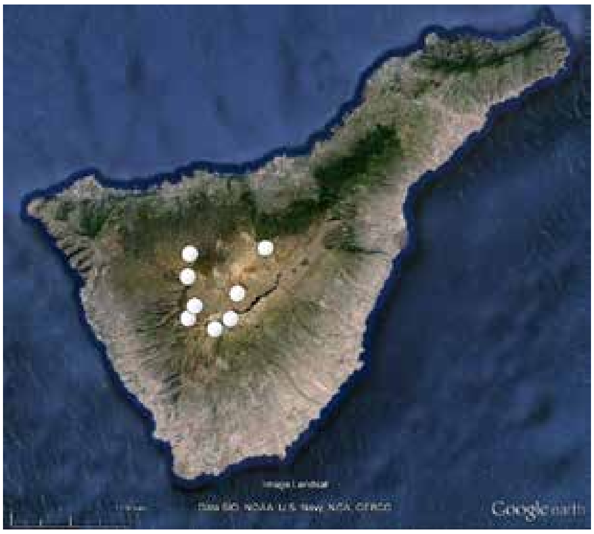
Phylogeny. A sequence taken from apothecia of the isotype comprises ITS (with incomplete 5'-end) and LSU. A DNA isolate (partial 5.8S and entire ITS2) from *Pinus heldreichii* needles in Montenegro differs by only 1 nt in the ITS2. In our analyses, *O. adenocarpi* clustered strongly (ITS+LSU, Phyl. 9), medium (ITS, Phyl. 10), or weakly (LSU, S13) supported with *O. concoloris* and *O. sarothamni*, to which also *O. myriofusiclava* is associated. However, the ITS distance to *O. adenocarpi* is rather high (8.3–9.3%, to the latter 13%). In the LSU (D1–D2, 522 nt) the lowest distance is 1.3% to *O. myriofusiclava* and 1.7% *O. sarothamni*. The four species formed a medium supported subclade of the *cryptogena-sarothamni* clade (Phyl. 9). An environmental sequence from savannah soil in Texas (ITS+LSU) clustered with *O. adenocarpi* (Phyls 9–10, S13; ITS distance 7.5%, LSU 1%).

Ecology. *O. adenocarpi* grows in the upper meso- to supra-mediterranean semihumid high plateau (caldera) and on the south and west-exposed slopes outside the rim around the volcano Teide (Tenerife, Macaronesia). The species was recorded on bark of xeric branches of the dwarf shrub *Adenocarpus viscosus* (codeso del Teide), either dead or sometimes internally still alive (Quijada

Plate 311. **1–2**: *Orbilia adenocarpi*. – **1a**. *Spartocytisetum supranubii*, Luis Quijada with *Adenocarpus viscosus*; **2**. dry apothecia on exterior of bark; **1h**. apothecium in median section; **1b–g**. rehydrated apothecia; **1i**. basal ectal excipulum in median section; **1j**. id., marginal ectal excipulum; **1k–m**. mature asci; **1n**. ascospores. – Living state. – **1a**: phot. J. Rodríguez-Armas; **1m**, **2**: phot. L. Quijada. — **1a**. holotype locality, **1m**. TFC Mic. 21741 (holotype), **1b–l**, **n**. H.B. 9056 (isotype): Tenerife, Las Cañadas del Teide, on *Adenocarpus*; **2**. TFC 19428: ibid., on *Adenocarpus*.

et al. 2012), lying on the ground or attached. The first collection was made in 1978 on '*Spartocytisus supranubius*' (retama del Teide), but a revision of the bark structure by L. Quijada (pers. comm.) revealed that it is *A. viscosus*, in coincidence with all later samples of L. Quijada between 2008–2009. The eight collection sites lie mainly in the dry summit broom scrub (retamar-codesar, *Spartocytisetum supranubii,* facies with *A. visosus*), twice in adjacent plant communities (*Sideritido solutae-Pinetum canariensis spartocytisetosum subranubii* and *Erysimo scoparii-Pterocephaletum lasiospermi*), including almost vegetation-less lava areas. The host plant is endemic to the Canary islands and occurs in Tenerife mainly in the caldera, but also on La Palma and Gomera at similar altitudes. It is known to act as condensator of the air humidity and thus experiences a (sub)humid microclimate in spite of the dry climatic conditions there (Brullo et al. 2008).

Specimens included. **MACARONESIA** (all on bark of branches of *Adenocarpus viscosus*: **Canary Islands**, **Tenerife**, **La Orotava**, las Cañadas del Teide, 8 km ENE of Teide, NW of El Portillo, 2098 m, 18.II.1978, R. Agerer (H.B. 2280a, **topotype**, erron. as *Spartocytisus* or *Cytisus supranubius*). – ibid., 25.III.2009, L. Quijada, E.V. Rodríguez & R. Castro (TFC Mic. 21741, **holotype**; H.B. 9056, **isotype**; sq.: KT222366. – ibid., 15.VI.2009 (TFC Mic. 21742, 21743, **topotypes**, non vid.). – 4.8 km SE of Teide, Tabonal Negro, Callao Teide, 2230 m, 17.X.2008, E. Beltrán-Tejera, A. Losada & L. Quijada (TFC-Mic 18428, doc. vid.). – 4 km WSW of Teide, W of Pico Viejo, 2660 m, 13.XII.2008, L. Quijada (TFC Mic. 22996, doc. vid.). – **Vilaflor**, 7.3 km



Map 54: Known distribution of *O. adenocarpi* in Tenerife (Macaronesia).

SSE of Teide, Los Riachuelos, 2340 m, 28.XI.2008, L. Quijada (TFC Mic. 20873, doc. vid.). – 8.3 km S of Teide, El Andén del Gato, 2410 m, 5.IV.2009, L. Quijada (TFC Mic. 21983, non vid.). – **Adeje**, 8 km SSW of Teide, Casa de Juan Evora, 2050 m, 1.III.2008, L. Quijada (TFC Mic. 19118, non vid.). – 5.8 km SSW of Teide, Asientos de Pedro Méndez, 2090 m, 13.XII.2008 (TFC Mic. 21078, non vid.). – **Icod de los Vinos**, 4.2 km NW of Teide, Los Asientos de Luis González, 1920 m, 29.XII.2009, L. Quijada (TFC Mic. 22725, non vid.). — **MONTENEGRO**: 20–23 km ENE of Podgorica, Kučka korita, 1300–1450 m, needles of *Pinus heldreichii*, V.2015 (2814_272, Lazarević & Menkis 2020, mol. extr., sq.: MT242134).

Series *Hemiorbilia*

Orbilia subgenus ***Orbilia*** section ***Hemiorbilia*** series ***Hemiorbilia*** – Type species: *Orbilia occulta* (Rehm) Sacc.

(?)= *Trinacrium* Riess in Fresenius, Beitr. Mykol. 2: 42 (1852) – Type species: *T. subtile* Riess

(?)= *Radotinea* Velen., Monogr. Discomyc. Bohem.: 298 (1934) – Type species: *R. caudata* Velen. [(?)= *Orbilia aristata* (Velen.) Velen.]

= *Orbilia* subgroup V *Aristula* Velen., Monogr. Discomyc. Bohem.: 102 (1934, unranked, in 1947 as '*Aristulae*') – Type species: not designated

?= *Descalsia* A. Roldán & Honrubia, Mycol. Res. 92: 494 (1989) – Type species: *D. cruciata* A. Roldán & Honrubia, *Mycol. Res.* 92: 495 (1989)

Etymology: *Aristula*: referring to the ascospores with long tails; *Descalsia*: named after the Spanish mycologist Enrique Descals; *Hemiorbilia*: named after the ± hemispherical shape of the ascus apex (in both living and dead state); *Radotinea*: after the village Radotín near Praha (Czechia); *Trinacrium*: according to the triradiate (Y-shaped) conidia with 1 main axis and 2 divergent arms.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–0.7(–1.5) mm diam. (incl. teeth), pale to bright orange to rose, margin smooth or often finely to strongly crenulated or toothed, rarely with long hyaline hairs, sessile or with a ± distinct short stipe. **Asci** *(35–)40–75(–90)((–103)) × (5–)5.5–8.5(–10) µm, rarely *22–32 × 3.6–4.5 µm, 8-spored, 0–4(–6) lower spores inverted; **apex** (†) hemispherical to slightly (rarely medium) truncate, with (0.6–)1–2(–3) µm thick dome, often with apical chamber; **base** L-, T-, Y- or h-, exceptionally H-shaped. **Ascospores** *3.5–9 or mostly (9–)11–20(–29.5) × (1.6–)2.2–4(–4.8) µm, usually divided into an inflated head and a distinct tail, head cylindrical or narrowly to broadly ellipsoid to fusiform, rarely strongly inequilateral to triangular, SB-containing end rounded to mostly obtuse to subacute, rarely acute to acuminate, tail ± abruptly delimited from head, short to very long, *0.2–1.2 µm thick, basally sometimes swollen, rarely absent, straight to slightly curved, sometimes strongly geniculate near base or below head. **SBs** apically affixed to spore wall (except for *O. aviceps* and *O. triangulispora* with laterally attached SBs), (1.6–)2–5(–6.5) × (0.4–)0.6–1.5(–1.7) µm, rarely only 1.3–1.5 µm long or 2–2.2 µm wide, rod-shaped (vermiform) to subulate or tear-, pear- to dumbbell-shaped or ampulliform, straight, apically narrowed to a small to wide point, with or without a very short filum. **Paraphyses** uninflated or slightly to medium, rarely strongly clavate-capitate, in *O. fimbriata* predominantly slightly lageniform, terminal cells (1–)1.5–2(–2.5)× as long as the lower cells, sometimes of equal length. **Ectal excipulum** cells near base *(5–)8–20(–30) × (4–)8–15(–20) µm, near margin of t. angularis to t. prismatica or t. porrecta, outer part oriented at a high to often medium or low angle, with **glassy processes** of 1–5 up to 30–100 µm length, rarely without, in *O. fimbriata* instead with 60–300 µm long septate hairs. **SCBs** globose (rarely absent), in some species also crystalloid. **Exudate** 0.2–0.5 up to 1–3(–5) µm thick, continuous-cloddy or granular, loosely attached, hyaline or pale yellowish, rarely absent. — **ANAMORPH**: trinacrium-like, descalsia-like, dwayaangam-like. **Conidiophores** not observed. **Conidia** staurosporous, of 3 types: 2-armed (Y- or rarely T-shaped), *20.5–80 × 18–100 µm, arms straight or somewhat curved downwards; 3-armed (descalsia-like), *18–73 × 25–85 µm; 4-armed (dwayaangam-like): *27–95 × 29–115 µm, arms straight; exceptionally a few conidia unbranched (phragmosporous), straight.

Habitat: on wood and bark of both gymno- & angiosperms, rarely on leaves or bryophytes, all species desiccation-tolerant, in humid to semiarid, boreal to subtropical climates.

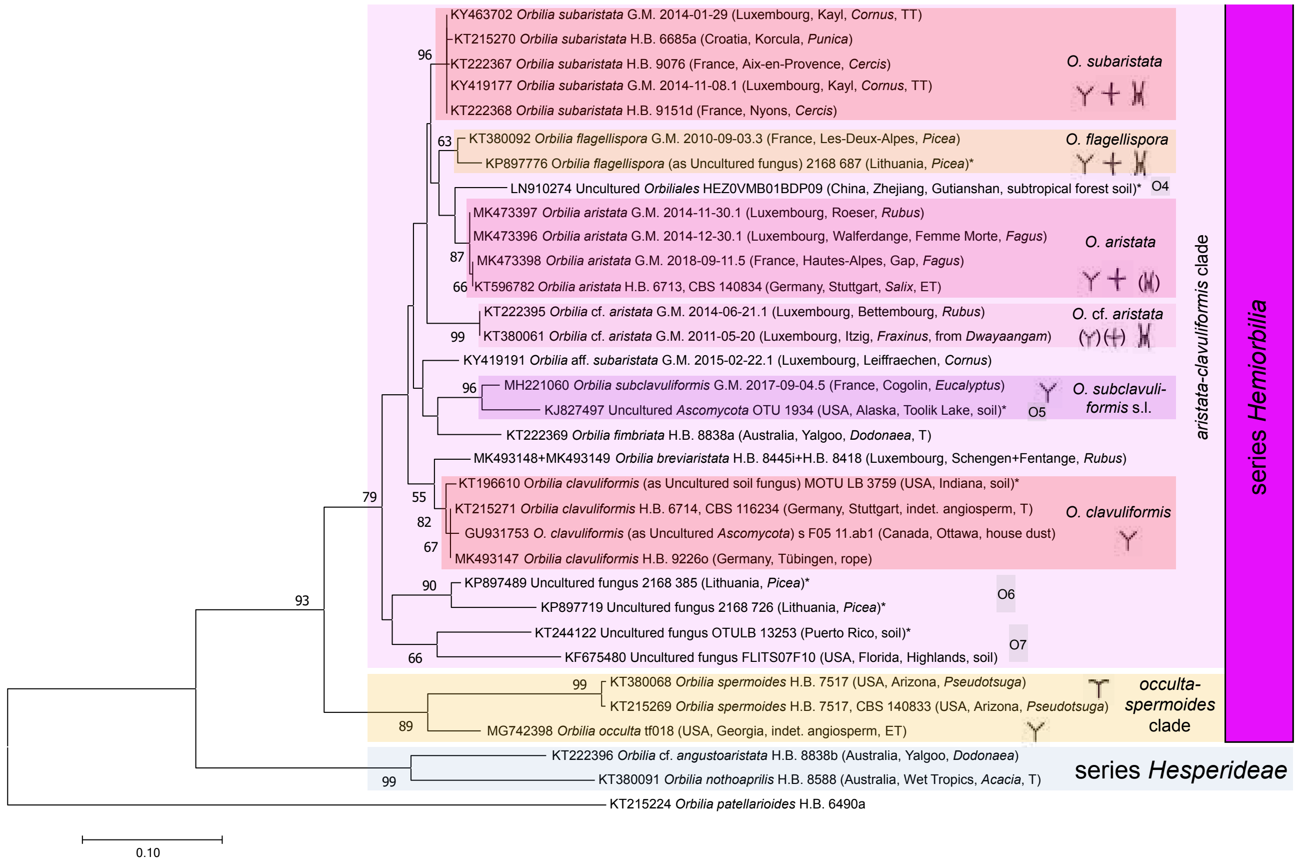
Recognized species: 24, plus 3 unnamed species ('affinis').

Taxonomic remarks. Within section *Hemiorbilia* series *Hemiorbilia* is characterized by ascospores with mostly distinct basal tails, also by the frequent presence of glassy processes that are agglutinated to form minute to large marginal teeth. The spore tails are not wider than 1.2 µm in their middle part, but may be swollen to 1.5–2 µm at the base. As a further peculiarity, all included species are 8-spored, and mostly only a few of the lower spores are inverted. In many of the species the terminal cells of paraphyses tend to be 1.5–2 × as long as the lower cells, while those of series *Hesperideae* range mainly around 0.5–1.5 ×. The variously branched conidia of the so far known anamorphs of series *Hemiorbilia* tend to have longer and narrower arms than those of series *Hesperideae*.

O. aviceps and *O. triangulispora* are exceptional in their strongly asymmetrical (triangular) ascospores with laterally attached SBs and short or even absent tails. They somewhat resemble *O. corculispora* in spore shape, but are retained in series *Hemiorbilia* because of their prominent glassy processes and 8-spored asci with only a few inverted lower spores. These features point to a relationship with *O. aviflagellata* and *O. aviaristata*, which have similar asymmetrical spore heads, although their SBs point in subapical direction and the spores have long tails. Also *O. colombiana* lacks a spore tail but is compared with *O. clavuliformis* for similar reasons.

O. nanosperma deviates from the other members of this series in remarkably small asci and spores, short SBs, and very long marginal teeth. *O. megaocculta* and *O. fimbriata* deviate by spores being distinctly wider than the average, the former species also by very wide SBs and short tails, and the latter by very long, septate hairs that are not agglutinated. In *O. fimbriata* the paraphysis apices are predominantly slightly lageniform. Here and in *O. spermoides* no exudate could be observed over the paraphyses. As an exception within series *Hemiorbilia*, *O. brevicauda* was collected in a humid subtropical forest on bark lying on the moist ground, nevertheless, we assume that also this species tolerates desiccation, as do all the others of section *Hemiorbilia*.

Velenovský (1934) included in his subgroup 'V *Aristula*' three species: *O. occulta*, *O. herbarum*, and *O. carpathica*. His *O. occulta* corresponds to *O. aristata* in the present study, while



Phylogenetic analysis 12. Phylogram of series *Hemiorbilia* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (29 sequences, 610 positions, aligned with MUSCLE) using the K2+G model in MEGA6 (500 replicates). 9 environmental strains from GenBank are included, 4 of them representing unidentified species (O4–O7). The tree is rooted with *O. patellarioides*. Asci 8-spored in all taxa; T = type, ET = epitype, TT = topotype. * = without ITS1 and partial 5.8S.

the latter two taxa resemble *O. flagellispora* but are of uncertain identity. *O. carpathica* resembles also some members of section *Arthrobotrys*, see p. 1664). Later (Velenovský 1947), the author changed the name of this subgroup to *Aristulae*, again without stating its taxonomic rank.

Species delimitation. Series *Hemiorbilia* contains a rather large aggregate of species, which includes the type species *O. occulta* and which is quite problematic in regard to species delimitation. Its members are characterized mainly by spore shape and size, and by presence and length of glassy processes. Some of them, e.g., *O. aristata*, *O. subaristata*, *O. flagellispora*, and *O. clavuliformis*, were quite frequently collected within Europe in the present study, and could not clearly be identified in every case. They are rather variable in their spore characters, such as length of inflated apical part, length of tail, and strength of basal inflation of the tail. It is also impossible to recognize different subgroups of species, because quite a few intermediate species exist, e.g., *O. clavuliaristata* as a link between *O. aristata*/*O. subaristata* and *O. clavuliformis*/*O. subclavuliformis*.

Anamorph. Members of series *Hemiorbilia* produce a variety of staurosporous conidial types. Often several types were observed within a species or single strain: (1) trinacrium-like (Y-shaped) conidia were observed in 11 species, in four of them also or only in ascospore isolates (*O. clavuliformis*, *O. occulta*, *O. spermoides*, *O. subaristata*); (2) descalsia-like (┼-shaped) conidia occurred in six species, in two of them also in ascospore isolates (*O. aristata*, *O. subaristata*); (3) dwayaangam-like conidia were observed in three species in which also trinacrium- and descalsia-like conidia occurred, in one also in a conidial isolate that was sequenced (*O. aristata*).

Descalsia cruciata was described with almost exclusively tetraradiate (┼-shaped), apparently plane conidia, besides Y-shaped and unbranched ones. It was isolated from foam in a stream in the mountainous supramediterranean region of Calar del Mundo in Albacete, southern Castilla-La Mancha (Spain) and could possibly provide an older name for *O. subaristata* or *O. flagellispora*, or be a synonym of *O. aristata*. A living culture was not preserved (A. Roldán & L. Marvanová pers. comm.). Efforts by one of us (G.M.) to gain DNA from a permanent slide failed. Descalsia-like conidia observed by us in series *Hemiorbilia* have a spatial, tetraradiate shape when floating in thicker water films. They appear as plane cross-like structures only when exposed to pressure in the narrow water film under the cover slip. Possibly the 4-armed conidia of *D. cruciata* were also tetraradiate in three dimensions when floating in water.

Although conidial branching varied on the natural substrate within a given population between trinacrium-, descalsia- and dwayaangam-like, we obtained in four ascospore isolates only one type of conidia: trinacrium-like in *O. clavuliformis* and *O. spermoides*, descalsia- or dwayaangam-like in *O. aristata*, whereby the isolates of *O. aristata* showed a distinct molecular distance between descalsia- and dwayaangam-like (Phyl. 12). On the other hand, trinacrium- and descalsia-like conidia developed in our isolate of *O. subaristata* (H.B. 6685a, CBS 116217, unillustrated). Likewise Ando (1992) figured a very similar conidial state which he identified as *T. subtile* (without teleomorph). In addition to the Y-shaped trinacrium-like conidia, he observed four further conidial forms: *Sigmoidea* (unbranched), *Lambdasporium* (2-armed, sometimes with 1 arm again branched), *Articulospora* (┼-shaped), and *Dwayaangam*

(4-armed). The author concluded that the current system of conidial shapes is artificial. Quite probably, Ando was dealing with the anamorph of a species of series *Hemiorbilia*. Since the morphology of a given conidial type within this series is rather uniform, we are unable to decide to which species Ando's isolate belongs. Possibly it represents a species of the *O. aristata* aggregate. The same uncertainty applies to the type of *Trinacrium subtile*, which is very probably the anamorph of a species of series *Hemiorbilia* and resembles particularly those of *O. clavuliformis*, *O. subclavuliformis*, and *O. clavuliaristata*.

At the present state of knowledge we may conclude that some species of series *Hemiorbilia* are able to produce two or three types of conidia whereas others produce only one type.

Phylogeny. Molecular data were available for nine of the 24 species included here in series *Hemiorbilia*. Seven of them form in our analyses a strongly (ITS+LSU, Phyl. 9) or medium supported (ITS, Phyl. 12; LSU, S13) monophyletic clade which is called *aristata-clavuliformis* clade here. It includes *O. aristata*, *O. breviaristata* (not shown in analyses), *O. subaristata*, *O. flagellispora*, *O. clavuliformis*, *O. subclavuliformis*, and *O. fimbriata*. Another strongly (ITS) or medium (ITS+LSU) supported clade includes *O. spermoides* and *O. occulta* and is called *occulta-spermoides* clade here. Both clades show a remarkable distance between each other, despite a close morphological similarity between *O. occulta* and *O. aristata*/*O. breviaristata*. They clustered with strong (ITS) or medium support (ITS+LSU) as sister groups in a clade which represents series *Hemiorbilia*. However, the sequence of a tenth taxon, *O.* cf. *angustoaristata*, is even more surprising: it shows a strong distance to those nine species of series *Hemiorbilia* and clustered instead in the *vinosa-velutina* clade. The distance in the ITS region among the seven species of the *aristata-clavuliformis* clade ranges at 3.5–8% and between *O. spermoides* and *O. occulta* at 9%, while the distance between both clades lies at 10–17%. All these species show a distance of 16–22% to *O.* cf. *angustoaristata*.

Specific nucleotide positions. In the LSU D1–D2, pos. 153 is unique and consistent within series *Hemiorbilia* (excluding *O.* cf. *angustoaristata*) in having TTTG**T**AGA vs. TTTG**A**AGA in all remaining taxa of *Orbiliomycetes*, except for the *Hyalorbilia*-*Vermispora* clade which has TCTG**G**AGA or TCTG**C**AGA or rarely TCTG**A**AGA. In the ITS1 occurs a long, highly conservative motif with only 2 variable positions (ACCAAACTTGTTATTTCTG*DW*CAGTCTGAAAAACATTTTTTG), which is unique for the six species of the *aristata-clavuliformis* clade. *O. spermoides* and *O. occulta* deviate hereof by various nucleotides and indels, but differ also strongly between each other. This region is very different in other members of section *Hemiorbilia*, including *O.* cf. *angustoaristata*.

Ecology. Many species of series *Hemiorbilia* were found in temperate to boreal-subalpine, more or less humid regions, but many others predominantly or exclusively occur in subtropical semihumid to semiarid regions. The apothecia often grew on wood and more often bark of xeric branches and trunks of gymno- and predominantly angiosperms, but various species were occasionally or exclusively found on more or less herbaceous substrates: *O. aristata* on stems of *Heracleum* and *Humulus*, also on *Pinus* leaves, *O. breviaristata* on stems of *Euphorbia* and *Rubus*, *O.* cf. *angustoaristata* on *Dryas* leaves, *O. parviclava* on *Livistona* petiole, *O.* cf. *clavuliaristata* on *Phragmites* culm, and *O. subclavuliformis* on *Melilotus* stem. Several species were recorded on stems of *Rubus*, and *O. frullaniae* grew on leaves of *Frullania*. Members of series *Hemiorbilia* occur worldwide: records are known from Europe, Northern, Middle and South America, Africa, Asia, and Australia.

Orbilia colombiana Baral & Priou, **sp. nov.**, MB 813600 — Pls 312–313

Etymology: named according to the geographical origin of the holotype, Colombia (South America).

Typification: Colombia, Bogotá, branch of *Eucalyptus*, 30.X.1994, W. Jaklitsch (ex H.B. 5187, M-0276459, holotype).

Latin diagnosis: *Apothecia 0.3–1 mm diam. in statu umido, sessilia, superficialia, aurantio-rosea, margine valde albido-denticulata. Asci 8-spori. Ascosporae *6–9.8 × 2.1–2.5 µm, ellipsoideo- vel fusoideo-clavatae, apice rotundatae vel subacutae, subrectae, in statu vivo corpusculum refringens pyriformem, ad apicem affixum continentes Cellulae vivae excipuli et paraphysium corpuscula globosa continentes, excipulum marginale processis vitreis longis praeditum. Habitat ad corticem putridum ramulorum subsiccorum* Eucalypti *et* Polylepidis *in zona subtropica (sub)humida montana Americae australis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1 mm diam., 0.14–0.23 mm high, pale rose or light to bright orange-rose, round, scattered to gregarious in small groups; disc flat, margin and exterior with ± prominent whitish or pale orange teeth projecting 30–60 µm beyond disc; sessile, superficial. **Asci** *42–50 × 5.3–6 µm {T}, †(35–)40–48(–53)((–60)) × (4–)4.5–5(–5.3) µm {2}, 8-spored, spores biseriate, (1–)2(–3) lower spores inversely oriented {2}, pars sporifera *18–27 µm long; **apex** (†) hemispherical (to slightly truncate), dome (†) 0.7–1.3 → 0.5–1 µm thick {2}, with very slight apical chamber; **base** with short to long, thin or thick, flexuous stalk, L-, T- or Y-shaped. **Ascospores** *(6–)7–9(–9.8) × 2.1–2.5((–2.7)) µm {2}, †6.5–8 × (1.8–)2–2.3 µm {T}, subcylindric- or ellipsoid-clavate with rounded apex {T}, or fusoid to fusoid-clavate with (obtuse to) subacute apex {1}, base slightly to strongly attenuated, straight to very slightly curved below; **SBs** *(1.8–)2.3–2.8(–3.2) × 0.7–1.3 µm {2}, pyriform to dumbbell-shaped or slightly ampulliform, rarely tear-shaped, apically narrowed to a small to wide point {T} or to a very short filum {1}. **Paraphyses** apically uninflated to slightly clavate-capitate, terminal cells *(8–)11–18 × 1.8–3 µm {2}, lower cells *7–13.5 × 1.6–2.5(–3.2) µm {2}; never branched at upper septum; hymenium very pale reddish. **Medullary excipulum** hyaline, 40–100 µm thick, of dense to loose textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** hyaline, of (†) thin-walled, indistinctly oriented t. globulosa-angularis from base to margin, 40–60 µm thick near base, cells *11–21(–30) × 10–15 µm {1}, †7–20 × 6–12 µm {T}; 20–25 µm thick at mid flanks and margin, of t. angularis oriented at a 60–90° angle, cells *7–11 × 6–9 µm {T}, outer marginal layer of t. porrecta oriented at 20–30°, marginal cortical cells *6–13 × 1.5–3.4 µm {2}, giving rise to **glassy processes** of 18–80 × 1.8–3.5 µm {2}, stratified, low- to medium-refractive, curved in- {2} or outwards {1}, coherent to form 30–100 × 50–90 µm large teeth. **Anchoring hyphae** (very) abundant, *2–3(–4)((–5)) µm wide, walls 0.2(–0.3) µm thick {2}, forming strands, near base gradually emerging from ectal excipulum as thick moniliform hyphae, intergrading at flanks into glassy hairs. **SCBs** in paraphyses and excipular cells (sub)globose, 1.2–2.3 µm diam. {2}. **Exudate** over paraphyses (0.5–)1–2.5(–3.5) µm thick, broken in clods, very pale yellowish, loosely attached; on teeth sparse or abundant. — **ANAMORPH**: descalsia-like (presumed, from natural substrate {1}). **Conidiophores** not seen. **Conidia** 3–4-armed (by repeated dichotomous branching), total size *~18–28 × 25–30 µm {1}, stipe *10–18 × 2.8–3.5 µm, 1–2-septate, arms tapering, *11–17 × 2.5–3 µm, 1–3(–4)-septate.

Habitat: lying on somewhat moist ground {2}, corticated, 4–8 mm thick semixeric twigs and branches of *Eucalyptus* sp. {1}, *Polylepis* sp. {1}, on medium decayed bark {2} (in deep cross-cracks, on bast), somewhat greyed, sometimes blackened, green algae very sparse. **Associated**: brown ?conidiomata. **Desiccation tolerance**: fully viable for at least

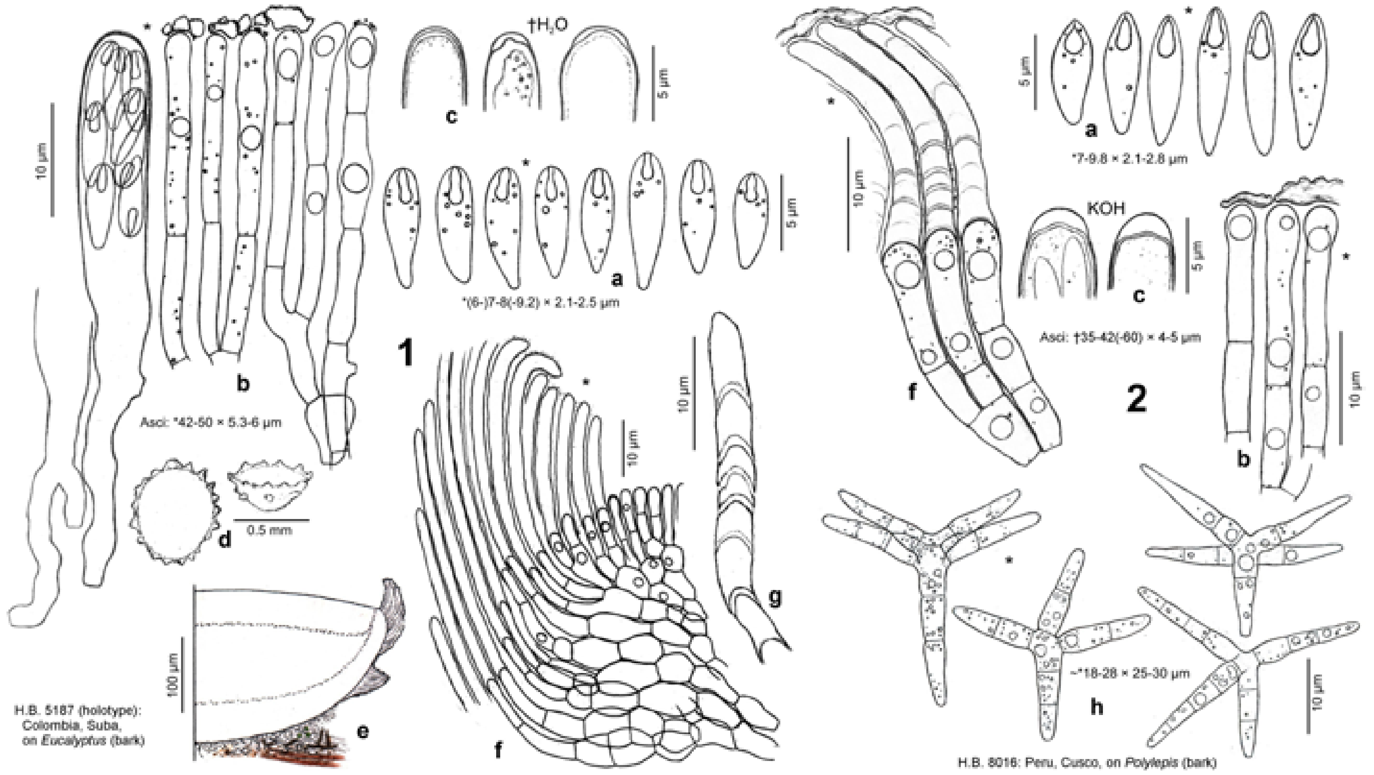


Plate 312. **1–2**: *Orbilia colombiana*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia with dentate margin (rehydrated); **e**. apothecium in median section; **f**. id., marginal ectal excipulum with long glassy processes; **g**. glassy process; **h**. conidia from substrate.

3 weeks, paraphyses, excipular cells, ascospores and conidia after 2 months. **Altitude**: 2620–3820 m a.s.l. **Phenology**: X (tropical belt).

Taxonomic remarks. *Orbilia colombiana* resembles *O. montigena*, *O. alpigena*, and *O. hesperidea* (series *Hesperideae*) in the shape of ascospores and SBs. It differs in long glassy processes and shorter spores, from *O. hesperidea* also in the absence of crystalloid SCBs. *O. colombiana* is tentatively placed in series *Hemiorbilia* because of showing only a few inverted spores in the asci and the presumed descalsia-like anamorph. *O. colombiana* resembles particularly *O. clavuliformis*, in which the spore tails are sometimes rather short or even absent (Pls 314: 6; 315: 9). From this species it differs in smaller spores being consistently without a tail, and in longer glassy processes which form distinct teeth.

Variation. The holotype differs in cylindric-clavate spores with rounded apices from the collection on *Polylepis* with fusoid spores with obtuse to subacute apices, also shape and attachment of the SBs are slightly different. The glassy processes are curved inwards in the holotype but outwards in the *Polylepis* specimen, though here teeth with slightly inwards curved processes also occur. It cannot be excluded that the two collections belong to two different taxa. Yet, similar variation in spore morphology was noted, e.g., in *O. hesperidea*.

Anamorph. The conidia found in the paratype of *O. colombiana* resemble descalsia-like conidia of some typical members of series *Hemiorbilia*, e.g., *O. aristata*. They are also similar to trinacrium-like conidia typical of series *Hesperideae*, but differ in 1 or 2 more branches.

Ecology. *O. colombiana* grew on medium decayed bark of semixeric twigs and branches of *Eucalyptus* and *Polylepis* at two subtropical highland areas in the mountain range of northwestern and western South America. That on *Eucalyptus* was in the humid high basin of Colombian Andes, that on *Polylepis* in a subhumid highland in the Peruvian Andes. Although collected on rather moist ground, *O. colombiana* is desiccation-tolerant and possibly survives drought for a much longer period of time than evaluated at present.

Specimens included. **COLOMBIA**: **Cundinamarca**, Cordillera oriental, 16 km N of Bogotá, Suba, 2620 m, branch of *Eucalyptus*, on bark, 30.X.1994, W. Jaklitsch (ex H.B. 5187, M-0276459, **holotype**). — **PERU**: **Cusco**, 5 km N of Cusco, 2.6 km NW of Yuncaypata, Tambo Machay, 3820 m, twig of *Polylepis*, on bark, 18.X.2005, J.P. Priou (H.B. 8016, anam. substr.).

Orbilia clavuliformis Baral & G. Marson, **sp. nov.**, MB 814366 — Pls 314–317, Map 55

Etymology: referring to the club-shaped ascospores.

Typification: Germany, Stuttgart, branch of indet. angiosperm, 23.VI.2000, H.O. Baral (ex H.B. 6714, M-0276457, holotype; CBS 116234; sq.: KT215271).

Latin diagnosis: *Apothecia rehydratata 0.15–0.7 mm diam., roseo-aurantiaca, (sub)sessilia, margine subtiliter vel distincte crenulata. Asci 8-spori. Ascosporae *13–21.5 × 2.8–3.7 µm, ellipsoideae, cauda basali 3–10 × 0.8–1.5 µm, basi non inflata praeditae, in statu vivo corpusculum refringens bacilliformem, ad apicem affixum continentes. Cellulae vivae excipuli marginalis et paraphysium corpuscula globosa continentes, excipulum marginale processis vitreis dentes minutos formantibus praeditum. Habitat ad corticem putridum, etiam lignum, ramulorum vel ramorum siccorum fruticum vel arborum angiospermarum, raro coniferarum, in zona temperata ad submediterranea (semi)humida atlantica ad continentale Europae et hemiboreale humida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.5(–0.9) mm diam., 0.12–0.2 mm high (receptacle 0.08–0.13 mm), pale to bright orange-rose, medium translucent, round, scattered to (sub) gregarious; disc ± flat, margin thin, 0–12 µm protruding, finely rough to distinctly crenulate; sessile or with a very indistinct stipe up to 50 × 250 µm; superficial but sometimes immersed in biofilm; dry bright orange-red to dark brick-red. **Asci** *(47–)50–70(–85) × 6.8–8.5(–10) µm {12}, †42–68 × 5.5–7.3 µm {6}, 8-spored, spores 2–4-seriate, 1–3(–4)((–6)) lower spores inversely oriented {12} (mostly not mixed), pars sporifera *26–47 µm long; **apex** (†) hemispherical to slightly truncate, dome

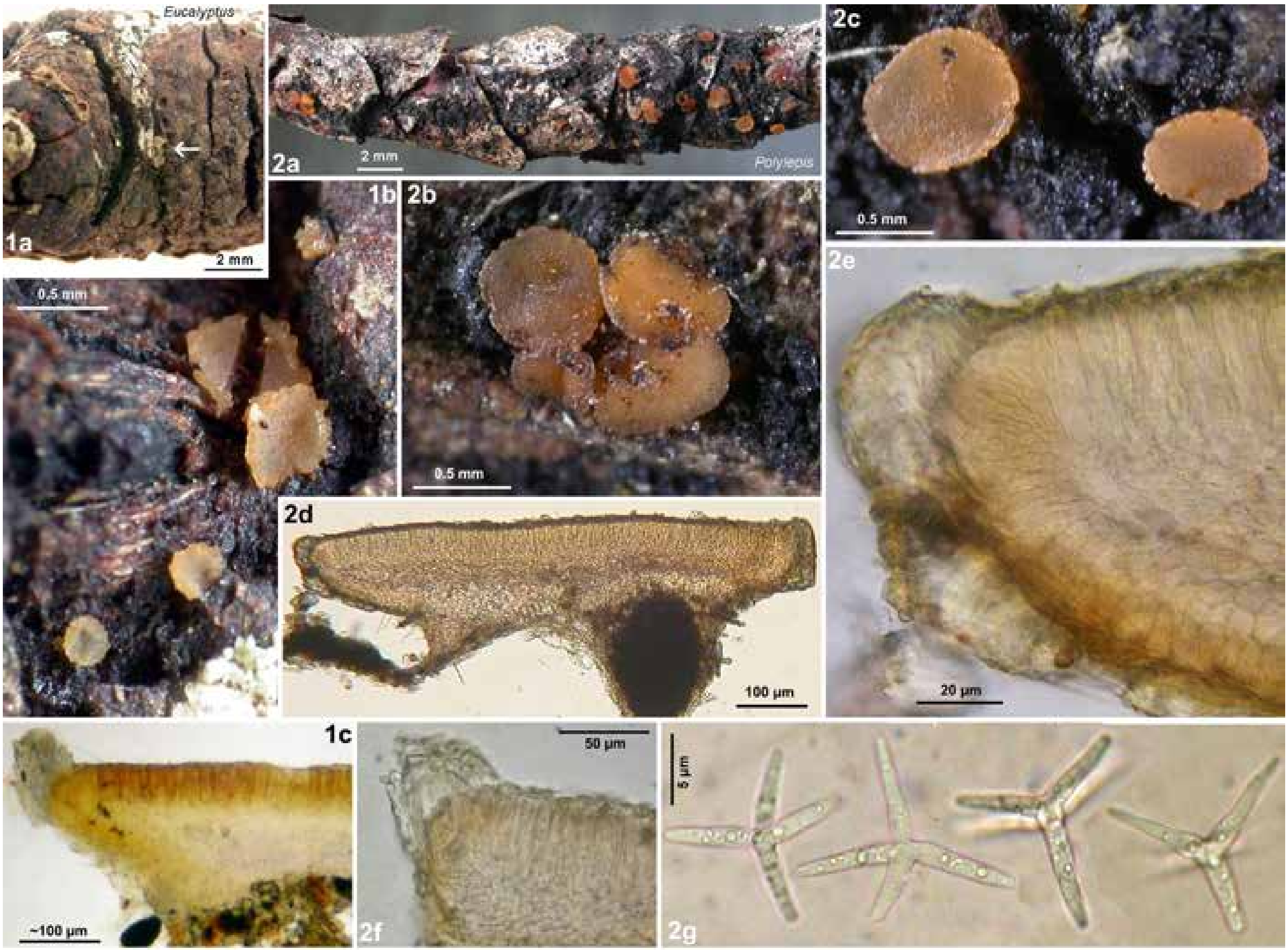


Plate 313. **1–2**: *Orbilia colombiana*. – **1a**, **2a**. corticated xeric branches (rehydrated); **1b**, **2b–c**. rehydrated apothecia; **1c**, **2d**. apothecia in median section; **2e–f**. id., marginal region; **2g**. conidia from substrate. – Living state, except for **1c** (in KOH+IKI). — **1a–b**. H.B. 5187 (holotype): Colombia, on *Eucalyptus*; **2a–g**. H.B. 8016: Peru, on *Polylepis*.

†1–2 → (0.5–)1–1.3 µm thick {6}, mostly with small distinct apical chamber; **base** with short to medium long, medium thick, flexuous stalk, T- or Y-shaped. **Ascospores** *((9.5–))(13–)15–19(–21.5) × (2.5–)2.8–3.5(–3.7) µm {23}, †15–20.5 × 2.7–3.3 µm {4}, composed of an ellipsoid head (*~9–11 µm long, with rounded or obtuse apex) which gradually attenuates in a tail-like base or mostly distinct tail *(3–)4–8(–10) × 0.8–1.3(–1.5) µm (†0.8–1.2 µm thick), tail never inflated at base, always shorter than head (rarely of equal length), straight to slightly (rarely strongly) curved near base, exceptionally with an eccentrical septum near tail {1}; **SBs** *((3.5–))(4–)4.5–6.5(–7) × (0.7–)0.8–1.2(–1.3) µm {14}, rod-shaped, often slightly ampulliform or dumbbell-shaped, rarely pyriform, apically narrowed to a small or mostly wide point, overmature *3–4 × 1.4–1.7 µm. **Paraphyses** apically uninflated, sometimes slightly or medium clavate-capitate or sublageniform, terminal cells *(5.5–)7–20 × 2–3.5((–4.5)) µm {4}, lower cells *(4–)7–14 × 1.5–2.6 µm {5}; sometimes branched near apex. **Medullary excipulum** subhyaline to pale rose-orange, 30–70 µm thick, of dense textura intricata with many inflated cells, medium sharply delimited (mainly at flanks). **Ectal excipulum** pale rose, of thin-walled, vertically oriented t. angularis(-prismatica) from base to mid flanks, 40–80 µm thick near base, cells *(7–)10–20(–25) × (5–)8–13(–15) µm {4}; 20–35 µm thick at flanks and margin, cells *5–10 × 5–7 µm, at margin of t. prismatica oriented at a 45–70° angle to the surface, outer cells hyphoid, oriented at 10–20°, marginal cortical cells *6–14 × (2.5–)3–3.5(–5.3) µm {3}, **glassy processes** present {24}, 1–7 {8} or 8–20(–30) {9} × (2–)2.5–3.5(–5.5) µm, refractive, ± stratified, ± straight or curved inwards, coherent to form indistinct or distinct teeth up to 15–20 × 25–40 µm. **Anchoring hyphae** sparse to abundant, */†2–3.5(–5) µm wide, walls 0.2–0.3(–0.6) µm thick {3}, sometimes forming a medium dense hyaline t. intricata (sometimes t. prismatica-angularis) 20–50 µm thick at base, covering apothecia at flanks as a thin layer. **SCBs** globose to subglobose, in paraphyses 0.7–2.5 µm diam.; in marginal excipulum 1–3 µm; **LBs** sometimes present in basal excipular cells, 1.5–2.3 µm diam., pale orange (carotenoids). **Exudate** over paraphyses (0.5–)1–3(–4) µm thick, ± continuous, externally coarsely rough, loosely attached; on margin and flanks finely granular, very thin to absent, but over glassy processes sometimes ~1–2 µm thick. — **ANAMORPH**: trinacrium-{1/6} (Y) or descalsia-like {-/4} (┼) (from ascospore isolate {1} and natural substrate {6}). **Conidiophores** not seen. **Conidia** Y-shaped, total size *(34–)40–55(–60) × (33–)48–65(–69) µm (†60–62 × 43–73 µm), stipe *17–29 × 3–4 µm (†24.5–33 × 2.5 µm), (2–)3–5-septate, arms slightly tapering or cylindrical, *29–42 × 2.5–4 µm (†37.5–44 × 2.5–3 µm), 3–6(–9)-septate {5}; rarely unbranched; in some collections in addition also some cross-shaped tetraradiate conidia (*Descalsia*) found on the substrate near apothecia: *50–60 × 52–64 µm (†45–55 × 55–66 µm), stipe *19–28 × 2.6–3 µm (†16–17 × 2 µm), 3-septate, arms *24–33 × 2.5–3.2 µm (†23–39 × 2–2.5 µm), 3–6-septate {3}.

Habitat: collected 0.2–4 m above the ground, corticated, more rarely ± decorticated, 2–25 mm thick branches of *Acer pseudoplatanus* {1}, *A. platanoides* {1}, *Cornus alba* {1}, *C. alternifolia* {1}, *C. mas* {2/1}, *C. sanguinea* {2}, *Cytisus scoparius* {1}, *Eucalyptus gunnii* {1}, *Euonymus europaeus* {1}, *Fraxinus* sp. {1}, *Fraxinus ornus* {1}, *Ligustrum vulgare* {2}, *Malus domestica* {3}, *Picea abies* {2}, *Pinus sylvestris* {2}, *Populus* sp. {1}, *Punica granatum* {2}, *Quercus* sp. {2}, *Rosa* sp. {1}, *R. canina* {1}, *Salix sp.* {2}, *S.* cf. *alba* {1}, *S. caprea* {3}, *S. cinerea* {1}, *S. eleagnos* {1}, *Tilia tomentosa* {1}, *Ulex europaeus* {1}, *Vitis vinifera* {3}, indet. angiosperm {2}, stems of

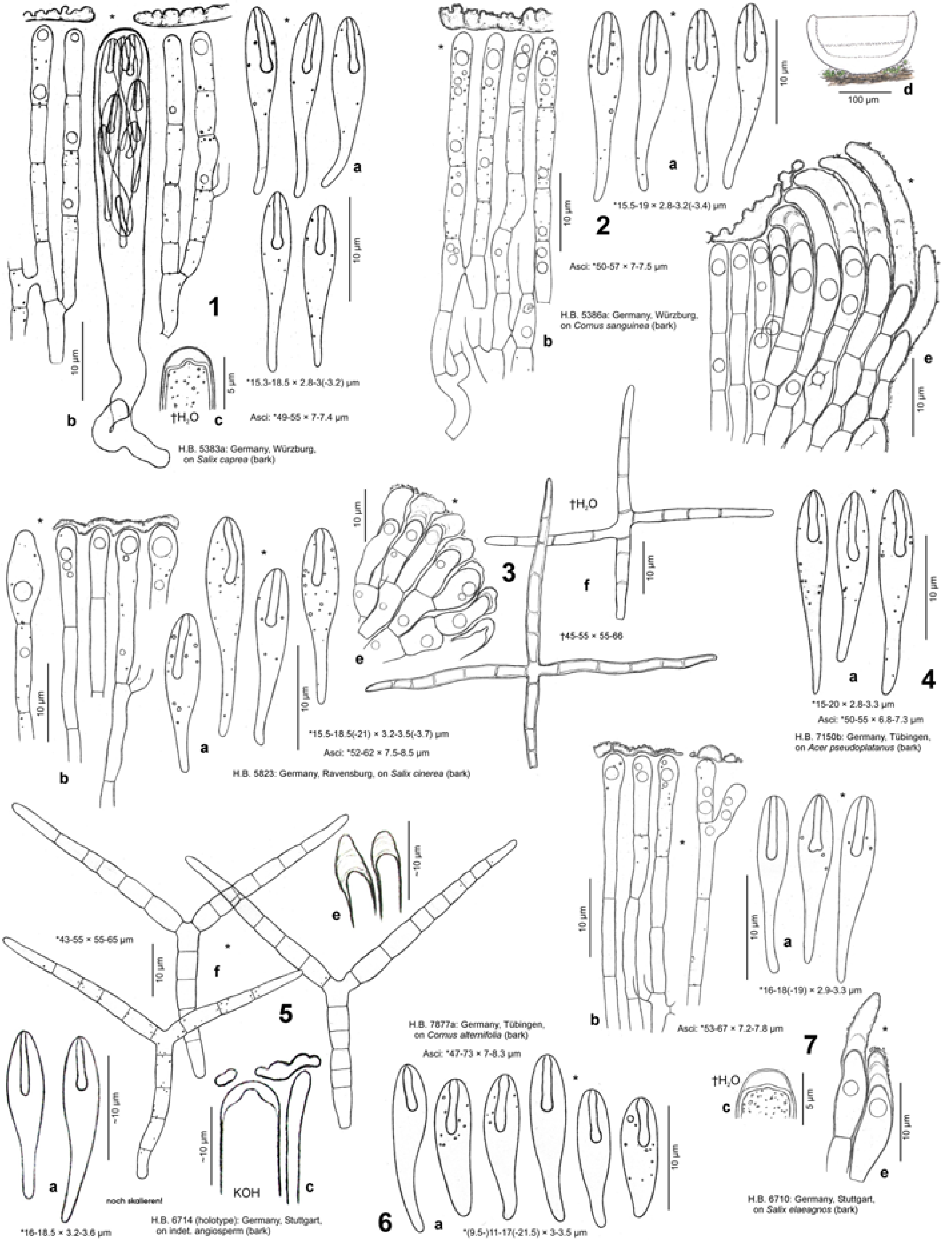


Plate 314. **1–7**: *Orbilia clavuliformis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum, cortical cells with glassy processes; **f**. conidia from culture (**5**) or substrate (**3**).

Rubus fruticosus {3}, on medium to strongly decayed bark {37}, on periderm {9} or bast {13} (in small cracks or larger periderm-free areas), sometimes on inner surface of detaching bark, rarely on wood {9}, on a thorn of *Rosa* {1}, on textile {1}, slightly to strongly greyed, green algae sparse or abundant. **Associated**: ?*Calloria* sp. {1}, ?*Ciliolarina* sp. {1}, *Dacrymyces* sp. {1}, *Diatrype* sp. {1}, *Hyalorbilia latispora* {1}, *H. multiguttulata* {1}, *H. subfusispora* {3}, *Karstenia rhopaloides* {2}, *Lasiosphaeria* sp. {1}, *Lecophagus ellipsoideus* {1}, *Lophiostoma compressum* {1}, *Melanelia glabratula* {1}, *Melaspileella* ?*proximella* {1}, *Merismodes* sp. {2}, *Micropeziza* sp. {1}, *Mollisia* sp. {2}, *M. ligni* {1}, *Neodasyscypha cerina* {1}, *Nitschkia cupularis* {1}, *Orbilia aristata* {11}, *O. aurantiorubra* {2}, *O. breviaristata* {3}, *O. eucalypti* {1}, *O. flavida* {1}, *O. gambelii* {1}, *O. mali* {1}, *O. pseudoaristata* {1}, *O. quaestiformis* {1/1}, *O. septispora* {1}, *O. subaristata* {1}, *O. subclavuliformis* {1}, *O. trapeziformis* {1}, *O. vinosa* {1}, *O. vitalbae* {2/1}, *Orthotrichum* sp. {1}, *Olla scrupulosa* {1}, *Parmelia sulcata* {1}, *Patellaria atrata* {2}, *Phaeophyscia orbicularis* {1}, *Physcia* sp. {1}, *P. tenella* {1}, *Phyllactinia guttata* {1}, *Pseudolachnea hispidula* {1}, *Pyrenopeziza rubi* {1}, *Rutstroemia punicae* {1}, *Sporidesmium* sp {1}, *Trimmatostroma salicis* {1}, *Tympanis ligustri* {1}, *Xanthoria parietina* {1}. **Desiccation tolerance**: fully viable for at least 2 weeks, many spores and some paraphyses still alive after 5 months. **Altitude**: 10–480 m a.s.l. **Geology**: Cambrian-Ordovician shale, silt, greywacke, Muschelkalk, Keuper (Gipskeuper, Stubensandstein, Knollenmergel), Cretaceous lime-, clay- & marlstone, flysch, Tertiary molasse, sand & clay, Pleistocene loess & sand; rhyolite, dacite, mica schist, gneiss; USA: Carboniferous calcareous sediment. **Phenology**: throughout the year (long-lived).

Phenology of *O. clavuliformis*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2	2	4	1	5	14	5	2	1	5	5	3

Taxonomic remarks. *Orbilia clavuliformis* is characterized by rather broad, ellipsoid-clavate ascospores with a well-defined thick tail, and by the presence of glassy processes. Similar spores as in *O. clavuliformis* are found in several more or less closely related species, such as *O. subclavuliformis*, *O. breviclava*, *O. parviclava*, and *O. clavuliaristata* (for the differences see there). *O. aristata* and *O. flagellispora* are readily distinguished by much thinner spore tails. *O. clavuliformis* resembles also the mediterranean *O. hesperidea*, from which it differs in the presence of glassy processes and rather distinct spore tails, further in the consistent absence of crystalloid SCBs. However, our molecular data suggests placement of *O. clavuliformis* in the *aristata-clavuliformis* clade.

Variation. *O. clavuliformis* is a rather constant species. Variability is mainly observed in spore length, especially due to variation in tail length. In one collection the tails were often very short or rarely even absent (Pls 314: 6; 315: 9). Also the glassy processes varied strongly in length among the collections. In only one specimen (1.X.2000, Stuttgart) a single free mature spore with a fully developed SB possessed an eccentrical septum near the tail.

Not included collections. The only known two collections from North America (Arizona, on bark of *Pinus edulis*, soc. *O. spermoides*, 17.V.1995, unillustrated; North Carolina, on *Cornus*, soc. *O. occulta*, Pl. 317) each consisted of a single apothecium. Both are tentatively referred to *O. clavuliformis* but are not included in the description. The former was only studied in the dead state. The glassy processes were short or absent and the spores had a short, rather thin tail. In that on *Cornus* the rehydrated apothecium measured 0.8 mm diam., the glassy processes were exceptionally long (20–40 µm), the asci comparatively large (*8.5–9.7 µm wide, †60–70 × 6.8–8 µm), and the spores had often subacute apices and somewhat shorter and thicker SBs. Further records are needed to clarify whether populations from North America are specifically distinct.

Anamorph. Trinacrium-like conidia in pure culture of the holotype (Pl. 314: 5f) were only obtained after flooding with water. They closely resemble those observed on the natural substrate and are very similar to the type of *Trinacrium subtile*. In four collections of *O. clavuliformis* we found together with triradiate also tetraradiate conidia near apothecia, which strongly resemble the descalsia-like anamorph obtained in pure culture of *O. aristata* and *O. subaristata*. Since *O. aristata* was sometimes found growing in association with *O. clavuliformis*, they might in fact belong to this species. In the North American collection on *Cornus* (IVV: H.B. 7402b) two trinacrium-like conidia were observed (†30–35 × 42 µm, arms 2.5–2.8 µm wide).

Phylogeny. A sequence from the ex-type culture of *O. clavuliformis* (H.B. 6714) comprises SSU (without S1506 intron), ITS and LSU (D1–D2), and one taken from apothecia of H.B. 9226o (as H.B. 9226a = *O. aristata*) likewise lacks the intron and fully coincides in the ITS and LSU. Obviously, collection H.B. 9226 included, besides abundant *O. aristata* and one apothecium of *O. subclavuliformis*, also *O. clavuliformis* which was overlooked during microscopic examination.

In our phylogenetic analyses *O. clavuliformis* clustered in the *aristata-clavuliformis* clade (Phyls 9, 12, S13). In the ITS region *O. clavuliformis* shows a distance of 4.5–6% to *O. subaristata*, *O. aristata*, and *O. flagellispora*, 6.5% to *O. subclavuliformis*, 7% to *O. fimbriata*, 16% to *O. spermoides*, and 19% to *O. angustoaristata*. When analysing LSU (D1–D2), *O. clavuliformis* clustered with medium support and a 0.8% distance with *O. subclavuliformis* in a clade (S13), the next close taxon being *O.* aff. *subaristata* (KY419191) with 1%, whereas in the ITS analysis *O. clavuliformis* clustered distant from *O. subclavuliformis* (Phyl. 12).

Two environmental ITS sequences from North America are undoubtedly conspecific with *O. clavuliformis* (see Phyl. 12). One from Ottawa (GU931753) differs by 3 nt and 1 gap (0.6%) in the ITS region (2 nt in ITS2), and that from Indiana (KT196610), comprising only partial 5.8S and entire ITS2, deviates from *O. clavuliformis* in the ITS2 by 5 nt and 2 gaps (in 2 of these 5 nt it concurs with the Ottawa strain).

Ecology. *O. clavuliformis* grows on ± rotten bark and also wood of xeric twigs and branches of various trees and shrubs of angiosperms, sometimes gymnosperms, also on stems of *Rubus*, in thermophilous (sun-exposed) but also shady forests and scrubs, including a swampy *Salicetum* with *Filipendula*. The rather numerous collections and environmental DNA data suggest that the species is restricted to more or less temperate humid, oceanic to continental areas of Europe and North America. In Europe it was repeatedly found growing in association with *O. aristata*. In samples from western France the climate is mesotemperate humid (oceanic), in those from Montenegro mesosubmediterranean (semi)humid, and in the two DNA-extracts from North America hemiboreal humid (Ottawa) and warm-continental humid (Indiana). Records from montane, boreal, and eumediterranean areas are so far absent. The not included samples from North America are from the cold-temperate (sub)humid southern Appalachian Mountains and Colorado Plateau (pinyon-juniper woodland).

Specimens included. **GREAT BRITAIN**: **East Midlands**, **Nottinghamshire**, 5 km NW of Retford, 2 km NE of Barnby Moor, Daneshill Energy Forest, 15 m, trunk *Eucalyptus gunnii*, on bark, 26.V.2011, C. Hobart (ø, doc. vid.).

Plate 315. **1–10**: *Orbilia clavuliformis*. – **1a**. living *Malus* tree with detaching bark; **2a**, **3a**. dead corticated xeric branches (**2a** with *Xanthoria parietina* & *Physcia tenella*, **3a** with *Orthotrichum*); **1b**, **d**, **f**, **2a**, **3a–b**, **4a**. rehydrated apothecia; **1c**, **e**, **4b**. dry apothecia (**4b** with *Nitschkia cupularis* & *Physcia tenella*); **1g–h**. apothecia in median section; **1i**. id., marginal ectal excipulum; **10a**. marginal cortical cells in squash mount (with globose SCBs); **1j**, **5b**, **6b**, **10b**. asci (**6b** fully turgescent) and paraphysis; **2b**, **5a**, **6a**, **7**, **8**, **9**. ascospores. – Living state. – **1a**, **10a–c**: phot. P. Perz. — **1a–j**. H.B. 8212: Poland, Kłodzko, on *Malus*; **2a–b**. H.B. 9253b: Germany, Tübingen, on *Salix*; **3**. H.B. 8231: Luxembourg, Grevenmacher, on *Cornus*; **4a–b**. H.B. 7150b: Tübingen, on *Acer*; **5a–b**. H.B. 7817: ibid., on *Salix*; **6a–b**. H.B. 8390: ibid. on *Rubus*; **7**. H.B. 8437a: ibid., on *Rubus*; **8**. P.P. 20061028: Kłodzko, on *Picea*; **9**. H.B. 7877a: Tübingen, on *Cornus*; **10a–b**. P.P. 20061228: Kłodzko, on *Cornus*.

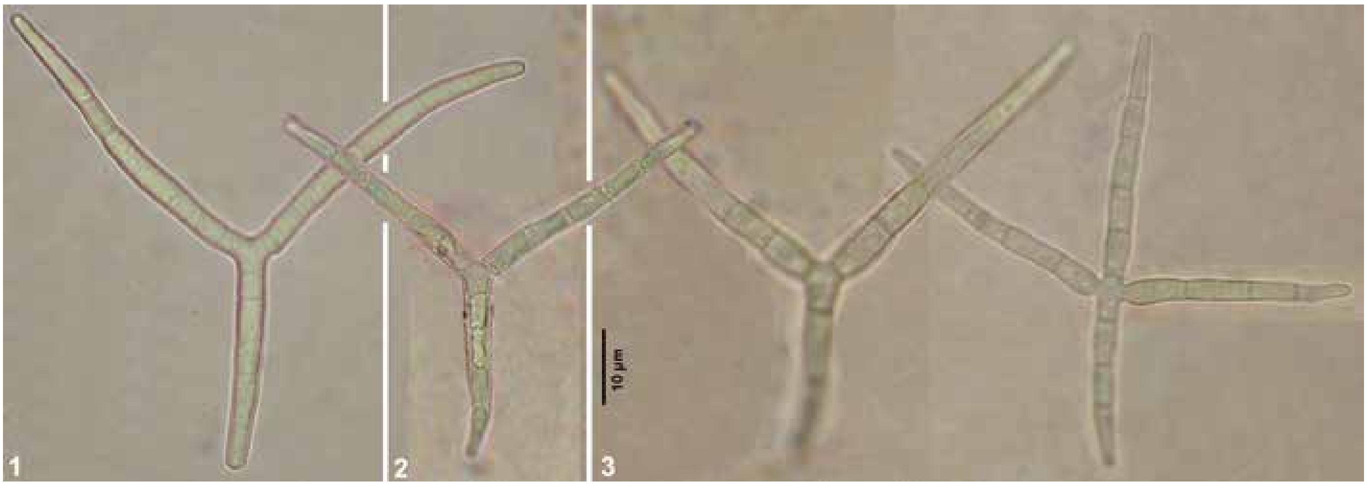


Plate 316. **1–3**: *Orbilia clavuliformis*. – Trinacrium- (**1–3**) and descalsia-like (**3** right) conidia from substrate. – Living state, except for **2** (in H_2O). — **1**. 28.III.2009: Netherlands, Boxmeer, on *Cornus*; **2**. H.B. 5823: Germany, Ravensburg, on *Salix*; **3**. H.B. 8212: Poland, Kłodzko, on *Malus*.

– **West Midlands**, **Worcestershire**, 5 km NW of Bromsgrove, 1.8 km E of Chaddesley Corbett, Chaddesley Wood, 120 m, branch of *Rosa canina*, on thorn, 25.I.2011, P. Thompson (K(M) 169475, doc. vid.). — **NETHERLANDS**: **Noord-Brabant**, 0.3 km NE of Boxmeer, Weijerpark, 13 m, branch of *Cornus alba*, on bark, 28.III.2009, S. Helleman (S.H. 605, doc. vid., anam. substr. Y). — **LUXEMBOURG**: **Gutland**, **Esch-sur-Alzette**, 1.5 km E of Bettembourg, Bierg, 290 m, branch of *Malus domestica*, on bark, 24.VI.2007, G. Marson (ø, anam. substr. Y & ┼). – **Grevenmacher**, 6 km NE of Grevenmacher, 1.5 km N of Wasserbillig, N of Langsur, S-exposed slope at Sauer River, 150 m, branch of *Cornus sanguinea*, on bark, 15.VII.2006, G. Marson (H.B. 8231). — **FRANCE**: **Bretagne**, **Morbihan**, 3.5 km ESE of Malestroit, NE of Nazareth, 94 m, branch of *Ulex europaeus*, on wood, 29.III.2008, J.P. Priou (J.P.P. 28055, doc. vid.). – 3.2 km NNE of Malansac, SW of La Saulais, Moulin de Quiban, 14 m, branch of indet. angiosperm, on wood, 20.V.2005, J.P. Priou (J.P.P. 25105, H.B. 8380 ø). – **Pays-de-la-Loire**, **Loire-Atlantique**, 13 km WSW of Nantes, NW of St.-Jean-de-Boiseau, W of La Rivière, 13 m, branch of *Cytisus scoparius*, on wood, 15.XI.2009, J.P. Priou (J.P.P. 29213, doc. vid.). – **Aquitaine**, **Gironde**, 7.5 km SSE of Langon, 1.5 km WSW of Coimères, 100 m, branch of *Quercus*, on wood, 6.I.2007, J.P. Priou (J.P.P. 27012, doc. vid.). — **GERMANY**: **Baden-Württemberg**, 5.5 km SW of Heidelberg, 2.5 km SSW of Eppelheim, Eppelheimer Wäldchen, 108 m, branch of *Cornus mas*, on bark, 12.V.2012, M. Bemmann (ø, doc. vid., anam. substr. Y). – 8.5 km NW of **Stuttgart**, 1.8 km W of Korntal, Grüner Heiner, 330 m, branch of *Salix ?alba*, on bark, 24.VI.2000, H.O. Baral (ø). – 6 km NW of Stuttgart, S of Weilimdorf, SW of Köstlinschule, 335 m, twig & branch of *Salix eleagnos*, on bark, 23.VI.2000, E. Weber & H.O. Baral (H.B. 6710, anam. substr. Y & ┼). – ibid., branch of indet. angiosperm, on bark, 23.VI.2000, H.O. Baral (ex H.B. 6714, M-0276457, **holotype**, CBS 116234, anam. cult. Y; sq.: KT215271). – 0.8 km E of Weilimdorf, Lake at Goslarer Straße, 325 m, branch of *Cornus mas*, on bark, 1.X.2000, H.O. Baral (ø). – 2.5 km NW of **Tübingen**, Morgenstelle, University Campus, 455 m, branch of *C. alternifolia*, on bark, 22.VIII.2005, H.O. Baral (H.B. 7877a ø). – 1.8 km WNW of Tübingen, Schnarrenberg, 430 m, branch of *Salix*, on bark, 19.VI.2005, H.O. Baral (H.B. 7817 ø). – 1 km W of Tübingen, Rheinlandstraße, 330 m, branch of *Acer pseudoplatanus*, on bark, 16.VI.2002, H.O. Baral (H.B. 7150b). – 5.5 km NE of Tübingen, N of Pfrondorf, Brand, 440 m, stem of *Rubus fruticosus*, on bark, 3.III.2007, H.O. Baral (H.B. 8437a). – Pfrondorf, Blaihofstraße, 430 m, twig of *Ligustrum vulgare*, on bark, 1.VII.2002, H.O. Baral (ø). – ibid., on a rope, 24.XI.2009, H.O. Baral (H.B. 9226o, non vid., sq.: MK493147). – S of Pfrondorf, Obere Mähder, 390 m, stem of *Rubus fruticosus*, on wood, 24.VII.2002, H.O. Baral (H.B. 7171c, in M-0276444 [*O. breviaristata*]). – ibid., 13.XII.2006 (H.B. 8390). – ibid., branch of *Salix caprea*, on bark, 22.III.2010, H.O. Baral (H.B. 9253b). – **Oberschwaben**, 6.7 km N of Ravensburg, 2.8 km WNW of Baienfurt, SSE of Staig, 440 m, branch of *S. cinerea*, on bark, 28.VI.1997, G. Marson (H.B. 5823, anam. substr. Y & ┼). – 7 km NW of Überlingen, NW of Sipplingen, Gasthof Niederhohenfels, 480 m, branch of *Pinus sylvestris*, on wood, 1.IX.2001, H.O. Baral (H.B. 7017a). – **Bayern**, **Unterfranken**, 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz, 260 m, branch of *Salix caprea*, on bark, 11.XI.1995, H.O. Baral (H.B. 5383a, Krieglsteiner 1999: 271, as 10.XI., *Orbilia* sp. 1). – ibid., branch of *Cornus sanguinea*, on bark, 11.XI.1995, H.O. Baral & L.G. Krieglsteiner (H.B. 5386a, Krieglsteiner l.c.). — **AUSTRIA**: **Steiermark**, 22 km NNW of Graz, 3 km SSW of Frohnleiten, S of Burg Rabenstein, 430 m, branch of *Malus domestica*, on bark, 3.II.2019, G. Friebes (G.F. 20190019). – 4.5 km SE of Graz, SE of St. Peter, Messendorfberg, 450 m, branch of *Quercus*, on bark, 29.XII.2013, R. Burkard, vid. B. Wergen (B.W. C00060). – **Burgenland**, 8.5 km SE of Eisenstadt, 3 km E of Siegendorf, Siegendorfer Puszta und Heide W of Neusiedler See, 170 m, branch of *Rosa*, on wood, 28.XI.2009, G. Friebes (G.F. 20090126, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 11.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, WSW of WWII memorial, 452 m, branch of *Tilia tomentosa*, on bark, 3.VII.2019, D. Savić (FG-1099, doc. vid.). – ibid., W of WWII memorial, 445 m, branch of *Fraxinus ornus*, on bark, 16.VII.2019, D. Savić (doc. vid.). – 15.5 km SW of Novi Sad, Orlovac, 470 m, branch of *Acer platanoides*, on bark, 19.VII.2019, D. Savić (doc. vid.). — **MONTENEGRO**: 15 km NNW of Podgorica, 1.9 km NE of Donje Selo, Glizica, 210 m, twig of *Punica granatum*, on bark, 8.V.2016, B. Perić & D. Raspopović (B.P. Dgf/C7D-08-05-16c, doc. vid.). – ibid., twig of *Fraxinus*, on bark, 15.V.2016, B. Perić & D. Raspopović (B.P. Dgf/C7D-15-05-16, doc. vid.). - 4.5 km NW of Herceg Novi, NW of Ratiševina, 170 m, branch of *Punica granatum*, on bark, D. Savić (FG-1093, doc. vid.). — **CZECHIA**: **Moravia-Silesia**, 17 km SW of Ostrava, 2.5 km SE of Studénka, northeast-border of Albrechtičky, 243 m, branch of *Salix caprea*, on bark, 17.X.2009, M. Chlebická (PRM 915867, doc. vid.). — **SLOVAKIA**: **Banská Bystrica**, 8.5 km S of Banská Štiavnica, 3 km NNW of Prenčov, 455 m, branch of *Pinus sylvestris*, on wood, 27.IV.2018, A. Polhorský (A.P. 18/48, doc. vid.). – **Bratislava**, 10 km SE of Bratislava, 4.8 km S of Podunajské Biskupice, Topol'ové hony, 133 m, branch of *Ligustrum vulgare*, on wood, 5.VI.2019, A. Polhorský (A.P. 19/30, doc. vid.). — **POLAND**: **Łódź**, 5 km N of Łódź, Bałuty, Warszawska road, 213 m, branch of *Vitis vinifera*, on bark, 2.VI.2013, P. Perz (P.P. 20130602-4, doc. vid.). – 8 km E of Sieradz, Stawiszcze, Grabowiec road, 165 m, branch of *V. vinifera*, on bark, 10.VI.2013, P. Perz (P.P. 20130610-7B, doc. vid.). – 5.7 km SE of Radomsko, 2 km W of Orzechówek, 245 m, branch of *Populus*, on bark, 21.II.2010, J. Nowicki, vid. P. Perz (P.P. 20100221-1 JN, doc. vid.). – **Opole**, 3 km E of Otmuchów, N of Wójcice, 222 m, branch of *V. vinifera*, on bark, 10.VI.2013, P. Perz (P.P. 20130610-1A, doc. vid.). – **Lower Silesia**, 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, branch of *Cornus ?mas*, on

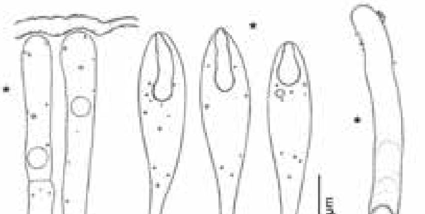


Plate 317. **1**: *Orbilia* cf. *clavuliformis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal cells terminated by a glassy process.

Map 55. Known distribution of *O. clavuliformis* in Europe.

bark, 28.XII.2006, P. Perz (P.P. 20061228-2, doc. vid.). – ibid., branch of *Salix*, on bark, 3.X.2007, P. Perz (ø). – 0.9 km NE of Kłodzko, Nałkowskiej ul., 320 m, trunk of *Malus domestica*, on bark, 15.VI.2006, P. Perz (P.P. 20060615_002, H.B. 8212, anam. substr. Y & ┼). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, young trunks of *Picea abies*, on bark, 28.X.2006, P. Perz (P.P. 20061028-3, doc. vid.). – ibid., 12.VIII.2006, P. Perz (P.P. 20060812-1, doc. vid.). — **RUSSIA (West)**: **Oryol**, **Znamenskoye**, 75 km ENE of Bryansk, 63 km NW of Oryol, 2.3 km NE of Elenka, Vytebet river, 174 m, twig of *Euonymus europaeus*, on bark, 19.X.2012, E.S. Popov (LE 248005, doc. vid.). — **CANADA**: **Ontario**, 25 km SW of Ottawa, Stittsville, 123 m, house dust, IX.2008 (Amend et al. ined., mol. extr.; sq.: GU931753). – **USA**: **Indiana**, 11 km SE of Bloomington, Lake Moore, ~200 m, deciduous forest soil, V–XI.2012 (Rosling et al. 2016, mol. extr.; sq.: KT196610).

Not included. **USA**: **North Carolina**, Appalachian Mts., Blue Ridge Mts., 31 km E of Franklin, 8 km NE of Cashiers, Big Green Mt., Panthertown Valley, 1200 m, twig of *Cornus*, on bark, 20.V.2003, W. Jaklitsch (W.J. 2174 ø, H.B. 7402b, anam. substr. Y). – **Arizona**, Grand Canyon, Kaibab Plateau, 28 km ESE of Fredonia, 13 km NNW of Jacob Lake, 2115 m, branch of *Pinus edulis*, on bark, 17.V.1995, G. Marson (ø).

Orbilia asturiensis Baral, E. Rubio & J. Linde, **sp. nov.**, MB 813601 — Pls 318–319

Etymology: named after the geographical origin (Asturias, northwestern Spain)
Typification: Spain, Villablino, branch of *Salix caprea*, 17.VIII.2008, J.L. Cheype (ex H.B. 8901, M-0276435, holotype).

Latin diagnosis: *Similis* Orbiliae clavuliformi *sed cauda ascosporarum distincte inflata, corpusculum refringens brevius, ab* O. flagellispora *cauda breviore, leniter constricta differt. Habitat ad lignum et corticem putridum ramorum siccorum* Salicis *in zona orotemperata humida Europae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.25–)0.5–1.2(–1.5) mm diam. (without teeth), 0.15–0.18(–0.3) mm high (receptacle 0.14 mm), light to bright yellowish-orange, slightly translucent, round to slightly lobate, scattered to ± gregarious in small groups; disc flat, margin not protruding but with prominent, 20 µm protruding white teeth of 40–70(–100) × 50–130(–200) µm; broadly sessile or with a stalk up to 0.15 × 0.25 mm, superficial; dry bright orange-red. **Asci** *65–80 × 7–8 µm {2}, †60–70 × 5.5–6.5 µm {T}, 8-spored, spores (*) biseriate, 2–4(–5) lower spores inverted {2} (not mixed), pars sporifera *~40–50 µm long; **apex** (†) hemispherical, dome †1.2–1.4 → 0.7–1 µm thick {T}, with distinct apical chamber; **base** with short to medium long, ± thick, flexuous stalk, T- to L-shaped. **Ascospores** *(13.7–)15–19(–21) × 3.3–3.8 µm {2}, †13.5–18 × 3.2–3.5 µm {T}, with ellipsoid head of *(8.5–)9–11(–12) µm length and a distinct *(3.5–)5–7(–8) µm long tail with a basal *1.5–2 µm wide inflation (rarely ± uninflated and *1.2–1.4 µm wide), above inflation *0.8–1.3 µm wide, apex obtuse to subacute, straight or somewhat inequilateral, rarely slightly to medium geniculate between head and tail; **SBs** *3–4 × 1–1.2(–1.4) µm {2}, cylindrical to pear- or dumbbell-shaped, apically abruptly narrowed to a very short filum (not visible on photographs), straight. **Paraphyses** apically uninflated to medium capitate, terminal cells *(12–)18–26(–32) × 2.5–3.3 µm {T}, lower cells *12–17 × 1.5–2.5 µm {T}; unbranched at upper septum, hymenium pale orange. **Medullary excipulum** pale orange, 40–70 µm thick, of loose to dense textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** pale orange, of (†) ± thin-walled, vertically oriented t. angularis-prismatica from base to margin, 40–75 µm thick near base, cells *9–25 × 6–12 µm {2}; 20–30 µm thick near margin, oriented at a 40–70° angle to the surface, outermost cells elongate, oriented at 20–40°, marginal cortical cells *6–9 × 2.5–3.5(–4.5) µm {T}; **glassy processes** (10–)20–70 × 2.5–3.5(–4.5) µm {2}, refractive, unstratified, curved outwards, coherent to form distinct teeth. **Anchoring hyphae** abundant, †2–3 µm wide, walls 0.2–0.7 µm thick {T}. **SCBs** in paraphyses and ectal excipulum absent {T} or globose, 1.8–2.1 µm diam. {1}; ectal excipular cells at flanks with some light yellow-orange **LBs** 1–2.5 µm diam. that contain carotenoids {2}. **Exudate** over paraphyses and teeth 1–3 µm thick, cloddy-continuous, pale yellowish-orange, loosely attached. **— ANAMORPH**: unknown.

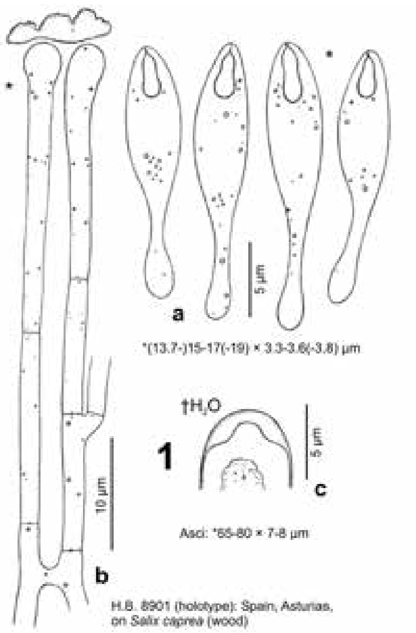


Plate 318. **1**: *Orbilia asturiensis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex.

Habitat: collected 1.5–3 m above the ground, decorticated, 13–15 mm thick branch of *Salix cantabrica* {1}, *S. caprea* {1}, on 0.2–0.3 mm deep strongly decayed wood {1} or on medium decayed bark {1}, slightly greyed, no algae. **Associated**: *Lindgomyces griseosporus* {1}, *Orbilia subtrapeziformis* {1} (both on another xeric branch of the same tree of paratype). **Desiccation tolerance**: mature asci still viable after 3 weeks. **Altitude**: 1365–1505 m a.s.l. **Geology**: acidic glacial deposits from Silurian-Devonian-Carboniferous quartzite, clay and slate. **Phenology**: VII–VIII (but probably long-lived).

Taxonomic remarks. *Orbilia asturiensis* resembles *O. clavuliformis*, from which it differs in the spore tails being consistently inflated at the base, also in shorter SBs with a very short filum, and larger marginal teeth made up of longer glassy processes. However, the filum is invisible on photographs and perhaps not always present. *O. asturiensis* differs from *O. flagellispora* in shorter spore tails which are much thicker above the basal inflation. In some collections here referred to *O. flagellispora* (e.g., Pl. 327: 3–4) the spore tails approach those of *O. asturiensis* in thickness, but here the spore heads are narrower and the SBs exceed 4 µm in length. An illustration of the paratype of *O. asturiensis* is also found in Rubio & Zapico (2018: 52).

Variation. In the paratype the spores tend to be slightly longer than in the holotype due to longer spore tails, otherwise the two samples concur very well.

Plate 319. **1–2**: *Orbilia asturiensis*. – **1a–c**, **e–g**, **2a–b**. rehydrated apothecia; **1d**. dry apothecium; **1h**. apothecium in median section; **1i**. id., marginal ectal excipulum with glassy processes that form teeth; **1k**. id., basal ectal excipulum; **1j**, **2c–e**. ascus and paraphysis apices; **1l**, **2f**. ascospores. – Living state (**2c–f** in CRB), except for **1j** (ascus and paraphyses), ascus in **2e**. – **1c**, **f–g**, **j**, **l**, **2a–f**: phot. E. Rubio. — **1a–l**. H.B. 8901 (holotype): Spain, Asturias, Monasterio de Hermo, on *Salix*; **2a–f**. id., El Puerto, on *Salix*.

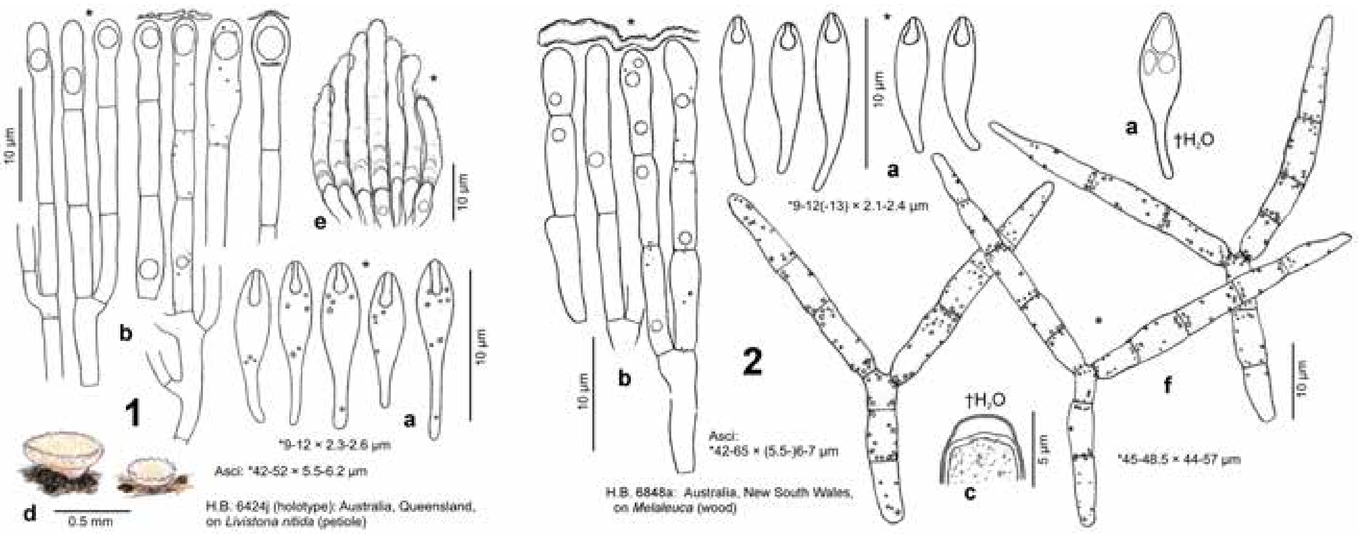


Plate 320. **1**: *Orbilia parviclava*; **2**: *O*. aff. *parviclava*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex; **d**. apothecia with dentate margin (rehydrated); **e**. marginal cortical cells with glassy processes (external view); **f**. conidia from substrate.

Ecology. *Orbilia asturiensis* was found on rotten wood and bark of xeric branches of *Salix* spp. in the orotemperate humid atlantic Cantabrian Mountains of Asturias (southwestern Europe). Despite repeated search at the type locality, apothecia could only be observed on the original tree individual. The vegetation was a *Fagus sylvatica* dominated forest on acidic soil, with *Betula pubescens*, *Corylus avellana* and *Salix caprea*, at a medium shaded forest edge. The paratype locality lies in a heath- and shrubland with, e. g., *Erica* spp., *Cytisus scoparius*, *Genista florida*, *Juniperus alpina*, *Thymelaea cordifolia*, and *Vaccinium myrtillus*, where *O. asturiensis* grew on an attached branch 1.5–2 m above the water of a streamlet bordered by shrubs of *Salix cantabrica*. The associated *Lindgomyces griseosporus* was considered to be an aquatic fungus but is obviously able to form perithecia also on xeric branches (here with *O. subtrapeziformis* about 2 m above the water, E. Rubio pers. comm.).

Specimens included. **SPAIN**: **Asturias**, 7 km S of Pola de Somiedo, 1.6 km W of El Puerto, N of Vega Cimera, 1505 m, branch of *Salix cantabrica*, on bark, 7.VII.2017, E. Rubio (E.R.D. 7104, doc. vid.). – 23 km SW of Pola de Somiedo, 4 km E of Monasterio de Hermo, 1365 m, branch of *S. caprea*, on wood, 17.VIII.2008, J.L. Cheype, vid. E. Rubio (ex H.B. 8901, M-0276435, **holotype**; E.R.D. 4549, **isotype**).

Orbilia parviclava Baral, **sp. nov.**, MB 813602 — Pls 320–321

Etymology: referring to the rather small clavate ascospores.

Typification: Australia, Queensland, Taroom, leaf of *Livistona nitida*, 22.X.1998, G. Marson (ex H.B. 6424j, BRI AQ799183, holotype).

Latin diagnosis: *Similis* Orbiliae clavuliformi *sed ascosporae multo minores, corpusculum refringens brevius differt. Habitat ad petiolum putridum siccum* Livistonae nitidae *in zona subtropica subhumida Australiae orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.22–0.55 mm diam., 0.07–0.15 mm high (receptacle 0.06–0.09 mm), pale cream-orange, translucent, round, ± scattered; disc flat (to slightly convex), margin thin,

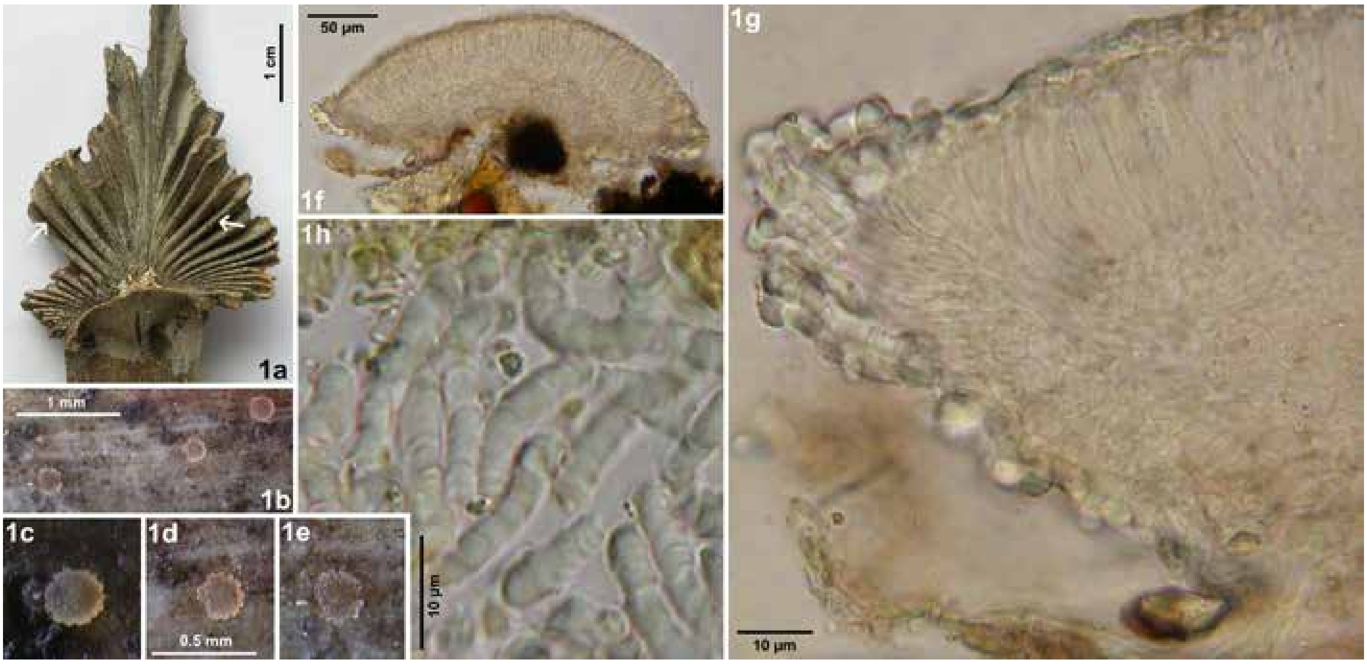


Plate 321. **1**: *Orbilia parviclava*. – **1a**. dead fan-shaped part of leaf of *Livistona nitida*; **1b–e**. rehydrated apothecia; **1f**. apothecium in median section; **1g**. id., marginal region; **1f**. marginal glassy processes (squash mount). – Dead state (in KOH). — **1a–g**. H.B. 6424j (holotype): Australia, Queensland, Taroom, on *Livistona*.

smooth or more often distinctly crenulate or toothed, teeth 30–50 × 15–30 µm; sessile or with a short, broad stipe, superficial. **Asci** *42–52 × 5.5–6.2 µm, †34–43 × 4–5 µm, 8-spored, 2–3 lower spores inversely oriented, pars sporifera *22–24 µm long; **apex** (†) ± hemispherical, dome immature †1–1.3 µm thick, without apical chamber, **base** with medium to long, thin, ± flexuous stalk, L-shaped. **Ascospores** *9–12 × 2.3–2.6 µm, ± clavate, with ellipsoid-fusoid head *6.2–7 µm long and a distinct, straight (to slightly curved) basal tail *2–5 × 0.6–0.9 µm; **SBs** *2.2–2.5 × 0.7–0.9 µm, rod-shaped to ampulliform, apically attached by a ± wide point. **Paraphyses** apically uninflated to slightly capitate, terminal cells *7–12(–17) × 2–3.3 µm, lower cells *6–11 × 1.3–2.7 µm; never branched near apex. **Medullary excipulum** 20 µm thick, of dense textura intricata with some inflated cells, medium sharply delimited. **Ectal excipulum** of (†) thin-walled, indistinctly oriented t. angularis from base to mid flanks, 30–40 µm thick near base, cells *10–17 × 8–13 µm, †8–13 × 5–7 µm; 15–20 µm thick near margin, of t. prismatica-porrecta oriented at a 20–40° angle to the surface, marginal cortical cells *8–13 × 2.5–4 µm. †5–7 × 2.8–3.2 µm, **glassy processes** 4–30 × 3–4 µm, refractive, stratified, slightly outwards curved, coherent to form 20–30 × 15–30 µm large teeth. **Anchoring hyphae** abundant, †1.5–2.5 µm wide, walls 0.2(–0.3) µm thick. **SCBs** globose, in paraphyses 1.5–2.5 µm diam., rarely with a needle-shaped (crystalloid) SCB. **Exudate** over paraphyses 0.3–1.5 µm thick, cloddy, loosely attached; over glassy processes scattered, granular, 0.2–0.5 µm thick. **— ANAMORPH**: unknown (but see below).

Habitat: collected ~1 m above the ground, upper end of dead petiole of *Livistona nitida*, on ridges and deep in clefts at the base of the leaf blade (upperside), medium decayed, strongly greyed, with or without many green algae. **Associated**: remotely (on different leaves) with *Gloniopsis* sp., *Mellitiosporiella* sp., *Orbilia acaciae*, *O. ?australiensis*, *O. ?commarosa*, *O. coronohesperidea*, *O. ?dixiensis*, *O. livistonae*, *O. multiserpens*, *O. myrioeuonymi*, *O. palmicola*, *O. pleiohesperidea*. **Desiccation tolerance**: fully viable for at least 9 months. **Altitude**: 200 m a.s.l. **Geology**: Jurassic sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia parviclava* is characterized by clavate ascospores similar as in the European *O. clavuliformis*, and glassy processes that form distinct teeth. It deviates in much smaller spores with shorter spore bodies. The European *O. breviclava* differs in longer spores with more cylindrical heads, longer SBs, larger apothecia without glassy processes, also in more abundant crystalloid SCBs.

Not included collections. Two very sparse Australian collections on wood of *Melaleuca* (Pl. 318: 2, also mentioned under *O. australiensis*) and bark of *Eucalyptus* (IVV: H.B. 6764b) differ in slightly longer and narrower spore heads and in the absence of glassy processes. Moreover, in that on *Melaleuca* the SBs are shorter and wider (no SBs were seen in H.B. 6764b which was only studied in the dead state).

Anamorph. No anamorph was observed in *O. parviclava*. However, in the *Melaleuca* collection trinacrium subtile-like conidia were found on the natural substrate (Y-shaped, total size *45–48.5 × 44–57 µm, stipe *18–21 × 3.5–4 µm, 2-septate, arms slightly tapering, *31–38.5 × 3.5–4 µm, 3–5-septate, Pl. 318: 2f).

Ecology. *O. parviclava* was found on a medium decayed xeric (attached) leaf of *Livistona nitida* in the Palm-Tree Creek in a subtropical subhumid (winter-dry savannah) eucalypt woodland (Great Dividing Range, eastern Australia). One of the two mentioned deviating collections grew on wood of *Melaleuca* under a similar climate, that on *Eucalyptus* in a warm-temperate humid mountainous eucalypt open forest in southeastern Australia (Great Dividing Range).

Specimens included. **AUSTRALIA**: **Queensland**, Brigalow Belt South, 69 km SSW of Theodore, 15 km N of Taroom, Palm-Tree Creek, Roy Staines Bridge, 200 m, leaf of *Livistona nitida*, 22.X.1998, G. Marson (ex H.B. 6424j, BRI AQ799183, **holotype**).

Not included. **AUSTRALIA**: **New South Wales**, Brigalow Belt South, 38 km SSW of Goondiwindi, 34 km SSW of Boggabilla, 230 m, branch of *Melaleuca*, on wood, 23.X.1998, G. Marson (H.B. 6848a ø). – Sydney Basin, 95 km WNW of Sydney, 11.5 km SE of Lithgow, 1.6 km SE of Mt. York, 1073 m, branch of *Eucalyptus*, on bark, 26.X.1998, G. Marson (ex H.B. 6764b, mixture in MEL 2389215 [type of *O. plurililacina*]).

Orbilia breviclava Baral, **sp. nov.**, MB 813603 — Pls 322–323

Etymology: named according to the clavate ascospores which are shorter than in *O. subclavuliformis* and *O. clavuliformis*.

Typification: Austria, Gmunden, trunk of *Frangula alnus*, 19.IV.1994, W. Dämon (ex H.B. 5072, M-0276445, holotype).

Latin diagnosis: *Similis* Orbiliae clavuliformi *sed ascosporae breviores, subcylindricae, excipulum marginale absque processis vitreis, cellulae vivae excipuli marginalis et paraphysium corpuscula crystalloidea continentes. Habitat ad lignum putridum trunci sicci* Frangulae alnus *in zona temperata humida Europae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.6 mm diam., 0.12–0.15 mm high (receptacle 0.11–0.13 µm), light orange-rose, semitranslucent, ± round, (densely) gregarious; disc flat to medium convex, margin thin, not protruding, smooth; sessile, superficial; dry bright orange. **Asci** *42–60 × 5.7–6.3 µm, †39–53 × 5–5.7 µm, 8-spored, spores *3–4-seriate, 2–6 lower spores inverted (scarcely mixed), pars sporifera *26–30 → 18 µm long; **apex** (†) hemispherical, dome mature 0.5–1 µm thick, with apical chamber; **base** with short to medium long, thin, flexuous stalk, L- to Y-shaped. **Ascospores** *(9–)11–14(–15) × 2.4–2.6(–2.7) µm, †9.5–12.5 × 2–2.5 µm, with cylindric to ellipsoid head *7.5–9 µm long, with rounded apex, and a medium sharply differentiated tail *(2–)3–5(–6) × 0.7–1(–1.2) µm, straight to slightly curved near base, sometimes slightly swollen at base;

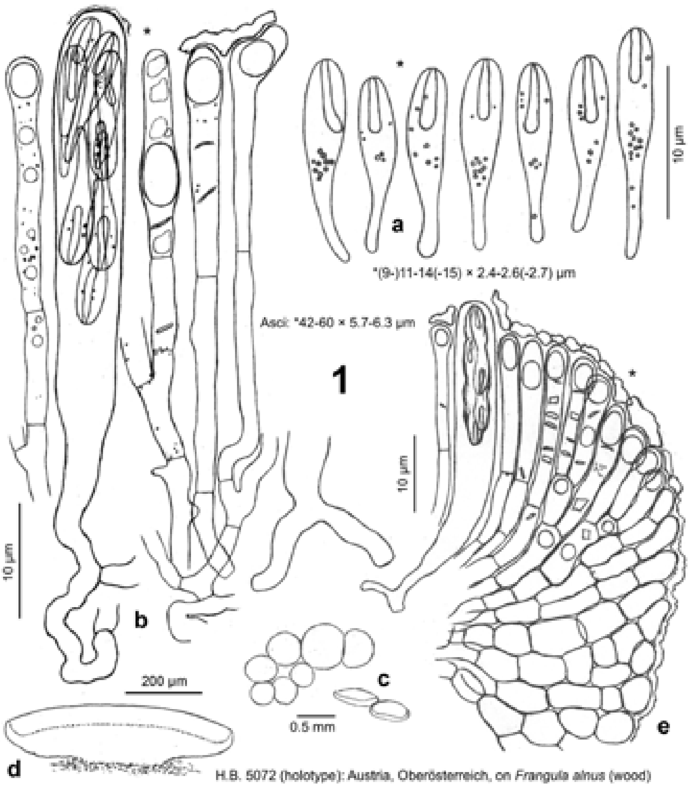


Plate 322. **1**: *Orbilia breviclava*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. apothecia (fresh); **d**. apothecium in median section; **e**. id., ectal excipulum (margin and mid flanks), with high-turgescent ascus.

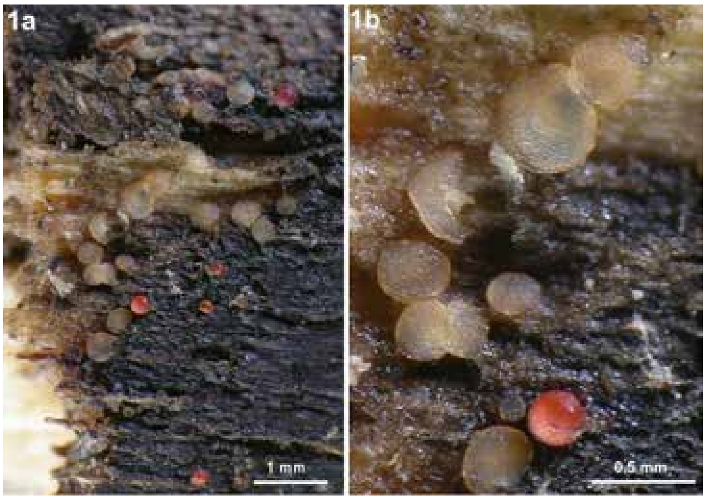


Plate 323. **1**: *Orbilia breviclava*. – **1a–b**. rehydrated apothecia (with *Neonectria coccinea*) (phot. after 12 years). — **1a–b**. H.B. 5072 (holotype): Austria, Oberösterreich, Gmunden, on *Frangula*.

SBs *(3–)4–5(–5.5) × (0.7–)0.8–1(–1.2) µm, rod-shaped to subulate, apically narrowed to a small to wide point, ± straight; with a number of small, often aggregated LBs. **Paraphyses** apically uninflated to slightly clavate-capitate, terminal cells *17–30 × 2.2–3.5 µm, lower cells *8–20 × 1.5–2(–3) µm; unbranched at upper septum, hymenium pale rose. **Medullary excipulum** 30 µm thick, of dense textura globulosa(-intricata), indistinctly delimited. **Ectal excipulum** pale rose, of thin-walled, indistinctly vertically oriented t. globulosa-angularis from base mid flanks, 60–80 µm thick near base, cells *8–18 × 8–15 µm; 30–40 µm thick at flanks, 20 µm near margin, of t. prismatica-porrecta oriented at a 45° angle to the surface, marginal cortical cells *(5–)9–18 × 3–4.5 µm; **glassy processes** absent. **Anchoring hyphae** rather abundant, *2–4 µm wide, walls 0.2–0.5 µm thick, somewhat gelatinized. **SCBs** in paraphyses and ectal excipulum (near margin) globose to ellipsoid, 2–3 µm wide, and rod-shaped to angular. **Exudate** over paraphyses 1–2 µm thick, cloddy, loosely attached; over margin and flanks 1–3 µm thick. **— ANAMORPH**: unknown.

Habitat: collected 1.5 m above the ground, on a partially decorticated, 5 cm thick standing trunk of a dead shrub of *Frangula alnus*, on medium decayed wood, sometimes blackened, without algae. **Associated**: *Neonectria coccinea*. **Desiccation tolerance**: not tested, probably at least slightly tolerant. **Altitude**: 470 m a.s.l. **Geology**: peat bog over Cretaceous-Paleogene flysch. **Phenology**: IV.

Taxonomic remarks. The ascospore characters of *O. breviclava* are very similar as in *O. subclavuliformis* and *O. clavuliformis*, from which this species differs in shorter spores and the presence of crystalloid SCBs, also in a tendency to more inverted spores within the asci. *O. clavuliformis* differs in wider, more ellipsoid spore heads, and in the presence of glassy processes. For the similar Australian *O. parviclava* see p. 688.

Not included collection. A very sparse collection from southwestern North America (on wood of *Larrea*, IVV: H.B. 5658c) shows a similar spore size (*10.5–13 × 2.4–3 µm) and shape, but the SBs are too short (~2.5–3.5 µm) and more ampulliform, and the tails rather thick. The sample was not studied thoroughly and the material is now without mature apothecia. The marginal excipulum was without devoid of glassy processes, and only globose SCBs were seen in the paraphyses.

Ecology. *O. breviclava* was collected on medium rotten wood of a xeric young trunk of *Frangula alnus* in a cold-temperate humid, subcontinental, submontane, *Sphagnum*-rich *Betula-Pinus* bog with *Alnus glutinosa* at the northern foothills of the Alps (central Europe). The not included collection was on very rotten wood of a xeric *Larrea tridentata* branch in the subtropical semiarid Sonoran paloverde-mixed cacti desert scrub with, e. g., *Cylindropuntia versicolor* and *Parkinsonia microphylla* on Cenozoic mixed sand- & mudstone and volcanic rock in Arizona (southwest of Northern America).

Specimens included. **AUSTRIA**: **Oberösterreich**, Salzkammergut Mts., 55 km SW of Linz, 1 km NE of Gmunden, SE of Schloss Cumberland, Krottensee, 470 m, trunk of *Frangula alnus*, on wood, 19.IV.1994, W. Dämon (ex H.B. 5072, M-0276445, **holotype**).

Not included. **USA**: **Arizona**, Sonoran Desert, 82 km NW of Phoenix, ~1.5 km SE of Wickenburg, 615 m, branch of *Larrea tridentata*, on wood, 4.V.1995, G. Marson (H.B. 5658c).

Orbilia subclavuliformis Baral, E. Weber & Priou, **sp. nov.**, MB 813605 — Pls 324–326, Map 56

Etymology: closely related to *O. clavuliformis*.

Typification: France, La Tranche-sur-Mer, branch of *Quercus ilex*, 2.VI.2003, H.O. Baral (ex H.B. 7382, M-0276592, holotype).

Latin diagnosis: *Similis* Orbiliae clavuliformi *sed ascosporae angustiores, subcylindricae, cauda basaliter saepe inflata, processi vitrei excipuli marginalis breves vel saepe absentes. Habitat ad lignum et corticem putridum ramorum siccorum fruticum vel arborum angiospermarum vel coniferarum in zona thermo- ad mesosubmediterranea vel temperata atlantica ad subcontinentale Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.15–0.5(–0.7) mm diam., 0.08–0.17 mm high (receptacle 0.08–0.11 mm), (pale to) light (to bright) (pinkish-)rose, orange-rose or orange, translucent, round (rarely elliptical), scattered to (sub)gregarious; disc flat, sometimes slightly convex, margin thin, sometimes indistinct, 0(–10) µm protruding, smooth, rarely very finely rough; broadly sessile or with a distinct stipe up to 0.05–0.06 × 0.1–0.18 mm, superficial; dry light to bright pinkish-rose or orange(-red). **Asci** *(35–)40–55(–58) × 6–7.2((–8)) µm {9}, †34–55(–60) × (5–)5.5–6.5(–6.8) µm {10}, 8-spored, spores 2–4-seriate, ((0–))(1–)2–3(–4)((–5)) lower spores inversely oriented {11} (mostly not mixed), pars sporifera *23–32 µm long; **apex** (†) hemispherical (rarely slightly truncate), dome †1–1.8 → 0.8–1.2 µm thick {10}, with distinct apical chamber; **base** with short to (very) long (rarely absent), thin to medium thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *((11–))(13–)14–18(–19)((–20.5)) {19} or (17–)18–21.5(–23) {3} × (2.2–)2.3–2.7(–3) µm {22}, †(12–)13–17(–18) × (2–)2.2–2.6 µm {10}, with cylindric(-ellipsoid) head *(7.5–)8.5–11(–12.5) µm long and a ± sharply differentiated tail *(4–)5–8(–11) µm long, tail shorter than head (rarely of equal length), apex rounded or obtuse, tail straight or slightly to medium curved, base not or often slightly, sometimes medium inflated, *((0.5–))0.8–1.2(–1.5)((–2)) µm wide; **SBs** *(3.5–)4–6 × (0.6–)0.7–1.2(–1.3) µm {13}, rod-shaped to subulate, sometimes slightly pyriform, ampulliform, or dumbbell-shaped, apically narrowed to a small to mostly wide point; overmature *2.5–3 × 1.4–1.5 µm. **Paraphyses** apically uninflated to often slightly (rarely medium) clavate-capitate, rarely spathulate, terminal cells *(7.5–)9–20(–23) × 2–3.5(–4) µm {7}, †6–15 × 1.8–3 µm {1}, lower cells *(3–)5–10(–12) × (1.5–)1.8–2.5(–3.7) µm {5}; sometimes branched at upper septum. **Medullary excipulum** subhyaline to pale rose, 10–30 µm thick, of dense textura intricata with many inflated cells, not or medium sharply delimited. **Ectal excipulum** pale rose, of thin-walled (†slightly gelatinized), ambiguously or ± vertically oriented t. globulosa-angularis from base to mid flanks, 25–150 µm thick near base, cells */†(8–)10–17(–21) × (6–)8–14(–17) µm {3}; 15–25 µm thick at flanks and margin, at margin of t. prismatica-porrecta oriented at a 30–60 or often 70–90° angle to the surface (including outer cells), marginal cortical cells */†6–11 × (2.3–)3–4(–5) µm {6} (at submargin *5–8 × 4–5 µm), **glassy processes** absent {25}, sometimes present on some or most cells, 1–5(–7.5) × 2.8–4 µm {8}, refractive, somewhat stratified. **Anchoring hyphae** sparse, †(1.7–)2–3(–4) µm wide, walls 0.2–0.3(–0.7) µm thick {2}, forming a medium dense, hyaline t. intricata 20–50 µm thick at base, covering apothecia at flanks as a thin layer. **SCBs** globose, in paraphyses 1–3 µm diam., in marginal excipulum 2–3.3 µm. **Exudate** over paraphyses (0.3–)1–2.5(–4) µm thick; over margin (0.3–)1–4(–5) µm, ± continuous to cloddy, externally coarsely rough, loosely attached, subhyaline to pale yellowish. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {3}). **Conidiophores** not seen. **Conidia** Y-shaped, total size *36–50 × 46–48 µm (†60–62 × 43–73 µm), stipe *24–31 × (2.6–)3.5–4 µm (†24.5–33 × 2.5 µm), 4–5-septate, arms slightly tapering or cylindrical, *(19–)23–29 × (2.8–)3.5–4.2 µm {H.B. 8106}, †37.5–44 × 2.5–3 µm {H.B. 5226a}, 4–9-septate {2}.

Habitat: collected (0–)0.2–5 m above the ground, corticated, more rarely ± decorticated, (2–)5–25(–40) mm thick twigs and branches, rarely cones, of *Anagyris foetida* {1}, *Buxus sempervirens* {1}, *Cedrus atlantica* {1}, *Cercis siliquastrum* {3}, *Clematis* (?)*flammea* {1}, *Cornus sanguinea* {1}, *Cytisus scoparius* {6}, *Eucalyptus* sp. {1}, *Euonymus europaeus* {1}, *Frangula alnus* {1}, *Lonicera implexa* {1}, *L. xylosteum* {1}, *Olea europaea* {1}, *Petteria ramentacea* {1}, *Pinus* sp. {1}, *P.* ?*contorta* {1}, *P. sylvestris* {3}, *Punica granatum* {1}, *Quercus ilex* {4}, *Q. suber* {1}, *Rosa* sp. {2}, *Rosmarinus officinalis* {1}, *Salix* sp. {1}, *S.* ?*aurita* × *caprea* {1}, *Ulex europaeus* {8}, *Vitis vinifera* {1}, stems of *Rubus armeniacus* {1}, *R.* (?)*bifrons* {1}, *R. fruticosus* agg. {1}, *R. grandifolius* {1}, on 0.1–0.2 mm deep (slightly to) medium to strongly decayed wood {23} or bark {23} (on periderm {2} or bast {9}), on cut, splitted, or eroded wood, sometimes in beetle galleries, in small to large cracks or large periderm-free areas when on bast, sometimes on inner surface of detaching bark, sometimes at border of resinous wounds, on herbaceous stem of *Melilotus* sp.{1}, on textile (rope) {1}, slightly to strongly greyed, green algae very sparse to abundant. **Associated**: *Baggea* sp. {1}, *B. pachyascus* {1}, *Bionectria ralfsii* {1}, *Bulbillomyces* sp. {1}, ?*Calloria* sp. {1}, *Caloplaca* sp. {1}, *C. holocarpa* {1}, *Capronia* sp. {1}, '*Chlorosplenium*' *viridulum* {1}, *Claussenomyces* spp. {2}, *C. atrovirens* {1}, *Coniochaeta* sp. {1}, *Corticiaceae* {1}, *Dacrymyces* sp. {1}, *Didymosphaeria futilis* {1}, *Hyalorbilia erythrostigma* {2}, *H. fusispora* {1}, *H. inflatula* {1}, *H. juliae* {1}, *H. subfusispora* {1}, *Hyaloscypha minuta* {1}, *Hysterium angustatum* {1}, *Hysterographium fraxini* {1}, *Karstenia idaei* {1}, *K. rhopaloides* {1}, *Lecanora* sp. {1}, *Lophiostoma caulium* {1}, *L.* ?*macrostomum* {1}, *Mellitiosporiella pulchella* {3}, *Mollisia* spp. {3}, *M.* ?*discolor* {1}, *M. ligni* {2}, *M. rosae* {1}, *Neodasyscypha cerina* {2}, *Nitschkia broomeana* {1/1}, *Olla scrupulosa* {1}, *Orbilia aristata* {3}, *O. aurantiorubra* {2}, *O. breviaristata* {2}, *O.* ?*caulicola* {1}, *O. cercidicola* {2}, *O. corculispora* {3}, *O. eucalypti* {2}, *O. filiformis* {1}, *O. flagellispora* {3}, *O. flavida* {2}, *O. gambelii* {5}, *O. microserpens* {1}, *O. myriolentiformis* {1}, *O. myriosphaera* {3}, *O. pleiogambelii* {4}, *O. polyspora* {3}, *O. quaestiformis* {2}, *O. rosicola* {1}, *O. sarothamni* {1}, *O. serpentina* {1}, *O. spermoides* {1}, *O. subaristata* {5}, *O. subocellata* {1}, *O. subovoidea* {3}, *O. trapeziformis* {1}, *O. vinosa* {2/1}, *O. vitalbae* {2}, *O. xanthoguttulata* {1}, *Orthotrichum* sp. {1}, *Patellaria atrata* {2}, *Patellariopsis dennisii* {1}, *Phyllactinia guttata* {1}, *Physcia* sp. {1}, *Pirottaea* ?*imbricata* {1}, *Propolis farinosa* {1}, *Pseudolachnea hispidula* {1}, *Pyrenopeziza rubi* {1}, *Rutstroemia fruticeti* {1}, *Sarea resinae* {1}, *Schizoxylon* sp. {1}, *Stereum hirsutum* {1}, *Unguiculariopsis* sp. {1}, *U. ilicincola* {1}, *Unguiculella eurotioides* {1}, fruticose lichen {1}. **Desiccation tolerance**: fully viable for at least 3 months, some spores after 5 months. **Altitude**: 2–1530 m a.s.l. **Geology**: Cambrian & Ordovician sand- & siltstone, quartzitic wacke, Keuper (marl & sandstone), Lower to Upper Jurassic and Cretaceous to Tertiary sand-, marl- & limestone, Minette & shale, dolomite, Pleistocene sand & loess; granite, migmatite, gneiss, mica schist. **Phenology**: throughout the year (long-lived).

Phenology of *O. subclavuliformis*

Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
3	4	3	1	3	8	3	4	7	6	3	5

Taxonomic remarks. *Orbilia subclavuliformis* differs from *O. clavuliformis* in the narrower and more cylindrical instead of ellipsoid ascospore heads, also in often slightly inflated tail bases. Concerning the long heads and inflated tail bases the species rather closely approaches *O. flagellispora*, in the first feature also *O. clavuliaristata*, but both species differ in more ellipsoid-fusoid spore heads and in often longer tails with a mostly thinner middle part (almost always > 0.7 µm wide). *O. flagellispora* differs also in mostly more strongly inflated tail bases. *O. subclavuliformis* differs from both *O. clavuliformis* and *O. flagellispora* in the glassy processes being often absent or at least very short. *O. breviclava* deviates in shorter spores and the presence of crystalloid SCBs.

Variation. *O. subclavuliformis* is somewhat variable in spore size and shape. Three atlantic collections (Pls 324: 3–4; 326: 4) have conspicuously longer spores, though the other features are quite the same as in typical specimens. Likewise, spore width (and also ascus width) varies somewhat among the populations. In many collections the spore heads are strikingly cylindrical (e. g., Pl. 325: 5), but this feature often varies to some extent towards subcylindrical or sometimes narrowly ellipsoid. The spore tails vary somewhat in length, thickness, and basal inflation. As an exception, they can be less than 0.8 µm thick in their middle part (Pls 325: 4; 326: 1i), thus obscuring the limits to *O. flagellispora*.

Not included collections. A sparse unpreserved sample on wood of *Pinus* from Bretagne deviated in exceptionally short spore heads (Pl. 325: 6). A sketchily documented collection on *Chamelaucium* from southwestern Australia did not clearly differ from European specimens (spores *15 × 2.2 µm, SBs 4.5 × 1 µm, glassy processes absent), but the single minute apothecium showed only a few living spores. A sample on *Arbutus* from southwestern Canada studied by O. & A. Ceska (pers. comm.) matches well *O. subclavuliformis* in the spores (*15–20 × 2–2.5 µm), but differs in apothecia with a minutely toothed margin.

Anamorph. The trinacrium subtile-like conidia observed on the natural substrate closely match those reported for *O. clavuliformis*. In the sample from Luxembourg (Pl. 325: 2e) the conidial arms were longer and narrower than in the Spanish collection (Pl. 326: 2h).

Phylogeny. A sequence from apothecia of *O. subclavuliformis* on *Eucalyptus* comprises SSU (with S1506 intron), ITS, and LSU. In our phylogenetic analyses (Phyls 9, 12, S13), the species clustered in the *aristata-clavuliformis* clade. When analysing LSU (D1–D2), S13), it clustered with medium support with *O. clavuliformis* in a clade, with a minimum distance of 0.8 %, the next close being *O. aristata* (KT222395) with 1.3 %. In the ITS region *O. subclavuliformis* shows a distance of 6.5 % to *O. clavuliformis*, but a similar distance to *O. aristata*, *O. fimbriata*, and other species of the *aristata-clavuliformis* clade can be noted. When analysing the intron (S12), *O. subclavuliformis* surprisingly clustered moderately supported with *O. spermoides*, though with a distance of 21 %.

An environmental sequence from northern Alaska (Toolik lake, arctic tundra soil, KJ827497), comprising only partial 5.8S and entire ITS2, clustered in a strongly supported clade with *O. subclavuliformis*, but deviates from it by 15 nt and 1 gap in the ITS2 (Phyl. 12).

Ecology. *O. subclavuliformis* grows on ± rotten wood and bark of xeric twigs and branches of various trees and shrubs of angio- but also gymnosperms, including stems of *Rosa* and *Rubus*. In the many records from western France the host was mostly *Ulex* (or *Cytisus*).

The rather numerous collections indicate occurrence from supra- or meso- to thermotemperate (rarely orotemperate and

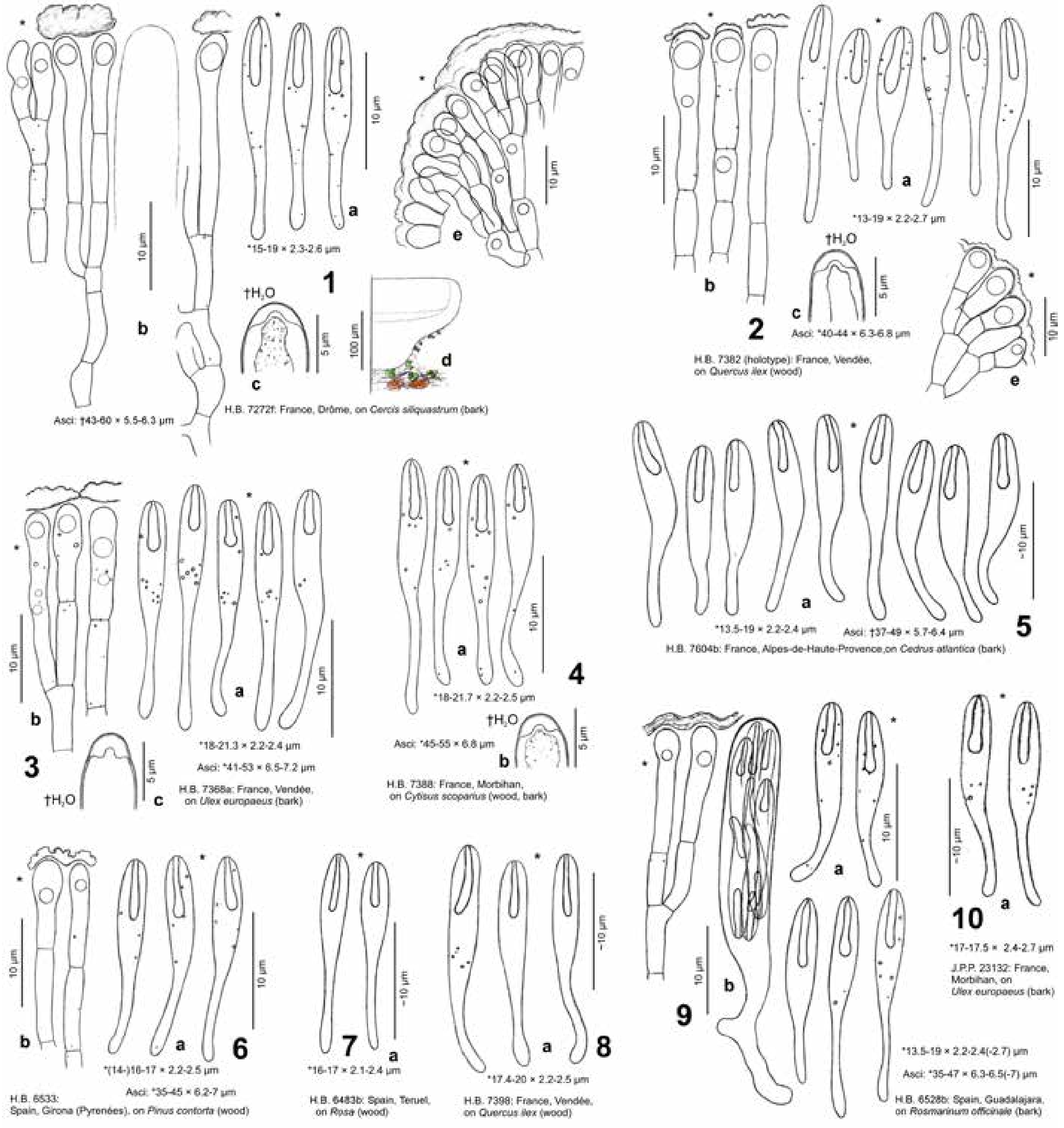


Plate 324. **1–9**: *Orbilia subclavuliformis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

orosubmediterranean) humid, suprasub- to mesosub- and even supra- to thermomediterranean semihumid areas in atlantic to subcontinental central, western, and southern Europe.

On Madeira (Macaronesia) *O. subclavuliformis* occurred in the supramediterranean humid ridge-crest laurel forest (*Ilici canariensis-Ericetum platycodonis*). The not included collections comprise a mild-maritime humid mixed evergreen forest with *Arbutus* in western Canada, a subtropical semihumid eucalypt low open forest (karri-tingle) in southwestern Australia, and an arctic tundra for the DNA-isolate from Alaska.

Specimens included. **NETHERLANDS**: **Noord-Brabant**, 1 km W of Boxmeer, Brestbos, 18 m, twig of *Frangula alnus*, on wood, 24.VII.2014, S. Helleman (ø, doc. vid.). — **LUXEMBOURG**: **L'Oesling**, **Diekirch**, 4.5 km SW of Diekirch, W of Ettelbruck, railway station, 197 m, stem of *Melilotus*, 6.VII.2002, G. Marson (H.B. 7169). – **Gutland**, **Luxembourg**, 5 km SSW of Luxembourg, NE of Kockelscheier, Kreuzhof, 305 m, branch of *Salix* (?)*aurita* × *caprea*, on bark & wood, 16.IX.1994, G. Marson (H.B. 5226a, anam. substr.). – 1 km SE of Kockelscheier, N of Uecht, 305 m, stem of *Rubus fruticosus*, 16.II.2007, G. Marson (ø). – **Esch-sur-Alzette**, 2 km SW of Kockelscheier, Nonneboesch, Neieweier, 285 m, stem of *R. armeniacus*, on bark, 30.XII.2006, G. Marson (ø). – 7.5 km WNW of Esch-sur-Alzette, S of Differdange, Rollesbierg, 358 m, twig of *Cornus sanguinea*, on bark, 1.VIII.2006, G. Marson (H.B. 8359c). – **Remich**, 8.5 km S of Remich, SW of Schengen, Stréimchen, 225 m, stem of *R.* (?)*bifrons*, on bark, 11.II.2007, G. Marson (H.B. 8445g ø). — **GERMANY**: **Baden-Württemberg**, 5.5 km NE of Tübingen, Pfrondorf, Blaihofstraße, 430 m, on a rope, 24.XI.2009, H.O. Baral (H.B. 9226b ø). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 17 km SW of Rennes, 2.6 km S of Bréal-sous-Montfort, 70 m, branch of *Cytisus scoparius*, on wood, 6.II.2009, J.P. Priou (J.P.P. 29011, doc. vid.). – 15 km SW of Rennes, 1 km SW of Le Pont-Réan, NNE of Guichen,

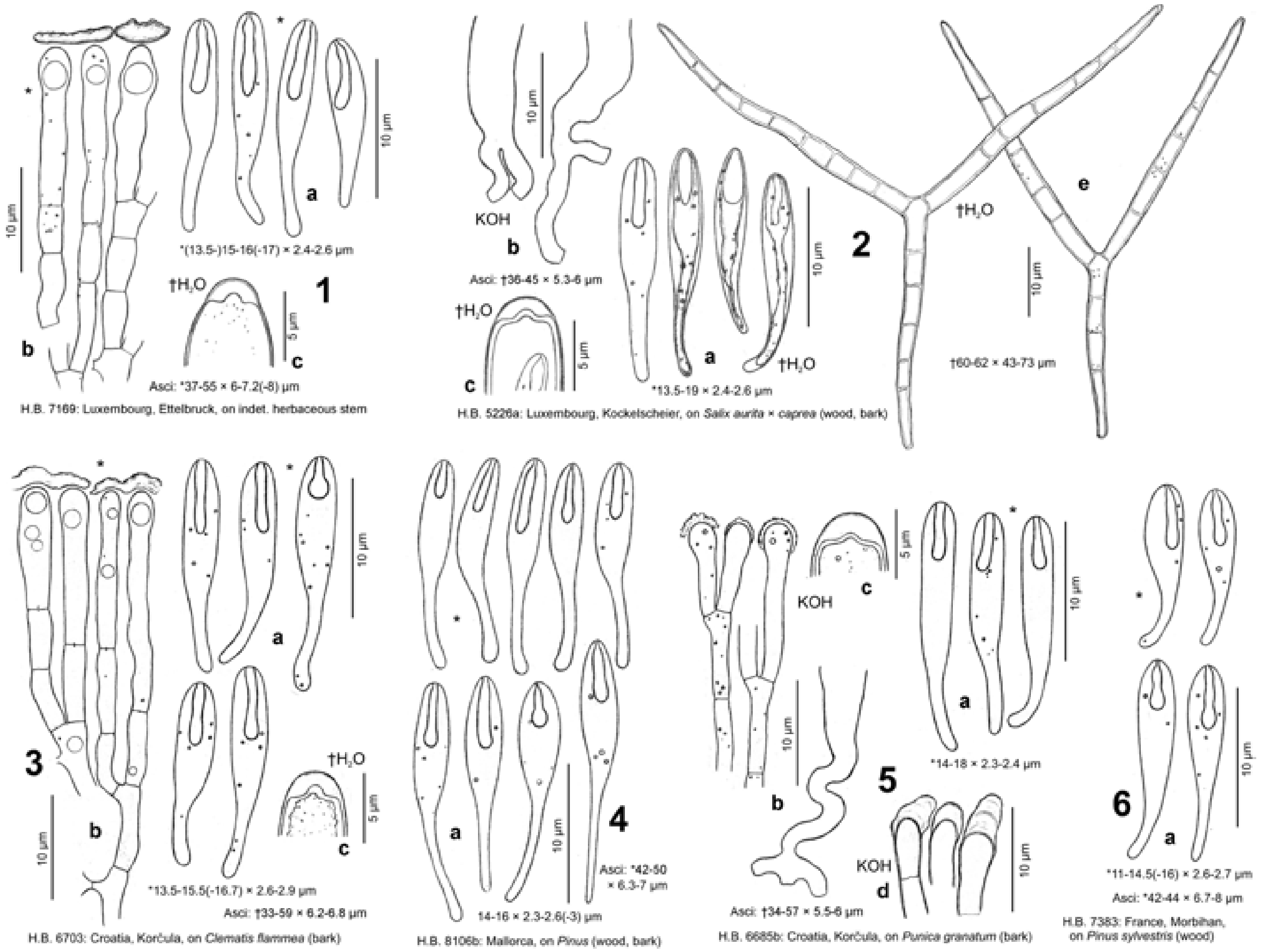


Plate 325. **1–5**: *Orbilia subclavuliformis*; **6**: *O.* cf. *subclavuliformis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. marginal cortical cells with short glassy processes; **e**. conidia from substrate.

La Massaye, 68 m, branch of *C. scoparius*, 15.II.2005, J.P. Priou (J.P.P. 25034, doc. vid.). – **Morbihan**, 8 km WNW of La Gacilly, S of St.-Nicolas-du-Tertre, Etang près La Croix, 47 m, branch of *C. scoparius*, on wood, 25.XII.2003, J.P. Priou (J.P.P. 23147, H.B. 8381). – 4.3 km W of La Gacilly, 3.5 km NE of Les Fougerêts, St.-André, 75 m, branch of *Ulex europaeus*, on bark, 14.XII.2003, J.P. Priou (in J.P.P. 23132, ø). – 1 km N of La Gacilly, Yves Rocher, 27 m, branch of *C. scoparius*, on wood, 22.I.2004, J.P. Priou (J.P.P. 24028, H.B. 8382). – 1.8 km WSW of La Gacilly, 1 km W of Graslia, 60 m, branch of *C. scoparius*, on wood & bark, 11.VI.2003, H.O. Baral (H.B. 7388). – 9 km WNW of Redon, 2 km E of St.-Jacut-les-Pins, Moulin de Calléon, 20 m, branch of *U. europaeus*, on wood, 24.I.2005, J.P. Priou (J.P.P. 25017, ø). – 1.8 km S of Vannes, park SE of harbour, 4 m, branch of *U. europaeus*, on wood, 12.VI.2003, H.O. Baral (ø). – 3 km ESE of Carnac, 1 km SW of La Trinité sur Mer, W of Kervourden, 7 m, branch of *U. europaeus*, on wood, 24.XI.2006, J.P. Priou (H.B. 8376b). – 1.6 km SW of Muzillac, 4.5 km ESE of Ambon, NW of St.-Mamert, 25 m, branch of *U. europaeus*, on bark, 13.XII.2009, J.P. Priou (J.P.P. 29242, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 3 km ESE of Piriac-sur-Mer, 0.5 km E of St.-Sébastien, 20 m, branch of *U. europaeus*, 10.XI.2007, J.P. Priou (J.P.P. 27123, doc. vid.). – **Vendée**, 33 km NW of La Rochelle, 1.5 km WNW of La Tranche-sur-Mer, W of Savinière, 12 m, branch of *Quercus ilex*, on wood, 2.VI.2003, H.O. Baral (ex H.B. 7382, M-0276592, **holotype**, anam. substr.). – ibid., 6.VI.2003 (H.B. 7398 ø). – 17 km SE of Les Sable-d'Olonne, 2.6 km W of Jard sur Mer, S of Ragounite, 15 m, twig of *U. europaeus*, on bark, 4.VI.2003, H.O. Baral (H.B. 7368a ø). – **Poitou-Charentes**, **Charente-Maritime**, Île de Ré, 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, branch of *Q. ilex*, on wood, 26.IV.2006, G. Marson (H.B. 8158, G.M.). – **Aquitaine**, **Gironde**, 4.5 km SW of St.-Savin, 3 km SE of St.-Christoly-de-Blaye, 0.4 km SE of Les Trias, 15 m, branch of *U. europaeus*, on wood, 21.XII.2007, J.P. Priou (J.P.P. 27141, doc. vid.). – **Bourgogne**, **Côte-d'Or**, 24 km NE of Dijon, N of Bèze, Les Combottes, 225 m, branch of *Euonymus europaeus*, on wood, 29.X.2009, J.P. Priou (J.P.P. 29206, doc. vid.). – 20 km NNE of Dijon, 1.8 km SW of Is-sur-Tille, La Gare, 345 m, twig of *Lonicera xylosteum*, on wood, 29.X.2009, J.P. Priou (J.P.P. 29208, doc. vid.). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 16 km SW of Sisteron, 6.5 km N of St.-Étienne-les-Orgues, SW of montagne de Lure, 1447 m, branch of *Cedrus atlantica*, on bark, 8.VIII.2003, G. Marson (H.B. 7604b). – **Var**, 10 km W of Cogolin, 5 km NW of Gorbière, SW of Capelude, 380 m, branch of *Eucalyptus*, on wood, 4.IX.2017, G. Marson (G.M. 2017-09-04.5; sq.: MH221060). – **Alpes Maritimes**, 24 km N of Nizza, ~ 1.5 km WSW of Utelle, Madone d'Utelle, ~ 1160 m, branch of *Pinus sylvestris*, on bark, 3.X.1993, G. Marson (H.B. 5144). – **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, Col du Pontias, 460 m, branch of *Cercis siliquastrum*, on bark, 11.X.2002, G. Marson (H.B. 7272f ø). – ibid., 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9151h). – 10 km ENE of Nyons, 1 km N of Curnier, 383 m, twig of *C. siliquastrum*, on bark, 12.IX.2009, G. Marson (H.B. 9182a). – 16.3 km E of Nyons, 1.5 km NNW of Bellecombe, SW of Col de Soubeyrand, 880 m, twig of *Cytisus scoparius*, 10.X.2002, G. Marson (H.B. 7251d ø). — **SPAIN**: **Asturias**, 2.4 km N of Pola de Somiedo, 2 km S of Castro, 703 m, branch of *Quercus ilex*, on wood, 7.VI.2013, H.O. Baral (H.B. 9819). – 3.5 km ESE of Gijón, Jardín Botánico Atlántico, 21 m, cone of *Pinus sylvestris*, 5.III.2015, E. Rubio (E.R.D. 6399, doc. vid.). – **País Vasco**, **Gipuzkoa** (border to Navarra), 11 km ESE of Tolosa, 3.8 km SE of Berastegi, 423 m, branch of *Salix*, on bark, 5.I.2008, J.P. Priou (J.P.P. 28004, doc. vid.). – **Cataluña**, **Girona**, eastern Pyrenees, 28 km NE of Ripoll, 5 km NE of Molló, Col d'Ares, 1530 m, branch of *P. ?contorta*, on wood, 28.IX.1999, H.O. Baral (H.B. 6533 ø). – **Castilla-La Mancha**, **Guadalajara**, Sierra de Guadarrama, 43 km NNW of Guadalajara, 2 km NNW of Tamajón, Ermita de los Enebrales, 1040 m, branch of *Rosa*, on bark, 14.V.1996, H.O. Baral (H.B. 5511f ø). – 38 km ESE of Guadalajara, 8 km S of Alocén, NW of Sacedón, Pantano de Entrepeñas, 755 m, branch of *Rosmarinus officinalis*, on bark, 25.IX.1999, H.O. Baral (H.B. 6528b). – **Cuenca**, Sierra de Cuenca, 16 km ENE of Cuenca, 3 km E of Buenache de la Sierra, Vía del Saca, 1370 m, branch of *Rosa*, on wood, 25.IX.1999, H.O. Baral (H.B. 6483b ø). – **Com. Valenciana**, **Castellón**, 13.5 km NNW of Castellón, 3.2 km WSW of

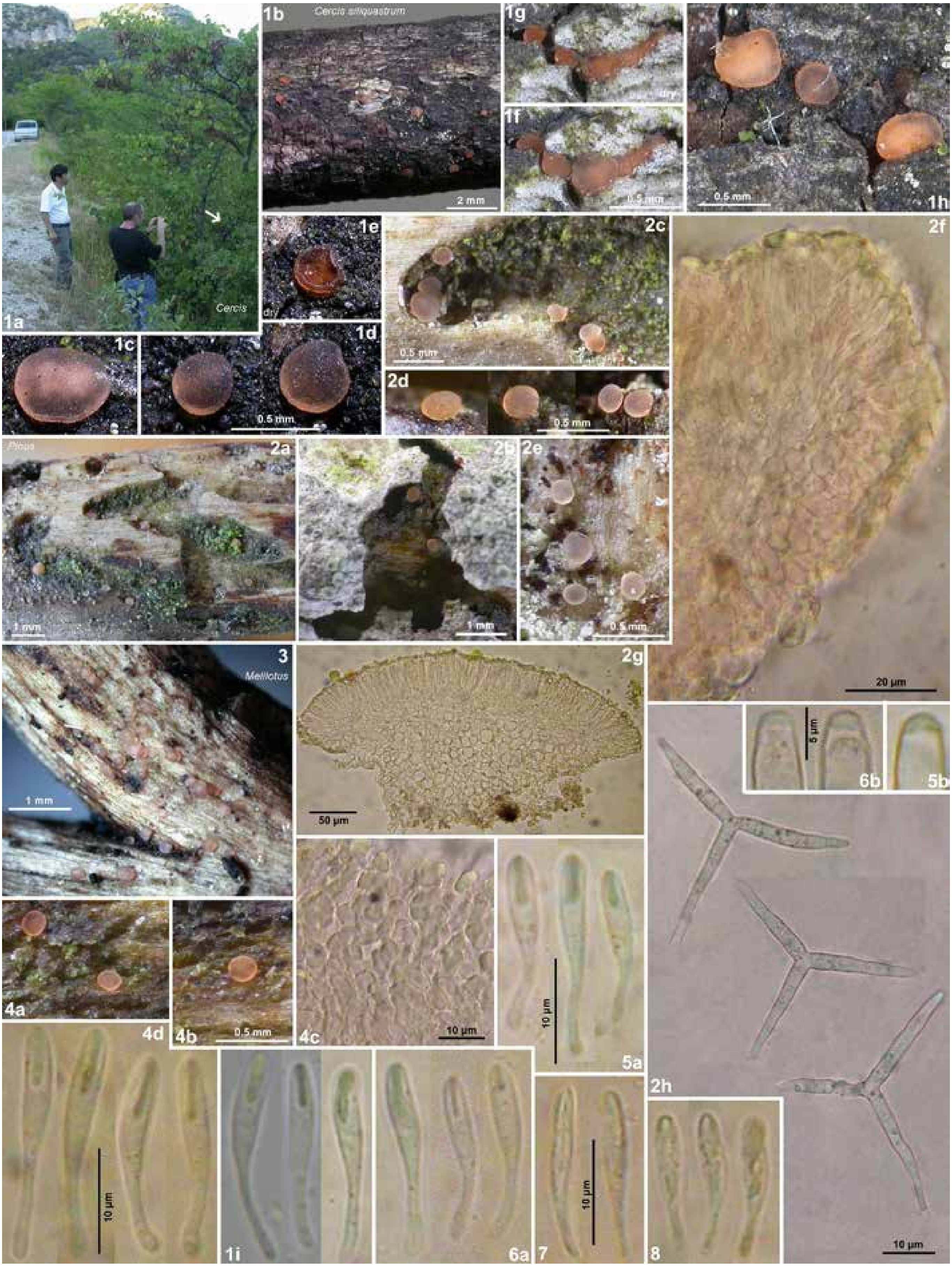


Plate 326. **1–8**: *Orbilia subclavuliformis*. – **1a**. mediterranean shrubland (macchia) with *Quercus ilex* and *Cercis siliquastrum*; **1b**, **2a**, **3**. dead xeric branches and herbaceous stem (rehydrated); **1b–d**, **f**, **2a–e**, **3**, **4a–b**. rehydrated apothecia; **1e**, **g**. dry apothecia; **2g**. apothecium in median section; **2h**. id., marginal ectal excipulum; **4c**. exudate on margin (external view); **5b**, **6b**. ascus apices; **1i**, **4d**, **5a**, **6a**, **7**, **8**. ascospores; **2h**. conidia from substrate. – Living state, except for **5b**, **6b**, **7**, **8** (in H_2O). — **1a–i**. H.B. 9182a: France, Nyons, on *Cercis*; **2a–h**. H.B. 8106b: Mallorca, on *Pinus*; **3**. H.B. 7169: Luxembourg, Ettelbruck, on *Melilotus*; **4a–d**. H.B. 8158: France, Ile de Ré, on *Quercus*; **5a–b**. H.B. 9226b: Germany, Tübingen, on rope; **6a–b**. H.B. 8376b: France, La Trinité sur Mer, on *Ulex*; **7**. H.B. 8381: France, Malestroit, on *Cytisus*; **8**. 8359c: Luxembourg, Differdange, on *Cornus*.

Map 56. Known distribution of *O. subclavuliformis* in Europe and Macaronesia.

Vilafamés, Camí Costur, 400 m, branch of *Olea europaea*, on bark, 27.IX.1999, H.O. Baral (H.B. 6530d). – **Islas Baleares**, **Mallorca**, 15 km NNW of Palma, 4.3 km WSW of Valldemossa, NE of Coll de Claret, 480 m, branch of *Pinus*, on wood & bark, 26.III.2006, R. Reuter (H.B. 8106b, anam. substr.). — **PORTUGAL**: **Leiria**, 12 km SW of Fátima, 1.3 km SE of Alcaria, 280 m, twig of *Quercus suber*, on bark, 4.V.2009, J.P. Priou (J.P.P. 29124, H.B. 9115 ø). — **CROATIA**: **Split-Dalmatia**, Dinaric Alps, 3.2 km ENE of Zagvozd, 11 km WSW of Imotski, 635 m, branch of *Petteria ramentacea*, on wood, 27.VII.2000, N. Matočec (CNF 2/4564 & 4566, doc. vid.). – **Dubrovnik-Neretva**, Korčula island, 11.5 km W of Korčula, 2 km W of Račišće, Samograd bay, 2 m, branch of *Punica granatum*, on bark, 4.VI.2000, N. Matočec & H.O. Baral (H.B. 6685b ø). – 8 km W of Korčula, Pupnat, south-slope of Veli vrh, 400 m, branch of *Clematis* (?)*flammula*, on bark, 11.VI.2000, H.O. Baral (H.B. 6703). – 2.5 km W of Korčula, NW of Žrnovska Banja, 2 m, trunk of *Lonicera implexa*, on bark, 24.VIII.2000, N. Matočec (CNF 2/4717, doc. vid.). — **MONTENEGRO**: 15 km NNW of Podgorica, 1.9 km NE of Donje Selo, Glizica, 210 m, twig of *Vitis vinifera*, on wood, 2.V.2016, D. Raspopović (B.P. Dgf/C7D-02-05-16a, doc. vid.). — **GREECE**: **South Aegean**, **Rhodos**, 17 km WNW of Archangelos, 1 km SSE of Salakos, NNE of Profitis Ilias, 495 m, branch of *Anagyris foetida*, on bark, 20.III.2010, V. Kummer (H.B. 9353c ø). — **MACARONESIA**: **Madeira**, 4.5 km NNE of Arco da Calheta, SE of Rabaçal, 1305 m, stem of *Rubus grandifolius*, 15.X.2009, J.P. Priou (J.P.P. 29182, doc. vid.).

Not included. **FRANCE**: **Bretagne**, **Morbihan**, 15 km ESE of Ploermel, 2 km NE of Monteneuf, Les Pierres Droites, 140 m, branch of *Pinus sylvestris*, on wood, 9.VI.2003, H.O. Baral (H.B. 7383 ø). — **USA**: **Alaska**, Toolik lake, ~730 m, arctic tundra soil (Semenova et al. 2014, mol. extr.; sq.: KJ827497). — **CANADA**: **British Columbia**, 11 km NNW of Victoria, Observatory Hill, NW of planetarium, 175 m, branch of *Arbutus menziesii*, on wood, 13.II.2017, O. & A. Ceska (O.C. 2170213, doc. vid.). — **AUSTRALIA**: **Western Australia**, Jarrah Forest, 47 km WNW of Albany, 13 km NNE of Denmark, NE of Mt. Lindesay, 75 m, branch of *Chamelaucium ciliatum*, on wood, 15.XII.2001, G. Marson (H.B. 7213c ø).

Orbilia flagellispora (Raitv. & R. Galán) Baral & G. Marson, **comb. nov.**, MB 813607 — Pls 327–330, Map 57

Basionym: *Hyalinia flagellispora* Raitv. & R. Galán in Galán et al., Mycol. Res. 98: 1142 (1994)

?= *Orbilia herbarum* Velen., Monogr. Discom. Bohem.: 102, pl. 11 fig. 19 (1934)

Etymology: *flagellispora*: referring to the very long and narrow tails of the ascospores; *herbarum*: growing on herbaceous substrate.

Typification: Mexico, Baja California, El Sauzal, leaf of *Rhus laurina*, 14.III.1990, R. Galán (AH 6780, holotype of ***Hyalinia flagellispora***). — Czechia, Mnichovice, 'stem of *Lotus corniculatus*' (?leaf of *Carex*), 21.XI.1929, J. Velenovský (PRM 152431, holotype of ***Orbilia herbarum***).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.7(–0.9)((–1.2)) mm diam., 0.11–0.18(–0.23)((–0.36)) mm high (receptacle 0.09–0.15 mm), light to bright orange to rose, not or slightly translucent, ± round; scattered or often subgregarious to gregarious in small groups; disc flat, margin distinct, 0–30 µm protruding, finely crenulate or with prominent whitish teeth, sometimes smooth; broadly sessile or mostly with ± distinct obconical stipe 0.04–0.1(–0.24) × 0.1–0.2 mm, superficial or slightly immersed in biofilm or furrows; dry bright to deep rose-orange or orange-red, somewhat contracted. **Asci** *(47–)50–73 × 6–7.7(–8) µm {7}, †(40–)45–65(–70) × (5–)5.3–6.5(–7) µm {8}, 8-spored, spores 2(–4)-seriate, 1–3(–4) lower spores inversely oriented {12} (not mixed), pars sporifera *30–40 µm long; **apex** (†) hemispherical to slightly truncate, dome †1–2(–3) → 0.7–1.5 µm thick {10}, with distinct, small apical chamber; **base** with short to long, medium thick stalk, L- or h-shaped. **Ascospores** *(14–)16–26.5(–28.5) × (2.3–)2.6–3.3(–3.6) µm {18}, †16–26(–29.5) × (2–)2.3–3(–3.3) µm {11}, sperm-shaped: with ellipsoid-fusoid head and sharply differentiated filiform tail, apex obtuse to subacute (rarely rounded or acute), head *(9–)9.5–12(–12.5) µm long, straight or sometimes slightly inequilateral, tail */†(7.5–)9.5–15(–18) × (0.2–)0.3–0.6(–0.9) µm {8}, base nearly always slightly to strongly swollen to *0.9–1.7(–2.3) µm thick {8}, †0.7–1.8(–2.3) {3}, ± bulbous, rarely in all spores only †0.2–1 µm thick {1 Canada}, straight or slightly to medium (rarely very strongly) curved at base or above; **SBs** *(3–)3.3–5(–5.3) × 0.8–1.3(–1.5) µm {11}, rod-shaped, subulate, pear-shaped to ampulliform, apically narrowed to a small or wide point, overmature *3–4 × 1.4–1.7 µm. **Paraphyses** apically uninflated or slightly to medium clavate-capitate, terminal cells *(7–)12–18(–24) × (1.8–)2.2–3.5(–4.5) µm {8}, †13–18 × 2–2.7 µm {T}, lower cells *((3.5–))(6–)8–13(–17) × 1.5–2.5(–3)((–3.7)) µm {7}; not or sometimes branched near apex, sometimes flexuous; hymenium very pale rose. **Medullary excipulum** hyaline to very pale rose, 30–85 µm thick, of medium dense textura intricata with many inflated cells, very sharply delimited at flanks. **Ectal excipulum** pale rose, of (†) thin-walled to slightly gelatinized, vertically oriented t. (globulosa-)angularis(-prismatica) from base to mid flanks, 20–100 µm thick near base, cells *(8–)10–20(–24) × (5–)7–14(–16.5) µm {6}; 20–40 µm thick on lower flanks, cells *8–12 × 5–8 µm, oriented at a 70–80° angle to the surface, 15–30(–40) µm near margin, inner part of t. prismatica-angularis oriented at 45–80°, outer part of t. prismatica-porrecta oriented at 20–50°, marginal cortical cells *(5–)6–11(–14) × (2–)2.3–4 µm {5}, or outer part of t. prismatica oriented at 60–80°, then cortical cells *5–10 × 3–5 µm {5}, **glassy processes** 0–12 {8} or 10–40 {8} or up to 40–60 {5} × (2–)2.5–4(–4.5) ((–6)) µm, refractive, sometimes stratified, ± straight, sometimes curved outwards or inwards, coherent to form indistinct small squamules or very prominent teeth 40–60 × 50–100 µm. **Anchoring hyphae** sparse to medium abundant, */†2–3(–4) µm wide, walls 0.2–0.4(–0.8) µm thick {6}. **SCBs** in paraphyses and ectal excipulum absent {1} or globose {7}, 1–2.5 µm diam., rarely some needle-shaped {1}; excipular cells at base and lower flanks with globose, pale yellowish(-orange) **LBs** 1.3–3 µm diam. {2} (carotenoids). **Exudate** over paraphyses hyaline, 0.5–2.5(–3) µm thick; over marginal excipulum 1–3 µm thick, granular to cloddy, mostly loosely, sometimes firmly attached. — **ANAMORPH**: trinacrium- {5} (Y), descalsia- {5} (┼), and dwayaangam-like {1} (dw) (presumed, from natural substrate {11}). **Conidiophores** not seen. **Conidia** variable in shape: 2-armed, Y-shaped (trinacrium subtile-like): total size †36–40 × 39–40 µm, stipe †15–17 × 2.5–4 µm, 2–4-septate, arms †25–27 × 3.5–4.8 µm, 6-septate {2}; 3-armed (┼-shaped, descalsia-like): total size †/*40–55 × (25–)35–53 µm, stipe †/*18–21(–35) × 2–4 µm, 3–4-septate, arms †/*11–26 × 2.5–3.5 µm, 3–5-septate {3}; 4-armed or 6–7-armed (dwayaangam-like): total size *64–65 × 68 µm, stipe *13–15 × 2.4–3.2 µm, 2–3-septate, arms *20–42 × 2.7–3.6 µm, 3–7-septate {1}.

Habitat: collected (0–)0.5–5 m above the ground, on corticated to decorticated, 3.5–27 mm thick twigs and branches, also 10–15 cm thick trunks, of *Alnus alnobetula* {5}, *Crataegus* sp. {1}, *Cedrus atlantica* {1}, *Cercis siliquastrum* {1}, *Cornus sanguinea* {4}, *Crataegus* sp. {1}, *Juniperus communis* {3}, *Larix* sp. {1}, *Picea* sp. {1}, *P. abies* {4}, *Pinus* ?*contorta* {1}, *P. sylvestris* {3}, *Salix* sp. {1}, *S. appendiculata* {1}, *S. aurita* {1}, *S. caprea* {2}, *S.* (?) *cinerea* {1}, *S. glauca* {1}, *S. phylicifolia* {1}, sometimes on slightly resinous wounds, on bark (periderm and mainly bast) {26}, also on wood {7} or blackened resin {4}, often on edges of bark or in small cracks, slightly to medium decayed; on stem of *Rubus fruticosus* {1}, rotten, non-sceletonized leaf of *Rhus laurina* {T}; greyed or blackened, with a few to many green algae (sometimes included within the basal excipulum: Pl. 328: 1e), **Associated**: *Amphosoma*

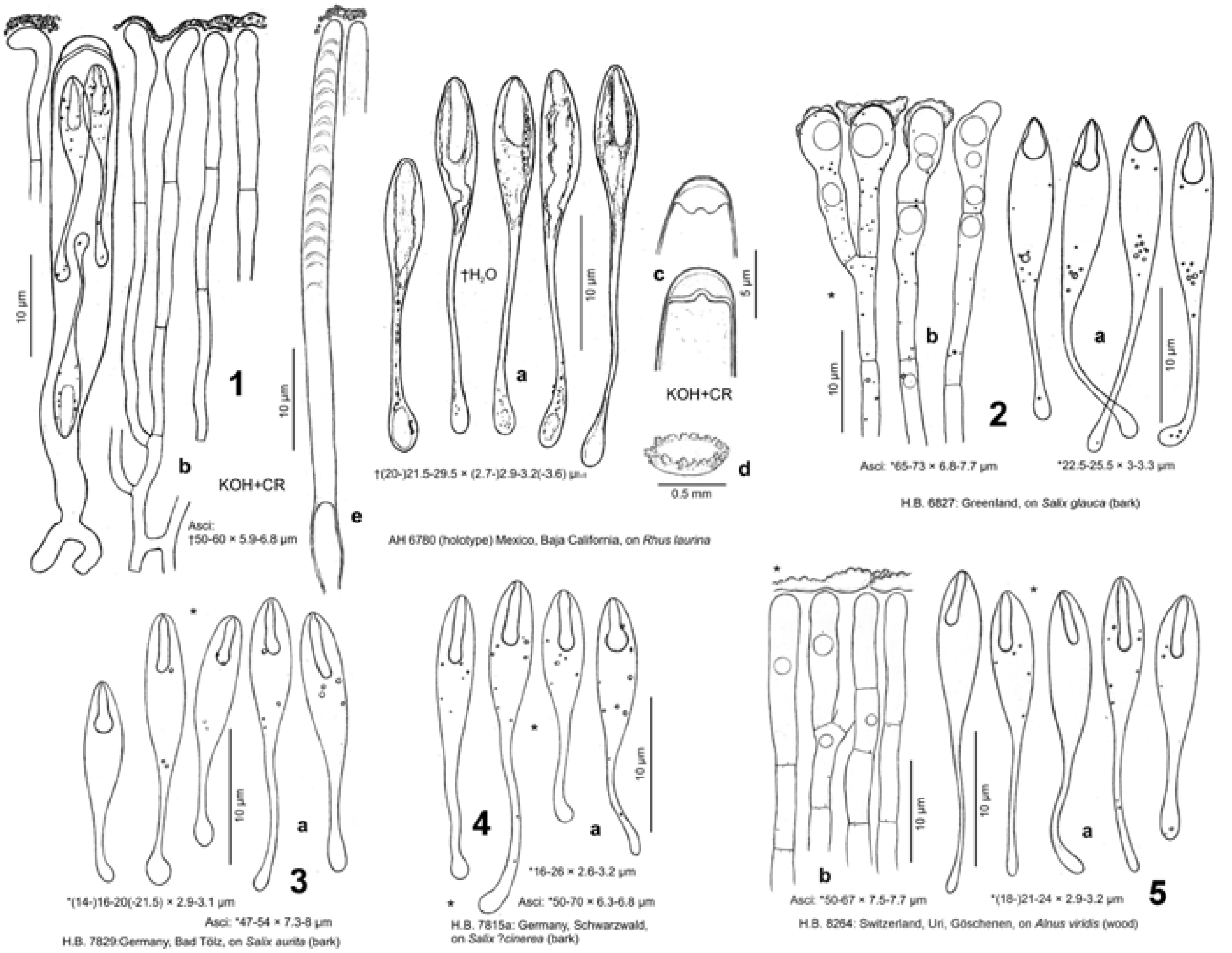


Plate 327. **1–5**: *Orbilia flagellispora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium with dentate margin (rehydrated); **e**. marginal cortical cell with long glassy process.

atroolivaceum {2}, *A. resinicola* {3}, *Caloplaca holocarpa* {1}, *Capronia* sp. {1}, *Ciliolarina pinicola* {1}, *Claussenomyces* sp. {1}, *C. olivaceus* {2}, *Coniochaeta* sp. {1}, *Crumenulopsis pinicola* {1}, *Diplolaeviopsis resinae-pini* {1}, *Dothideales* {1}, *Echinosphaeria strigosa* {1}, *Evernia prunastri* {1}, *Exarmidium inclusum* {1}, *Exidia* sp. {1}, *Hyalorbilia orbiliicola* (parasitic on *O. flagellispora*) {1}, *Hyphodiscus theiodeus* {1}, *Hypogymnia physodes* {1}, *H. vittata* {1}, *Hysterium angustatum* {1}, *Hysteropatella elliptica* {2}, *Lachnellula resinaria* {1}, *Lilapila oculispora* {1}, *L. oculisporella* {1/1}, *Melanomma pulvis-pyrius* {1}, *Melaspileella proximella* {1}, *Mollisia ?discolor* {1}, ?*Mytilinidion* sp. {1}, *Nitschkia broomeana* {1}, *Orbilia alpigena* {2}, *O. arachnovinosa* {1/1}, *O. aristata* {6}, *O. cercidicola* {1}, *O. eucalypti* {1}, *O. filiformis* {1}, *O. gambelii* {1}, *O. myriolentiformis* {1}, *O. myriosphaera* {1}, *O. spermoides* {1}, *O. subaristata* {3}, *O. subclavuliformis* {3}, *O. subocellata* {1}, *O. subtrapeziformis* {1}, *O. trapeziformis* {2}, *O. tremulae* {1}, *O. vinosa* {3}, *Orthotrichum* sp. {2}, *Parmelia* sp. {2}, *P. ?sulcata* {1}, *Parmelina carporrhizans* {1}, *Patellariopsis atrovinosa* {1}, *Perrotia flammea* {1}, *Pezicula ocellata* {1}, *Physcia* sp. {2}, ?*Pragmopora* sp. {1}, *Propolis farinosa* {1}, *Hymenochaetopsis tabacina* {1}, *Resinomyces griseus* {3/1}, *R. kirschsteinianus* {2}, *Sarea difformis* {3}, *S. resinae* {2}, *Sclerococcum* sp. {1}, *Usnea* sp. {1}, *Xanthoria* sp. {1}. **Desiccation tolerance**: fully viable for 15 months. **Altitude**: 250 m (Greenland), 350 m (Mexico), 320–1650 m a.s.l. (central Europe), 460–1800 m (southern Europe). **Geology**: Greenland: Precambrian sediment, Canada: Devonian-Mississippian sedimentary rock; Europe: Buntsandstein, Keuper (marl- & sandstone), Triassic dolomite, Lower to Upper Jurassic Minette, marl- & limestone, Cretaceous sand- & limestone, Eocene flysch; granite, quartzite, phyllite, mica schist, wacke, ophiolite, biotite-amphibole. **Phenology**: III–X (but certainly throughout the year, long-lived).

Taxonomic remarks. *Orbilia flagellispora* differs from *O. aristata* and *O. subaristata* mainly in longer spore heads (9–12 instead of 7–10 µm). The width of the spore heads and the middle parts of tails is very similar in the three taxa, but the tail bases are always slightly to strongly bulbous in *O. flagellispora* and mostly also in *O. subaristata*, but not or only very slightly so in *O. aristata*. The tails in *O. flagellispora* and *O. subaristata* are sometimes strongly bent just above the bulbous base, reminiscent of golf clubs. However, such curved tail bases did not occur in the holotype of *O. flagellispora* (Pl. 327: 1a, see also Galán et al. 1994). For the similar *O. asturiensis* see p. 686. Confusion is easily possible with the rare Australian *O. pseudoflagellispora* (series *Albovinosae*, section *Aurantiorubrae*), which differs from *O. flagellispora* mainly in truncate thin-walled ascus apices (dead state) and in wider SBs.

A very sparse, unpreserved Australian collection on bark of *Eucalyptus*, mentioned under *O. pseudoflagellispora* (Pl. 526: 2, section *Aurantiorubrae*), differs in slightly narrower spores (*19–22 × 2.2–2.6 µm) being frequently 1-septate (apparently when overmature). It is possibly more closely related to *O. clavuliaristata* or *O. angustoaristata* which, however, both differ in spores with uninflated tail bases, the latter also in

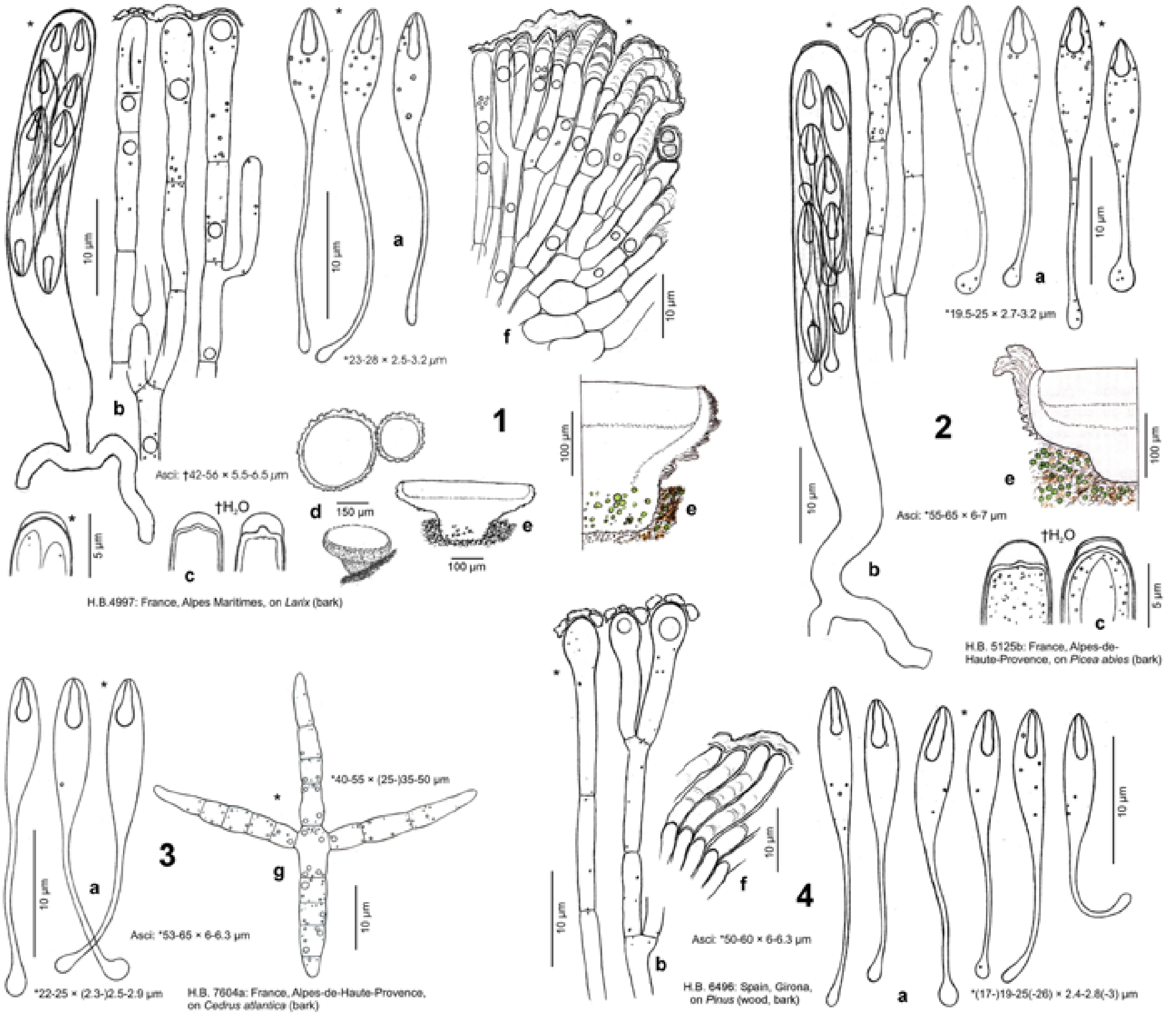


Plate 328. **1–4**: *Orbilia flagellispora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia with crenulate margin (rehydrated); **e**. apothecia in median section; **f**. id., marginal cortical cells with glassy processes; **g**. conidium from substrate.

much narrower SBs and in the presence of crystalloid SCBs. Because of the tear-shaped SBs the specimen might be related to *O. pseudoflagellispora*, but whether it was devoid of an apical thickening was not clarified.

Variation. Considerable variation in the maximum length of the glassy processes and consequently the length of the teeth at the apothecial margin was found among the collections but also within a collection. A length of up to 40–60 µm was noted in the holotype (on leaves of *Rhus*, Mexico) but also in some bark-inhabiting central and southern European specimens, without showing any further morphological deviations that would allow separation from specimens with inconspicuous teeth, i. e., with glassy processes 2–20 µm long. The only feature that was more or less correlated with such short or nearly absent glassy processes was found in the somewhat wider and shorter marginal cortical cells which run under a higher angle to the surface. Possibly, long glassy processes require longer cortical cells from which they emerge. Also the curvature of the glassy processes in specimens with distinct teeth is not consistent. Sometimes they are curved outwards (e. g., Pls 328: 2e; 329: 5c–d), sometimes inwards (e. g., H.B. 6827), and apparently rather straight in the holotype and some other collections. In those samples with short teeth, the processes were also either ± straight or inwards or outwards curved, even within a single apothecium. The observed differences in length and curvature of glassy processes did not correlate with the substrate.

Two collections (H.B. 7815a, H.B. 9163a) showed large, yellowish LBs in the cells of the basal ectal excipulum (Pl. 329: 6e), a feature not seen in other specimens, and in H.B. 9163a only in the largest of the five apothecia examined, showing the deepest pigmentation.

In a few collections on *Cornus sanguinea* from Luxembourg, *O. aristata* grew in more or less close association with both *O. flagellispora* and *O. subaristata*. The apothecia of *O. aristata* were here recognizable by their very short marginal teeth, whereas the other two appear to be macroscopically indistinguishable. In a mixed collection on *Alnus* (H.B. 8269) both *O. aristata* and *O. flagellispora* had very short processes and, therefore, looked macroscopically almost identical.

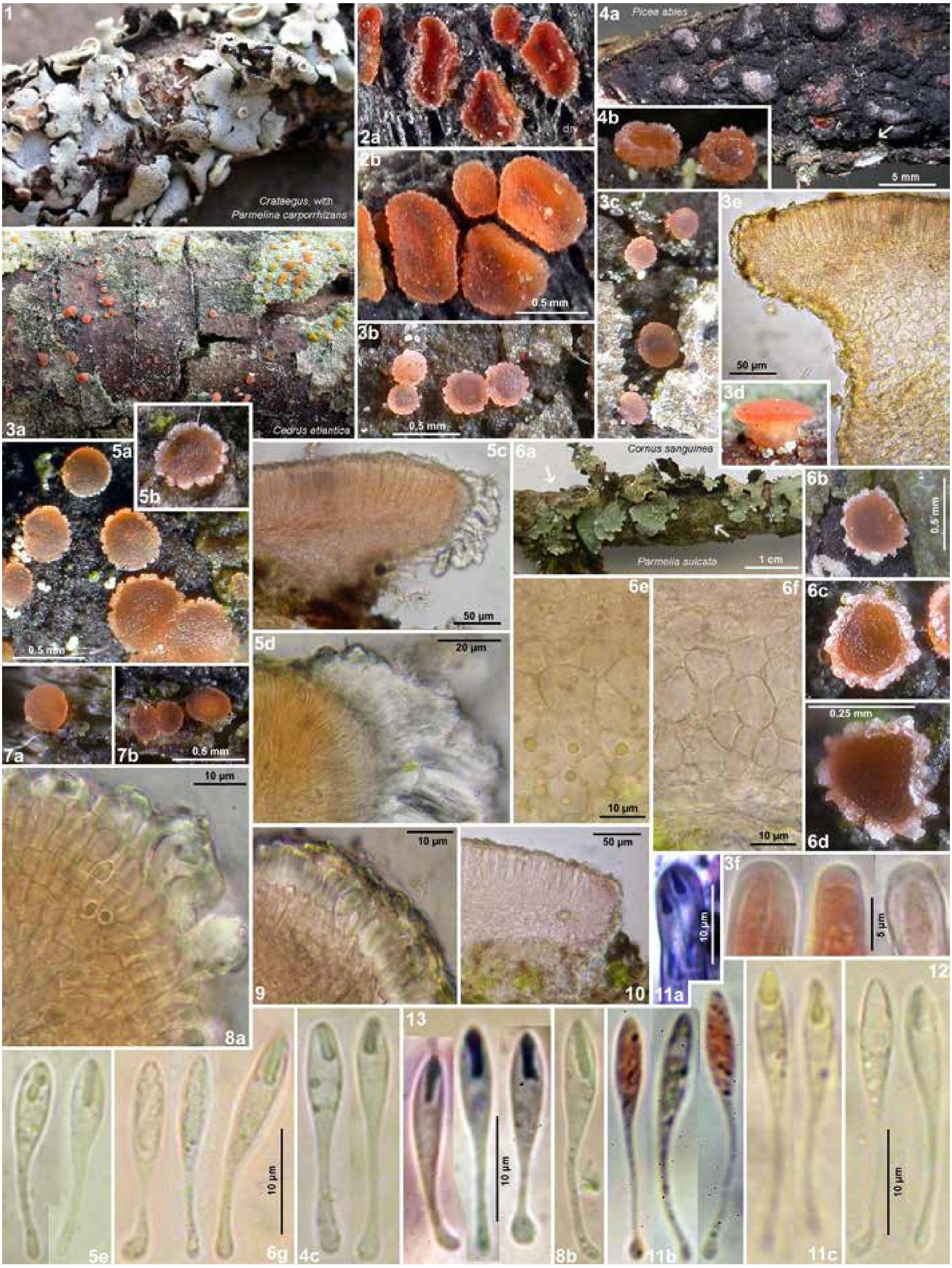


Plate 329. **1–13**: *Orbilia flagellispora*. – **1**, **3a**, **6a**. dead corticated xeric branches (**3a** with *Caloplaca holocarpa*); **4a**. living branch of *Picea abies*, with blackened resinous wound; **2b**, **3a–d**, **4b**, **5a–b**, **6b–d**, **7a–b**. rehydrated apothecia; **2a**. dry apothecia; **3e**, **5c**, **10**. apothecia in median section; **5d**, **8a**, **9**. id., marginal ectal excipulum; **6e–f**. id., basal ectal excipulum (**6e** cells with yellowish LBs); **3f**, **11a**. ascus apices; **4c**, **5e**, **6g**, **8b**, **11b–c**, **12**, **13**. ascospores. – Living state (spores in **11a** & **13** with SBs stained deep blue in CRB), except for **6g** left, **12** left (in H_2O), **11b** (in CR), **5d** (in KOH), **3f** (in KOH+CR), ascus in **11a** (in CRB). – **1**: phot. S. Helleman, **11a–b**, **13**: phot. E. Rubio, **11c**: phot. M. Hairaud. — **1**. S.H. 360: Spain, Málaga, on *Crataegus*; **2a–b**. H.B. 6827: Greenland, on *Salix*;

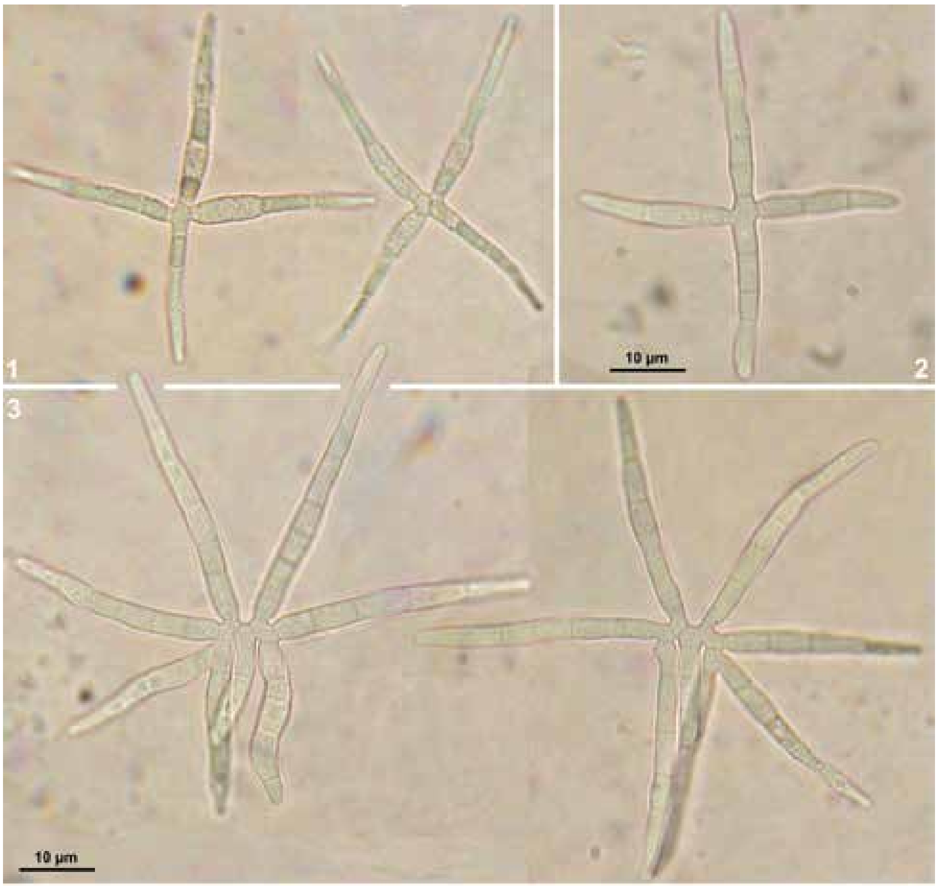


Plate 330. **1–3**: *Orbilia flagellispora*. – Conidia from substrate (living state, except for some cells). — **1**. H.B. 7829: Germany, Lenggries, on *Salix*; **2**. H.B. 8264: Switzerland, Uri, on *Cornus*; **3**. H.B. 8272b: Switzerland, Obwalden, on *Picea*.

Spore length varies strikingly among the collections of *O. flagellispora*, but often also within a single apothecium. The holotype showed the longest spores (Galán et al. 1994: 20–30 × 2.5–3.5 µm), but also in some European specimens the spores measured 24–28 µm (Pls 328: 1a; 329: 12, H.B. 9151f). This variation is mainly due to a variable tail length, but also the length of the spore head varies to some extent. In some collections the head measured 10–13 µm (e.g., Pl. 327: 2a; 328: 3a) but in others only 9–11 µm (Pl. 328: 1a, H.B. 8248c), so that the delimitation from *O. subaristata* with 7–10 µm long spore heads may become obscure, if only a few spores are available for comparison. The width of the bulbous tail bases may also vary rather considerably, even within a collection. In the only North American collection the tail bases were exceptionally narrow, varying from uninflated to medium bulbous (†0.2–1 µm thick, unillustrated).

Type studies. In the type of ***O. flagellispora***, Galán et al. (l.c.) apparently saw a few living spores with SBs as they stated 'sometimes with 1 large oil inclusion'. In any case, their photos of dead spores in MLZ clearly show the transparent region of the SBs (see Fig. 67g). In the present reexamination (Pl. 327: 1a) the SBs of some spores were visible when mounted in water, measuring ~5–6 µm in length, whereas in all collections on bark referred to *O. flagellispora* the SBs of living spores measured 3–5.3 µm. Future collections on leaves should, therefore, be explored for SB length, also for spore length and basal curvature.

The description of ***Orbilia herbarum*** Velen. (1934: 102, pl. 11 fig. 19) somewhat resembles *O. flagellispora*. The holotype (PRM 152431) contains a minute plant fragment which looks like a leaf tip of possibly *Carex*, not like a stem of *Lotus corniculatus* as stated by Velenovský. No apothecia could be found by Svrček (1954) and in the present study. Based on the description, Svrček considered *O. herbarum* to be very close to *O. aristata* (as '*O. occulta*'). The rather narrow and elongated spore heads resemble *O. flagellispora*, from which *O. herbarum* differs, besides the substrate, in basally uninflated tails. *O. herbarum* could perhaps also be close to *O. subclavuliformis*, although Velenovský's drawing shows very narrow spore tails, or to the mainly extra-European *O. angustoaristata* or *O. clavuliaristata*.

Not included collection. A sample on bark of *Fraxinus* from Switzerland studied in the dead state (IVV: H.B. 9242b) differs in rather short spores (†13.3–19 × 2.3–2.6 µm) with not or hardly inflated tail bases, also in short asci (†31–38 × 5–5.5 µm) and might be more related to *O. clavuliaristata*.

Anamorph. Conidia with a different number of arms were detected on the substrate near apothecia of 11 collections. These were mostly Y-shaped trinacrium-like or ┼-shaped descalsia-like conidia. Two times dwayaangam-like conidia were seen, either 6–7-armed (Pl. 330: 3) or 4-armed (H.B. 4997). No pure culture was available, but the different conidial types from substrate are similar to the anamorphs of the closely related *O. aristata* and *O. subaristata*.

Phylogeny. A sequence of a sample from southern France (on *Picea*, G.M. 2010-09-03.3, from apothecia) comprises S1506 intron, ITS, and LSU. When analysing ITS+LSU (Phyl. 9), *O. flagellispora* clustered in a strongly supported clade with *O. subaristata* (3 strains) and *O. aristata* (H.B. 6713) with a distance of 2.8–3 % and 3.5 % in the ITS (0.7–0.9 and 0.2 % in LSU), respectively. When analysing the intron, *O. flagellispora* clustered unresolved within section *Hemiorbilia* by showing a very high distance (~23–28 %) to any other species of *Orbilia*.

Five environmental sequences from *Picea* shoots and needles in Lithuania and one from *Pinus heldreichii* needles in Montenegro comprise partial 5.8S and entire ITS2. The *Pinus* isolate (Lazarević & Menkis 2020, GenBank MT242053) fully coincides with *O. flagellispora*, whereas those from *Picea* (A. Menkis pers. comm., Menkis et al. 2015, KP897776) differ by 3(–4) nt in the ITS2. The medium support of the *O. flagellispora* clade in Phyl. 12 is due to the missing ITS1 in KP897776; the clade is strongly supported when restricting the analysis to the ITS2 region (not shown).

3a–g. H.B. 7604a: France, Sisteron, on *Cedrus*; **4a–c**. H.B. 9162d: France, Le Labouret, on *Picea*; **5a–e**. H.B. 8359a: Luxembourg, Differdange, on *Cornus*; **6a–g**. H.B. 9163a: Luxembourg, Kayl, on *Cornus*; **7a–b**. H.B. 8264: Switzerland, Uri, on *Cornus*; **8a–b**. H.B. 7815a: Germany, Schwarzwald, on *Salix*; **9**. H.B. 8266: Switzerland, Uri, on *Alnus*; **10**. H.B. 7829: Germany, Lenggries, on *Salix*; **11a–c**. E.R.D. 4825: Spain, Asturias, on *Juniperus*; **12**. H.B. 8269c: Switzerland, Uri, on *Alnus*; **13**. 7.V.2011: Spain, Asturias, on *Rubus*.

Ecology. Within Europe, *O. flagellispora* grows on slightly to medium decayed bark, exceptionally wood, of xeric twigs, branches or trunks of gymno- and angiosperm trees and shrubs. It mainly occurs at higher altitudes in orotemperate (montane to subalpine) and orosubmediterranean humid forests, but it was sometimes also recorded at colline altitude in cold-temperate humid (Luxembourg, Steiermark) or hemiboreal (Lithuania, DNA-extract) or supra- to mesosubmediterranean semihumid areas. When growing on resin of conifers, some branches or trunks were still alive. The five DNA isolates of Menkis et al. (2015) were from *Picea* shoots and needles damaged by the spruce bud scale (*Physokermes piceae*), whereas trees with undamaged needles at the same locality were without the fungus, suggesting that it does not occur as an endophyte in living plant tissue.

Two records from northern Europe are from the supraboreal (on *Salix*) and hemiboreal zone (DNA isolate from *Picea* needles), one sample is from a subarctic humid tundra vegetation in western Greenland (on the dwarf shrub *Salix glauca*), and one from a boreal humid Douglas fir mixed conifer forest of northwestern North America (Northern Rocky Mountains, on *Picea*). The type collection was on a dry coriaceous leaf of *Rhus laurina* in a subtropical semiarid chaparral with *Quercus agrifolia* in Baja California (Sonoran Desert, Middle America).

Specimens included. **NORWAY**: **Sør-Trøndelag**, 33 km S of Oppdal, SW of Kongsvoll, Botanical Garden, 900 m, twig of *Salix phylicifolia*, on bark, 18.VII.2012, S. Helleman (S.H. 732, doc. vid.). — **LITHUANIA**: **Šiauliai**, 35 km WNW of Šiauliai, 10.5 km WNW of Kuršėnai, 100 m, shoots/needles of *Picea abies* (Menkis et al. 2015, mol. extr.; sq.: KP897776). — **LUXEMBOURG**: **Gutland**, **Diekirch**, 5.5 km SE of Diekirch, 1.8 km WSW of Ermsdorf, Kieselshéicht, 320 m, branch of *Picea abies*, on bark, 28.IV.1995, G. Marson (H.B. 5273, anam. substr. ┼). – **Esch-sur-Alzette**, Terres rouges, 6.7 km W of Esch-sur-Alzette, 1.5 km S of Obercorn, Ronnebierg, 410 m, branch of *Cornus sanguinea*, on bark, 25.III.2001, G. Marson (H.B. 6984c, anam. substr. Y). – 7.5 km WNW of Esch-sur-Alzette, S of Differdange, Rollesbierg, 358 m, twig of *C. sanguinea*, on bark, 1.VIII.2006, G. Marson (H.B. 8359a, anam. substr. ┼). – 2.2 km S of Esch-sur-Alzette, 1.5 km ENE of Audun-le-Tiche, Ellergronn, 345 m, branch of *Salix caprea*, on bark, 26.IV.2001, H.O. Baral & G. Marson (H.B. 6925). – 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, branch of *C. sanguinea*, on bark, 8.VIII.2009, G. Marson (H.B. 9163a). — **GERMANY**: **Baden-Württemberg**, Schwarzwald, 10 km ESE of Bühl, 7.5 km WSW of Forbach, Herrenwies, Schwarzenbach, 760 m, branch of *S.* (?)*cinerea*, on bark, 13.VI.2005, E. Weber (H.B. 7815a). – **Bayern**, **Oberbayern**, Kocheler Berge, 4.8 km SW of Lenggries, 1.3 km SE of Brauneck, W of Florianshütte, Finstermünzalm, 1200 m, branch of *S. aurita*, on bark, 20.VI.2005, P. Karasch (H.B. 7829, anam. substr. ┼). — **SWITZERLAND**: **Bern**, 11 km E of Thun, 3.8 km E of Schwanden, Sigriswilergrat, northwest-slope of Rothorn, 1620 m, branch of *Alnus alnobetula*, on wood, 27.VIII.2008, H.O. Baral (H.B. 8915d ø). – Nidwalden, 8.2 km SSW of Luzern, 3.2 km W of Hergiswil, NE of Pilatus, N of Gschwänd, 1200 m, branch of *S. appendiculata*, on wood, 18.VIII.2006, H.O. Baral (H.B. 8248c). – 8.5 km NE of Brienz, 7.5 km WSW of Giswil, Glaubenbielen, 1555 m, branch of *Picea abies*, on bark, 17.VIII.2006, H.O. Baral (H.B. 8272b, anam. substr. dw). – **Uri**, Glarner Alpen, 9 km ESE of Altdorf, 1.2 km SW of Unterschächen, N of Sittlisalp, E of Obsaum, 1650 m, branch of *A. alnobetula*, on bark, 21.VIII.2006, H.O. Baral (H.B. 8269c). – 1.7 km SSW of Unterschächen, N of Vorder Boden, 1620 m, branches of *A. alnobetula*, on wood, 21.VIII.2006, H.O. Baral (H.B. 8266, anam. substr. Y, 8270c). – Urner Alpen, 4 km NW of Andermatt, 2.5 km WSW of Göschenen, Steglaui, 1300 m, branch of *A. alnobetula*, on wood, 20.VIII.2006, H.O. Baral (H.B. 8264, anam. substr. ┼). — **AUSTRIA**: **Steiermark**, 15.5 km SW of Hartberg, 1 km NW of Schloss Herberstein, Buchberg, 500 m, branch of *Pinus sylvestris*, 10.IV.2011, G. Friebes (ø, doc. vid.). – **Tirol**, Großklockner, 24 km NNW of Lienz, 3 km NNW of Kals, NE of Spöttlinghof, 1630 m, branch of *Salix*, on bark, 9.VII.2011, T.R. Lohmeyer (H.B. 9581). — **MONTENEGRO**: 45 km E of Podgorica, 8 km SSW of Gusinje, Ropojana, 1195 m, twig of *Juniperus communis*, on bark, 2.VI.2014, B. Perić (doc. vid.). – NNW & NE of Podgorica, Prekornica and Kuči Mt., 1200–1800 m, needles of *Pinus heldreichii*, V.2015 (2814_135, Lazarević & Menkis 2020, mol. extr., sq.: MT242053). — **FRANCE**: **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, Col du Pontias, 460 m, twigs of *Cercis siliquastrum*, on bark, 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9151f). – 20 km SW of Serres, 8 km WNW of Ballons, Col de Perty, 1300 m, branch of *Pinus sylvestris*, on bark & wood, 23.VIII.1996, G. Marson (H.B. 5624b). – **Isère**, 38 km SE of Grenoble, 1.5 km SSE of Les-Deux-Alpes, 1780 m, trunk of *Picea abies*, on resin, 3.IX.2010, G. Marson (G.M. 2010-09-03.3; sq.: KT380092). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 16 km SW of Sisteron, 6.5 km N of St.-Étienne-les-Orgues, SW of montagne de Lure, 1447 m, branch of *Cedrus atlantica*, on bark, 8.VIII.2003, G. Marson (H.B. 7604a, anam. substr. Y & ┼). – 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *P. abies*, on bark, 17.VII.1994, G. Marson (G.M. 5206, H.B. 5125b, anam. substr. Y). – ibid., branch of *P. abies*, on resin, 14.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9162d). – **Alpes Maritimes**, 25 km N of Monte Carlo, 3 km N of Col du Turini, l'Authion, ~1800 m, branch of *Larix*, on bark, 3.X.1993, G. Marson (H.B. 4997). — **SPAIN**: **Asturias**, 12.5 km ESE of Pola de Somiedo, 5 km SE of Saliencia, E of Lago Cerveiriz, 1705 m, branch of *Juniperus communis*, on bark, 13.VI.2009, M. Hairaud, vid. E. Rubio (E.R.D. 4825, doc. vid.). – ibid., 22.IV.2011, J. Linde (ø, doc. vid.). – 22 km NE of Villablino, NW of Endriga, Ponteixina, 1050 m, stem of *Rubus fruticosus*, 7.V.2011, E. Rubio (E.R.D. 7898, doc. vid.). – **Navarra**, 17 km N of Pamplona, 1 km W of Olague, 595 m, branch of *Cornus sanguinea*, on bark, 30.III.2015, F.J. Balda (F.J.B. 30314, doc. vid.). – 18 km W of Pamplona, 2 km NNW of Muniáin, 878 m, branch of *Crataegus*, on bark, 12.III.2016, F.J. Balda (F.J.B. 12316, doc. vid.). – **Cataluña**, **Girona**, eastern Pyrenees, 26 km NE of Ripoll, 2.3 km NE of Molló, WSW of Col d'Ares, 1310 m, branch of *Salix caprea*, on bark, 28.IX.1999, G. Marson (H.B. 6495b). – 5 km NE of Molló, Col d'Ares, 1525 m, twig & branch of *Pinus* ?*contorta*, on bark, wood & resin, 28.IX.1999, H.O. Baral & G. Marson (H.B. 6496). – **Andalucía**, **Málaga**, Sierra de Grazalema, 21 km W of Ronda, 2.7 km WSW of Grazalema, 1195 m, branch of *Crataegus*, on bark, 14.VI.2004, S. Helleman (S.H. 360, doc. vid.). — **GREENLAND**: **Qeqqata**, 21 km ENE of Kangerlussuaq, Russell Glacier, 250 m, branch of *Salix glauca*, on bark, 12.VIII.2000, A. Raitviir (TAAM 137755, H.B. 6827, anam. substr. Y). — **CANADA**: **Alberta**, 310 km WSW of Edmonton, 7 km NE of Jasper, Maligne Canyon, 1165 m, branch of *Picea*, on bark & resin, 17.VIII.1997, G. Marson (H.B. 5926b). — **MEXICO**: **Baja California**, California Chaparral, 16 km NW of Ensenada, 10 km N of El Sauzal, NW of Antonio de las Minas, Las Lomas, Rancho La Cruz, 350 m, on leaf blade of *Rhus laurina*, 14.III.1990, R. Galán (AH 6780, **holotype**, H.B. 5503 ø).

Map 57. Known distribution of *O. flagellispora* in Europe (yellow = not included collection, cyan = *O. herbarum*).

Not included. **SWITZERLAND**: **Luzern**, 24 km NNW of Luzern, 1.2 km E of Aesch, Gitzitobel, 540 m, twig of *Fraxinus excelsior*, on bark, 9.I.2010, U. Graf (H.B. 9242b). — **CZECHIA**: **Central Bohemia**, ~1.5 km ENE of Mnichovice, Myšlín, 'stem of *Lotus corniculatus*' (?leaf of *Carex*), 21.XI.1929, J. Velenovský (PRM 152431, **holotype** of *Orbilia herbarum*, doc. vid.).

Orbilia angustoaristata Baral & G. Marson, **sp. nov.**, MB 813608 — Pls 331–332

Etymology: referring to the ascospores which are much narrower than in the otherwise similar *O. aristata*.
Typification: Australia, Northern Territories, Curtin Springs Roadhouse, twigs of *Acacia jennerae*, 10.X.1998, G. Marson (ex H.B. 6277f, MEL 2389201, holotype).

Latin diagnosis: *Apothecia rehydratata 0.18–0.8 mm diam., vivide rosea, sessilia vel substipitata, margine subtiliter crenulata vel distincte albido-dentata. Asci 8-spori. Ascosporae *12–17 × 1.6–2.4 µm, anguste ellipsoideo-fusoideae, cauda basali 3.5–7.5 × 0.3–0.7 µm, basi non inflata praeditae, in statu vivo* *corpusculum refringens bacilliformem vel subulatum, ad apicem affixum continentes. Cellulae vivae excipuli marginalis et paraphysium corpuscula globosa et crystalloidea continentes, excipulum marginale saepe processis vitreis, dentes minutos formantibus praeditum. Habitat ad lignum vel corticem putridum ramulorum vel ramorum siccorum* Acaciae *et* Pittospori phillyreoidis *in zona subtropica arida ad temperata subhumida Australiae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.18–)0.25–0.45(–0.8) mm diam., 0.09–0.2 mm high (receptacle 0.08–0.15 mm), (pale to) light to bright rose-pink to rose-red, round, scattered to subgregarious; disc flat, margin rising 0–5 µm above disc, finely whitish crenulate or with distinct small teeth (10–20 × 15–30 µm), rarely smooth; sessile to (sub)stipitate, stipe 0.08 × 0.2 mm, superficial or half immersed in biofilm. **Asci** *(40–)48–56(–68) × 5–6 µm {2}, †39–58 × 4.5–5.6 µm {2}, 8-spored, spores 3–4-seriate, (0–)1–3 lower spores inversely oriented {2} (not mixed), pars sporifera *26–28 µm long; **apex** (†) hemispherical to slightly truncate, dome 1.2–1.6 → 0.5–1 µm thick, with or without apical chamber; **base** with short to very long, ± thin, flexuous stalk, L- to Y-shaped. **Ascospores** *12–15(–17) × 1.6–2.4 µm {2}, †12–15(–18.5) × 1.7–2 µm {2}, with (subcylindrical to) narrowly ellipsoid-fusoid, *8–10 µm long head and medium sharply differentiated narrow tail of *3.5–7.5 × 0.3–0.7 µm, apex rounded to obtuse, tail straight to slightly curved, never widened at the base; **SBs** *(2–)2.5–3.5 × 0.4–0.5 µm {2}, rod-shaped to subulate, more overmature *0.8(–1) µm wide, ampulliform, apically narrowed to a small or often wide point, with a few minute LBs. **Paraphyses** apically uninflated to slightly clavate-capitate, terminal cells *9–24 × (2–)2.3–3.5(–4) µm {2}, lower cells *8–12 × 1.8–2.2(–3.5) µm {2}; unbranched near apex, hymenium light rose. **Medullary excipulum** hyaline to pale rose, 20–130 µm thick, of medium dense textura intricata-globulosa, sharply delimited. **Ectal excipulum** hyaline to pale rose, of medium gelatinized {2}, vertically oriented t. angularis(-prismatica) at base and flanks, 20–50 µm thick near base, cells */†10–21 × 7–14 µm {2}, common walls †1–1.3(–2) µm thick; 15–30 µm thick near margin, inner part of t. prismatica-angularis oriented at a 30–50° angle to the surface, outer part abruptly of t. prismatica(-porrecta) oriented at 20–45°, marginal cortical cells *5–16 × 3–4 µm {2}, **glassy processes** absent {1} or present {2}, 10–20 × 3.5–4(–4.5) µm, stratified, ± coherent to form teeth. **Anchoring hyphae** sparse, */†2–4 µm wide, walls 0.2–0.7 µm thick {2}, sometimes covering lower flanks by a 10 µm thick layer. **SCBs** in paraphyses and ectal excipulum globose, 1–2.7 µm diam., also crystalloid {2}. **Exudate** over paraphyses 0.5–1 µm thick, continuous to granular-cloddy, loosely attached; over margin and flanks rough-cloddy, 0.5–1 µm thick. — **ANAMORPH**: unknown.

Habitat: collected 0–1.5 m above the ground, ± decorticated, 1.5–9 mm thick twigs & branches of *Acacia jennerae* {1}, *Pittosporum phillyreoides* {1}, on wood {1} or remnants of bast {2} (outer layers of bark removed), outer 0.3 mm deep medium to strongly decayed, greyed, green algae sparse or absent. **Associated**: *Baggea* sp. {1}, *Claussenomyces* sp. {1}, *Coccomycetella* sp. {1}, *Dacrymyces* sp. {1}, *Dothideomycetes* {1}, *Exidia* sp. {1}, *Gloniopsis* sp. {1}, *Orbilia austropleiomicrosoma* {1}, *O. coronohesperidea* {1}, *O. ?livistonae* {1}, *O. megahesperidea* {1}, *O. multiaustraliensis* {1}, *O. multiserpens* {2}, *O. myriella* {1}, *O. myrionamibica* {1}, *O. ?myrioolneyae* {1}, *O. pleioaustraliensis* {2}, *O. pleiocoronohesperidea* {1}, *Peniophora* sp. {1}, *Symbiotaphrina desertorum* {2}, *?Triblidium* sp. {1}, *Xylobolus* sp. {1}. **Desiccation tolerance**: fully viable for at least 2 months. **Altitude**: 248–480 m a.s.l. **Geology**: Cenozoic regolith. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia angustoaristata* is characterized by rather elongate and narrow spore heads which gradually attenuate into a comparatively short tail. *O. herbarum* Velen. (1934: 102) was described with similar spores, but the holotype is now empty and the substrate (herbaceous) and geographical origin is different. The northern hemispheric *O. aristata*, *O. clavuliaristata*, *O. clavuliformis*, *O. frullaniae*, and *O. subclavuliformis* differ in mostly wider spores, wider SBs, and in the absence of crystalloid SCBs, *O. aristata* also in much shorter spore heads and longer, more abrupt tails. For the similar *O. brevicauda* see p. 705.

Variation. The two collections of *O. angustoaristata* closely resemble each other in their micromorphology. Variation was mainly observed in the length of the glassy processes and consequently in the length of the margin teeth. This variation occurred within both collections, the margin being either distinctly crenulate to denticulate or almost to entirely smooth.

Not included collections. Two European samples on leaves of *Dryas* (Pl. 331: 4), with minute (0.2 mm diam.), whitish to pale cream apothecia, were only studied in the dead state and might represent a separate species. They were among the specimens published by Nograsek & Matzer (1991: 460) from Sweden and Austria under the provisional name *O. inconspicua* which turned out to be a mixture (see p. 1674). The fungus of Pl. 331: 4 was probably not studied by the authors who only reported spores without a tail. Besides typical *O. angustoaristata*, this fungus resembles also *O. frullaniae*, *O. brevicauda*, and *O. clavuliaristata* in spore shape, but consistently deviates in rather short tails (†2.5–3.5 × 0.3–0.4 µm). The glassy processes have a size of 1–9 × 3–3.5 µm.

A collection from southwestern Australia on bark of *Dodonaea viscosa* subsp. *angustissima* (Pls 331: 3; 332: 2) is not included because it differs in slightly wider asci and spores, slightly larger, especially wider SBs (3–3.8 × 0.6–0.8 µm) with an often narrow attachment, and longer glassy processes (15–50 × 2.5–3.5 µm) forming much larger teeth (40–75 × 40–160 µm). Though studied in the living state, crystalloid SCBs were only seen in some of the apothecia examined. This collection showed a drought tolerance of 20 months.

Phylogeny. A sequence comprising S1506 intron, ITS, and LSU was gained from two different apothecial extracts of the not included sample on *Dodonaea* (H.B. 8838b). In the combined analysis (Phyl. 9) it clustered unexpectedly with *O. velutina* in a moderately supported clade within the strongly supported *vinosa-velutina* clade in spite of its close similarity with species of series *Hemiorbilia*. A medium supported association with *O. velutina* was also observed when analysing LSU (Phyl. S13).

In the ITS region *O.* cf. *angustoaristata* shows a distance of 11.5–15 % to other members of the *vinosa-velutina* clade. In the LSU the distance to *O. velutina* is 1.5 %, to *O. multicurvula* 3 %, to *O. nothoaprilis* 3.5 %, and to members of the *aristata-clavuliformis* clade 5–8.3 %. This raises the question whether the sequence might originate from another, macroscopically similar *Orbilia* that grew in association. However, none of the five *Orbilia* species that were recorded in association with it on the same branches, including *O. fimbriata*, show a micromorphology similar to *O. velutina*. We retained *O. angustoaristata* in series *Hemiorbilia* because of its morphology which is reminiscent of, e. g., *O. flagellispora*.

Ecology. *O. angustoaristata* was found on ± rotten bark and wood of xeric twigs and branches of *Acacia* and *Pittosporum*. In the holotype most apothecia grew on decorticated wood, while in the paratype they equally grew on bark and wood. The holotype was from a subtropical arid acacia open shrubland in central Australia (south of MacDonnell Ranges), the paratype from a warm-temperate subhumid eucalypt woodland in eastern Australia west of the Great Dividing Range. The not included collection on *Dodonaea* was in a subtropical semiarid acacia open shrubland on Cretaceous sedimentary rock in southwestern Australia, while those on *Dryas* were from a calcareous humid shrubland and pasture (*Dryadetum*) in the (sub)alpine, cryorotemperate eastern Alps of central Europe.

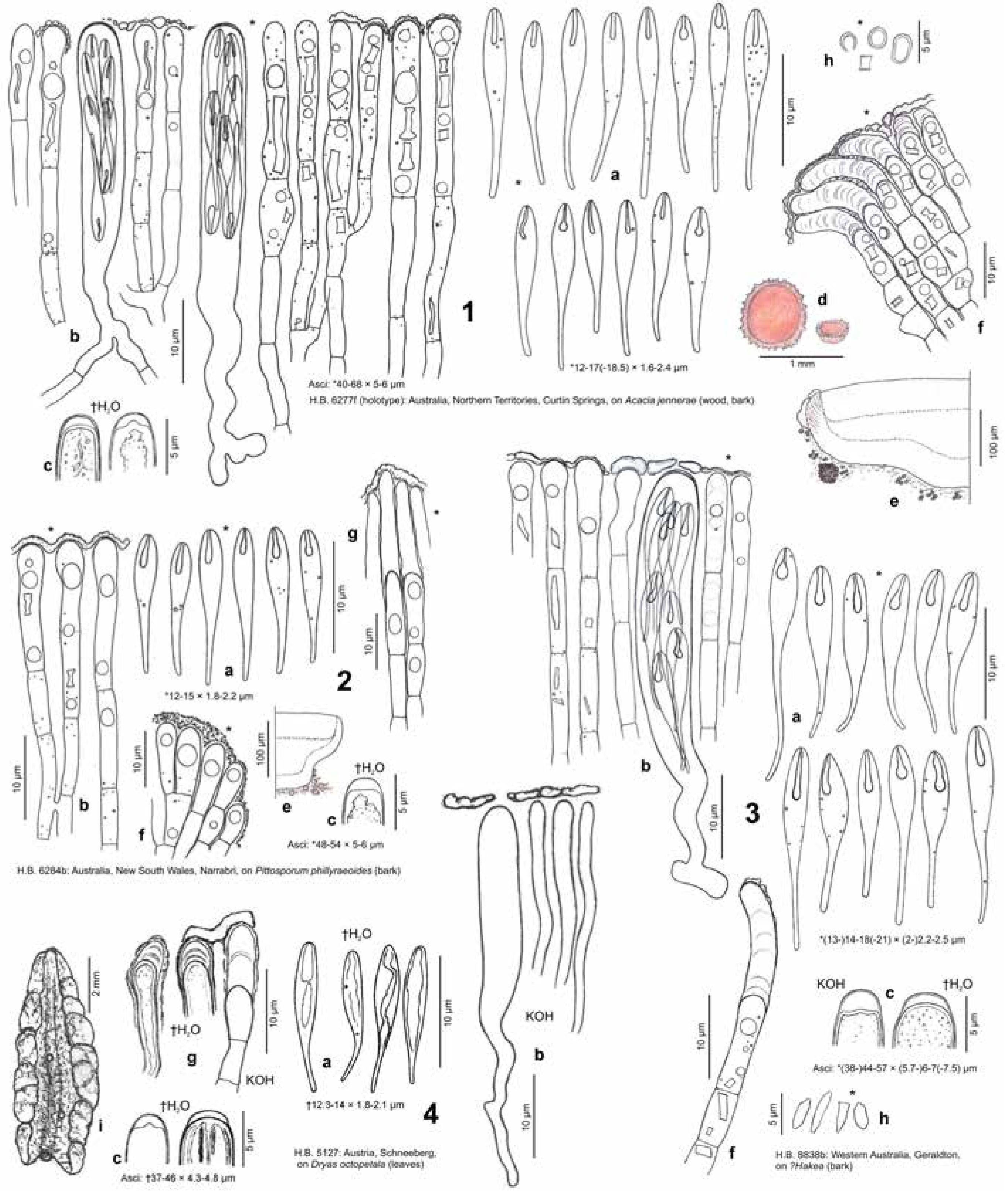


Plate 331. **1–2**: *Orbilia angustoaristata*; **3–4**: *O.* cf. *angustoaristata*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia with dentate margin (rehydrated); **e**. apothecia in median section; **f**. id., marginal ectal excipulum, cortical cells with or without glassy processes; **g**. id., external view; **h**. crystalloid SCBs in ectal excipular cells (lower flanks); **i**. leaf of *Dryas* (underside, with two apothecia).

Specimens included. **AUSTRALIA**: **Northern Territories**, Finke, 100 km E of Yulara, 24 km ENE of Curtin Springs Roadhouse, 28 km NNE of Mt. Connor, 480 m, twigs of *Acacia jennerae*, on wood & bark, 10.X.1998, G. Marson (ex H.B. 6277f, MEL 2389201, **holotype**; MEL 2389203B, **isotype** [in type of *O. multiaustraliensis* MEL 2389203A]). – **New South Wales**, Brigalow Belt South, 20 km SW of Narrabri, 248 m, branches of *Pittosporum phillyreoides*, on bark, 24.X.1998, G. Marson (H.B. 6284b).

Not included. **AUSTRIA**: **Niederösterreich**, 6.7 km WSW of Puchberg, 2.2 km ESE of Hochschneeberg, between Waxriegel and train station, ~1840 m, leaves of *Dryas octopetala*, 19.VIII.1990, A. Nograsek, W. Pongratz & K. Waltl (H.B. 5127 ø, GZU 63-92, as *O. inconspicua*). – **Steiermark**, 13 km NE of Schladming, 4.3 km N of Aich, Stoderzinken, 2010 m, leaf of *Dryas octopetala*, 21.VII.1987, J. Hafellner & A. Nograsek (GZU 37-92, as *O. inconspicua*). — **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, Nerren Nerren, W of Toolonga 190 m, trunk of *Dodonaea viscosa* subsp. *angustissima*, on bark, 8.XI.2007, G. Marson (H.B. 8838b; sq.: KT222396).

Plate 332. **1**: *Orbilia angustoaristata*; **2**: *O.* cf. *angustoaristata*. – **2a**. semiarid acacia shrubland; **1a**. dead, partially decorticated xeric branches of *Pittosporum phillyreoides*; **2b**. detached xeric bark of *Dodonaea viscosa*; **1b–g**, **2c–i**. rehydrated apothecia; **1h**, **2m**. apothecia in median section; **2l**. id., marginal ectal excipulum; **2j**. id., basal ectal excipulum; **1i**, **2k**. ascus apices; **2n**. ascospores. – Living state, except for **1h** (in KOH), **1i** (in KOH+IKI), ascus in **2k**. — **1a–i**. H.B. 6284b: Australia, New South Wales, on *Pittosporum*; **2a–n**. H.B. 8838b: Western Australia, Yalgoo, on *Dodonaea*.

Orbilia frullaniae Baral & Priou, **sp. nov.**, MB 813609 — Pls 333–334

Etymology: named after the substrate, *Frullania dilatata*.

Typification: France, Besançon, leaves of *Frullania dilatata*, 3.II.2008, J.M. Moingeon & G. Moyne (ex H.B. 8760, M-0276487, holotype).

Latin diagnosis: *Similis* Orbiliae angustoaristatae *sed cellulae vivae excipuli et paraphysium absque corpusculis crystalloideis, capites ascosporarum breviora, corpuscula refringentia latius, asci apice leniter crassitunicati, ab* O. brevicauda *ascosporis majoribus, corpusculis refringentibus et processis vitreis longioribus differt. Habitat ad folia senescentia vel emortua sicca* Frullaniae dilatatae *in zona temperata humida subatlantica Europae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** fresh 0.25–0.65 mm diam., 0.19–0.4 mm high (receptacle 0.11–0.16 → 0.07–0.1 mm), light to bright orange-rose, non-translucent, round, scattered; disc slightly concave, margin 10–80 µm protruding (incl. teeth), with white incurved teeth 40–80 × 40–70 µm; sessile on a broad obconical base or mostly with a distinct stipe 0.12–0.25 × 0.2–0.25 mm; dry somewhat contracted, bright pink-red with whitish marginal teeth. **Asci** *44–54 × 5.5–6 µm, †33–43 × 4.5–5.3 µm, 8-spored, spores *4-seriate, (1–)2(–4) lower spores inverted (not mixed), pars sporifera *22–25 µm long; **apex** (†) slightly to medium truncate, hemispherical in profile view, dome †0.6–0.8 → 0.5–0.6 µm thick, without apical chamber; **base** with short to medium long, thick, flexuous stalk, L- to h-shaped. **Ascospores** *(11.5–)14–16(–17.5) × 2.1–2.4 µm, †13.5–15.5 × 2–2.2 µm, head fusoid, apex obtuse (to subacute), *7–8 µm long, tail *7–8(–9) × 0.4–0.7 µm (towards head 0.5–0.8 µm), straight to slightly flexuous; **SBs** *2–2.8 × 0.7–0.9(–1) µm, subcylindrical (to tear-shaped), apically narrowed to a small or medium wide point, ± straight. **Paraphyses** apically uninflated or mostly slightly capitate, terminal cells *(12–)15–19 × 2.7–3.3 µm, lower cells *7.5–11 × 1.7–2.4 µm. unbranched at upper septum, hymenium pale rose. **Medullary excipulum** pale rose-orange, 70 µm thick, of dense textura globulosa-intricata, indistinctly delimited. **Ectal excipulum** very pale rose, of thin-walled, indistinctly oriented t. globulosa from base to mid flanks, 70–90 µm thick at lower flanks, cells *10–20(–23) × (6–)9–12(–14) µm; 20–25 µm thick near margin, inner part of t. (prismatica-)angularis oriented at a 60–80° angle to the surface, outer part of t. porrecta oriented at 20–40°, marginal cortical cells *8–12 × 2.5–3.5(–4) µm; **glassy processes** (5–)20–60 × 2.5–3.5(–4.5) µm, high-refractive, indistinctly stratified, at margin strongly inwards curved, coherent to form distinct teeth. **Anchoring hyphae** very abundant, */†1.7–3.5(–5) µm wide, walls 0.2–0.3(–0.8) µm thick, forming a medium dense, hyaline, slightly gelatinized t. intricata up to 90 µm thick at base, covering flanks as a 5–10 µm thick layer, intergrading with glassy processes. **SCBs** globose, in paraphyses 1.3–2 µm diam., in ectal excipulum (near margin) 1.5–2.5 µm. **Exudate** over paraphyses 0.2–0.5 µm thick, granular, hyaline, loosely lying over gel, on glassy processes 1–3 µm thick, cloddy-continuous. — **ANAMORPH**: unknown.

Habitat: collected 1.6 m above the ground, corticated, 15 cm thick living trunk of *Prunus mahaleb*, on necrobiotic or dead, darkened leaflets of *Frullania dilatata*. **Associated**: ?*Brachythecium* sp., *Lepraria* sp., *Metzgeria furcata*, *Normandia pulchella*, *Orthotrichum* sp., *Rhytidium rugosum*. **Desiccation tolerance**: ectal excipular cells still viable after 2 weeks. **Altitude**: 370 m a.s.l. **Geology**: Middle Jurassic limestone (marble). **Phenology**: II.

Taxonomic remarks. *Orbilia frullaniae* is similar to the Australian *O. angustoaristata*, from which it is tentatively separated by the absence of crystalloid SCBs, also by slightly shorter spore heads, wider SBs, and thinner ascus apical thickenings. However, in one of the collections mentioned under *O. angustoaristata* (H.B. 8838b) crystalloid SCBs were also often absent. Another close relative of *O. frullaniae* is the Chinese *O. brevicauda* which is tentatively separated by smaller ascospores and shorter SBs, also by shorter glassy processes. The North American *O. clavuliaristata* differs in slightly wider spores and larger SBs, also in slightly thicker domes and much shorter glassy processes. *O. subclavuliformis* distinctly differs in thicker spore tails, longer SBs, and in very short or absent glassy processes. A collection on *Hedera* in remote association with *Frullania* (Pl. 339: 11, atlantic Europe) differs in much longer SBs and almost smooth apothecia and is, therefore, considered as an aberrant form of *O. aristata*.

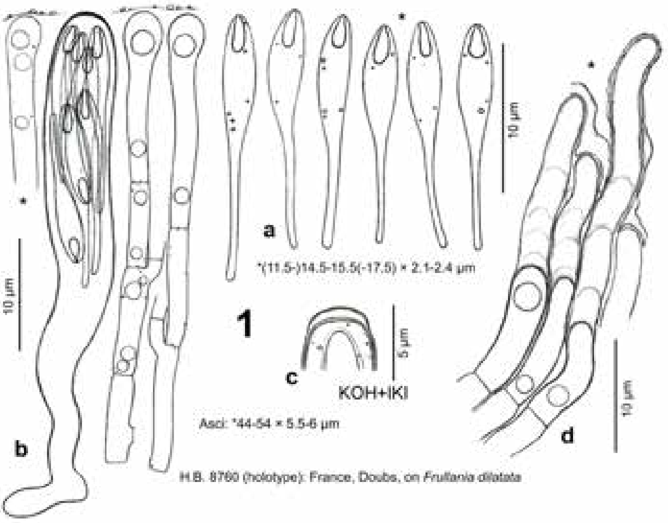


Plate 333. **1**: *Orbilia frullaniae*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. marginal cortical cells with glassy processes (median section).

Not included collection. A sample on a 5 mm thick corticated xeric twig of *Cornus* (on periderm, closely associated with an acrocarpous moss and lichens, Pl. 334: 2) showed a similar spore size [*14–16.5 × 2.3–2.5(–2.7) µm] but has spores with longer, more cylindrical heads and shorter tails, and much wider, tear-shaped SBs 2.4–3 × 1.3–1.6 µm (only a few living spores could be seen). The shorter glassy processes (10–20 µm) and particularly the presence of rod-shaped SCBs 3.5–4 × 0.8–1 µm in the ectal excipular cells at mid flanks are further diagnostic features. This sample seems to be intermediate to *O. clavuliaristata*, which was also recorded on *Cornus*, but deviates in, e. g., more dumbbell-shaped SBs, more distinct spore tails, and the absence of crystalloid SCBs.

Ecology. *O. frullaniae* grew on old but still-living leaflets of *Frullania dilatata* on a standing trunk of *Prunus* in a cold-temperate humid, subatlantic, medium shady *Prunus mahaleb*-*Buxus sempervirens* forest on calcareous Jurassic soil in southwestern central Europe. The species is probably rare or is not confined to *Frullania*, otherwise it would have been encountered earlier on this thoroughly investigated bryophyte. The not included collection was on rotten bark of a xeric twig of *Cornus* from the northern foothills of central Pyrenees in a warm-temperate humid, atlantic forest with *Robinia* and *Cornus sanguinea* on calcareous soil (Cretaceous).

Specimens included. **FRANCE**: **Franche-Comté**, **Doubs**, 15.5 km SSW of Besançon, 1 km N of Courcelles-Les-Quingey, 370 m, trunk of *Prunus mahaleb*, on leaves of *Frullania dilatata*, 3.II.2008, J.M. Moingeon & G. Moyne (ex H.B. 8760, M-0276487, **holotype**; J.P.P. 28020, **isotype**).

Not included. **FRANCE**: **Midi-Pyrénées**, **Ariège**, 16.5 km ENE of St.-Girons, 0.7 km NE of Castelnau-Durban, les Mouns, 450 m, twig of *Cornus sanguinea*, on bark, 30.X.2011, J.P. Priou (H.B. 9622a).

Plate 334. **1**. *Orbilia frullaniae*; **2**. *O.* cf. *frullaniae*. – **1a**. subatlantic forest with *Buxus sempervirens* and *Prunus mahaleb*; **1b**. living *Prunus mahaleb* tree after pieces of bark were harvested; **1c–d**. apothecia on *Frullania dilatata*, with *Metzgeria*; **1e**, **g**. fresh apothecia; **1f**, **h–j**, **2a–c**. rehydrated apothecia (**2a–c** with acrocarpous moss & foliose lichen), **1k**. dry apothecia; **1l–n**. apothecium in median section; **1o–p**. id., ectal excipulum and anchoring hyphae near base; **1q**, **2d–e**. ascospores. – Living state (**1q** right in CRB), except for **2d** (in H_2O). – **1a–b**: phot. G. Moyne; **1e**, **g**, **l–o**, **1q** right: phot. J.P. Priou. — **1a–p**. H.B. 8760 (holotype): France, Doubs, on *Frullania* (on *Prunus*); **2a–e**. H.B. 9622a: France, Ariège, on *Cornus*.

Orbilia brevicauda Ying Zhang, Baral & K.Q. Zhang, in Zhang et al., Fungal Diversity 36: 143 (2009) — Pls 335–336

Etymology: named after the short-tailed ascospores.

Typification: China, Yunnan, Yimen, branch of indet. angiosperm, 1.VII.2006, Z.F. Yu (ex YMFT1.01851 & ex H.B. 8715, M-0140891, holotype).

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated 0.4–1 mm diam., 0.1–0.12 mm high (receptacle 0.09 → 0.06 mm), light cream-yellow-orange, medium translucent, round, scattered; disc flat, margin distinctly crenulate by small whitish, hardly protruding teeth; sessile, superficial. **Asci** *36–50 × 5.2–5.4 µm, †(30–)35–40 × (4.2–)4.5–5(–5.3) µm, 8-spored, spores (*) biseriate, 1–2 lower spores inverted, pars sporifera *22–25 µm long; **apex** (†) hemispherical to very slightly truncate, dome †1 → 0.3–0.8 µm thick, with slight apical chamber; **base** with short to medium long, ± thin, flexuous stalk, L-, T- or Y-shaped. **Ascospores** *11.5–13.5 × 2–2.2 µm, †10.8–12.5 × 1.7–1.9 µm, with a narrowly ellipsoid-fusoid head *7–8 µm long (†6–7 µm) and an abrupt thin tail *4.5–5.5 × 0.6–

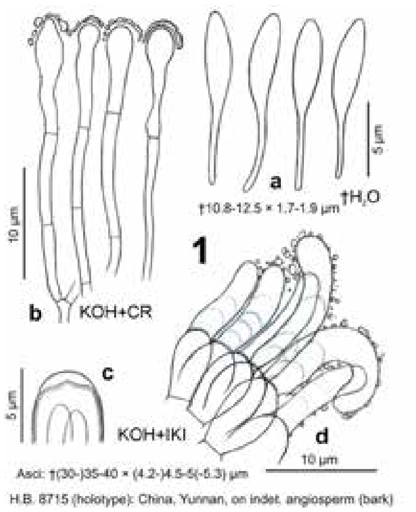


Plate 335. **1**: *Orbilia brevicauda*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex; **d**. marginal cortical cells with glassy processes (median section).

0.7(–0.9) µm (†4–5 × 0.3–0.5 µm), apex obtuse, head straight to slightly inequilateral, tail straight to slightly curved, rarely basally slightly inflated; **SBs** *1.6–2.2 × 0.7–0.9 µm, tear-shaped to almost cylindrical, apically narrowed to a ± wide point, straight. **Paraphyses** apically slightly to medium clavate-capitate, sometimes spathulate, terminal cells *12 × 2–4 µm, †8–11 × (1.7–)2–2.5(–3) µm, lower cells *9.5–11 × 1.4–2.2 µm, †7–11 × 1–1.7 µm; unbranched at upper septum. **Medullary excipulum** 15–30 µm thick, of dense textura intricata-porrecta, ± horizontally oriented, with many inflated cells, sharply delimited. **Ectal excipulum** of (†) thin-walled, indistinctly oriented t. globulosa-angularis from base to mid flanks, 20–45 µm thick near base, cells †6–11 × 5–10 µm; 20 µm thick near margin, of t. prismatica-angularis oriented at a 40–80° angle to the surface, marginal cortical cells †6–8 × 4–5.5 µm; **glassy processes** absent or usually present, 6–16 × 2.5–3.5 µm, medium refractive, hardly stratified, ± coherent to form small teeth. **Anchoring hyphae** medium abundant, †1.5–2.5 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses globose, 1.3–2.7 µm diam., in ectal excipulum not examined. **Exudate** over paraphyses 0.3–1.3 µm thick, granular-cloddy, ± loosely attached, over margin 0.3–1 µm thick, granular. **— ANAMORPH**: unknown.

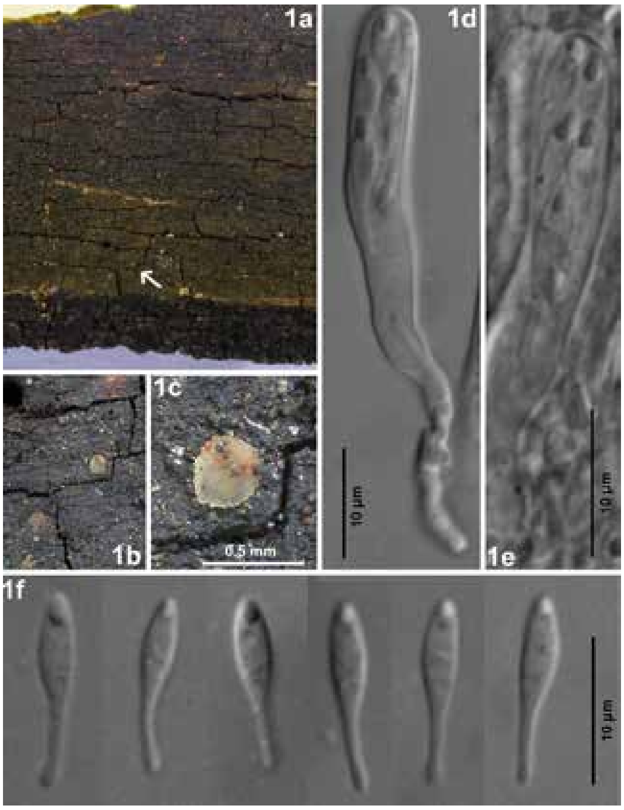


Plate 336. **1**: *Orbilia brevicauda*. – **1a**. blackened underside of detached bark of indet. angiosperm; **1b–c**. rehydrated apothecium; **1d–e**. mature asci; **1f**. ascospores (perhaps overmature because SBs smaller than in **1d–e**); — Living state. – **1b–f**: phot.Zhang et al. (2009b, DIC). — **1a–f**. H.B. 8715 (holo-/isotype): China, Yunnan, on indet. angiosperm.

Habitat: collected on moist ground on detached bark of ~10 cm thick branch or trunk of unidentified angiosperm tree, on medium decayed inner surface of bark, strongly blackened, no algae. **Associated**: none observed. **Desiccation tolerance**: not tested. **Altitude**: 2000 m a.s.l. **Geology**: Jurassic-Cretaceous-Paleogene sedimentary rock. **Phenology**: VII.

Taxonomic remarks. *Orbilia brevicauda* is similar to the Australian *O. angustoaristata*, from which it differs in shorter ascospores and spore heads, shorter and wider SBs, thinner apical domes, and apparently also in the absence of crystalloid SCBs. The Australian *O. parviclava* and the North American *O. clavuliaristata* differ in distinctly wider spore heads, the latter also in a tendency to longer spores. Also *O. frullaniae* is similar (for the differences see p. 704).

Ecology. The very sparse, apparently only two apothecia in the single collection of *O. brevicauda* grew on rotten, detached bark of an unidentified angiosperm tree in a shady subtropical humid (winter-dry) evergreen mountain forest in southeastern Asia. Considering the relationship within series *Hemiorbilia*, *O. brevicauda* is probably a desiccation-tolerant species that grows on exposed, attached branches. In fact, the bark fragment in the holotype shows a xeric appearance, which permits to assume that the branch recently fell to ground.

Specimens included. **CHINA**: **Yunnan**, **Yuxi**, Yimen, 75 km SW of Kunming, 53 km NW of Yuxi, Longkou Forest Park, 2000 m, branch of indet. angiosperm, on bark, 1.VII.2006, Z.F. Yu (ex YMFT1.01851, ex H.B. 8715, M-0140891, **holotype**).

Orbilia clavuliaristata Baral & E. Weber, **sp. nov.**, MB 813610 — Pls 337–338

Etymology: named after the ascospores that resemble *O. clavuliformis*, though having narrow tails similar as in *O. aristata*.

Typification: Germany, Traunreut, branch of *Frangula alnus*, 18.VIII.2010, T.R. Lohmeyer (ex H.B. 9419, M-0276456, holotype).

Latin diagnosis: *Similis* Orbiliae clavuliformi *sed ascosporae caudis longioribus et multo angustioribus*, *corpusculis refringentibus multo brevioribus differt. Habitat ad corticem putridum ramulis siccis* Corni *vel* Frangulae *in zona temperata humida Americae septentrionalis et Europae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.3–0.5(–0.7) mm diam., 0.09–0.17 mm high, (pale to) light rose-orange, medium translucent, round, scattered; disc flat (to slightly convex), margin indistinct, 0–5 µm protruding, smooth to finely crenulate; broadly sessile, superficial but sometimes ± immersed in cracks of periderm; dry light to bright orange-rose. **Asci** *(31–)40–60(–70) × 6–6.5(–7.2) µm {2}, †(32–)35–48(–55) × (4–)4.3–5.5(–6) µm {4}, 8-spored, spores *3-seriate, (1–)2–3(–4) lower spores inverted {4} (not mixed); **apex** (†) hemispherical to slightly truncate, dome †1–1.3(–1.5) → 0.7–1 µm thick {4}, apical chamber distinct or not; **base** with very short to very long, thin ot thick, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *(11–)12–16.5(–18) × (2.3–)2.4–2.6(–2.7) µm {4}, †10–15 × 2–2.4 µm {1}, with ellipsoid-fusoid head and sharply differentiated thin tail, head *7–10(–11) µm long (1/2–2/3 of spore length), straight or sometimes slightly inequilateral, apex obtuse (to subacute), tail *4–7(–8) × 0.3–0.6 µm, not swollen at base, straight to slightly curved or flexuous; **SBs** *(2.2–)2.5–3.5(–4.2) × (0.8–)1–1.2(–1.4) µm {4},

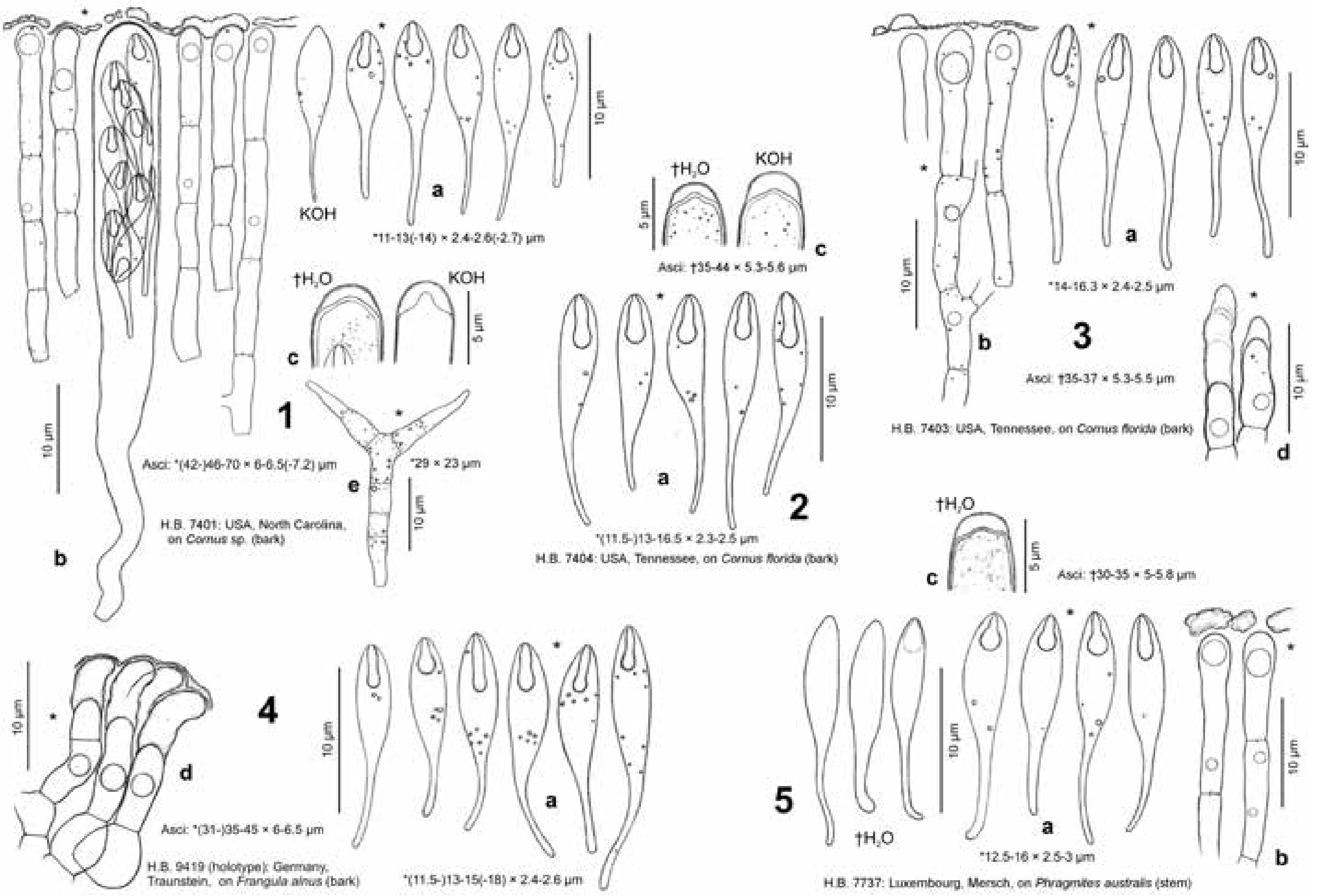


Plate 337. **1–4**: *Orbilia clavuliaristata*; **5**. *O.* cf. *clavuliaristata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal cortical cells with glassy processes (**4d** in median section); **e**. conidium from substrate.

pyriform to dumbbell-shaped, also rod-shaped, apically narrowed to a ± wide point, straight, overmature 2–2.5 × 1.2–1.3 µm {1}. **Paraphyses** apically slightly (rarely medium) clavate-capitate, terminal cells *(5.5–)7–17(–19) × (1.8–)2.2–2.7(–3.3) µm {3}, lower cells *(5.3–)6.5–11(–12) × 1.5–2.5(–3.3) µm {3}; sometimes branched at upper septum. **Medullary excipulum** 15–50 µm thick, of dense textura intricata with some or many inflated cells, sharply delimited. **Ectal excipulum** of thin-walled, irregularly or vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 25–60 µm thick near base, cells *8–20(–24) × 6–12 µm {2}; 15–20 µm thick near margin, pale rose, inner part of t. prismatica-angularis oriented at a 50–80° angle to the surface, outer part of t. prismatica-porrecta oriented at 20–50°, marginal cortical cells */†(4–)6–11(–13) × 2.5–3.5(–4) µm {4}; **glassy processes** absent {2} or present, 1–4 {3} or 4–10(–20) {3} × 2.5–4 µm {4}, high-refractive, ± stratified or not, sometimes outwards curved. **Anchoring hyphae** very sparse to medium abundant, †1.7–3 µm wide, walls 0.2–0.3 µm thick {2}, sometimes forming a 30 µm thick, slightly gelatinized, rather dense t. intricata. **SCBs** in paraphyses and ectal excipulum (near margin) globose, (0.8–)1.2–2(–2.7) µm diam. {3}. **Exudate** over paraphyses and exterior 0.2–1(–2) µm thick, cloddy-continuous, hyaline, loosely or firmly attached. **— ANAMORPH**: trinacrium-like (presumed, from natural substrate {2}). **Conidiophores** not seen. **Conidia** Y-shaped, total size */†(29–)44–50 × (23–)40–55 µm, stipe †(17–)21–31 × 2.2–3 µm, 3–5-septate, arms slightly (also strongly) tapering, */†(12–)20–33 × 2–3 µm, 2–6-septate {2}.

Habitat: collected 0.1–1 m above the ground, corticated, 2–9 mm thick twigs and branches of *Cornus* sp. {1}, *C. florida* {2}, *Frangula alnus* {1}, on medium decayed bark {4} (periderm {3} and bast {4}), along or in holes and cross fissures of periderm, sometimes on inner surface of detaching periderm, slightly greyed, also blackened and close to old pyrenomycete, green algae sparse or abundant. **Associated**: *Caloplaca* sp. {1}, *Graphis scripta* {1}, *Physcia* sp. {1}, various discocarpous lichens. **Desiccation tolerance**: fully viable for at least 2 months, paraphyses still alive after 11 months. **Altitude**: 2–570 m a.s.l. **Geology**: USA: Late Proterozoic sedimentary rock, Quaternary sediments; Germany: Pleistocene calcareous till. **Phenology**: V, VIII (but rather long-lived).

Taxonomic remarks. *Orbilia clavuliaristata* resembles *O. clavuliformis* in its ellipsoid-fusoid ascospore heads, but differs in longer and much narrower spore tails and much shorter SBs. From *O. angustoaristata* it differs in wider spores and SBs, and in the absence of crystalloid SCBs. However, in one of the Australian collections mentioned under *O. angustoaristata* (Pl. 331: 3) crystalloid SCBs were often also absent. That collection, but also the similar *O. frullaniae*, are actually very similar to *O. clavuliaristata* but differ in much longer glassy processes forming prominent teeth, also in narrower SBs and slightly narrower spores. A European collection on *Cornus* mentioned under *O. frullaniae* deviates by crystalloid SCBs.

O. clavuliaristata is segregated from *O. aristata* by narrower spore heads and shorter tails. A European collection on *Hedera* (Pl. 339: 11) mentioned under *O. aristata* differs from *O. clavuliaristata* in slightly longer, sometimes basally a bit swollen spore tails, somewhat longer SBs, and in shorter asci with thinner apical domes.

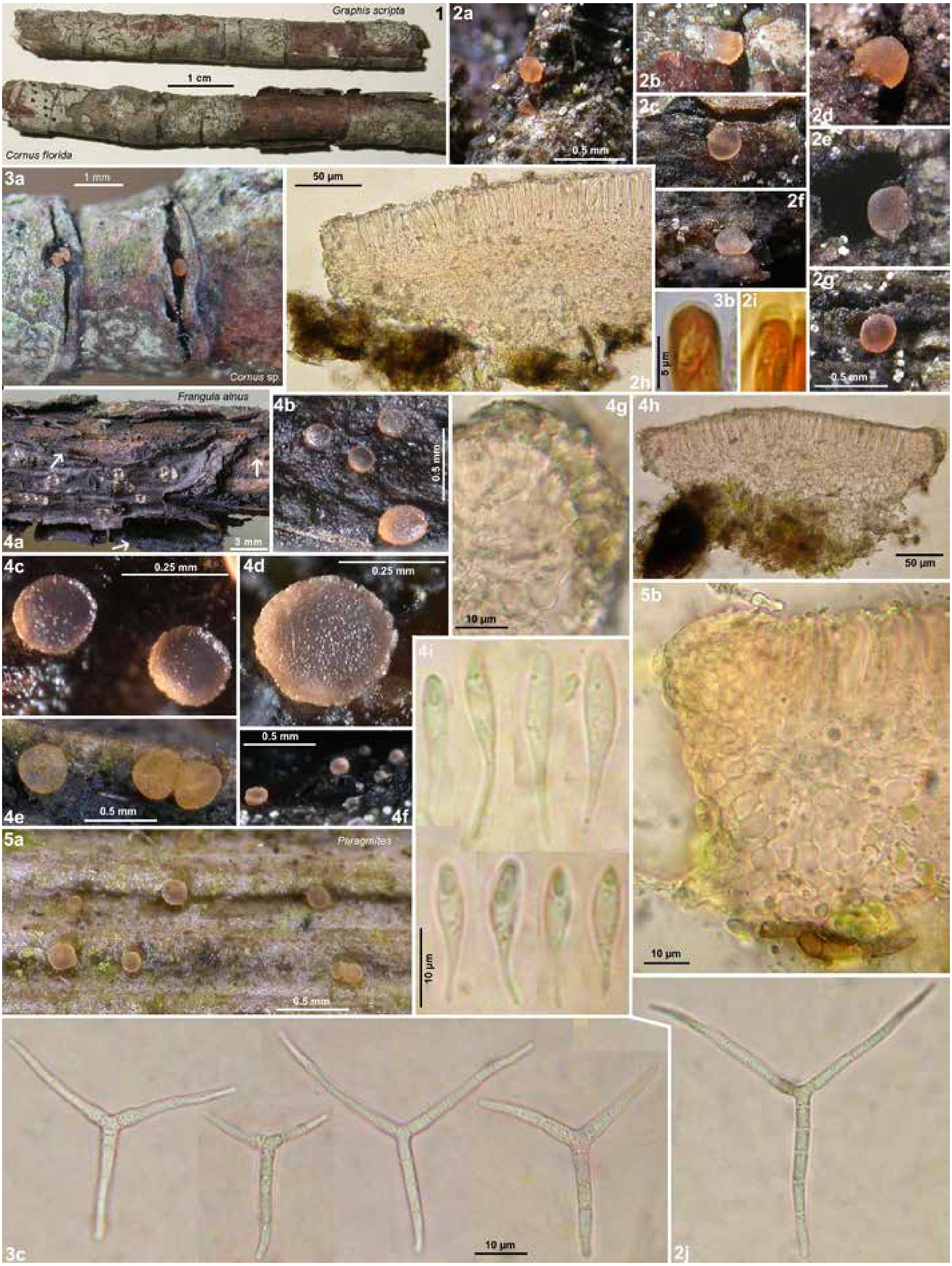


Plate 338. **1–4**: *Orbilia clavuliaristata*; **5**: *Orbilia* cf. *clavuliaristata*. – **1**, **3a**, **4a**. dead corticated xeric branches; **4b–f**. fresh apothecia; **2a–g**, **3a**, **5a**. rehydrated apothecia; **2h**, **4h**. apothecia in median section; **4g**, **5b**. id., marginal region; **2i**, **3b**. ascus apices; **4i**. ascospores; **2j**, **3c**. conidia from substrate. – Living state, except for **2h** (in KOH), **2j** (in H_2O), **3c** (3 left conidia, in H_2O), **4i** (2 spores on upper right). — **1**. H.B. 7403: USA, Tennessee, on *Cornus*; **2a–j**. H.B. 7404: ibid., on *Cornus*; **3a–c**. H.B. 7401: USA, North Carolina, on *Cornus*; **4a–i**. H.B. 9419 (holotype): Germany, Traunreut, on *Frangula*; **5a–b**. H.B. 7737: Luxembourg, Mersch, on *Phragmites*.

O. breviaristata differs in shorter and thicker spore heads and apothecia with prominent marginal teeth. The spore heads of *O. clavuliaristata* resemble those of *O. flagellispora* but that species sharply differs in mostly longer tails with always swollen bases.

Variation. Within the three North American specimens some variation can be noted. The one from North Carolina (18 m a.s.l., *Cornus* sp.) has distinctly shorter spores and SBs whereas those from Tennessee (500–540 m a.s.l., *Cornus florida*), tend to have inequilateral spores. Despite the short spores, the sample from North Carolina showed the longest asci. The European sample on *Frangula* fits quite well these specimens. Also here the ascus length is at the lower end of the range, while the spores attain the highest length (18 µm), also the heads of the spores are a bit longer compared to the North American specimens.

Not included collections. A sample on *Euphorbia* from Madeira (J.P. Priou, IVV: J.P.P. 15165, spores *13–17 × 2.1–2.5 µm, SBs 2.5–4 × 0.8–1.2 µm) fits quite well *O. clavuliaristata*, but is not included because of its different ecology. A collection from Boston Harbor Islands is intermediate to *O. subclavuliformis* in having wider spore tails and less fusoid heads but an SB length that fits *O. clavuliaristata* (IVV: bhi-F665). A central European collection on *Phragmites* (Pl. 337: 5) is not included because of the unusual substrate, rather thin (70–80 µm), pale rose apothecia, comparatively short asci, and slightly wider spores with rather short and wide SBs (SB size could be a result of overmaturity). *O. herbarum* Velen. differs from the latter collection in longer tails, according to the protologue (see p. 699).

Anamorph. The conidia observed on the substrate near apothecia of *O. clavuliaristata* are hardly different from those trinacrium-like conidia found in *O. clavuliformis* and related species.

Ecology. *O. clavuliaristata* was collected on medium decayed bark of xeric twigs and branches of angiosperms. Three samples on *Cornus* derive from warm-temperate humid forests of the southern Appalachian Mountains and coastal lowlands of eastern North America, while the type collection was on *Frangula* in a cold-temperate humid colline high moor (*Salici-Franguletum* among *Vaccinio-Pinetum*) in central Europe. The not included collection from cold-temperate humid central Europe was on a xeric culm of *Phragmites* in a *Phragmitetum* along a rivulet within a mixed forest, that from Macaronesia on *Euphorbia* in thermosubmediterranean semihumid southern Madeira, and that from Boston in cold-temperate humid northeastern North America.

Specimens included. **GERMANY**: **Bayern**, **Oberbayern**, 6.7 km NE of Traunreut, 2.8 km ESE of Palling, W of Lampertsheim, Harpfetshamer Filz, 570 m, branch of *Frangula alnus*, on bark, 18.VIII.2010, T.R. Lohmeyer (ex H.B. 9419, M-0276456, **holotype**). — **USA**: **North Carolina**, 33 km SE of Franklin, 6 km NE of Gatesville, Merchants Millpond State Park, Cypress Point Trail, 2 m, twigs of *Cornus*, on bark, 16.V.2003, W. Jaklitsch (H.B. 7401, W.J. 2134 ø, anam. substr.). – **Tennessee**, Appalachian Mts., Blue Ridge Mts., Great Smoky Mts., 23 km SE of Maryville, 9 km SSW of Townsend, Cades Cove, 540 m, twigs of *Cornus florida*, on bark, 22.V.2003, W. Jaklitsch (H.B. 7404, W.J. 2190 ø, anam. substr.). – Great Smoky Mts., 40 km ESE of Maryville, ~5 km SSW of Gatlinburg, Old Sugarlands Trail, 520 m, branch of *Cornus florida*, on bark, 24.V.2003, W. Jaklitsch (H.B. 7403, W.J. 2215 ø).

Not included. **LUXEMBOURG**: **Gutland**, **Mersch**, Luxembourg Plateau, 4.3 km S of Larochette, 1.2 km N of Koedange, below Folkend, Mäschpesch, 300 m, culm of *Phragmites australis*, 1.IV.2005, G. Marson (H.B. 7737). — **MACARONESIA**: **Madeira**, 2 km NW of Funchal, Jardín Botánico, twig of *Euphorbia balsamifera*, 265 m, 19.IX.2015, J.P. Priou (J.P.P. 15165, doc. vid.). — **USA**: **Massachusetts**, 16 km SE of Boston, 3.5 km NNE of Hingham, Slate Island, 2 m, branch of indet. angiosperm, on wood, 21.III.2017, A.C. Dirks & L.A. Kappler, vid. L. Quijada (bhi-F665, doc. vid.).

Orbilia aristata (Velen.) Velen., Opera Bot. Čech. 4: 104 (1947) — Pls 339–343, Map 58

≡ *Orbilia occulta* (Rehm) Sacc. var. *aristata* Velen., Monogr. Discom. Bohem.: 102 (1934)

(?) = *Radotinea caudata* Velen., Monogr. Discom. Bohem.: 298, pl. 17 figs 57, 58, 70 (1934) [non *Orbilia caudata* Starbäck]

Etymology: *aristata*: referring to the long and thin, awn-shaped ascospore tails; *caudata*: likewise from the spores having prominent basal tails.

Typification: Czechia, Mnichovice, branch of *Salix aurita*, 7.XII.1927, J. Velenovský (PRM 152468, holotype of ***Orbilia occulta* var. *aristata***); Germany, Stuttgart, Weilimdorf, branch of *Salix eleagnos*, 23.VI.2000, H.O. Baral & E. Weber (ex H.B. 6713, M-0291760, epitype, designated here, MBT385115, CBS 140834; sq.: KT596782, genotype 1) — Czechia, Radotín, branch of *Cornus mas*, 31.III.1927, J. Velenovský (PRM 151698, holotype of ***Radotinea caudata***, without apothecia).

Misapplied name: Rehm (1891: 459), Velenovský (1934: 102), Kirschstein (1936: 204), Svrček (1954: 10, 1960: 16), Ellis & Ellis (1985: 12), Beyer (1998: 191), as *O. occulta*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–0.6(–1) mm diam., (0.09–)0.1–0.2(–0.38) mm high (receptacle 0.075–0.13 mm), pale to bright rose or (ochraceous-)orange(-apricot), rarely reddish-cream, ± translucent, round, rarely elliptical, very scattered to densely gregarious; disc (slightly concave) flat to slightly (rarely medium) convex, margin thin, 0–15 µm protruding (5–25 µm incl. glassy processes), smooth or often finely powdered, or crenulate by small whitish teeth up to 20–30 × 30–40 µm; sessile or sometimes with an obconical or cylindrical stipe 0.06–0.08 or up to 0.15–0.2 × 0.12–0.2 mm, superficial but slightly immersed in biofilm; dry bright to deep orange-red(-apricot), somewhat contracted. **Asci** *(40–)45–62(–70) × (6–)6.2–7.5(–8) µm {18}, †(34–)38–55(–58) × (5–)5.5–6.5(–7) {11}, 8-spored, spores 2–4-seriate, 1–**2**–3(–4)((–5)) lower spores inversely oriented {49} (never mixed), pars sporifera *(29–)30–35(–40) µm long; **apex** (†) hemispherical to slightly truncate, dome †(1.1–)1.3–1.8(–2)((–2.3)) → 0.8–1 µm thick {14}, with or without apical chamber, endotunica bright red in $\mathrm{CR}_{\mathrm{SDS}}$; **base** with short to very long, thin to thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *((11.5–))(13–)14–22(–23)((–26)) × (2.5–)2.7–3.3(–3.5)((–4)) µm {77}, †(12–)14–20(–22) × (2.2–)2.5–3(–3.2) µm {18}, sperm-shaped: with ellipsoid-fusoid (rarely clavate) head and sharply differentiated filiform tail, head *(6–)7–9(–10) µm long, apex obtuse, sometimes subacute, rarely rounded, tail *(6–)8–12(–13)((–15)) × (0.25–)0.3–0.6(–0.8) µm, base usually not or only slightly inflated to *0.8(–1) µm wide {~160}, exceptionally bulbous, 0.8–1(–1.3) µm wide {6}, †0.2–0.6(–0.9) µm) wide, tail straight to slightly flexuous, exceptionally strongly bent; **SBs** *(2.5–)3–4(–4.5)((–4.8)) × (0.8–)0.9–1.3(–1.5) µm {25}, pyriform, also rod-shaped to subulate, apically narrowed to a small to ± wide point, overmature *2–3 × 1.2–1.7 µm, tear-shaped to ampulliform. **Paraphyses** apically (cylindrical to) slightly to medium (rarely strongly) clavate-capitate, rarely spathulate, terminal cells *(6–)10–25(–32) × (2–)2.3–3.5(–5.5) µm {7}, †10–22 × 1.8–2.7 µm {3}, lower cells *6–14(–16) × 1.5–2.5 µm {6}; sometimes branched at upper septum; hymenium very pale rose to light rose-orange. **Medullary excipulum** very pale to light rose, 30–80(–100) µm thick, of medium loose or dense textura intricata with many inflated cells, or t. globulosa-angularis, sharply or very indistinctly delimited. **Ectal excipulum** hyaline to pale rose, pale to light orange-rose near margin, of (†) thin-walled, vertically oriented t. angularis-prismatica from base to mid flanks, 20–80(–100) µm thick near base, cells *8–26 × (4–)7–16(–20) µm {9}; 15–40(–50) µm thick near margin, of t. prismatica-angularis oriented at a 50–90° angle to the surface, outer cells of t. porrecta oriented at 10–30°, marginal cortical cells *(6–)7–12(–16) × 1.8–4 µm {5}, **glassy processes** always present {> 80}, attaining a length of 1–5 {23}, 5–10 {19}, 10–15 {16}, 15–20 {12}, 20–30 {14}, or 30–40 {2} µm, (2–)2.5–4(–5) µm wide, refractive, sometimes ± stratified, straight or slightly curved up- or downwards, often forming ± distinct coherent teeth. **Anchoring hyphae** sparse to abundant, */†(1.5–)2–3(–5) µm wide, walls 0.2–0.4 µm thick {5}. **SCBs** in paraphyses and sometimes in ectal excipulum globose, 1–2.5 µm diam. {16}, rarely absent {3}.

Large pale yellowish **LBs** (carotenoids) in basal excipular cells usually absent, rarely present {3}, 1.5–3.5 µm diam. **Exudate** over paraphyses 1–3.5 µm thick, hyaline to pale yellowish-chlorinaceous, continuous to mostly cloddy-granular, loosely attached; on margin and flanks among glassy processes ± scattered, cloddy, 0.5–2 µm thick. — **ANAMORPH**: trinacrium- {–/9} (Y), descalsia- {1/9} (┼), and dwayaangam-like {2/10} (dw) (from ascospore or conidial isolate {3}/natural substrate {23}). **Conidiophores** not seen. **Conidia** variable in shape: 2-armed (Y-shaped, trinacrium subtile-like), total size †/*42–80 × 48–100 µm, stipe †/*22.5–55 × 2.2–3.5 µm, 3–6-septate, arms †/*27–51 × 2.2–3.5 µm, 4–7-septate {3}; 3-armed (┼-shaped, descalsia-like, tetraradiate in 3 dimensions when floating), total size †/*33–73 × 30–63 µm, stipe †/*13–31 × 2.1–3.5 µm, 2–5-septate, arms †/*12–41 × 2.3–3.5 µm, (1–)3–6-septate {6}; 4(–7)-armed (dwayaangam-like), total size *37–75 × 29–70 µm, stipe *12–20 × 2.8–3.8 µm, 2–4-septate, arms *13–42 × 3–3.5 µm, (1–)2–6-septate, 4–7-armed {4}; very rarely unbranched.

Habitat: collected (0–)0.2–3(–8) m above the ground, corticated (to partly, rarely entirely decorticated), dead or sometimes still-living, (2.5–)5–25 mm, rarely 30–50 mm thick branches or up to 20 cm thick trunks of *Abies alba* {3}, *Acer campestre* {1}, *A. glabrum* {1}, *A. pseudoplatanus* {2/1}, *Alnus alnobetula* {4}, *Amelanchier lamarckii* {1/1}, *Aronia melanocarpa* {1}, *Betula pendula* {1}, *Cornus* sp. {2}, *C. alternifolia* {1}, *C. sanguinea* {16}, *Corylus cornuta* {1}, *Cotinus coggygria* {1}, *Crataegus* sp. {1}, *Cytisus scoparius* {1}, *Fagus sylvatica* {13}, *Frangula alnus* {4}, *Fraxinus excelsior* {5}, *Ilex aquifolium* {2}, *Larix decidua* {1}, *Laburnum alpinum* {1}, *Ligustrum vulgare* {1}, *Lonicera periclymenum* {1}, *L. xylosteum* {1}, *Malus domestica* {5/1}, *Picea* sp. {1}, *P. abies* {5}, *Pinus* sp. {2}, *P. sylvestris* {4}, *Prunus domestica* {1}, *P. padus* {1}, *P. spinosa* {6}, *Punica granatum* {1}, *Pyrus communis* {1}, *Quercus rubra* {2}, *Rhus typhina* {2}, *Robinia pseudoacacia* {1}, *Rosa* sp. {5}, *Rubus* (?)*bifrons* {1}, *R. fruticosus* {9}, *R. idaeus* {1/1}, *R.* (?)*silesiacus* {1}, *Salix* sp. {22/1}, *S. alba* {1}, *S. aurita* {2}, *S.* ?*aurita* × *caprea* {1}, *S. caprea* {12/1}, *S. cinerea* {1/1}, *S. eleagnos* {1}, *S.* ?*fragilis* {1}, *S. rhamnifolia* {1}, *Sorbus* sp. {1}, *S. aria* {1}, *S. aucuparia* {3}, *Syringa vulgaris* {3}, *Taxus baccata* {1}, *Thuja plicata* {1}, *Tilia tomentosa* {1}, *Ulmus* sp. {1}, *U. minor* {1}, *Viburnum lantana* {1}, *Vitis vinifera* {2}, indet. angiosperm {1}, on 0.1–0.5(–1) mm deep (slightly to) medium (to strongly) decayed bark {146} (bast {69} or periderm {24}), more rarely wood {39}, often in small cracks of bark, or on detaching bark (on edges and inner surface), frequently along old wounds, sometimes on blackened resin {3}, also on largely decorticated wood, rarely on boring dust of bark beetles; on leaves of *Pinus sylvestris* {2}, herbaceous stems of *Humulus lupulus* {2}, *Rumex* sp. {1}, on textile (rope) {1}; sometimes close to or on old or still-living pyrenomycetes (*Diatrype* spp., *Xenotypa aterrima* {1} etc.), greyed, covered by sparse or often abundant green algae (sometimes included within the basal excipulum). **Further associated**: *Allantoporthe tessella* {1}, *Amphosoma atroolivaceum* {2}, *A. resinicola* {2}, *Bulbillomyces* sp. {1}, ?*Calloria* sp. {1}, ?*Calycellina* sp. {1}, *Cenangium acuum* {1}, *Ciliolarina* sp. {1/2}, *C. pinicola* {1}, *Claussenomyces olivaceus* {2}, *Coniochaeta* sp. {1}, *C. subcorticalis* {1}, *Crepidotus sphaerosporus* {1}, *Cryptocoryneum condensatum* {1}, *Cryptodiscus foveolaris* {2}, *Dacrymyces* sp. {1}, *Diaporthe* sp. {1}, *Diatrype bullata* {1}, *Diplolaeviopsis* sp. {1}, *Durandiella gallica* {1}, *Durella atrocyanea* {1}, *D. connivens* {2}, *Echinula resinicola* {1}, *Eustilbum aureum* {1}, *Eutypa* sp. {1}, *Evernia prunastri* {1}, *Flagelloscypha* sp. {1}, *Gelatinopsis hysteropatellae* {1}, *Helicogonium orbiliarum* (parasitic in *O. aristata*) {1}, *Hyalorbilia orbiliicola* (parasitic on *O. aristata*) {3}, *H. juliae* {1}, *H. latispora* {1}, *H. rotifera* {2}, *H. subfusispora* {8}, *Hyaloscypha minuta* {1}, *Hypogymnia physodes* {1}, *H. vittata* {1}, *Hymenoscyphus infarciens* {1}, ?*Hyphodiscus* sp. {1}, *H. theiodeus* {2}, *Hypogymnia physodes* {2}, *Hypoxylon* sp. {1}, *Hysterium angustatum* {1}, *Hysteropatella elliptica* {1}, *H. prostii* {1}, *Jattaea ceanothina* {1}, *Karstenia idaei* {1}, *K. rhopaloides* {6}, *Lachnellula abietis* {1}, *L. resinaria* {1}, ?*Laetinaevia* sp. {1}, *Lasiosphaeria* sp. {1}, *Lecanora* sp. {3}, ?*Leptorhaphis* sp. {1}, *L. parameca* {1}, *Lophiostoma compressa* {1}, *L. macrostomoides* {1}, *L.* ?*macrostomum* {1}, *Melanelia glabratula* {4}, *Melanomma pulvis-pyrius* {2}, *Mellitiosporiella pulchella* {1}, *Merismodes* sp. {1}, *Micropeziza* sp. {1}, *Mollisia* sp. {2}, *M.* ?*discolor* {1}, *M. ligni* {4}, *M.* ?*oblonga* {1}, *M. prunicola* {2/1}, *M. rosae* {1}, *Mollisina rubi* {2}, *Nectria cinnabarina* {1}, *Neodasyscypha cerina* {1}, *Nitschkia cupularis* {2}, *Octospora affinis* {1}, *Olla scrupulosa* {1}, *Orbilia aprilis* {1}, *O.* ?*arachnovinosa* {1}, *O. aradi* {5}, *O. aurantiorubra* {3}, *O. auricolor* {1}, *O. breviaristata* {1}, *O. clavuliformis* {11}, *O. eucalypti* {12}, *O. euonymi* {2}, *O. fabacearum* {1}, *O. filiformis* {7}, *O. flagellispora* {6}, *O. flavida* {2}, *O. fraxini* {1}, *O. gambelii* {2}, *O. lentiformis* {1}, *O. maeandrina* {1}, *O. magnifica* {1}, *O. mali* {2}, *O. ocellata* {3}, *O. patellarioides* {1}, *O. pseudoaristata* {2}, *O. pseudocylindrospora* {1}, *O.* ?*pubescens* {1}, *O. quaestiformis* {2}, *O. sphaerospora* {1}, *O. subaristata* {2}, *O. subclavuliformis* {3}, *O. subtrapeziformis* {4}, *O. subvinosa* {1}, *O. trapeziformis* {1}, *O. vinosa* {5}, *O. vitalbae* {2}, *O. xanthoguttulata* {1}, *Otthia spiraeae* {1}, *Parmelia* sp. {2}, *P.* ?*saxatilis* {1}, *P. sulcata* {7}, *Patellaria atrata* {1}, *Patellariopsis atrovinosa* {2}, *Patinellaria sanguinea* {1}, *Peniophora lycii* {1}, *Perzia triseptata* {1}, *Pezicula cinnamomea* {1}, *Phaeomarasmius erinaceus* {1}, *Phyllactinia guttata* {1}, *Physcia aipolia* {1}, *P. tenella* {4}, *P. stellaris* {1}, *Pirottaea* ?*imbricata* {1}, *Platystomum obtectum* {1}, *Pleurosticta acetabulum* {1}, *Porina aenea* {1}, *Proliferodiscus pulveraceus* {2}, *Propolis farinosa* {4/1}, *Pseudevernia furfuracea* {1}, *Pseudohelotium sordidulum* {2}, *Pseudolachnea hispidula* {1}, *Pyrenopeziza* spp. {3}, *P. caespiticia* {1}, *P. rubi* {2}, *Resinomyces griseus* {1}, *R. kirschsteinianus* {1}, *Rutstroemia punicae* {1}, *Sarea difformis* {3}, *S. resinae* {1}, *Sclerococcum* sp. {1}, *Sordariales* {1}, *Stictis* sp. {2}, *Taeniolella stilbospora* {1}, *Thyronectria coryli* {1}, *Unguiculariopsis* sp. {4}, *U. rehmii* {1}, *Usena* sp. {1}, *Valsa* ?*ambiens* {1}, *Velutarina rufoolivacea* {2}, *Vulpicida pinastri* {1}, *Xanthoria parietina* {5}. **Desiccation tolerance**: fully viable for at least 7 months, some ascospores still alive after 2 years. **Altitude**: 50–900 m a.s.l. (Scandinavia), 4–1795 m (central Europe), 880–1495 m (southern Europe), 695–1600 m (Asia), 1885–2680 m (western North America). **Geology**: Cambrian-Ordovician & Carboniferous siltstone & greywacke, Permian lime- & sandstone (Rotliegend), Buntsandstein, Muschelkalk, Keuper (marl & sandstone), Jurassic & Cretaceous clay-, marl-, silt-, sand- & limestone, flysch, Minette, Eocene flysch, Tertiary molasse, Quaternary loess & gravel; migmatite, granite, diorite, rhyolite, dacite, quartzite, gneiss, mica schist, biotite-amphibolite, serpentinite, gabbro, basalt. **Phenology**: throughout the year (long-lived).

Phenology of *O. aristata*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
12	17	12	18	21	19	16	31	11	11	18	6

Taxonomic remarks. *Orbilia aristata* is characterized by sperm-shaped ascospores composed of an ellipsoid-fusoid head and an abrupt, long and thin tail which is usually not inflated at the base, also in short to medium long glassy processes that may form small whitish teeth at the margin. For the very similar *O. subaristata*, *O. breviaristata*, *O. flagellispora*, *O. clavuliaristata*, and *O. fimbriata* see there. The North American *O. occulta* and *O. spermoides* and Australian *O. austroocculta* are sharply separated from all these species by much shorter though equally wide spore heads, the former two also by the presence of crystalloid SCBs. Confusion with the much more rare *O. pseudoaristata* (series *Albovinosae*, section *Aurantiorubrae*) is easily possible. This species sharply differs in truncate thin-walled ascus apices in the dead state, also in wider, more tear-shaped SBs.

Variation. *O. aristata* is somewhat variable in length and width of the ascospores, also in shape of spore heads, length and occasional basal inflation of spore tails, and in SB length.

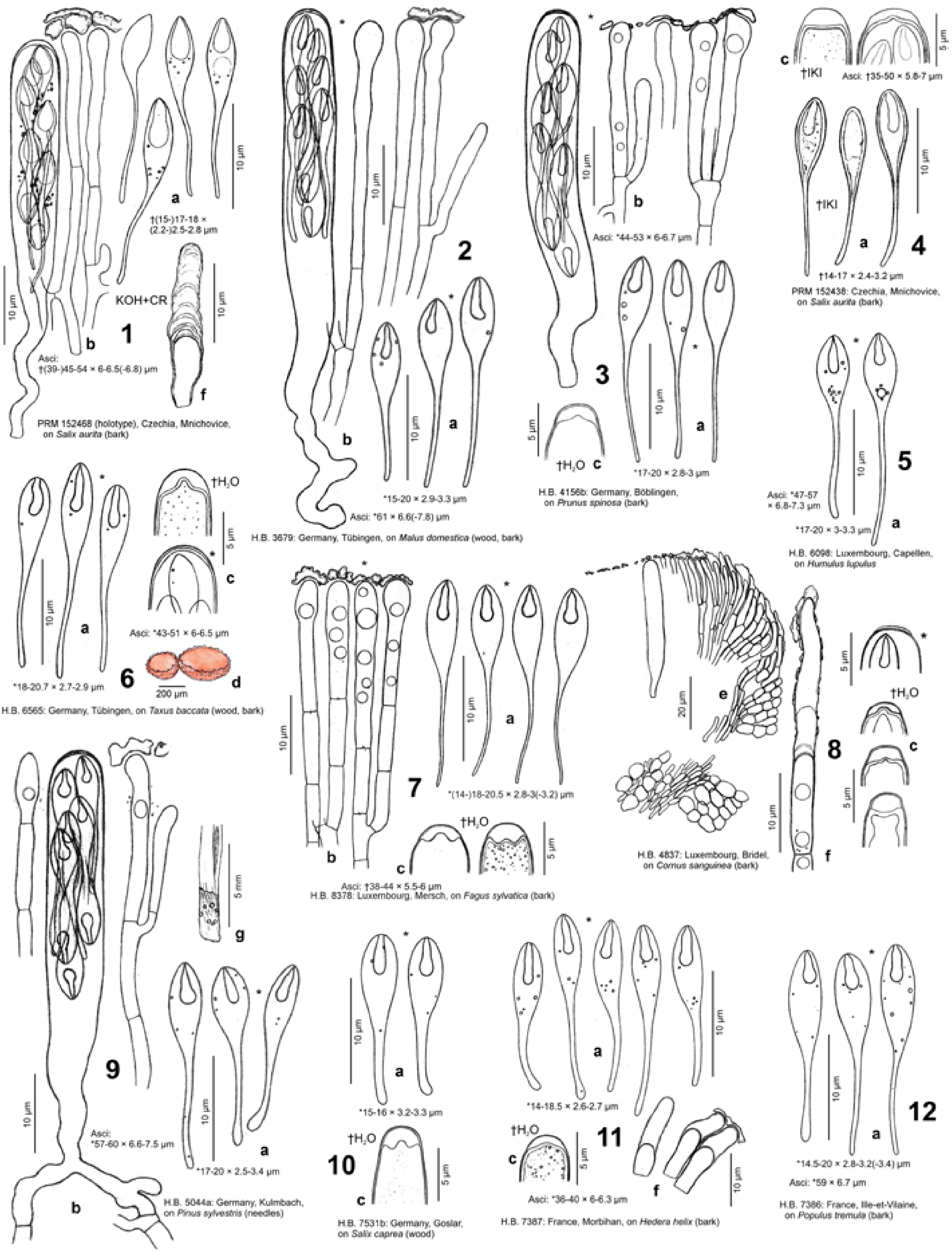


Plate 339. **1–9**: *Orbilia aristata*; **10–12**: *O.* cf. *aristata*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia with dentate margin (rehydrated); **e**. median section of ectal excipulum (margin and flanks); **f**. marginal cortical cells with glassy processes (**1f** in median section); **g**. base of *Pinus* leaves with apothecia.

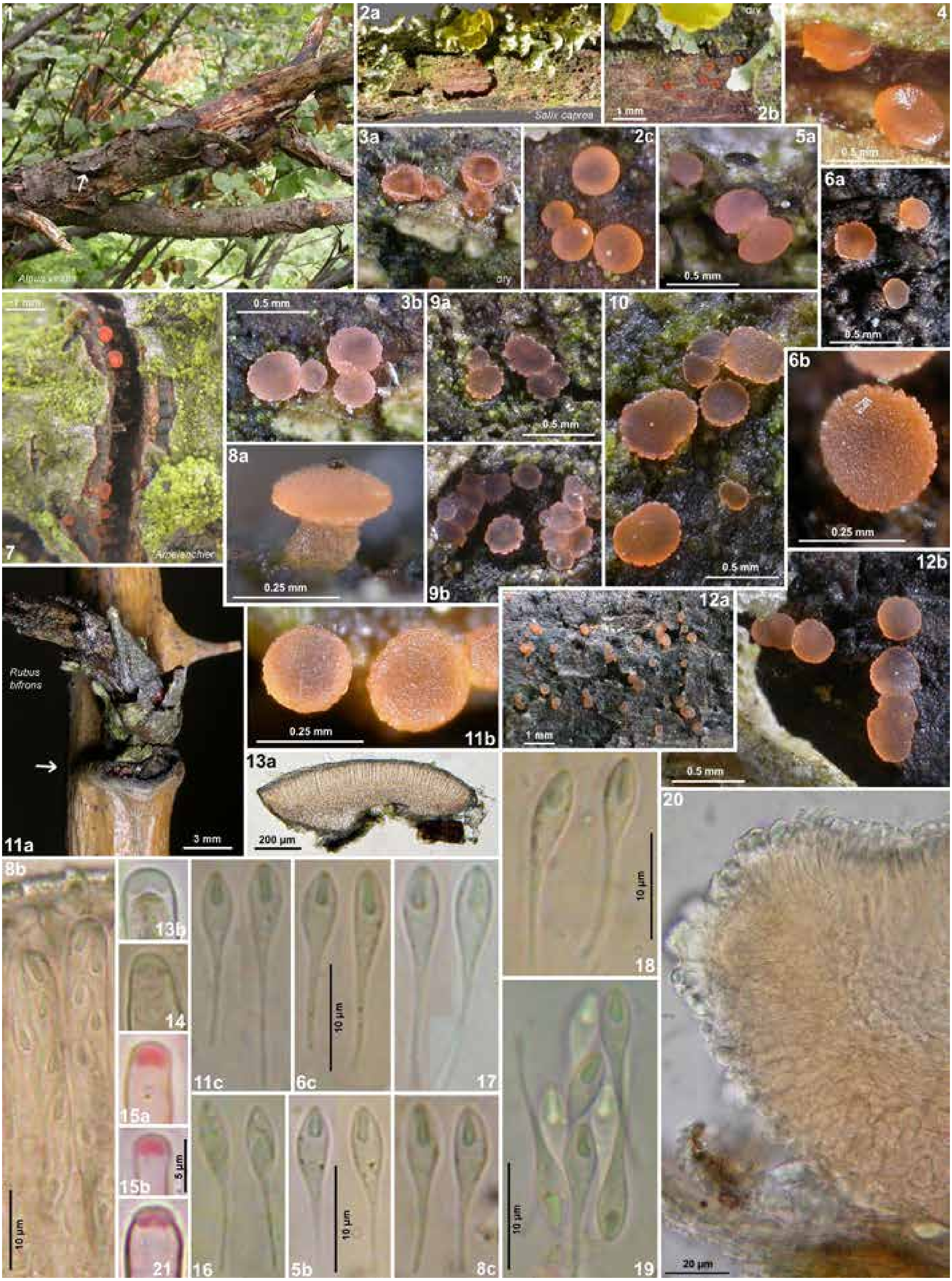


Plate 340. **1–21**: *Orbilia aristata*. – **1a**. subalpine alder bush (*Alnetum viridis*), dead branch of *Alnus alnobetula*; **2a**. dead corticated xeric branch of *Salix caprea* with *Xanthoria parietina* and *Physcia tenella*; **11a**. dead xeric stem of *Rubus bifrons*; **3b**, **4**, **5a**, **6a–b**, **7**, **8a**, **9a–b**, **10**, **11b**, **12a–b**. rehydrated apothecia; **2b**, **3a**. dry apothecia; **13a**. apothecium in median section; **20**. id., marginal ectal excipulum; **8b**. mature asci; **13b**, **14**, **15a–b**, **21**. ascus apices; **5b**, **6c**, **8c**, **11c**, **16–19**. ascospores. – Living state, except for **13b**, **14** (in H_2O), **15a–b**, **21** (in CR_{SDS}), **16** (in KOH), asci in **8b**. – **4**, **19**: phot. P. Perz; **21**: phot. M. Bemmann. —

Spore length varies from *13–17 to 18–23 µm, spore width from *2.5–2.8 to 3–3.5 µm, with exceptionally values of 26 µm in length or 3.8–4 µm in width. Variation in spore length is mainly due to a variable tail length, but also to a different length of the head. SB length varies from *3–3.5 to 3.5–4.5 µm. A specimen from Mongolia had extraordinarily long spore tails (11–15 µm, J.P. Priou pers. comm.), whereas the spores in a collection from Altay Republic (E.S. Popov pers. comm.) were with (7–)9–11 µm long tails quite typical (the other Mongolian sample had hardly any developed spores; all three samples were on *Salix*).

The tail bases are usually not thicker than their middle part, but in some collections a bulbous basal inflation was seen in a few spores. In *O. subaristata* and *O. flagellispora* this bulbous inflation is more frequently present, but due to an often great variability within each population, the taxonomic importance of the feature should not be overestimated.

A German collection on *Pinus* needles (Pl. 339: 9) seems to belong to *O. aristata*, although the spore tails had sometimes a bulbous base reminiscent of *O. subaristata*. However, Beyer (1998: 191, fig. 59) did not notice such inflation in the same specimen, and also in another collection on pine needles (I. Wagner, IVV: 16.II.2012) no distinctly inflated tail bases were seen. Probably this is only a matter of how many free spores were available for study. Inflated tail bases were rarely seen in a few spores of some other collections of *O. aristata*, e.g., on *Malus* (Poland, IVV: 9.VIII.2006), *Salix* (Luxembourg, 8.V.1997, unillustrated), and *Rubus* (Germany, 9.VIII.1999, unillustrated).

The length of the glassy processes varied rather strongly among the populations, but often also within them. Usually they did not exceed a length of 15–20 µm, but in a number of samples they attained 25, 30, 35, or even 40 µm. For instance, a length of 20–35 µm was noted on *Picea* from Poland (P.P. 20060625-4), and 5–25 µm on *Sorbus* from Lapland (H.B. 9406a). In a sample on the inner surface of bark of a standing trunk of *Fagus* from Luxembourg (Pl. 340: 3), the processes varied between 10–20 and 15–35 µm. A correlation to the substrate or geographical origin could so far not be seen within European records. Also a North American collection (on *Acer glabrum*, IVV: H.B. 5672a) had extraordinarily long glassy processes (up to 20–40 µm), but another (on *Corylus cornuta* IVV: H.B. 6030) only 2–8 µm. Both were from Colorado, and their consistently uninflated spore tails appear to forbid placement in *O. subaristata*. Rather short glassy processes (up to 5 or 10 µm) were noted in quite a lot of European collections, but also in specimens from central Asia, and intermediate cases were also frequent. This variation in length of glassy processes results in striking macroscopical differences in the apothecial margin (see Pl. 340). But even if some or all apothecia of a population had smooth margins, they always possessed at least very short processes.

Apothecial size varied among the populations between (0.1–)0.15–0.25 and 0.3–0.7(–1) mm, and colour from pale to bright and between rose and orange. Also the thickness of the apothecia differed between 0.1–0.12 and 0.15–0.2 mm, exceptionally 0.38 mm, especially depending on the occasional presence of a stalk which was characteristic of some collections.

In three collections (P.P. 20060809-3, P.P. 20070303, H.B. 9226a), large hyaline to pale yellowish LBs in the basal cells of the ectal excipulum were seen. This feature was not observed in any other collection of *O. aristata*, whenever the ectal excipulum was studied (a similar variation was noted in *O. flagellispora*).

Nomenclature and type studies. The first report of *O. aristata* (under the name *O. occulta*) appears to be that of Rehm (1891), who believed that his European collections fit exactly the North American type material of *O. occulta*. Also later authors have adopted the name *O. occulta* for European specimens with spores with ovoid-ellipsoid heads and long, thin tails. However, *O. occulta* differs in several points from *O. aristata* (see below) and is so far only known from the east of North America.

Velenovský (1934: 102, Pl. XI fig. 5) reported and figured under the name *O. occulta* [var. *occulta*] several Bohemian collections (on dry, sun-exposed branches of *Populus tremula*, *Frangula alnus*, *Crataegus*, *Carpinus*, Pl. 341: a, see also Fig. 154), with apothecia 0.3–0.6 mm diam., fire-red or rose, asci 25–30 × 5 µm, and spores up to 20 µm, with heads 6–10 µm and tails of same length. From these samples he separated in a note under this species in a few words a sample on bark of *Salix aurita* as a new variety *O. occulta* var. *aristata* (Pl. 341: b), based on smaller (0.2–0.3 mm), amber-coloured apothecia, much larger asci (50 × 8–10 µm, only shown in unpublished manuscript), and shorter spores (total length 12–15 µm, spore heads ~6–7 µm long according to sketch). The author compared both varieties with the South American *O. caudata*. Although Velenovský's diagnoses are very brief, his illustrations leave little doubt that he was dealing in both cases with *O. aristata* as circumscribed in the present study.

Reexamination of the holotype of ***O. occulta* var. *aristata*** confirms identity with our concept of this species. Contrary to Svrček's (1954) statement, the type specimen is not empty: it contains about 20 apothecia growing on bark (rehydrated ~0.13–0.25 mm diam., now pale cream). The abundant glassy processes measure 8–15 × 3–4 µm and form only very indistinct teeth at the margin. The asci concur in their length with the original data but are much narrower (Pl. 339: 1) which better meets the length/width ratio in Velenovskýs sketch. The material does not show any clear microscopic differences to Velenovský's description under the name *O. occulta* [var. *occulta*]. Two larger, whitish, *Orbilia*-like fructifications grew in association. They contained only narrowly cylindrical phialides with rod-shaped conidia ~4–5 × 1 µm, and certainly do not belong to the *Orbilia*.

Later, Velenovský (1947: 104) attributed his var. *aristata* species rank on the basis of two further collections, on bark of *Salix aurita* and *S. caprea*. Svrček named one of them (the *S. aurita* collection) 'holotypus speciei', but could not detect any apothecia also here. No material of the other sample seems to exist. Since Velenovský (1947) did not provide a description, but clearly referred to his monograph as '*Orbilia aristata* Vel. Mon. 102', this name has to be considered as a status novum for *O. occulta* var. *aristata*, not a new species, and the 'holotypus speciei' is only authentic material. On the ± detached bark of this material a single minute apothecium could be detected, with fully

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1. H.B. 8263c: Switzerland, Uri, *Alnus*; **2**. H.B. 9253a: Germany, Tübingen, on *Salix*; **3a–b**. H.B. 7628a: Luxembourg, Gréngewald, on *Fagus*; **4**. P.P. 20061203: Poland, Kłodzko, on *Sambucus*; **5a–b**. H.B. 9123: Germany, Villingen, on *Salix*; **6a–c**. H.B. 8486a: Sweden, Umeå, on *Betula* (on *Xenotypa aterrima*); **7**. 17.IV.2004: Germany, Weiskirchen, on *Amelanchier*; **8a–c**. H.B. 8692: Germany, Fürstenwalde, on *Quercus*; **9a–b**. H.B. 8378: Luxembourg, Mersch, on *Fagus*; **10**. H.B. 8456c: ibid., Grevenmacher, on *Cornus*; **11a–c**. H.B. 8445a: ibid., Remich, on *Rubus*; **12a–b**. H.B. 8543: ibid., Grevenmacher, on *Salix*; **13a–b**. H.B. 7627a: ibid., Walferdange, on *Salix*; **14**. H.B. 8255: Switzerland, Uri, on *Diatrype*; **15a–c**. H.B. 9226a: Germany, Tübingen, on a rope; **16**. H.B. 8359b: Luxembourg, Differdange, on *Cornus*; **17**. H.B. 8269b: Switzerland, Uri, on *Alnus*; **18**. H.B. 8179b: Germany, Tübingen, on *Fagus*; **19**. P.P. 20071028: Poland, Kłodzko, on *Salix*; **20**. H.B. 7891a: Mongolia, on *Salix*; **21**. 29.I.2012, Germany, Heidelberg, on *Syringa*.

mature asci and glassy processes of 15–25 × 2.5–3 µm which form agglutinated teeth at the margin (Pl. 339: 4). Also here numerous discoid yellowish fructifications of an imperfect fungus grew in association, with rod-shaped conidia 3.5–5 × 1 µm.

Because *O. aristata* turned out to be genetically heterogeneous (see below), though being rather invariable in the morphology of the teleomorph, a solution must be found which fixes the name. We here designate a sample from Germany (Stuttgart-Weilimdorf, on *Salix*, ex H.B. 6713, CBS 140834) as **epitype** of *O. aristata*, because it is on the type substrate and in the clade with the majority of available sequences.

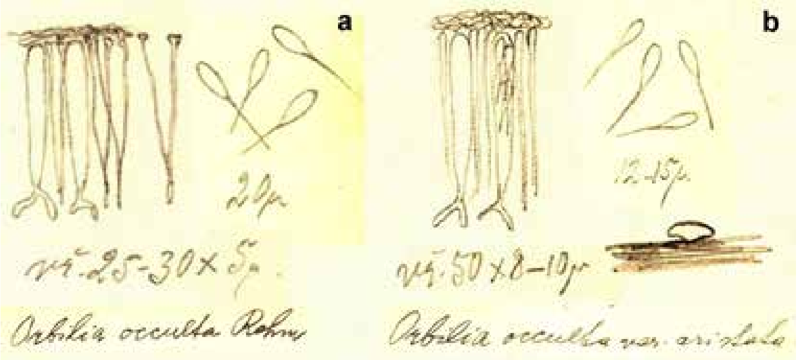


Plate 341. **a**. *Orbilia occulta* var. *occulta*, **b**. *O. occulta* var. *aristata* (holotype); both from Velenovský's unpublished manuscript (= *O. aristata*), with ascus and spore size.

In the holotype of ***Radotinea caudata*** (Czechia, Radotín, on corticated branch of *Cornus mas*, 31.III.1927, J. Velenovský, PRM 151698) no apothecia could be found, neither by Svrček (in sched.) nor in the present study, although it contains fairly many fragments of bark. The presence of a crustose lichen with black apothecia and a *Lophiostomataceae* indicate that the branch protruded in the air, which is also evident from the protologue (sun-exposed, dry, thermophilous slope). As already suspected by Svrček (1960, as *O. occulta*), the detailed original description appears to refer to *O. aristata* or perhaps *O. subaristata*, judging from the drawn 15–20 µm long ascospores and 15–35 µm long glassy processes (see Fig. 173). Velenovský depicted rather long glassy processes for *Radotinea caudata* reminiscent of *O. subaristata*, but this species seems improbable because he did not figure the least inflation at the tail bases, although his sketch on the manuscript plate shows 16 free spores. We also cannot exclude with certainty *O. pseudoaristata* (series *Albovinosae*), a species which differs from *O. aristata* mainly in truncate thin-walled ascus apices. Velenovský considered *Radotinea* to be intermediate between the hyaloscyphaceous genus *Olla* Velen. (because of solid hairs with a lumen only at the very base) and *Orbilia* (because of asci with a 'pedicello flexuoso, basi bilobo').

Since Velenovský attributed his variety *aristata* species rank not until 1947, *Radotinea caudata* has priority over *Orbilia aristata*. However, a new combination for *R. caudata* is blocked by *Orbilia caudata* Starbäck, therefore, the name *O. aristata* has to be chosen for the present taxon (Art. 53.1, Turland et al. 2018).

Not included collections. Two collections from northwestern France (Pl. 339: 11–12, on *Hedera* and *Populus*) somewhat resemble *O. clavuliaristata* in their more elongate spore heads. Spore heads similar to that on *Hedera* occurred also in other collections of *O. aristata* (e.g., Pl. 339: 6), but on *Hedera* the asci were extraordinarily short, and the apical domes thinner than usual (†0.8 → 0.5 µm). From *O. frullaniae* the *Hedera* specimen differs in wider spores and longer SBs, and in short glassy processes. In the collection on *Populus* the spore heads seem too large when compared with typical *O. aristata*. The associated conidia (Y-shaped on *Hedera*, Y- and ┼-shaped on *Populus*) do not differ from those of *O. aristata*. Also in this relationship appears to belong a very recent sample from Denmark on *Cryptomeria* (T. Læssøe, IVV: 24.I.2020).

In a sparse sample on *Salix* from northern Germany (Pl. 339: 10) only a single mature ascus was seen; it contained spores with rather thick spore tails, but the heads are too short to refer it to *O. clavuliformis*. A sample on *Acacia* from Réunion (Mascarene Islands, IVV: H.B. 9722e) includes a single, pale cream apothecium which was only studied in the dead state; it deviates from *O. aristata* in smaller, especially narrower spores (†11.5–15 × 2–2.2 µm). For *Radotinea caudata* from Czechia see above.

Anamorph. The anamorph of *O. aristata*, like that of the similar *O. subaristata* and *O. flagellispora*, is characterized by the occurrence of different conidial types: Y-shaped conidia with long arms and stipes similar to *Trinacrium subtile*, ┼-shaped descalsia-like conidia (3-dimensional), and 4- to more-armed dwayaangam-like conidia (probably also 3-dimensional).

One conidial and two ascospore isolates were available. In pure culture conidial production was stimulated by flooding with water. In one ascospore isolate (H.B. 6713: Stuttgart, on *Salix* bark) only tetraradiate (descalsia-like) conidia were seen, whereas in the two other isolates (G.M. 2014-06-21.1: Luxembourg, on *Rubus*, from ascospores; 20.V.2011: on *Fraxinus* bark, from conidia) only dwayaangam-like conidia were obtained. In the *Rubus* sample also a curucispora-like conidium was seen on the natural substrate besides many dwayaangam-like ones. This result, which is supported by deviating molecular data (see below), suggests that different species are involved which cannot be recognized by the teleomorph alone.

However, Ando (1992) reported in a Japanese isolate identified as *Trinacrium subtile* besides typical 2-armed conidia, which occurred in a frequency of more than 90%, five further conidial types, which are mostly comparable to those observed by us. He named them *Sigmoidea* (unbranched), *Lambdasporium* (2-armed), *Articulospora* (3-armed), and *Retiarius* or *Dwayaangam* (4-armed).

On the natural substrate we frequently observed trinacrium-, descalsia-, or dwayaangam-like conidia in association with apothecia, sometimes two together in a given population, e.g., *Trinacrium* & *Descalsia*, *Descalsia* & *Dwayaangam*, rarely *Trinacrium* & *Dwayaangam*, or all three together. Several transitional conidial forms were sometimes observed, similar as in *O. subaristata*. *O. aristata* sometimes grew in association with *O. subaristata* and *O. flagellispora* on the same branch, therefore, the observed mixture of conidial types might be due to the presence of different species. In two not included collections being intermediate to *O. clavuliformis* (Pl. 339: 11–12) we found similar trinacrium- and descalsia-like conidia: in H.B. 7386 predominantly descalsia-like, in H.B. 7387 solely trinacrium-like.

Phylogeny. Two different genotypes were observed within *O. aristata*. Sequences of genotype 1 were taken from an

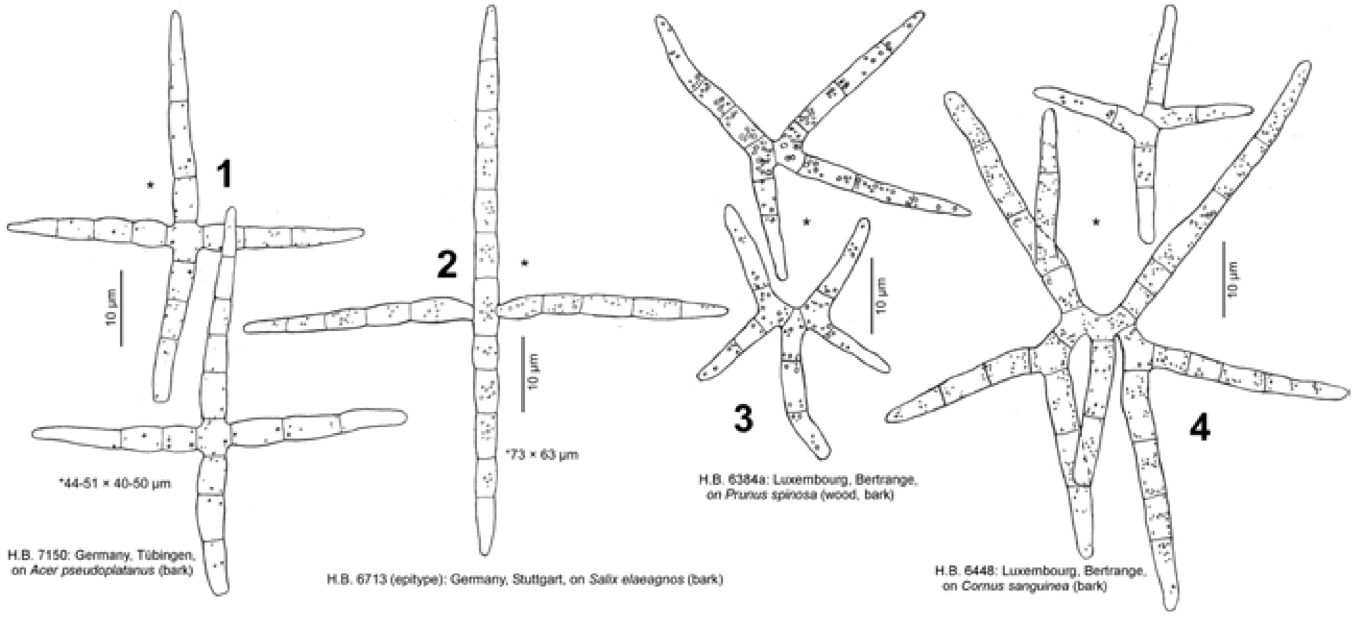


Plate 342. **1–4**: *Orbilia aristata*: conidia from culture (**2**) and substrate (**1**, **3–4**).

ascospore isolate of H.B. 6713 (Stuttgart-Weilimdorf, *Salix*, conidia descalsia-like, Pl. 342: 2) and from apothecia of three samples in which no conidia were observed: G.M. 2014-11-30.1 (Luxembourg, Roeser, *Rubus*, IVV), G.M. 2018-09-11.5 (France, Gap, *Fagus*, IVV) and G.M. 2014-12-30.1 (Luxembourg, Walferdange, *Fagus*, unillustrated).

Sequences of genotype 2 (conidia dwayaangam-like, Pl. 343: 5) derive from an ascospore isolate of G.M. 2014-06-21.1 (Luxembourg, Roeser, *Rubus*) and a conidial isolate of G.M. 2011-05-20.1 (Itzig, Luxembourg, *Fraxinus*). Sequences of type 1 comprise SSU+ITS+LSU, those of type 2 ITS+LSU or ITS, respectively. All are without S1506 intron (in the sample from Itzig the intron region is not covered).

In the ITS region the two strains with dwayaangam-like conidia (genotype 2) are identical, and likewise the strains with descalsia-like or without observed conidia (genotype 1) concur with 1 nt deviation in the ITS1 (A in Germany & France, G in Luxembourg). In the available parts of SSU (V8–V9) and LSU (D1–D2/D3) the strains of genotype 1 are identical. However, the two genotypes show a distance of 5 % in ITS (22–23 nt and 6 gaps) and 1.5 % in LSU D1–D2. This distance in the ITS/LSU exceeds that between *O. aristata* genotype 1 and *O. flagellispora* (3.5–3.8/0.2 %) or *O. subaristata* (3.5–3.8/0.8–1 %), while the distance between *O. aristata* genotype 2 and *O. flagellispora* or *O. subaristata* lies around 4.5–5/1.8–2.3 %. The two genotypes of *O. aristata* do not even form a clade of their own in our analyses of the ITS and/or LSU region (Phyls 9, 12, S12).

This preliminary result strongly suggests that two species are involved which might turn out to be characterized by different types of predominantly formed conidia. In the teleomorph no differences could be detected regarding ascospore and SB size. The length of the glassy processes varied within genotype 1 between 1–3 µm (*Salix*), and 18–35 µm (*Rubus* and *Fagus*), while no data were available for genotype 2.

A Chinese environmental strain (LN910274, almost entire ITS2) clustered unsupported with *O. aristata* s.str. and with a 7 % distance (Phyl. 12). Since the relationship of most of our collections and also the holotype of *O. aristata* remains unclear due to an uncertain or unknown connection to a conidial type, we feel unable at present to split *O. aristata* into two taxa.

Ecology. *O. aristata* occurs on ± rotten bark (rarely wood) of xeric branches and trunks of various gymno- or predominantly angiosperm trees and shrubs, rarely on coniferous leaves. The most favourite substrates were *Salix* {44}, *Cornus* {19}, *Fagus* {13}, *Rubus* {12}, *Prunus* {8}, *Malus* {6}, *Rosa* {5}, and *Sorbus* {5}, but also on different conifers {17}. Only a single record on *Quercus* and none on *Carpinus* came to our notice. Exceptional collections were on herbaceous substrates (*Humulus*, *Heracleum*). *O. aristata* has been reported in the literature under the name *O. occulta* on bark of *Malus* (Rehm 1891) and *Pyrus* (Kirschstein 1936), also on wood of *Populus*, *Frangula*, *Crataegus*, *Carpinus* (Velenovský 1934), *Prunus spinosa* (Svrček 1960), and *Salix* (Ellis & Ellis 1985). Especially Velenovský and Kirschstein emphasized the sun-exposed xeric habitat.

O. aristata is a very common species in cold-temperate humid areas of central Europe, where it occurs in moist or dry, ± thermophilous forests, especially at sun-exposed borders or in hedges, also in plantations and ruderal places. A few collections are from hemi- to oroboreal forests in Scandinavia, orotemperate (subalpine) alder bushes (*Alnetum viridis*) in the Alps, and mesotemperate atlantic lowland forests. Some other records are from orotemperate to orosubmediterranean humid forests in southern France and a mesosubmediterranean (semi)humid site in Montenegro. A few records indicate that the species also occurs in western North America and in central Asia: in the cold-temperate humid ponderosa pine and Douglas fir mixed forests of Southern Rocky Mountains and Colorado Plateau, in a continental, orotemperate subhumid, montane *Picea-Betula* mountain taiga in the Sayan mountains of Altay and a willow steppe in the altimontane (sub)humid (winter-dry) highland forests of central Mongolia. *O. aristata* was only exceptionally found in the summer-dry semihumid eumediterranean belt, where the very similar *O. subaristata* occurs.

The not included sample on bark of *Acacia* from Mascarene Islands east of Madagascar was from a warm-temperate subhumid (winter-dry) angiosperm woodland.

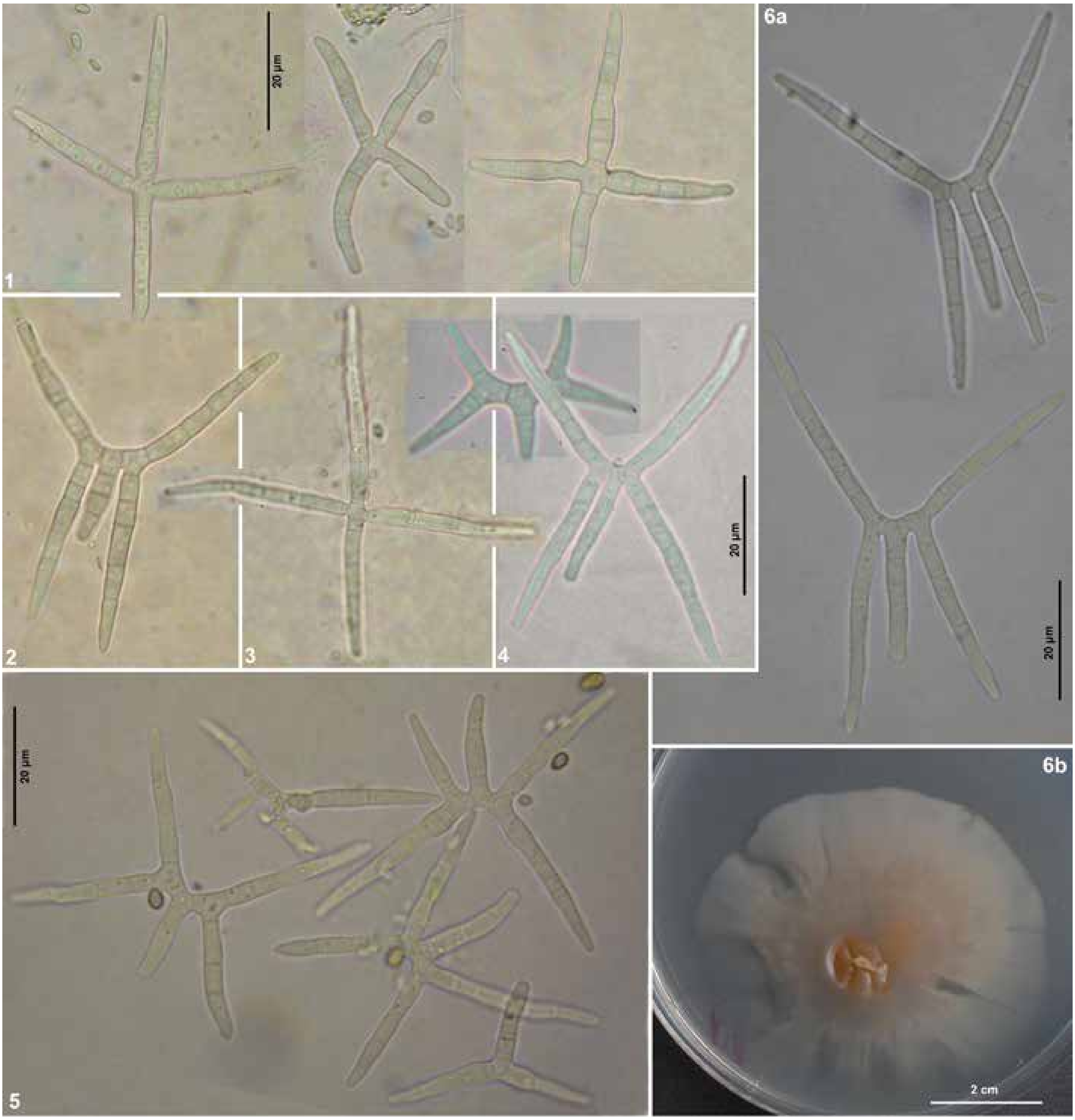


Plate 343. 1–4: *Orbilia aristata*; 5–6: *O.* cf. *aristata*. – Conidia (living state); 6b. pure culture on CMA. – 1. H.B. 8269b: Switzerland, Uri, on *Alnus*; 2. H.B. 8543: Luxembourg, Grevenmacher, on *Salix*; 3. H.B. 8915: Switzerland, Thun, on *Alnus*; 4. 7.V.2004: Luxembourg, Hesperange, on *Salix*; 5. G.M. 2011-05-20.1: ibid., Itzig, on *Fraxinus*; 6a–b. G.M. 2014-06-21.1: ibid., Bettembourg, on *Rubus*.

Specimens included. **NORWAY**: **Oslo**, 3.5 km NW of Oslo, Marienlyst, Blindern University, 88 m, branch of *Acer pseudoplatanus*, on bark, 13. VIII.2002, G. Marson (ø). — **SWEDEN**: **Västerbotten**, 12 km NW of Umeå, SW of Brännland, railway station, 50 m, branch of *Betula pendula*, on bark and *Xenotypa aterrima*, 6.V.2007, O.E. Eriksson (H.B. 8486a). – Vilhelmina, 6 km ESE of Saxnäs, Trappstegsforsen, 525 m, branches of *Sorbus aucuparia*, on wood & bark, 28.VII.2010, H.O. Baral (H.B. 9406a). — **FINLAND**: **North Karelia**, 42 km WNW of Joensuu, WNW of Outokumpu, Raivionmäki, 140 m, twig of *Syringa vulgaris*, on bark, 10.II.2011, M. Pennanen (ø, doc. vid.). – **Pirkanmaa**, 9.3 km SW of Tampere, 5 km SSE of Pirkkala, Keskinen, 130 m, branch of *Salix*, on bark, 1.IV.1994, U. Söderholm (TUR 56025, as *O. occulta*). — **POLAND**: **Łódź**, 8 km E of Sieradz, Stawiszcze, Grabowiec road, 165 m, branch of *Vitis vinifera*, on bark, 10.VI.2013, P. Perz (P.P. 20130610-7B, doc. vid.). – **Lower Silesia**, 8 km NW of Kłodzko, 1 km E of Swiecko, E of Huberek, 375 m, branch of *Pinus*, on bark, 3.IV.2006, P. Perz (ø, doc. vid.). - Kłodzko, Nałkowskiej ul. 12, 320 m, branch of *Vitis vinifera*, on bark, 20.VI.2006, P. Perz (P.P. 20060620-1, doc. vid.). – ?ibid., garden of Z. Perz, branch of *Pyrus communis*, on wood, 11.VIII.2006, P. Perz (P.P. 20060811-2, doc. vid.). – 22.5 km WSW of Kłodzko, 3.5 km SW of Duszniki Zdrój, 810 m, branch of *Abies alba*, on bark, 1.IX.2009, P. Perz (P.P. 20090901-1, doc. vid.). – 16 km W of Kłodzko, 1.5 km NW of Szczytna, Polna ulica, 480 m, branch of *Malus domestica*, on bark, 8.VIII.2006, P. Perz (P.P. 20060809-3, 20060808-6, doc. vid.). – 9 km S of Kłodzko, 2 km S of Żelazno, Bielica Mt., 430 m, branch of *Salix*, on bark, 3.X.2007, P. Perz (ø). – 7 km SSE of Bystrzyca Kłodzka, 2 km SW of Wilkanów, 435 m, branch of *Salix*, on bark, 6.XI.2006, P. Perz (P.P. 20061106-1a, doc. vid.). – 13 km SE of Bystrzyca Kłodzka, 11 km SW of Stronie Slaskie, WNW of Śnieżnick, 790 m, branch of *Salix*, on wood, 28.X.2007, P. Perz (ø, doc. vid.). – 14 km SE of Bystrzyca Kłodzka, 7.5 km NE of Miedzylesie, S of Nowa Wies, branch of *Salix*, on wood, 15.IV.2006, P. Perz (P.P. 20060415-1, doc. vid.). – 10 km SSE of Bystrzyca Kłodzka, 1.5 km E of Domaszków, Polna ulica, 445 m, board of *Picea abies*, on bark, 25.VI.2006, P. Perz (P.P. 20060625-4, anam. substr. Y). – 9 km SSW of Stronie Śląskie, NNE of Śnieżnik, 1125 m, branch of

Picea abies, on resin, 9.IX.2009, P. Perz (P.P. 20090909-2, doc. vid.). – unlocalized (P.P. 20070225, P.P. 20070303, P.P. 20090904-3, doc. vid.). — **CZECHIA**: **Central Bohemia**, 27 km SE of Praha, W of Mnichovice, 'in nostro horto' (E of railway), 370 m, branch of *Salix aurita*, on bark, 7.XII.1927, J. Velenovský (PRM 152468, **holotype**, H.B. 6179 ø). – 1 km WSW of Mnichovice, NW of Božkov, Božkov lake, 400 m, branch of *S. aurita*, on bark, XI.1940, J. Velenovský (PRM 152438, H.B. 6057 ø). — **SLOVAKIA**: **Žilina**, 5.5 km WNW of Hruštín, 3 km SW of Lomná, 824 m, branch of indet. angiosperm, on wood, 29.VII.2017, A. Polhorský (A.P. 18/43, anam. substr. ┼ & dw, doc. vid.). – 3.5 km SSE of Dolný Kubín, 3 km SW of Vyšný Kubín, 548 m, branch of *Aronia melanocarpa*, 24.XII.2017, A. Polhorský (A.P. 18/44, doc. vid.). – **Banskobystrický kraj**, 8.5 km S of Banská Štiavnica, 3 km NNW of Prenčov, 455 m, branch of *Pinus sylvestris*, on wood, 27.IV.2018, A. Polhorský (A.P. 18/48, doc. vid.). — **GERMANY**: **Schleswig-Holstein**, 17 km SE of Husum, 1.3 km NNW of Süderstapel, branch of *Salix*, on bark, 29.X.2017, T. Richter (H.B. 10135 ø). – **Brandenburg**, 8.5 km NW of Fürstenwalde, 3 km NE of Hangelsberg, Forst Hangelsberg, 55 m, branch of *Quercus rubra*, on bark, 24.XI.2007, R.K. Schumacher (R.S., H.B. 8692 ø). – **Sachsen-Anhalt**, ~3.5 km ENE of Eisleben ~SE of Oberrißdorf, Oberrißdorfer Tal, ~140 m, on bark of *Malus domestica*, III.1879, J. Kunze (M, herb. J. Kunze, F. selecti 282, as '*Calloria occulta* Rehm in herb.'). – **Thüringen**, 3 km W of Sonneberg, 1 km W of Bettelhecken, Mürschnitzer Sack, 370 m, branch of *Frangula alnus*, on bark, 24.I.2012, I. Wagner (ø, doc. vid.). – ibid., 1.5 km W of Bettelhecken, 355 m, 23.II.2012 (ø, doc. vid.). – ibid., 1.8 km W of Bettelhecken, 375 m, 24.I.2013, I. Wagner (ø, doc. vid.). – 0.8 km SSE of Bettelhecken, Stolze, 363 m, twig of *Salix*, on bark and old pyrenomycete, 25.I.2009, P. Püwert & I. Wagner (ø, doc. vid.). – 5 km SE of Sonneberg, 1.3 km ENE of Rottmar, 370 m, needles of *Pinus sylvestris*, on pyrenomycete, 16.II.2012, I. Wagner (ø, doc. vid.). – 7 km SSE of Sonneberg, 1.5 km E of Ölsdorf, branch of *Frangula alnus*, on bark, 373 m, 18.I.2013, I. Wagner (ø, doc. vid.). – 8 km SE of Sonneberg, NNE of Lindenberg, 360 m, branch of ?*Salix*, on bark, 5.XII.2013, I. Wagner (ø, anam. substr. Y, doc. vid.). – **Nordrhein-Westfalen**, 9.5 km E of Bergisch-Gladbach, 1.5 km NW of Schmitzhöhe, Kollenbachtal, branch of *Salix*, 23.VI.2013, B. Wergen (ø, doc. vid.). – **Saarland**, 18 km NE of Merzig, park in Weiskirchen, 360 m, branch of *Amelanchier* ?*lamarckii*, on bark, 17.IV.2004, H. Aeberhard (ø). – 2.5 km SE of Weiskirchen, 1.5 km NE of Thailen, Bildchen, 325 m, branch of *Cornus*, on bark, 17.IV.2004, G. Marson (ø). – **Baden-Württemberg**, 9 km E of Heidelberg, 1 km N of Neckargemünd, E of Kleingemünd, 129 m, twig of *Syringa vulgaris*, on wood, 29.I.2012, M. Bemmann (ø, doc. vid.). – 15 km SE of Heidelberg, 1.8 km ESE of Meckesheim, Schwarzbach, 152 m, branch of *Salix caprea*, on bark, 10.IV.2011, M. Bemmann (ø, doc. vid.). – **Schwarzwald**, 10 km ESE of Bühl, 7.5 km WSW of Forbach, Herrenwies, Schwarzenbach, 760 m, branch of *S.* (?) *cinerea*, on bark, 13.VI.2005, E. Weber (H.B. 7815b ø). – 3 km WNW of Villingen, 4.3 km ESE of Unterkirnach, SE of train station, Brigach, 732 m, twig of *S.* ?*fragilis*, on bark, 5.VIII.2009, H.O. Baral & B. Liu (H.B. 9123). – 3 km SE of Altensteig, 1.1 km E of Egenhausen, Egenhäuser Kapf, Heide NW of Freizeitheim, 620 m, trunk of *Rosa*, on wood, 10.X.2009, H.O. Baral (H.B. 9207a ø). – 5 km SSE of Calw, 1.3 km NE of Holzbronn Garweiden, 560 m, branch of *Prunus spinosa*, on bark, 25.III.1994, A. Gminder (H.B. 5037a). – 6 km NW of **Stuttgart**, S of Weilimdorf, SW of Köstlinschule, 335 m, branch of *S. eleagnos*, on bark, 23.VI.2000, H.O. Baral & E. Weber (ex H.B. 6713, M-0291760, **epitype** of *O aristata*, anam. cult. ┼, CBS 140834; sq.: KT596782, genotype 1). – 1.2 km NW of Weilimdorf, 1.5 km WSW of Korntal, train station, 305 m, stem of *Rubus fruticosus*, on bark, 18.VIII.2002, H.O. Baral (ø). – 5 km NNW of Stuttgart, 1 km N of Feuerbach, Lemberg, 320 m, branch of *Rosa*, on bark, 26.I.2003, H.O. Baral (ø). – 8 km S of Böblingen, 3.5 km S of Holzgerlingen, S of Schaichhof, Schleißenhau, 510 m, branch of *Prunus spinosa*, on bark, 2.VII.1990, H.O. Baral & G. Marson (H.B. 4156b ø). – 4 km N of **Tübingen**, 1 km WSW of Bebenhausen, Goldersbach, Schwefelbrünnele, 380 m, branch of *P. spinosa*, on bark, 27.II.1992, E. Weber & H.O. Baral (H.B. 4618a). – 3.3 km NNE of Tübingen, 2 km N of Lustnau, Goldersbach, Sonntagsstelle, 330 m, branch of *P. spinosa*, on bark, 17.III.1992, H.O. Baral (ø). – 2.5 km NW of Tübingen, Morgenstelle, University Campus, 455 m, branch of *Cornus alternifolia*, on bark, 22.VIII.2005, H.O. Baral (H.B. 7877b ø). – 1 km W of Tübingen, Rheinlandstraße, 330 m, branch of *Acer pseudoplatanus*, on bark, 16.VI.2002, H.O. Baral (H.B. 7150c, anam. substr. ┼, also Y & dw). – 0.3 km SE of Tübingen, Österberg, Wielandshöhe, 390 m, branch of *Cotinus coggygria*, on wood & bark, 13.VII.2002, H.O. Baral (ø). – Pfrondorf, 5 km NE of Tübingen, 1.5 km NW of Pfrondorf, Sophienpflege, 458 m, branch of *Cornus sanguinea*, on bark, 5.VII.1990, H.O. Baral (ø). – ibid., 450 m, trunk of *Fagus sylvatica*, on bark, 27.VIII.2005, H.O. Baral (ø). – 1.2 km NW of Pfrondorf, Lange Äcker, 457 m, trunk of *Malus domestica*, on bark, 20.I.2005, H.O. Baral (ø). – 1.5 km NNE of Pfrondorf, Brand, 460 m, trunk of *F. sylvatica*, on bark, 21.V.2006, H.O. Baral (H.B. 8179b). – 0.9 km N of Pfrondorf, 440 m, branch of *Rubus fruticosus*, on bark & wood, 3.III.2007, H.O. Baral (ø). – ibid., Brandklinge, 430 m, branch of *Taxus baccata*, on wood & bark, 13.II.2000, H.O. Baral (H.B. 6565). – NE of Pfrondorf, Gähklinge, 410 m, branch of *Prunus spinosa*, on bark, 30.XI.2011, H.O. Baral (ø). – ibid., 430 m, branch of *Ulmus minor*, on bark, 16.IX.2012, H.O. Baral (H.B. 9725 ø). – Pfrondorf, Blaihofstraße, 430 m, branch of (?)*Malus domestica*, on wood & bark, 15.II.1989, H.O. Baral (H.B. 3679). – ibid., 4. IV.1989 (ø). – ibid., branch of *Ligustrum vulgare*, on bark, 29.VI.1994, H.O. Baral (ø). – ibid., branch of *Robinia pseudoacacia*, on wood, 3.VIII.2002, H.O. Baral (ø). – ibid., branch of *Syringa vulgaris*, on wood, 14.II.2006, E. Weber (ø). – ibid., on a rope, 24.XI.2009, H.O. Baral (H.B. 9226a). – ibid., pole of *Picea abies*, on wood, 6.II.2010, H.O. Baral (H.B. 9245c ø). – E of Pfrondorf, Auchtert, 400 m, twig of *Cornus sanguinea*, on bark, 24.V.2003, H.O. Baral (ø). – ibid., Einsiedlerweg, 415 m, branch of *Sorbus aria*, on bark, 14.III.2007, H.O. Baral (H.B. 8444a ø, anam. substr. Y). – 1.2 km E of Pfrondorf, 420 m, branch of *Salix caprea*, on bark, 25.XI.2001, H.O. Baral (ø). – 1 km SE of Pfrondorf, Rauhalde, 380 m, branch of *Fraxinus excelsior*, on bark, 30.XI.2003, H.O. Baral (ø). – 0.6 km S of Pfrondorf, Obere Mähder, 390 m, twig of *Rubus fruticosus*, on bark, 9. VIII.1999, H.O. Baral (ø). – ibid., 30.VII.2002 (ø). – ibid., 17.XI.2002 (ø). – ibid., 9.II.2003 (ø). – branch of *S. caprea*, on bark, 14.X.2005, H.O. Baral & E. Weber (ø). – ibid., 22.III.2010 (H.B. 9253a ø). – ibid., stem of *Rumex*, 14.III.2009, H.O. Baral (H.B. 9018b ø). – ibid., 395 m, branch of *Malus domestica*, on wood, 4.X.1994, H.O. Baral & K. Siepe (ø). – ibid., 405 m, branch of *Rhus typhina*, on wood, 6.IV.2003, H.O. Baral (ø). – ibid., on bark, 19.II.2006, H.O. Baral (H.B. 8064 ø). – 1.2 km SSW of Pfrondorf, Beunke, 390 m, branch of *Prunus domestica*, on wood & bark, 2.XI.2003, H.O. Baral (ø). – 1.6 km SE of Pfrondorf, Neckar river, 320 m, branch of *Acer* (?)*pseudoplatanus*, on bark & wood, 19.I.2003, E. Weber & H.O. Baral (H.B. 7275a). – ibid., branch of *Cornus sanguinea*, on bark, 30.X.2005, H.O. Baral (ø). – **Schwäbische Alb**, 6 km E of Reutlingen, 2 km E of Eningen, NE of Drackenberg, 760 m, branch of *Crataegus*, on bark, 30.X.2001, H.O. Baral (ø). – 5.3 km ESE of Eningen, 1.8 km NW of Würtingen, Mutschlenbühl, 700 m, twig of *Rosa*, on bark, 30.X.2001, H.O. Baral (ø). – 11 km SE of Reutlingen, 1.6 km ENE of Holzelfingen, Hohrot, 785 m, branch of *Sorbus*, on wood, 28.VI.2002, G. Marson (H.B. 7159c). – **Bodensee**, 6.5 km NW of Überlingen, 0.5 km WNW of Sipplingen, S of Gasthof Niederhohenfels, 430 m, trunk of *Malus domestica*, on bark, 1.IX.2001, H.O. Baral (H.B. 7016c). – **Bayern**, **Unterfranken**, 29 km NW of Würzburg, 6 km NW of Karlstadt, E of Wiesenfeld, Rammersberg, 320 m, branch of *Pinus sylvestris*, on bark, 11.XI.1995, L.G. Krieglsteiner & H.O. Baral (L.K.). – 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz, 260 m, branch of *Salix caprea*, on bark, 11.XI.1995, H.O. Baral (H.B. 5383c). – **Oberfranken**, 9.3 km S of Kulmbach, W of Neuenreuth, 340 m, needles of *P. sylvestris*, 29.III.1994, W. Beyer (H.B. 5044a). – **Oberpfalz**, 13 km NNE of Amberg, 1.3 km NW of Hirschau, Frühmeßweg, 445 m, branches of *Rosa*, on bark and *Diaporthe*, 3.VIII.1994, H.O. Baral (H.B. 5122a). – **Oberbayern**, 8.5 km SE of München, 1 km ESE of Neuperlach, 543 m, branch of *Salix*, on bark, 20.II.2019, B. Fellmann (doc. vid.). – 8 km NW of Tutzing, 3.5 km S of Andechs, Goaslweide, 720 m, branch of *Prunus padus*, on bark, 7.VI.2007, P. Karasch (ø). – 5 km SE of Wasserburg, 4 km NW of Amerang, Murner Filz, 500 m, twig of *Salix*, on bark, 20.X.2018, I. Rößl (doc. vid.). – 3.7 km S of Siegsdorf, SE of Hörgering, Zinnkopf, 675 m, stem of *Rubus idaeus*, 22.VII.2017, I. Rößl (doc. vid.). – 5.5 km

Map 58. Known distribution of *O. aristata* in Europe.

N of Bad Reichenhall, S of Aufham, Reitweg, 505 m, trunk of *Fraxinus excelsior*, on bark, 13.VIII.2018, H.O. Baral (H.B. 10171b). — **SWITZERLAND**: **Solothurn**, 2 km E of Solothurn, NE of Zuchwil, 433 m, branch of *Quercus robur*, on bark, 14.V.2019, J. Gilgen, vid. S. Blaser (doc. vid.). – **Bern**, 11 km E of Thun, 3.8 km E of Schwanden, Sigriswilergrat, 1620 m, branch of *Alnus alnobetula*, on wood, 27.VIII.2008, H.O. Baral (H.B. 8915a ø). – **Uri**, Glarner Alpen, 9 km ESE of Altdorf, 1.2 km SW of Unterschächen, N of Sittlisalp, Obsaum, 1650 m, branch of *A. alnobetula*, on bark, 21.VIII.2006, H.O. Baral (H.B. 8269b, anam. substr. ┼). – Urner Alpen, 4 km NW of Andermatt, 2.5 km WSW of Göschenen, Steglaui, 1300 m, branches of *A. alnobetula*, on bark & wood, 20.VIII.2006, E. Weber & H.O. Baral (H.B. 8263c, anam. substr. Y). – ibid., 1250 m, branch of *A. alnobetula*, on old *Diatrype* ?*stigma*, 20.VIII.2006, H.O. Baral (H.B. 8255). — **LIECHTENSTEIN**, 7 km NNW of Vaduz, 1 km SW of Bendern, Bannriet, 460 m, branch of *Cornus sanguinea*, on bark, 5.VII.1997, H.O. Baral (ø). — **AUSTRIA**: **Niederösterreich**, Wienerwald, 17 km SSW of Wien, 2 km S of Mödling, Eichkogel, 310 m, branch of *Fraxinus excelsior*, on bark, 6.V.1992, W. Jaklitsch (WU 13301). – **Steiermark**, Koralpe, 17 km E of Wolfsberg, 1.7 km W of Gschrepl, NE of Glashütten, foot of Kumpfkogel, 1280 m, branch of *Salix*, on wood, 31.VII.2010, G. Friebes (ø, doc. vid.). – 16.5 km W of Deutschlandsberg, 2.2 km SSW of Weinebene, 1795 m, branch of *Sorbus aucuparia*, on bark, 2.VI.2018, G. Friebes (G.F. 20180137, doc. vid.). – 14 km NE of Graz, W of Rein, St. Ulrich, 540 m, trunk of *Abies alba*, on bark, 22.II.2014, G. Friebes (G.F. 20140031). – 35 km S of Graz, 3 km WNW of Großklein, N of Burgstall, 395 m, twig of *Acer campestre*, on bark, 9.II.2019, G. Friebes (doc. vid.). – **Kärnten**, 12 km SE of Klagenfurt, NNE of St. Margareten im Rosental, Stariwald, 582 m, branch of *Viburnum lantana*, on bark, 4.I.1995, W. Jaklitsch (H.B. 5217). – ibid., N of St. Margareten, 585 m, branch of indet. angiosperm, on bark, 24.II.1992, W. Jaklitsch (W.J., H.B. 5116). – ibid., NE of St. Margareten, 585 m, branch of *Cornus sanguinea*, on bark, 16.XI.1994, W. Jaklitsch (H.B. 5186). — **GREAT BRITAIN**, **South East England**, **West Sussex**, 1.5 km S of Crawley, Tilgate Park, 100 m, branches of *Salix* ?*caprea*, on bark, 18.I.2013, N. Aplin (N.A. 235). — **NETHERLANDS**: **Gelderland**, 6 km SW of Nijmegen, SW of Aldenhof, Staddijkpark, 8 m, branch of *Cornus sanguinea*, on bark, 9.IV.2011, S. Helleman (ø, doc. vid.). — **BELGIUM**: **Vlaanderen**, **Oost-Vlaanderen**, 3.5 km NNE of Hamme, N of Tielrode, Roomacker, 30 m, branch of indet. angiosperm, on wood, 2.V.2018, V. Declercq, vid. B. Declercq (doc. vid.). – **Wallonie**, **Luxembourg**, 4.5 km SE of Arlon, S of Clairefontaine, 333 m, stem of *Humulus lupulus*, 7.V.1998, B. Declercq (B.D.). – 8 km SE of Arlon, SE of Sterpenich, 325 m, branch of *Salix*, on bark, 23.IV.2001, H.O. Baral & G. Marson (ø). – 13 km S of Arlon, Athus, railway station, 270 m, branch of *S. caprea*, 27.VII.1999, G. Marson (ø, anam. substr. dw). — **LUXEMBOURG**: **L'Oesling**, **Wiltz**, 7 km W of Wiltz, Doncols, 465 m, branch of *S. alba* var. *vitellina* f. *tristis*, on bark, 4.V.2002, M.T. Tholl (ø). – **Diekirch**, Ardennes, 4.5 km SW of Diekirch, W of Ettelbruck, railway station, 197 m, branch of *Salix*, on wood & bark, 6.VII.2002, G. Marson (ø). – **Gutland**, **Diekirch**, 9.5 km NE of Mersch, 2 km NW of Medernach, Seitert, 330 m, branch of *Lonicera periclymenum*, on wood, 24.IV.1994, H.O. Baral & G. Marson (ø). – **Echternach**, 11.5 km WNW of Echternach, 2.2 km W of Beaufort, Elteschmuer, 400 m, branch of *Pinus*, on bark, 25.IV.2001, G. Marson (ø). – 4 km SW of Echternach, 1.5 km E of Scheidgen, N of Michelshaff, 320 m, stem of *Rubus fruticosus*, 27.I.2007, G. Marson (ø). – **Mersch**, 8 km NE of Mersch, E of Nommern, W of Këngerboesch, 403 m, branch of *Fagus sylvatica*, on bark and *Cryptocoryneum condensatum*, 23.IV.1994, H.O. Baral (ø). – 7 km SE of Mersch, 2.5 km NE of Lorentzweiler, Préventsboesch, 425 m, trunk of *F. sylvatica*, on bark, 26.XI.2006, G. Marson (H.B. 8378, anam. substr. Y). – 4 km S of Larochette, 1.4 km NNE of Koedange, E of Folkend, 350 m, branch of *Ilex aquifolium*, on wood, ~20.IV.1994, G. Marson (ø). – ibid., twig of *Ilex aquifolium*, on bark, 25.IV.1994, G. Marson (ø). – **Redange**, 10 km W of Mersch, W of Kapweiler, 260 m, branch of *Salix cinerea*, on bark, 24.VII.1993, G. Marson (G.M. 5004, G.V.). – **Capellen**, 6.7 km ESE of Arlon, 1.3 km NW of Steinfort, Aechels, 330 m, stem of *Humulus lupulus*, 5.V.1998, B. Declercq (H.B. 6098 ø). – 4 km WNW of Capellen, 2 km E of Steinfort, Treisch, 325 m, branch of *Salix*, on bark, 8.V.1997, G. Marson (ø). – 4.5 km NW of Capellen, 1 km N of Koerich, Haereboesch, 310 m, branch of *S. caprea*, on bark, 8.V.1998, G. Marson (H.B. 6121a). – **Luxembourg**, 9 km NE of Luxembourg, W of Rameldange, Rammeldangerhéicht, 400 m, trunk of *Fagus sylvatica*, on bark, 30.VIII.2005, G. Marson (ø). – 5.5 km NNW of Luxembourg, 1.5 km E of Bridel, Plakigebierg, 280 m, branch of *Cornus sanguinea*, on bark, 11.II.1993, G. Marson (H.B. 4837, G.M. 4945). – 6 km NNE of Luxembourg, 2.3 km E of Walferdange, Croix de la Femme Morte, 410 m, trunks of *F. sylvatica*, on bark, 20.XI.2004, G. Marson (H.B. 7620c). – ibid., 25.XI.2004 (H.B. 7627a). – ibid., 30.XII.2014 (G.M. 2014-12-30.1; sq.: MK473396, genotype 1). – 7 km NE of Luxembourg, 1.5 km WSW of Senningerberg, Kuelebierg, 395 m, trunk of *F. sylvatica*, on bark, 27.XI.2004, G. Marson (H.B. 7628a). – ibid., 3.XII.2004 (ø). – 2.7 km ENE of Luxembourg, Cents, 340 m, branch of *Amelanchier lamarckii*, 8.VII.2003, P. Thill (ø, anam. substr. ┼). – 11 km ESE of Luxembourg, 2 km E of Oetrange, Draf, 268 m, branch of *Salix*, 8.IX.1998, G. Marson (ø). – 7 km W of Luxembourg, 1 km NW of Bertrange, Brill, 300 m, branch of *Prunus spinosa*, on bark & wood, 23.V.1999, G. Marson (G.M. 1999-05-23.1, H.B. 6384, anam. substr. ┼ & dw). – branches of *Cornus sanguinea*, on bark, 13.VII.1999, G. Marson (H.B. 6448, anam. substr. ┼ & dw). – 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, branch of *Salix*, on bark, 10.II.2001, G. Marson (ø). – ibid., on *S. caprea*, 26.II.2001 (ø, anam. substr. dw). – 3.5 km S of Luxembourg, S of Howald, Drosbach, 288 m, branch of *Cornus sanguinea*, 3.XII.2011, G. Marson (ø). – 5 km SE of Luxembourg, 1.5 km E of Itzig, Reimeschbaach, 300 m, branch of *Fraxinus excelsior*, on bark, 20.V.2011, G. Marson (G.M. 2011-05-20.1 ø, dw, associated with immature apothecia, conid. isol.; sq.: KT380061, genotype 2). – 7 km SE of Luxembourg, 2 km ESE of Alzingen, Héid, 300 m, branches of *Salix*, on bark, 10.IX.1998, G. Marson (H.B. 6254, anam. substr. dw). – 5 km S of Luxembourg, 1.5 km W of Hesperange, Biersak/Géisselbierg, 290 m, branch of *S. caprea*, on bark & wood, 25.XI.2002, G. Marson (ø). – ibid., 7.V.2004 (ø, anam. substr. dw). – 2 km NNE of Kockelscheier, Kéisbierg, 320 m, branches of *S.* (?)*aurita* × *caprea*, on bark, 16.IX.1994, G. Marson (H.B. 5225a). – 0.7 km N of Kockelscheier, Weier, 300 m, on bark of *Ulmus*, 27.V.1999, G. Marson (ø, anam. substr. dw). – 1.8 km SW of Hesperange, Fennerholz, 292 m, stem of *Rubus fruticosus*, 31.I.2003, G. Marson (ø). – **Esch-sur-Alzette**, 3.7 km ENE of Bettembourg, 1.2 km SSE of Roeser, Herchesfeld, 290 m, stems of *R. fruticosus* agg., 21.VI.2014, G. Marson (G.M. 2014-06-21.1, anam. substr. dw, rarely ┼; sq.: KT222395, genotype 2). – ibid., 1 km SSE of Roeser, stems of *R. ?idaeus*, 30.XI.2014, G. Marson (G.M. 2014-11-30.1, non vid.; sq.: MK473397, genotype 1). – 8 km W of Esch-sur-Alzette, 1.5 km S of Obercorn, Ronnebierg, 410 m, branches of *Cornus sanguinea*, on bark, 25.III.2001, G. Marson (H.B. 6984b). – 7 km S of Luxembourg, 1.5 km NW of Berchem, Angelsbierg, 295 m, trunk of *Thuja plicata*, on bark, 19.III.2005, G. Marson (ø). – 0.5 km S of Differdange, Rollesbierg, 358 m, branch of *C. sanguinea*, on bark, 1.VIII.2006, G. Marson (H.B. 8359b). – 0.5 km NW of Belvaux, Galgebierg, 400 m, trunk of *Fagus sylvatica*, on bark, 24.V.2005, G. Marson (ø). – 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, branch of *Salix caprea*, on bark, 19.IV.1994, G. Marson (ø). – ibid., branch of *C. sanguinea*, on bark, 5.VI.1999, G. Marson (H.B. 6453). – ibid., 4.III.2003 (ø). – ibid., 8.VIII.2009 (H.B. 9163c ø). – 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, branch of *Cornus*, on bark, 27.IV.1993, G. Marson (H.B. 4867a, G.M. 4974). – **Grevenmacher**, 13.5 km NE of Luxembourg, 1.7 km WNW of Junglinster, Bierger 350 m, trunk of *F. sylvatica*, on bark, 21.VIII.2005, G. Marson (ø). – 5.5 km NE of Grevenmacher, Wasserbillig, railway station, 230 m, branch of *S. caprea*, on bark, 23.V.2007, G. Marson (H.B. 8543, anam. substr. Y & dw). – 0.8 km N of Wasserbillig, Sauer River, 138 m, branch of *C. sanguinea*, on bark, 15.VII.2006, G. Marson (ø). – 3 km NW of Wasserbillig, Neieberg, 195 m, branch of *C. sanguinea*, on bark, 17.III.2007, G. Marson (H.B. 8456c). – **Remich**, 8.5 km S of Remich, SW of Schengen, Stréimchen, 225 m, stem of *Rubus* (?)*bifrons*, on bark & wood, 11.II.2007, G. Marson (H.B. 8445a ø). — **FRANCE**: **Bretagne**, **Morbihan**, 0.5 km SSE of La Gacilly, ESE of La Grée St.-Jean, Rue de l'Aff, 9 m, branch of *Fraxinus excelsior*, on bark, 8.V.2001, J.P. Priou (J.P.P. 21079 ø, H.B. 6960). – **Lorraine**, **Vosges**, 10 km NW of Gérardmer, 2.3 km SW of Granges-sur-Volonge, NW of Faing Musqué, 730 m, branch of *Cytisus scoparius*, on wood, 7.IX.1996, G. Marson (ø). – 4 km NW of Gérardmer, SE of le Grand Liézey, Tourbière de Bassottes, 800 m, *Salix*, 8.VI.1998, J. Deny (ø, non vid.). – **Auvergne**, **Cantal**, 4.5 km SSE of Le Falgoux, S of Le Pont des Eaux, 1140 m, twig of *Lonicera xylosteum*, on wood, 29.IX.2016, J.P. Priou (J.P.P. 16242, doc. vid.). – **Rhône-Alpes**, **Drôme**, 55 km S of Grenoble, 5 km NW of Lus-la-Croix-Haute, Col de Grimone, 1330 m, branches of *Abies alba*, on bark, wood & resin, 3.VIII.1999, G. Marson (H.B. 6992b, anam. substr. ┼). – **Loire**, 16 km WNW of Boën, 1.5 km S of St.-Jean-la-Vêtre, Ventuel, 880 m, twig of *Picea abies*, on bark, 6.V.2010, P. Perz (ø). – 19 km WSW of Roanne, 4 km WSW of Arcon, le Gué de la Chaux, 1060 m, branch of *Salix*, on bark, 7.V.2010, H.O. Baral (H.B. 9299a ø). – **Savoie**, 19 km ENE of Albertville, 4.5 km ESE of Beaufort, N of Lac de Roseland, ~1320 m, on *Sorbus aucuparia*, 4.VIII.1995, G. Marson (ø). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 18 km WNW of Gap, 0.7 km W of La Montagne, SW of Pic de Bure, 1018 m, branch of *Fagus sylvatica*, on bark, 11.IX.2018, G. Marson (G.M. 2018-09-11.5; sq.: MK473398, genotype 1). – **Alpes-de-Haute-Provence**, 22 km NE of Digne-les-Bains, 1.6 km NE of Le Labouret, Col du Labouret, 1250 m, branch of *Picea abies*, on resinous bark, 14.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9136e ø). – 12 km SE of Gap, 3.5 km E of St.-Étienne-de-Laus, Mt. Colombis, 1455 m, branch of *Pinus sylvestris*, on resin, 14.VIII.2001, G. Marson (ø). – 2.8 km SW of Seyne, NE of Col du Fanget, 1385 m, branch of *Picea abies*, on resin, 24.VIII.1996, G. Marson (ø). – 9.7 km ESE of St.-André-les-Alpes, 3.2 km WSW of Annot, Colle Basse, 1475 m, branch of *Laburnum alpinum*, on bark, 17.VIII.2001, G. Marson (ø). – **Var**, 10 km ENE of Colmars-les-Alpes, 6,7 km S of Col de la Cayolle, 1455 m, branch of *Salix*, on bark, 15.VIII.2001, G. Marson (H.B. 7026b ø, anam. substr. Y). – **Vaucluse**, 9.5 km NE of Bedoin, 1.5 km NW of Mt. Ventoux summit, Mt. Serein, 1385 m, branch of *Pinus sylvestris*, on wood, 13.VIII.2009, G. Marson & H.O. Baral (H.B. 9173c ø). – **Languedoc-Roussillon**, **Pyrénées-Orientales**, 3 km SSE of Prats-de-Mollo, Col de la Seille, 1197 m, branch of *Rosa*, on bark, 28.IX.1999, H.O. Baral (ø). — **ITALY**: **Trentino-Alto Adige**, **Trento**, ~12 km NE of Trento, Baselga di Pine, ~990 m, twigs of *Salix*, on bark, 4.X.2002, A. Verbeeken (ø). — **SERBIA**: **Vojvodina**, Fruška Gora, 12 km SSE of Novi Sad, 6.5 km NNW of Irig, Iriški venac, N of TV tower, 511 m, branch of *Salix alba*, on bark, 26.VI.2019, D. Savić (FG-1096, doc. vid.). – 6 km NNW of Irig, WSW of WWII memorial, 452 m, branch of *Tilia tomentosa*, on bark, 3.VII.2019, D. Savić (FG-1099, doc. vid.). – ibid., W of WWII memorial, 430 m, branch of *Larix decidua*, on bark, 18.IX.2019, D. Savić (doc. vid.). – 13 km SSW of Novi Sad, E of Brankovac, stem of *Rubus* (?)*silesiacus*, 455 m, 28.VIII.2019, D. Savić (doc. vid.). — **MONTENEGRO**: 15 km NNW of Podgorica, 1.9 km NE of Donje Selo, Glizica, 210 m, twig of *Punica granatum*, on bark, 8.V.2016, B. Perić & D. Raspopović (B.P. Dgf/C7D-08-05-16a, doc. vid.). — **RUSSIA (East)**: **Altay**, **Turochak**, 116 km E of Gorno-Altaysk, 12.7 km N of Yaylyu, Bijka, 695 m, branch of *Salix caprea*, on bark, 17.VIII.2008, E.S. Popov (ø, doc. vid.). — **MONGOLIA**: **Töv**, 87 km NW of Ulaanbaatar, 14.5 km ESE of Jargalant, Dugana Park, 1240 m, branch of *Salix*, on wood, 22.VI.2011, J.P. Priou (J.P.P. 11084 ø, doc. vid.). – **Ulaanbaatar**, 25 km SE of Ulaanbaatar, 8 km W of Nalayh, Bogd Khan Uul, 1600 m, branch of *S. rhamnifolia*, on bark & wood, 1.VIII.2005, P. Karasch (P.K. 01082005-1, H.B. 7891a, anam. substr. dw). — **USA**: **Colorado**, Southern Rocky Mountains, 25 km SW of Denver, 11.5 km NE of Conifer, Tiny Town, 2100 m, branch of *Corylus cornuta*, on wood, 14.VI.1996, G. Marson (H.B. 6030, anam. substr. Y & ┼). – ~26 km NNW of Boulder, ~6 km WNW of Lyons, ~1885 m, branch of *Acer glabrum*, on bark, 13.VI.1996, G. Marson (H.B. 5672a, anam. substr. ┼). – **Arizona**, Grand Canyon, 3 km N of Kaibab Lodge, 2680 m, branch of *Picea*, on bark, 17.V.1995, G. Marson (ø).

Not included. **DENMARK**: **Sjælland**, 9.5 km SSE of Sorø, 1.2 km SSW of Næsby, Næsbyholm Storskov, twig of *Cryptomeria japonica*, on bark, 24.I.2020, T. Læssøe (doc. vid., anam. substr. ┼). – **GERMANY**: **Niedersachsen**, Harz, 5.5 km WSW of Goslar, southwest-end of Granestausee, 330 m, branch of *Salix caprea*, on wood, 2.VI.2004, H.O. Baral (H.B. 7531b ø, anam. substr. ┼). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 12 km E of La Gacilly, 1 km W of St.-Just, Moulin de Cojoux, 67 m, branch of *Populus tremula*, on bark, 9.VI.2003, H.O. Baral (H.B. 7386, anam. substr. ┼, also Y). – 0.5 km E of La Gacilly, forest SE of Ville Neuve, 35 m, branch of *Hedera helix*, on bark, 10.VI.2003, H.O. Baral (H.B. 7387, anam. substr. Y). — **CZECHIA**: **Central Bohemia**, ~10 km SW of Praha, Radotín, ~300 m, branch of *Cornus mas*, on bark, 31.III.1927, J. Velenovský (PRM 151698, **holotype** of *Radotinea caudata*, without apothecia). — **MASCARENE ISLANDS**: **Réunion**, 15.5 km E of St.-Gilles, Route du Maïdo, 2040 m, branch of *Acacia heterophylla*, on bark, 22.IX.2011, R. Reuter (H.B. 9722e ø).

Orbilia subaristata Baral, G. Marson & Matočec, **sp. nov.**, MB 813611 — Pls 344–347, Map 59

Etymology: named according to the close similarity with *O. aristata*.

Typification: Luxembourg, Esch-sur-Alzette, Kayl, twigs and branches of *Cornus sanguinea*, 17.VII.2001, G. Marson (ex H.B. 7005a, M-0276591, holotype).

Latin diagnosis: *Similis* Orbiliae aristatae *sed excipulum marginale processis vitreis longioribus*, *dentes albidos exiguos formantibus praeditum*, *ascosporae cauda paulo longiore*, *basi saepe inflata et curvata*, *asci paulo longiores. Habitat ad corticem putridum*, *raro lignum*, *ramulorum et ramorum siccorum fruticum vel arborum angiospermarum, raro coniferarum, in zona thermo-ad submediterranea semihumida, etiam (oro)temperata humida Europae meridionalis et occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.9(–1.4) mm diam., (0.11–)0.16–0.25(–0.38) mm high (receptacle 0.12–0.17 mm), light to bright orange(-rose) or orange(-ochraceous), round, very scattered to gregarious; disc flat, rarely slightly convex with age, margin 0–60 µm protruding (incl. teeth), usually with prominent whitish teeth, rarely smooth; broadly sessile or with distinct stipe 0.1–0.2 × 0.15–0.4 mm, superficial; dry deep orange-red. **Asci** *(45–)50–75(–94) × (6–)6.3–7.5(–8.3) µm {15}, †45–70 × 5.5–6.5 µm {2}, 8-spored, spores 2(–4)-seriate, (0–)1–3(–4) lower spores inversely oriented {22} (not mixed), pars sporifera *26–40 µm long; **apex** (†) hemispherical, dome †1.2–2.3 → 0.8–1.5 µm thick {8}, with apical chamber; **base** with short to medium long, ± thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *((13.5–))(16–)18.5–24.5(–27) × (2.5–)3–3.5(–3.8) µm {26}, †(15.5–)17–24(–25)((–29)) × 2.6–3.4(–3.6) µm {12}, sperm-shaped: with ellipsoid-fusoid (to fusiform) head and sharply differentiated filiform tail, head *7–10 µm long, apex obtuse to acute, tail *(10–)11–15(–16.5) × 0.3–0.6(–0.8) µm, base of tail in the majority of spores slightly to ± strongly inflated (bulbous), in some collections not or only slightly so, *(0.4–)0.7–1.3(–1.8) µm thick {13}, †0.5–1.2 µm {4}, head in profile view sometimes somewhat inequilateral, tail straight or slightly to medium curved (often only at base); **SBs** *(3–)3.5–4.2(–4.7) × (1–)1.1–1.3(–1.4) µm {12}, rod-shaped, subulate, pyriform to ampulliform, apically narrowed to a small or wide point. **Paraphyses** apically uninflated to medium (rarely strongly) clavate-capitate (rarely spathulate), sometimes flexuous, terminal cells *8–20(–24) × 2–4(–5.5) µm {5}, lower cells *9–13.5(–16) × 1.7–2.5 µm {3}; rarely or infrequently branched near apex, hymenium light orange. **Medullary excipulum** pale rose, 30–80(–100) µm thick, of medium dense textura intricata with many inflated cells, or t. globulosa, very indistinctly to rather sharply delimited. **Ectal excipulum** pale to light rose-orange, of (†) slightly gelatinized, vertically oriented t. angularis(-prismatica) from base to mid flanks, 30–150 µm thick near base, cells *8–20 × 6–12 µm {3}, common walls †0.5–1.3 µm thick; 20–30 µm thick at flanks, cells *4–9 × 3.5–6 µm, near margin 20–30 µm, of t. prismatica-porrecta oriented at a 45–90° angle to the surface, outer layer of narrower hyphae oriented at 20–30°, marginal cortical cells *(4–)6–11(–16) × 2–4 µm {4} (12–18 µm long at mid flanks), **glassy processes** present {47}, (8–)15–50(–80) × 2–3.5(–3.8) µm {14}, refractive, faintly stratified, coherent to form small to mostly large teeth (10–)20–60(–80) × (10–)20–60 µm. **Anchoring hyphae** sparse to abundant, *2–3 µm wide, walls 0.2(–0.3) ((–0.5)) µm thick {3}, forming an up to 50 µm thick dense t. intricata at base. **SCBs** globose, in paraphyses 1–2.5 µm diam., in excipular cells 1–3 µm diam. **Exudate** over paraphyses 1.5–4 µm thick, cloddy, loosely attached, hyaline to scarcely yellowish; over margin and flanks absent. — **ANAMORPH**: trinacrium- {1/4} (Y), descalsia- {1/12} (┼), and dwayaangam-like {-/4} (dw) (from ascospore isolate {1}/ natural substrate {12}). **Conidiophores** not seen. **Conidia** variable in shape: 2-armed (Y-shaped, trinacrium-like): total size *23–70 × 23–87 µm, stipe *10–45 × 2.8–3 µm, 1–7-septate, arms *15–64 × 2–3.5 µm, 3–9-septate {2}; 3-armed (┼-shaped, descalsia-like, tetraradiate in 3 dimensions when floating): total size */†52–70 × 50–85 µm, stipe */†17–25 × 2.7–3.5 µm, 2–3-septate, arms */†22–41 × 2.7–3.5 µm, 3–6-septate {5}; 4(–5)-armed (dwayaangam-like): total size */†27–95 × 34–115 µm, stipe */†15–30 × 2–3.5 µm, 2–4-septate, arms */†7–60 × 2–2.7 µm, 1–6-septate, 4–5-armed {3}; very rarely unbranched.

Habitat: collected 0.1–3 m above the ground, corticated to partially decorticated, 3–27(–70) mm thick twigs and branches of *Acer campestre* {1}, *Aeonium arboreum* {1}, *Arbutus unedo* {1}, *Carpinus* sp. {1}, *C. betulus* {1}, *Crataegus* sp. {1}, *C. monogyna* {2}, *Ceratonia siliqua* {1}, *Cercis siliquastrum* {5}, *Cistus* sp. {1}, *Cornus sanguinea* {6/1}, *Crataegus monogyna* {1}, *Echium leucophaeum* {1}, *Fraxinus* sp. {2}, *Juniperus communis* {1}, *Olea europaea* {2}, *Pistacia lentiscus* {1}, *Pinus brutia* {3}, *P. halepensis* {1}, *Punica granatum* {2}, *Pyrus spinosa* {2}, *Quercus* sp. {1}, *Q. coccifera* {1}, *Q. ilex* {2}, *Q. rotundifolia* {1}, *Q. pyrenaica* {1}, *Rhamnus alaternus* {1}, *Rosa* sp. {7}, *R. ?canina* {1}, *Rubus fruticosus* {1}, *Salix* sp. {2}, *S. caprea* {1}, *Spartium junceum* {1}, *Vitis vinifera* {1}, on 0.1–0.5 mm deep (slightly or) medium to strongly decayed bark {48} (bast, rarely periderm), rarely wood {10} or resin {1}, sometimes close to or on old pyrenomycetes, ± greyed, covered by sparse to abundant green algae. **Associated**: *Baggea* sp. {2}, *B. pachyascus* {1}, *Candelariella lutella* {1}, ?*Calloria* sp. {3}, ‘*Chlorosplenium*’ *viridulum* {1}, *Claussenomyces* sp. {1}, *Cryptodiscus* sp. {1}, *C. foveolaris* {1}, *C. pallidus* {1}, *Dacrymyces* sp. {1}, *Durella atrocyanea* {1}, *D. ?compressa* {1}, *D. connivens* {1}, *Hyalorbilia erythrostigma* {1}, *H. orbiliicola* (parasitic on *O. subaristata*) {1}, *Hyphodiscus theiodeus* {1}, *Hysterobrevium mori* {1}, *Hysteropatella* sp. {1}, *H. elliptica* {1}, *Ionomidotis fulvotingens* {1}, *Karstenia* sp. {2}, *K. idaei* {1}, *K. rhopaloides* {1}, *Lecidella elaeochroma* {1}, *Melanelia glabratula* {1}, *Mellitiosporiella pulchella* {3}, *Mollisia ligni* {1}, *M. rosae* {1}, *Nitschkia broomeana* {2/1}, *Orbilia aristata* {2}, *O. carpoboloides* {2}, *O. ?cejpii* {1}, *O. cercidicola* {3}, *O. clavuliformis* {1}, *O. delphinus* {3}, *O. eucalypti* {1}, *O. euonymi* {1}, *O. flagellispora* {3},

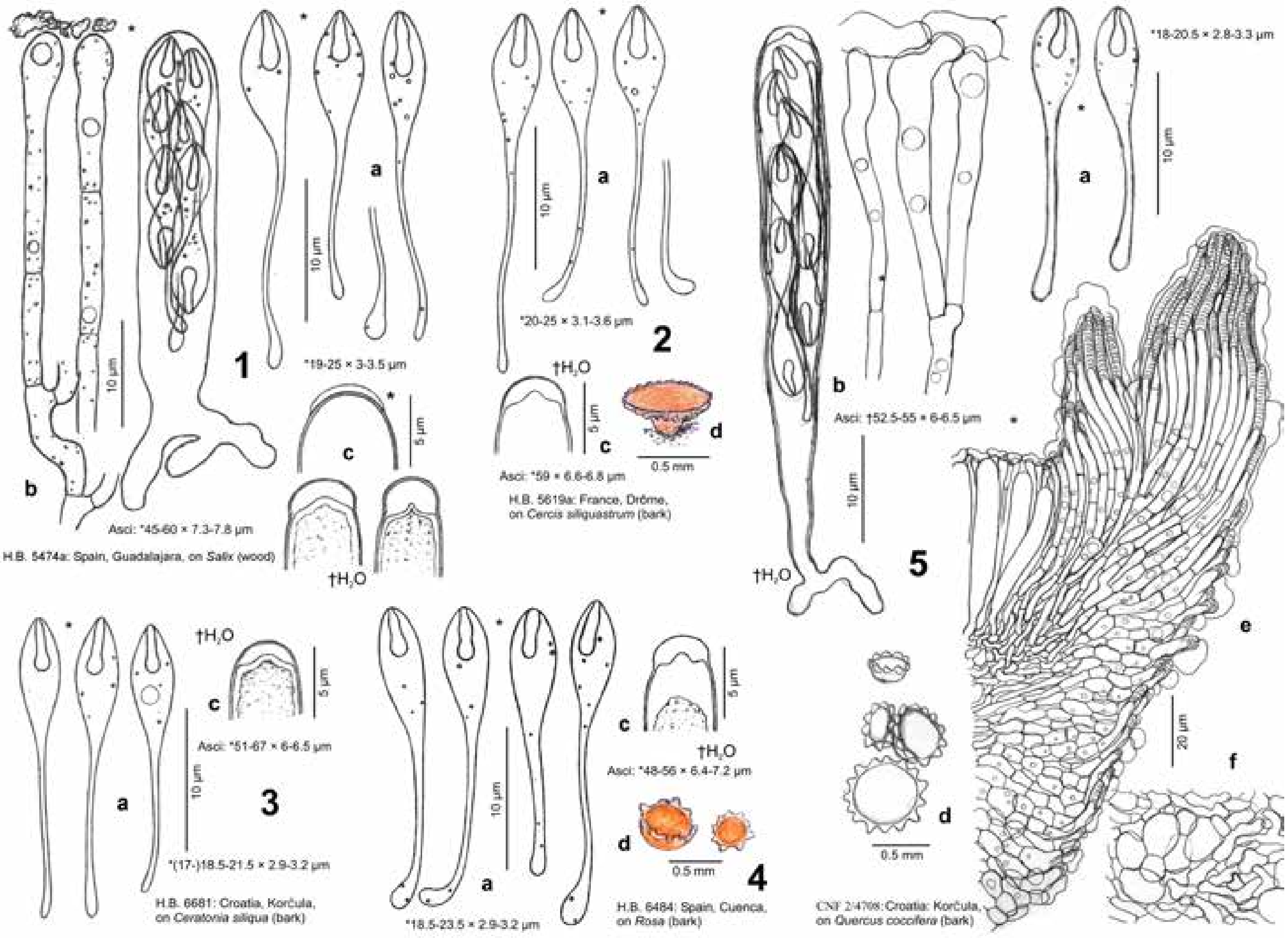


Plate 344. **1–5**: *Orbilia subaristata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia with dentate margin (rehydrated); **e**. apothecium in median section (marginal region); **f**. detail of the medullary excipulum. – **5**: del. N. Matočec.

O. gambelii {7}, *O. hesperidea* {1}, *O. mali* {1}, *O. myriolentiformis* {1}, *O. myriosphaera* {4}, *O. obtusispora* {1}, *O. ocellata* {1}, *O. ovalis* {1}, *O. pleiogambelii* {3}, *O. pleiomicrosoma* {1}, *O. pleioungulata* {1}, *O. polyspora* {3}, *O. rosicola* {1}, *O. subaristata* {2}, *O. subclavuliformis* {5}, *O. subocellata* {2}, *O. subovoidea* {3}, *O. subvinosa* {1}, *O. trapeziformis* {3}, *O. ?tremulae* {1}, *O. vinosa* {6}, *Ostropa barbara* {1}, *Ostropales* {1}, *Parmelia* sp. {2}, *P. sulcata* {1}, *Patellaria atrata* {2}, *P.* '*crassispora*' {1}, *Peniophora* sp. {1}, *Phragmiticola* sp. {1}, *Physcia tenella* {1}, *Propolis farinosa* {3/1}, *P. viridis* {2}, *Pseudovalsa longipes* {1}, *Pulcherricium coeruleum* {1}, *Rutstroemia punicae* {1}, *Schizoxylon* sp. {1}, *Xanthoria parietina* {4}. **Desiccation tolerance**: fully viable for at least 5 months. **Altitude**: 375–1063 m a.s.l. (central Europe), 1–1320 m (southern Europe). **Geology**: Lower Jurassic sandstone & Minette, marl & slate, Cretaceous limestone, dolomite, flysch, Miocene sandstone, Tertiary molasse, Pleistocene sand & loess; granite, basaltic and trachybasaltic flows and pyroclasts. **Phenology**: throughout the year (long-lived).

Phenology of *O. subaristata*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2	4	7	2	5	8	2	8	7	8	7	2

Taxonomic remarks. *Orbilia subaristata* differs from *O. aristata* in consistently longer glassy processes forming distinct whitish teeth, in slightly longer asci and spore tails, the latter being often basally swollen and more or less curved, also in sometimes somewhat inequilateral spore heads, finally in the occurrence in more thermophilous and (oro)mediterranean sites. The similar *O. flagellispora* differs from both species in distinctly more elongate spore heads.

Variation. *O. subaristata* varied mainly in the spore tails which, even within a collection, often showed a very different strength of curvature and basal inflation. In some collections the tail bases were consistently only slightly swollen, and in some spores or specimens even not at all. Although matching *O. aristata* in spore shape, these collections are included in *O. subaristata* because of the presence of rather long glassy processes and a mediterranean provenance. A collection on *Pinus brutia* from southeastern Turkey was reported by Kaya et al. (2018) under the name *O. aristata*, but the slightly bulbous base of the spore tails and the large apothecia with often distinct white teeth clearly refer it to *O. subaristata*.

Anamorph. The conidia of *O. subaristata* are very similar to those of *O. aristata* and comprise the same types: Y- and ┼-shaped, and dwayaangam-like with 4–5-arms. The ┼-shaped conidia (tetraradiate, descalsia-like) occurred in almost every collection in which conidia were observed, but the other types were only seen in some of them. However, usually only a few conidia were found on the natural substrate. As in *O. aristata*, conidia in pure culture were only formed when flooded with water. Descalsia-like conidia predominated in culture, while less often trinacrium- and no dwayaangam-like conidia could

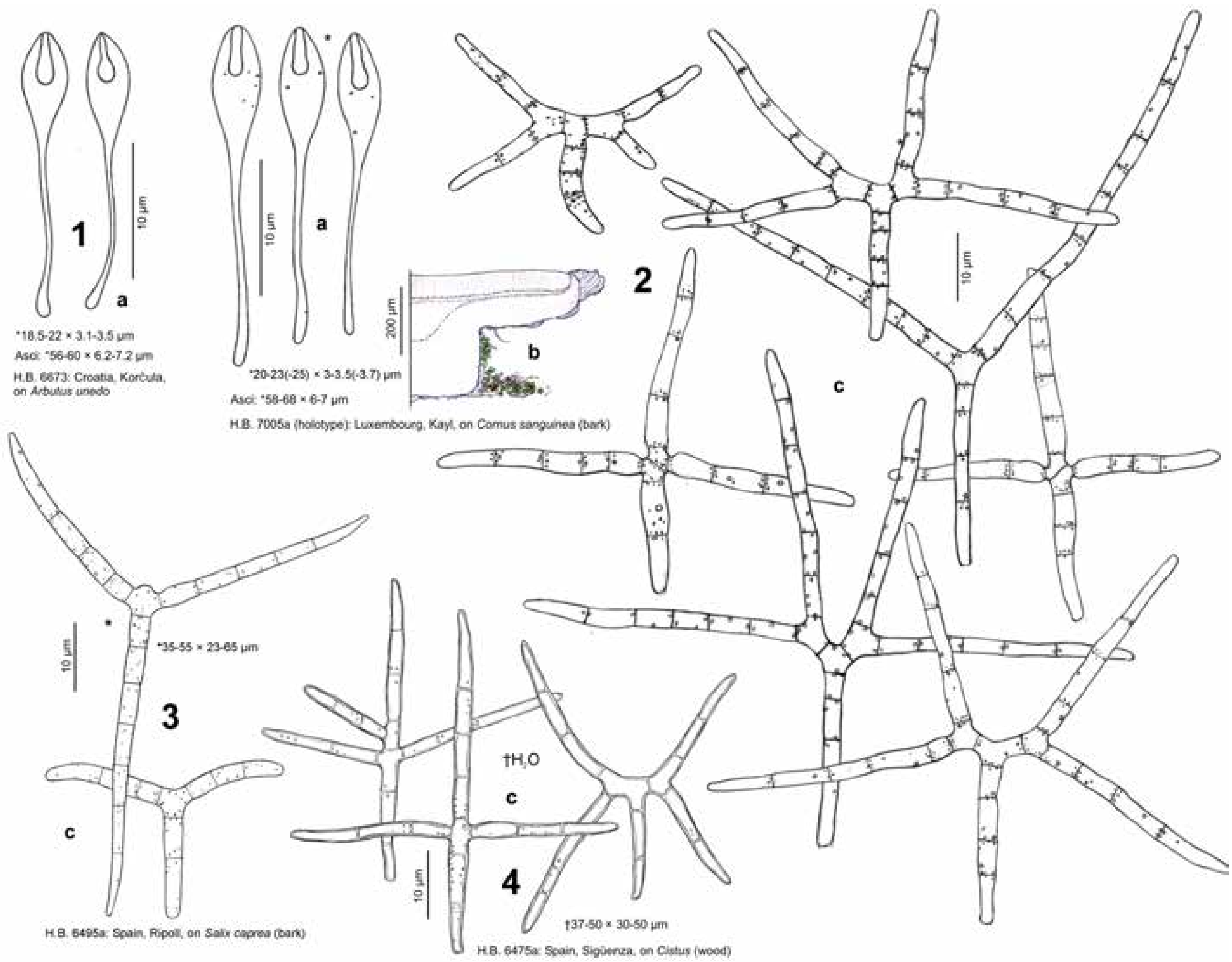


Plate 345. **1–4**: *Orbilia subaristata*. – **a**. ascospores; **b**. apothecium in median section; **c**. conidia from substrate.

be found. As a rule, descalsia-like conidia are in the majority also on the natural substrate, but sometimes spots with dwayaangam-like conidia occurred. The length of the arms varied rather strongly in all these conidial types.

Phylogeny. Sequences were taken from an ascospore isolate of a Croatian sample (H.B. 6685a, on *Punica*) comprising SSU, ITS, and LSU, and from apothecia of four samples comprising ITS and mostly also LSU, two from southern France (H.B. 9076 from Aix-en-Provence, H.B. 9151d from Nyons, both on *Cercis*) and three from Luxembourg (G.M. 2014-01-29.1, 2014-01-31.1, 2014-11-08.1, all from Kayl on *Cornus*). The S1506 intron is absent in all of them (G.M. 2014-01-31.1 includes only ITS2 and LSU). The six sequences are almost identical in the ITS region: the Croatian strain differs from all other samples by 2 nt in the ITS2, and that from Aix differs from all others by 1 nt. Between the strains from Nyons and Kayl no differences occur (a few positions are ambiguous).

The distance to *O. aristata* s.l. lies in the range of 3.5–5%, and to the other members of the *aristata-clavuliformis* clade at 2.8–3% (*O. flagellispora*), 4–5.5% to *O. clavuliformis*, 6% (*O. fimbriata*), and 6–7.5% to *O. subclavuliformis* (but 11–11.5% to *O. spermoides*/*occulta*). In the LSU (637 nt) the *O. subaristata* strains are identical and differ from *O. aristata* and *O. flagellispora* by 0.8–1% and from other species (including *O. aristata* with dwayaangam-like conidia) by min. 2–2.5%.

An unpreserved sample on *Cornus* from Luxembourg with unknown morphology (G.M. 2015-02-22.1), misidentified as *O. subaristata*, shows to *O. subaristata* a 6–6.5% distance in the ITS region (2% in the LSU D1–D2, no difference in D3), also it differs in possessing the S1506 intron. It clustered unresolved in the *aristata-clavuliformis* clade (Phyls 9, 12, S13), with a high distance to other species (*O. clavuliformis* ITS 5%, LSU 1%; *O. subclavuliformis* and *O. aristata* s.l. ITS 6–6.5%, LSU 1–1.5%; *O. fimbriata* ITS 6%, LSU 2%).

Ecology. *O. subaristata* was found on ± rotten bark (rarely wood) of xeric twigs and branches of various angiosperm trees and shrubs, exceptionally on gymnosperms (*Pinus brutia*, *P. halepensis*). Although *O. subaristata* sometimes grew in association with both *O. aristata* and *O. flagellispora*, it shows a rather different distribution area, being predominantly collected in the thermo- to supramediterranean phrygana or maquis, in supra- to mesosubmediterranean woodlands and orotemperate forests of southern Europe. However, *O. subaristata* was also repeatedly found in supratemperate humid subcontinental Europe, mainly at two sites in Luxembourg in thermophilous open woodlands with *Quercus*, *Salix*, *Cornus sanguinea*, *Crataegus*, *Prunus spinosa*, and *Sambucus nigra*. One of them represents the type locality, at which the *Cornus* bushes are scattered in a dry southeast-exposed grassland belt adjacent to a forest on a hill at the border of Lower and

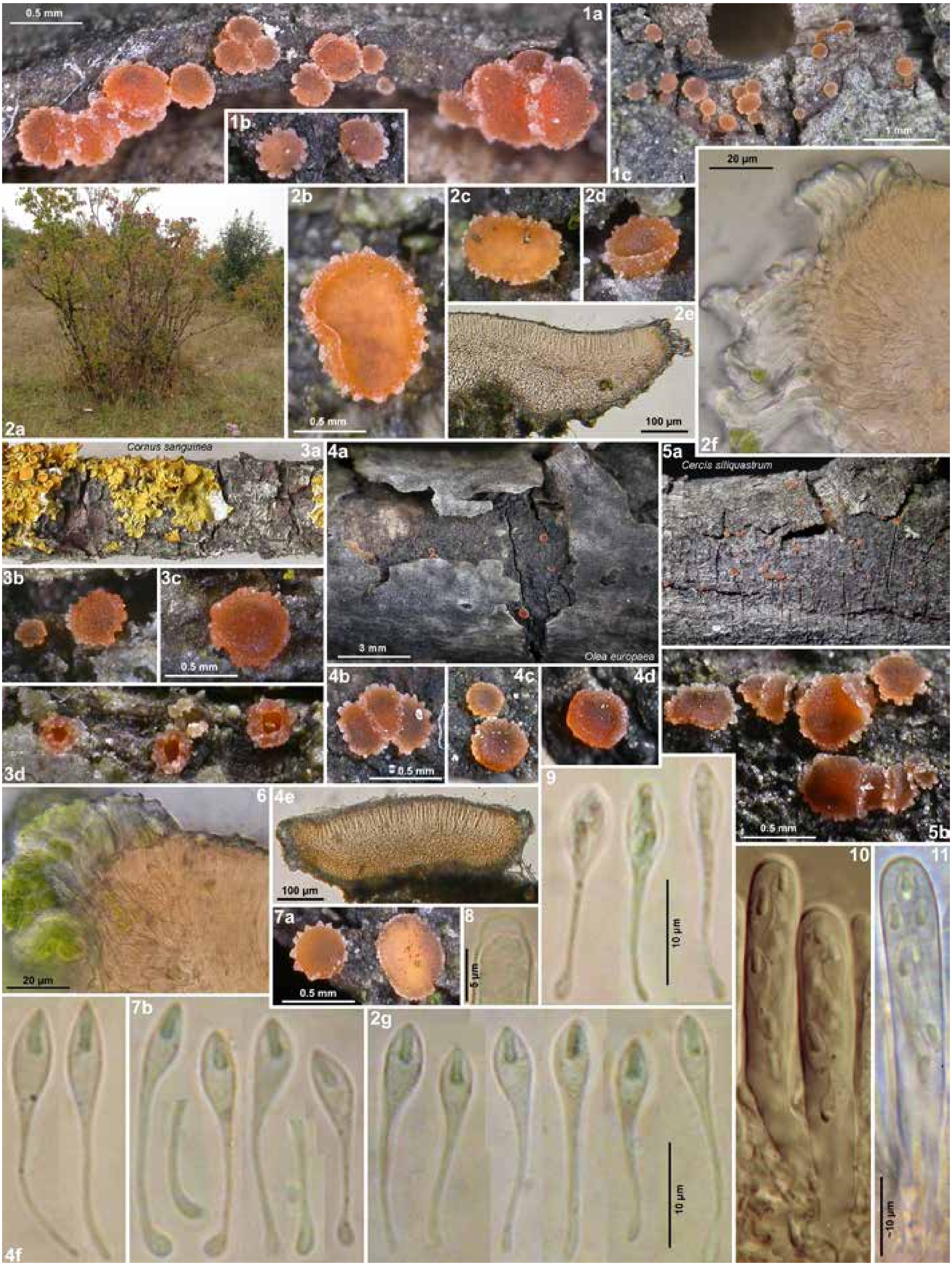


Plate 346. **1–11**: *Orbilia subaristata*. – **2a**. thermophilous grassland with *Cornus sanguinea* over Minette; **3a**. dead corticated xeric branch of *Cornus sanguinea* with *Xanthoria*; **1a–c**, **2b–d**, **3b–d**, **4a–d**, **5a–b**, **7a–b**. rehydrated apothecia; **2e**, **4e**. apothecia in median section; **2f**, **6**. marginal ectal excipulum in median section; **8**, **10**, **11**. asci; **2g**, **4f**, **7b**, **9**. ascospores. – Living state, except for **8–9** (in H_2O). **10**: phot. T. Askun (DIC). — **1a–c**. H.B. 9076: France, Aix-en-Provence, on *Cercis*; **2a–g**. H.B. 9163b (topotype): Luxembourg, Kayl, on *Cornus*; **3a–d**. H.B. 7005a (holotype): ibid., on *Cornus*; **4a–f**. H.B. 9101: Greece, Epidauros, on *Olea*; **5a–b**. H.B. 7272c: France, Nyons, on *Cercis*; **6**. H.B. 8365a: Luxembourg, Kayl, on *Cornus*; **7a–b**. H.B. 9151d: France, Nyons, on *Cercis*; **8**. H.B. 6685a: Croatia, Korčula, on *Punica*; **9**. H.B. 9076: France, Aix-en-Provence, on *Cercis*; **10**. T.A. 71: Turkey, Balıkesir, on *Carpinus*; **11**. T.A. 38: ibid., on *Quercus*.

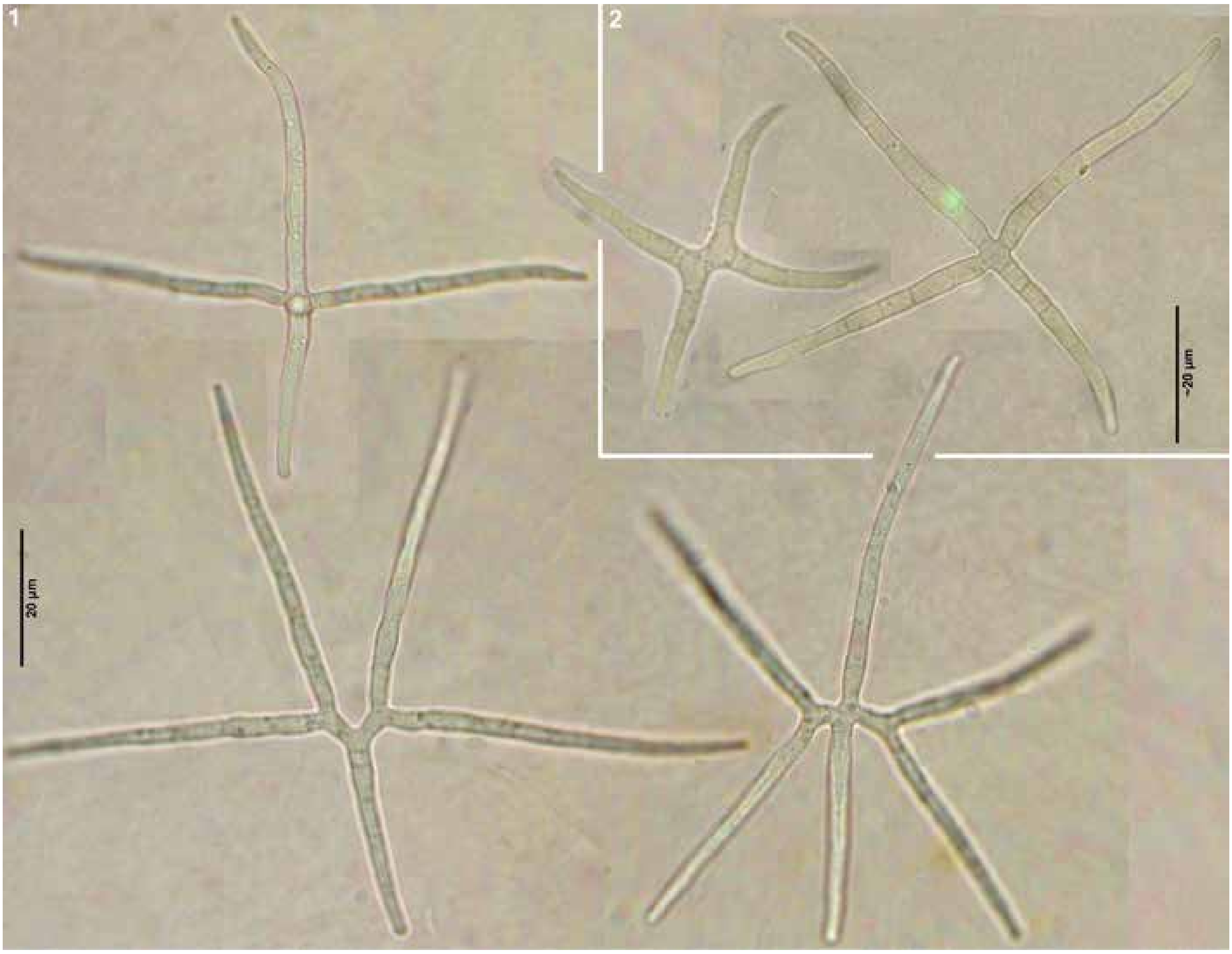


Plate 347. **1–2**: *Orbilia subaristata*. – Conidia from substrate (living state). — **1**. H.B. 8365a; **2**. T.A. 35d: Turkey, Balıkesir, on *Pinus*.

Middle Jurassic (a third site, Haard near Dudelange, was not documented). Collections from Macaronesia include infra- to thermomediterranean semiarid to semihumid cardonal (*Periploco laevigatae-Euphorbietum canariensis*), juniper woodland with *Euphorbia* spp. (*Junipero canariensis-Oleetum cerasiformis*), and Canary pine forest (*Sideritido solutae-Pinetum canariensis cistetosum monspeliensis*).

Specimens included. **LUXEMBOURG**: **Gutland**, **Mersch**, 5.5 km SE of Mersch, 2.5 km NE of Lorentzweiler, Lëtzert, 395 m, branch of *Cornus sanguinea*, on bark, 28.III.2007, G. Marson (ø). – **Esch-sur-Alzette**, 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, twigs & branches of *C. sanguinea*, on bark, 17.VII.2001, G. Marson (M-0276591, **holotype**; H.B. 7005a, **isotype**, anam. substr. ┼, also Y & dw). – ibid., 22.VI.2006 (ø, anam. substr. ┼). – ibid., 15.XI.2006 (H.B. 8365a, anam. substr. dw, also ┼). – ibid., 8.VIII.2009 (H.B. 9163b). – ibid., 3.III.2010 (ø). – ibid., 29.I.2014 (G.M. 2014-01-29.1; sq.: KY463702). – ibid., 31.I.2014, G. Marson (G.M. 2014-01-31.1; sq.: MK473390)– ibid., on bark & wood, 8.XI.2014, G. Marson (G.M. 2014-11-08.1; sq.: KY419177). — **FRANCE**: **Auvergne**, **Cantal**, 12.5 km WSW of Murat, 2 km NNE of St.-Jacques-des-Blats, S of Les Chazes, 1063 m, twig of *Crataegus monogyna*, on bark, 11.X.2006, J.P. Priou (J.P.P. 26156 ø). – ibid., branch of *Salix*, on bark, 23.VII.2015, J.P. Priou (J.P.P. 15162, doc. vid.). – **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, Col du Pontias, 460 m, branch of *Cercis siliquastrum*, on bark, 22.VIII.1996, G. Marson (H.B. 5619a, anam. substr. ┼). – ibid., 18.VIII.2001 (H.B. 7077j, anam. substr. ┼). – ibid., 11.X.2002 (H.B. 7272c, anam. substr. ┼). – ibid., 13.VIII.2009, G. Marson, H.O. Baral & B. Liu (H.B. 9151d, G.M. 2009-08-13.1; sq.: KT222368). – ibid., branch of *Quercus ilex*, on bark, 13.VIII.2009, H.O. Baral (H.B. 9149b ø). – **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 10 km ESE of Sederon, W of Curel, 765 m, branch of *Spartium junceum*, on wood & bark, 17.VIII.2001, G. Marson (H.B. 7032a, anam. substr. ┼, also dw). – 12 km WSW of Briançon, 2.7 km NNE of Vallouise, E of Pelvoux, l'Adret, 1495 m, branch of *Juniperus communis*, on bark, 11.IX.2008, J.P. Priou (J.P.P. 28202, doc. vid.). – ibid., twig of *Acer campestre*, on bark, 11.IX.2008, J.P. Priou (J.P.P. 28205, doc. vid.). – **Bouches-du-Rhône**, 3 km SW of Aix-en-Provence, La Baume, Chemin de la Blaque, 145 m, branch of *Cercis siliquastrum*, on bark, 31.X.2006, H. Aeberhard (H.B. 9076; sq.: KT222367). – **Languedoc-Roussillon**, **Pyrénées-Orientales**, 19 km SW of Perpignan, 0.5 km N of Tordères, 200 m, stem of *Rubus fruticosus*, 22.II.2011, U. Lindemann (ø, doc. vid.). – 7 km NE of Mont-Louis, Ayguatébia, Corral de Castanyet, 1514 m, branch of *Rosa*, on bark, 21.IX.2016, J.P. Priou (J.P.P. 16249 ø, doc. vid.). — **SPAIN**: **Asturias**, 2.4 km N of Pola de Somiedo, 2 km S of Castro, 703 m, branch of *Rhamnus alaternus*, on bark, 7.VI.2013, H.O. Baral (H.B. 9820c). – ibid., branch of *Quercus pyrenaica*, on bark (H.B. 9823). – 1.2 km N of Pola de Somiedo, twigs of *Crataegus monogyna*, on bark, J. Linde (E.R.D. 5716). –

Map 59. Known distribution of *O. subaristata* in Macaronesia, Europe, and eastern Asia (Turkey).

País Vasco, **Álava**, 9 km NW of Miranda de Ebro, WSW of Fontecha, 485 m, branch of *Rosa* ?*canina*, on bark, 23.XII.2004, C.E. Hermosilla (ø, doc. vid.). – **Aragón**, **Huesca**, western Pyrenees, 15 km N of Jaca, 0.8 km S of Canfranc, 1015 m, branch of *Rosa*, on bark & wood, 13.X.2010, J.P. Priou (J.P.P. 10161, doc. vid.). – ibid., 0.3 km N of Canfranc, Puente de Arriba, 1060 m, twig of *Rosa*, on bark & wood, 13.X.2010, J.P. Priou (J.P.P. 10167, doc. vid.). – 12.7 km N of Jaca, NNE of Villanúa, 970 m, branch of *Rosa*, on bark, 9.X.2016, H.O. Baral (H.B. 10027a). – ibid., branch of *Quercus rotundifolia*, on bark (H.B. 10028a). – **Zaragoza**, 25 km N of Zaragoza, 14 km NW of Villanueva de Gállego, 460 m, branch of *Pinus halepensis*, on resin, 5.II.2015, R. Blasco (ø, doc. vid.). – **Teruel**, 8.5 km WSW of Utrillas, 1.4 km SW of Las Parras de Martin, Hocino de las Parras, N of Cueva de las Brujas, 1117 m, branch of *Cornus* (?)*sanguinea*, on bark, 26.VIII.2011, R. Tena (ø, doc. vid.). – **Cuenca**: Sierra de Albarracín, 28 km NE of Cuenca, 1 km SW of Beamud, 1320 m, branch of *Rosa*, on bark, 25.IX.1999, G. Marson (H.B. 6484, anam. substr. ┼). – **Cataluña**, **Girona**, eastern Pyrenees, 26 km NE of Ripoll, 2.3 km NE of Molló, WSW of Col d'Ares, 1310 m, branch of *Salix caprea*, on bark, 28. IX.1999, G. Marson (H.B. 6495a, anam. substr. Y & ┼). – **Castilla-La Mancha**, **Cuenca**, 4.5 km ENE of Cuenca, 4 km NW of Palomera, 1077 m, branch of *Rosa*, on bark, 27.IV.2015, J.P. Priou (J.P.P. 15103, doc. vid.). – **Guadalajara**, 18 km SW of Sigüenza, 2.5 km NE of Almadrones, 1.5 km NW of E-90, 1065 m, branch of *Cistus*, on wood, 24.IX.1999, H.O. Baral & G. Marson (H.B. 6475a, anam. substr. ┼, also Y & dw). – 43 km NNW of Guadalajara, 2 km NNW of Tamajón, Ermita de los Enebrales, 1040 m, branches of *Rosa*, on bark, 14.V.1996, H.O. Baral (H.B. 5511l). – 55 km NNW of Guadalajara, 0.7 km NW of Majaelrayo, Arroyo La Matilla, 1180 m, branch of *Salix*, on wood, 14.V.1996, H.O. Baral (H.B. 5474a). — **AUSTRIA**: **Wien**, 5 km SSE of Wien, Laaer Wald, 235 m, twig of *Quercus*, on bark, 27.XII.2018, R. Moosbeckhofer, vid. B. Wergen (doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 12.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, W of WWII memorial, 445 m, branch of *Carpinus betulus*, on wood, 18.IX.2019, D. Savić (doc. vid.). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 11.5 km W of Korčula, 2 km W of Račišće, Samograd bay, 2 m, branches of *Punica granatum*, on bark, 4.VI.2000, N. Matočec & H.O. Baral (H.B. 6685a, CBS 116217, anam. cult. Y & ┼; sq.: KT215270). – ibid., branch of *Olea europaea*, on bark, 4.VI.2000, H.O. Baral (ø). – 2.5 km W of Korčula, NW of Žrnovska Banja, Vrbovica, 1 m, branch of *Arbutus unedo*, 2.VI.2000, H.O. Baral (H.B. 6673 ø). – ibid., 8 m, branch of *Ceratonia siliqua*, on bark, 6.VI.2000, H.O. Baral (H.B. 6681). – ibid., branch of *Quercus coccifera*, on bark, 24.VIII.2000, N. Matočec (CNF 2/4708, doc. vid.). — **MONTENEGRO**: 15 km NNW of Podgorica, 1.9 km NE of Donje Selo, Glizica, 210 m, twig of *Vitis vinifera*, on bark, 2.V.2016, D. Raspopović (B.P. Dgf/C7D-02-05-16b, doc. vid.). – ibid., twig of *Punica granatum*, on bark, 8.V.2016, B. Perić & D. Raspopović (B.P. Dgf/C7D-08-05-16d, doc. vid.). — **GREECE**: **Peloponnese**, 8 km SW of Epidauros, 4 km ESE of Asklipieio, amphitheatre, 365 m, branch of *Olea europaea*, on bark, 10.VI.2009, S. Helleman (H.B. 9101). – **South Aegean**, **Rhodos**, 17 km WSW of Archangelos, 4.5 km NNW of Laerma, 185 m, branch of *Pistacia lentiscus*, on bark, 21.III.2010, V. Kummer (H.B. 9334f ø). – 17 km WNW of Archangelos, 1 km SSE of Salakos, NE of Profitis Ilias, 525 m, branches of *Pyrus spinosa*, on bark, 20.III.2010, V. Kummer (H.B. 9355 ø). – 2 km E of Archangelos, N of Stegna, 12 m, branch of indet. angiosperm, on bark, 25.III.2010, V. Kummer (H.B. 9354c ø). – 3.5 km NE of Archangelos, 1.2 km ENE of Monastery of Tsambika, 165 m, branch of *Pyrus spinosa*, on bark, 18.III.2010, V. Kummer (H.B. 9273d ø). — **TURKEY**: **Marmara**, **Balıkesir**, 50 km WSW of Balıkesir, 17.5 km SW of Ivrindi, Korucu Forest, 1 km SSE of Büyükılıca, 340 m, branch of *Fraxinus*, on bark, 1.XI.2002, T. Askun (T.A. 37a, anam. substr. ┼). – 1 km ESE of Büyükılıca, Sarıpınar Mevkii, 410 m, branch of *Quercus ilex*, 1.XI.2002, T. Askun (T.A. 38a). – 1.3 km ESE of Büyükılıca, 425 m, branch of *Pinus brutia*, on wood, 1.XI.2002, T. Askun (T.A. 35d, anam. substr. Y & ┼). – 28 km N of Balıkesir, 1.2 km W of Hisaralan, NE of Toybelen Köyü, 250 m, branch of *Carpinus*, 15.XI.2003, T. Askun (T.A. 71c, doc. vid.). – 9 km NE of Balıkesir, 2.5 km SW of Ayvatlar, Değirmen Boğazı, 135 m, twig of *Fraxinus*, on bark, 4.II.2003, T. Askun (T.A. 44). – 28 km SE of Balıkesir, 8 km NW of Bigadiç, WSW of Kadıköy, 360 m, branch *Pinus brutia*, on bark, 10.II.2014, S. Yurtseven (doc. vid.). – **Southeastern Anatolia**, **Gaziantep**, 5 km NNE of Nurdağı, SE of Belpınar, 540 m, twigs of *Pinus brutia*, on bark, 9.III.2014, A. Kaya & Y. Uzun (A.Ky. 8596, KMU, as *O. aristata*, doc. vid.). — **MACARONESIA**: **Canary Islands**, **Tenerife**, San Cristóbal de la Laguna, 6 km NNE of Tegueste, 2.3 km E of Punta de Hidalgo, Andén de la Cruz, 345 m, branch of *Echium leucophaeum*, 20.V.2013, L. Quijada & C. García (TFC Mic. 24227, doc. vid.). – Guía de Isora, 5 km NNW of Guía de Isora, 1.7 km NW of Chío, Los Corchos, 640 m, branch of *Juniperus phoenicea* var. *turbinata*, on bark, 24.X.2014, L. Quijada, C. Quijada & J. Kout (L.Q.F.-9, doc. vid.). – Granadilla de Abona, 2.5 km SE of Vilaflor, La Martela, 1195 m, branch of *Aeonium arboreum*, on wood, 19.IV.2012, L. Quijada (TFC Mic. 23636, doc. vid.).

Not included. **LUXEMBOURG**: **Gutland**, **Esch-sur-Alzette**, 3.5 km SE of Esch-sur-Alzette, 1.7 km WSW of Kayl, Léiffraechen, 380 m, branch of *Cornus sanguinea*, 22.II.2015, G. Marson (G.M. 2015-02-22.1 ø, non vid.; sq.: KY419191).

Orbilia breviaristata Baral, Priou & G. Marson, **sp. nov.**, MB 813612 — Pls 348–350, Map 60

Etymology: referring to the tail of the ascospores which is much shorter than in *O. aristata*.

Typification: Germany, Tübingen, stem of *Rubus fruticosus*, 24.VII.2002, H.O. Baral (ex H.B. 7171a, M-0276444, holotype).

Latin diagnosis: *Similis* Orbiliae aristatae *sed ascosporae cauda multo breviore, asci paulo breviores. Habitat ad corticem vel lignum putridum ramulorum siccorum* Rubi, Euphorbiae *et fruticum* angiospermarum *in zona atlantica ad subcontinentale temperata locis thermophilis Europae occidentalis et centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.15–0.4(–0.5) mm diam., 0.06–0.12 mm high, pale to light rose or rose(-orange), medium to strongly translucent, round, subgregarious in small groups; disc flat, margin 5 µm protruding, with minute to often distinct whitish teeth; broadly sessile to subsessile, superficial; dry light to bright orange-rose, only slightly contracted. **Asci** *32–50 × (5.6–)6–7.3 µm {3}, †32–43 × 5.3–6.5 µm {3}, 8-spored, spores (*) biseriate, ((0–))1–2(–3)((–4)) lower spores inverted {4} (not mixed), pars sporifera *(21–)25–26(–31) µm long; **apex** (†) hemispherical, dome †1–1.8(–2) → 0.7–1 µm thick {3}, with slight to distinct apical chamber; **base** with short to long, medium thick, flexuous stalk, L-, T- or Y-shaped. **Ascospores** *(9.7–)10–13(–14) × 2.8–3.4(–3.6)((–3.8)) µm {10}, †(8–)9–12.5 × (2.5–)2.7–3 µm {5}, sperm-shaped: with ellipsoid-fusoid, *6.5–7.5(–8) µm long head and sharply differentiated filiform tail *(2–)3–5.3(–6) × 0.2–0.6 µm, apex obtuse to subacute, tail not swollen at base, straight to slightly (exceptionally strongly) geniculate towards head, ~½–¾ as long as head; **SBs** *2.8–3.8 × 1.1–1.3 µm {4}, pyriform to dumbbell-shaped, apically narrowed to a ± small point, overmature *2.5–2.8 × 1.4–1.5 µm. **Paraphyses** apically uninflated or often slightly (rarely strongly) clavate-capitate, terminal cells *(8.5–)12–20 × 1.8–3.5(–4.5) µm {3}, lower cells *4–9 × 1.7–2.3 µm {3}; not or rarely branched at upper septum. **Medullary excipulum** subhyaline, 15–40 µm thick, of dense textura intricata-globulosa with many inflated cells, very indistinctly to very sharply delimited. **Ectal excipulum** of light orange-rose, thin-walled t. globulosa(-prismatica) from base to mid flanks, 15–70 µm thick near base, cells *(5–)9–22 × (4–)7–19 µm {2}; 20–30 µm thick near margin, of t. prismatica oriented at a 50–70° angle to the surface, outer part of t. prismatica-porrecta oriented at 20–40°, marginal cortical cells *6–12 × 2.7–4 µm {1}, †7–12 × 2.2–3.2 µm {1}; **glassy processes** (3–)8–30(–40) × 2.5–3.5 µm {6}, high-refractive, sparsely stratified, coherent to form distinct teeth, predominantly curved inwards {3}. **Anchoring hyphae** medium sparse to abundant, */†1.5–3.2 µm wide, walls 0.2–0.3 µm thick {2}. **SCBs** in paraphyses and marginal excipular cells globose (to elongate), 1.8–3(–4) µm diam. **Exudate** over paraphyses 1–2.5(–3) µm thick, cloddy, coarsely rough, loosely attached, hyaline; over margin 0.2–0.3(–1) µm thick, continuous, rough. — **ANAMORPH**: descalsia-like (presumed, from natural substrate {1}). **Conidiophores** not seen. **Conidia** ┼-shaped, total size *62–66 × 47–50 µm, stipe *30–31 × 3.5–4 µm, 3–4-septate, arms *30–38 × 3.5–4 µm, 4–5-septate.

Habitat: collected 0.7–2 m above the ground, on partially to entirely decorticated stems of *Euphorbia characias* {1}, *Rubus fruticosus* agg. {3}, *Rubus* (?)*bifrons* {1}, 8–15 mm thick branches of *Cytisus scoparius* {2}, *Frangula alnus* {1}, *Pinus* ?*nigra* {1}, *Ulex europaeus* {4}, on very decayed wood {9} or bark {3} (periderm-free bast), also on splitted bark, along deep clefts, or in beetle galleries (sometimes on boring dust), sometimes on wounds, medium greyed, often with many green algae. **Associated**: *Hyalorbilia latispora* {1}, *H. multiguttulata* {1}, *H. subfusispora* {1}, *Hyaloscypha minuta* {1}, *Karstenia rhopaloides* {2}, *Lophiostoma compressum* {1}, *Orbilia aristata* {1}, *O. aurantiorubra* {2}, *O. clavuliformis* {3}, *O. corculispora* {2}, *O. eucalypti* {2}, *O. filiformis* {1}, *O. subclavuliformis* {2}, *O. vinosa*

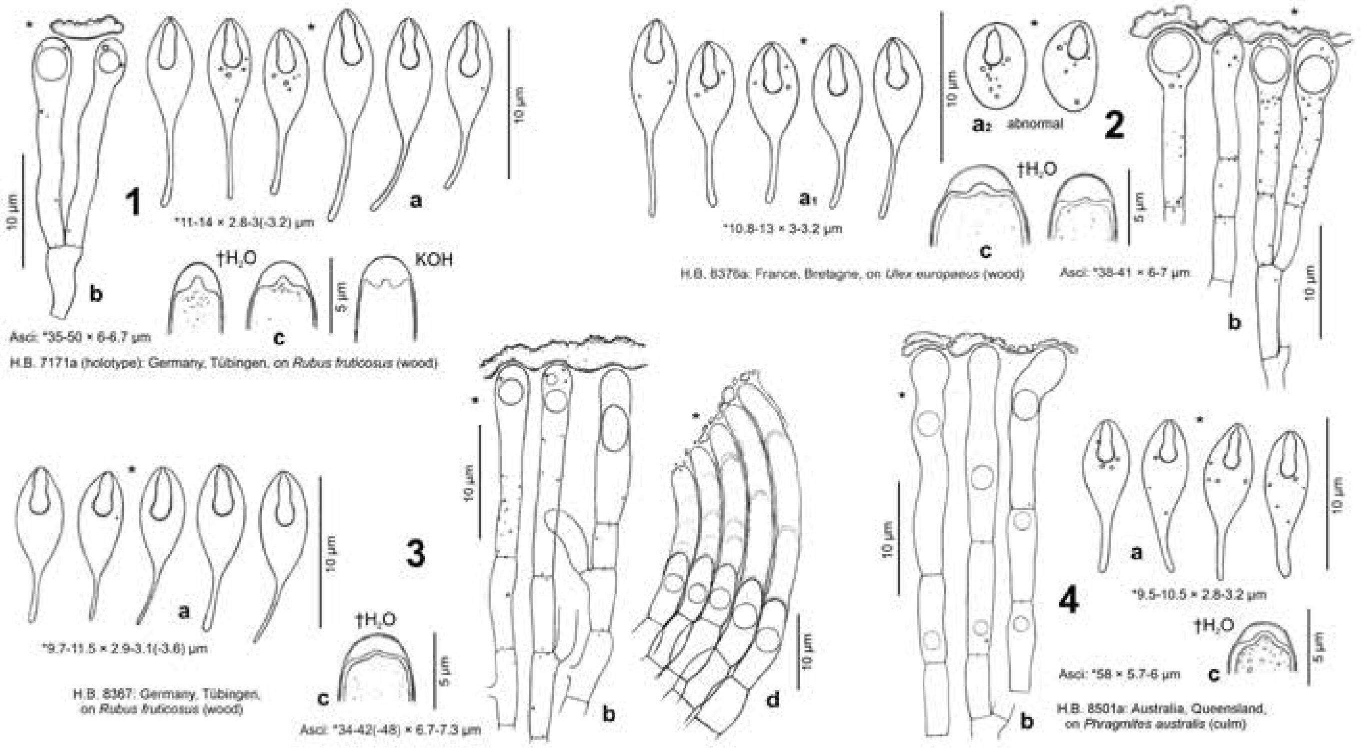


Plate 348. **1–3**: *O. breviaristata*; **4**. *O.* cf. *breviaristata*. – **a**. ascospores (**2a$_2$** 2 abnormal spores); **b**. paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section, cortical cells with glassy processes.

{1}, *O. vitalbae* {2/1}, *Pirottaea ?imbricata* {1}, *Pyrenopeziza rubi* {2}, *Sporidesmium* sp. {1}. *Unguiculariopsis* sp. {1}. **Desiccation tolerance**: excipular cells, paraphyses and immature asci still viable after 1 month, ascospores after 2 months. **Altitude**: 1–390 m a.s.l. **Geology**: Cambrian silt & wacke, Keuper (Knollenmergel etc.), Lower Jurassic & Cretaceous sand- & limestone, Quaternary sand & gravel; granite, gneiss. **Phenology**: II–IV, VI–VII, X–XII (throughout the year).

Taxonomic remarks. *Orbilia breviaristata* is very similar to *O. aristata*, except for the ascospore tails which are consistently and considerably shorter in all examined apothecia from all so far known collection sites. The asci are only slightly shorter than in *O. aristata*. If no free spores are found in a preparation, *O. breviaristata* is easily confused with *O. aristata* since the tails are often difficult to see in full length within the living asci. That this taxon is not an immature stage of *O. aristata* is indicated by the presence of fully developed SBs in the ascospores. Furthermore, the tails of immature ascospores (with not yet developed SBs) of both taxa are not shorter than those of mature spores, i. e., the tails attain their final length at an early stage of spore formation. Macroscopically, the apothecia of *O. breviaristata* tend to be smaller, paler and more translucent in comparison to *O. aristata*, and to have more distinct marginal teeth.

Also the spores of *O. occulta* and *O. spermoides* strongly resemble those of *O. breviaristata*, but their spore heads and SBs are shorter and slightly wider, and the excipular cells contain crystalloid SCBs. *O. multiaustraliensis* (series *Hesperidea*) resembles *O. breviaristata* in the spores, but differs, besides 32-spored asci, in the presence of crystalloid SCBs and absence of glassy processes. The Australian *O. megaocculta* differs in much wider asci and spores, much thicker spore tails, and much wider SBs.

Variation. In the collections on *Cytisus* and *Ulex* some of the glassy processes were very short (e. g., 3–12 µm in J.P.P. 29039, J.P. Priou pers. comm.) and, therefore, the margin was only finely denticulate or almost smooth (Pl. 349: 3a–b). In one collection of *O. breviaristata* a single aberrant ascus contained broader spores 5.7–6 × 3.7–4 µm, without any trace of a tail (Pl. 348: 2a$_2$).

Not included collections. In a Spanish sample on *Rubus* the apothecia entirely lack glassy processes and the spores tend to be more clavate (IVV: E.R.D. 7961). An Australian sample on culms of *Phragmites australis* (Pls 348: 4; 350, for a site photo see Pl. 620: 1a) differs merely in slightly thinner apical domes. The spore tails are comparatively short and thick. The specimen might be conspecific with European *O. breviaristata* but is not included mainly because of the deviating substrate

Map 60. Known distribution of *O. breviaristata* in Europe (yellow = not included collection).

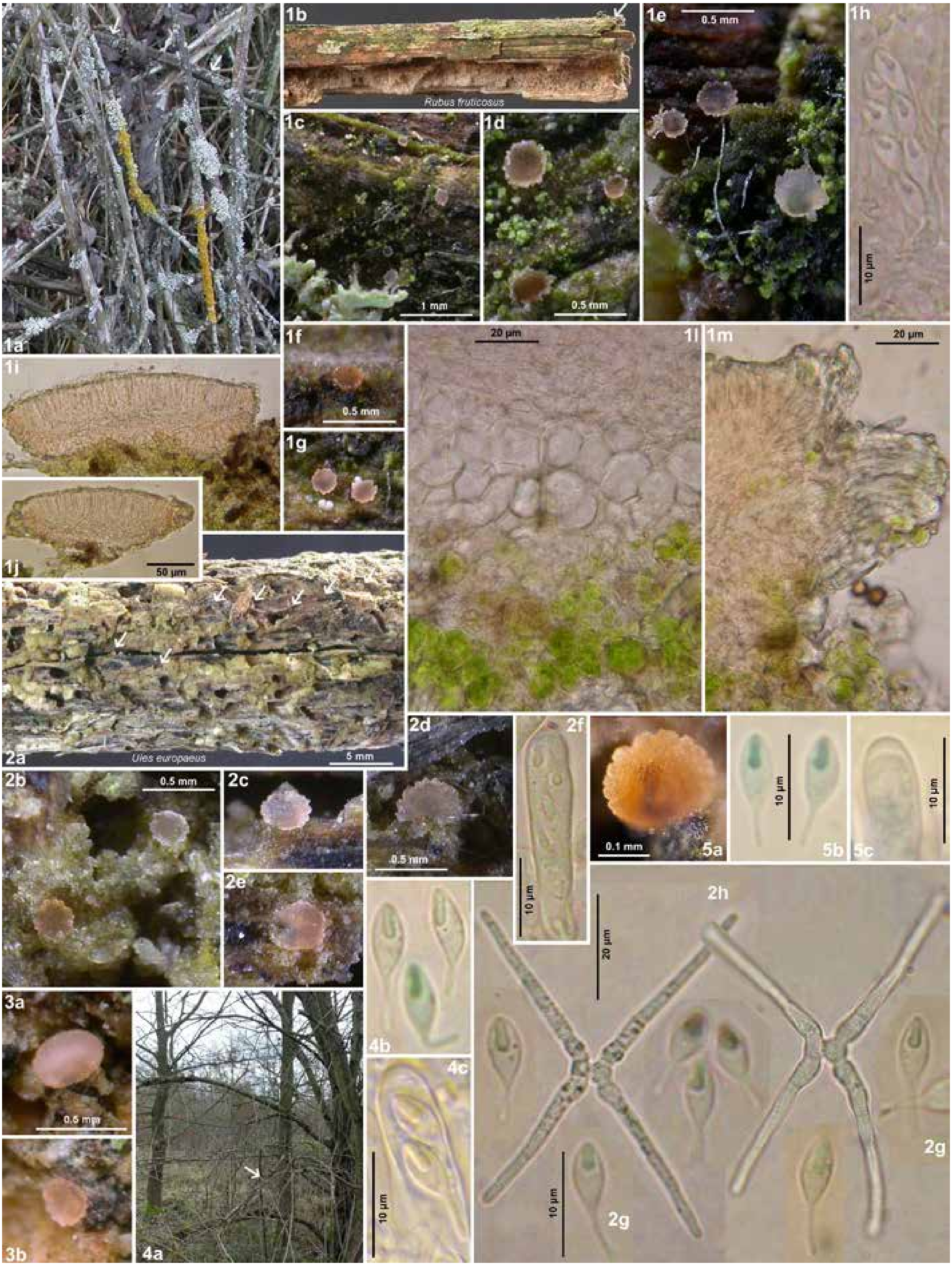


Plate 349. **1–5**: *Orbilia breviaristata*. – **1a**, **4a**. old stems of *Rubus fruticosus* ~ 1 m above the ground; **1b**. rotten stem of *Rubus fruticosus*; **2a**. decorticated xeric branch of *Ulex europaeus* with beetle galleries; **1c–g**, **2b–e**, **3a–b**, **5a**. rehydrated apothecia; **1i–j**. apothecia in median section; **1m**. id., marginal ectal excipulum with glassy processes; **1l**. id., basal ectal excipulum; **1h**, **2f**, **4c**. mature asci with spores; **5c**. apex of immature ascus; **2g**, **4b**, **5b**. ascospores; **2h**. conidia from substrate. – Living state (**4c**: oblique illumination) except for asci in **1h**, **2f**, **4c**, **5c** (in H_2O). – **3a–b**: phot. J.P. Priou, **5a–c**: phot. E. Rubio. — **1a–m**. H.B. 8367: Germany, Tübingen, on *Rubus*; **2a–h**. H.B. 8376a: France, Carnac, on *Ulex*; **3a–b**. J.P.P. 26155: France, Saintes, on *Ulex*; **4a–c**. H.B. 8418: Luxembourg, Fentange, on *Rubus*; **5a–c**. E.R.D. 5902, Asturias, Oviedo, on *Rubus*.

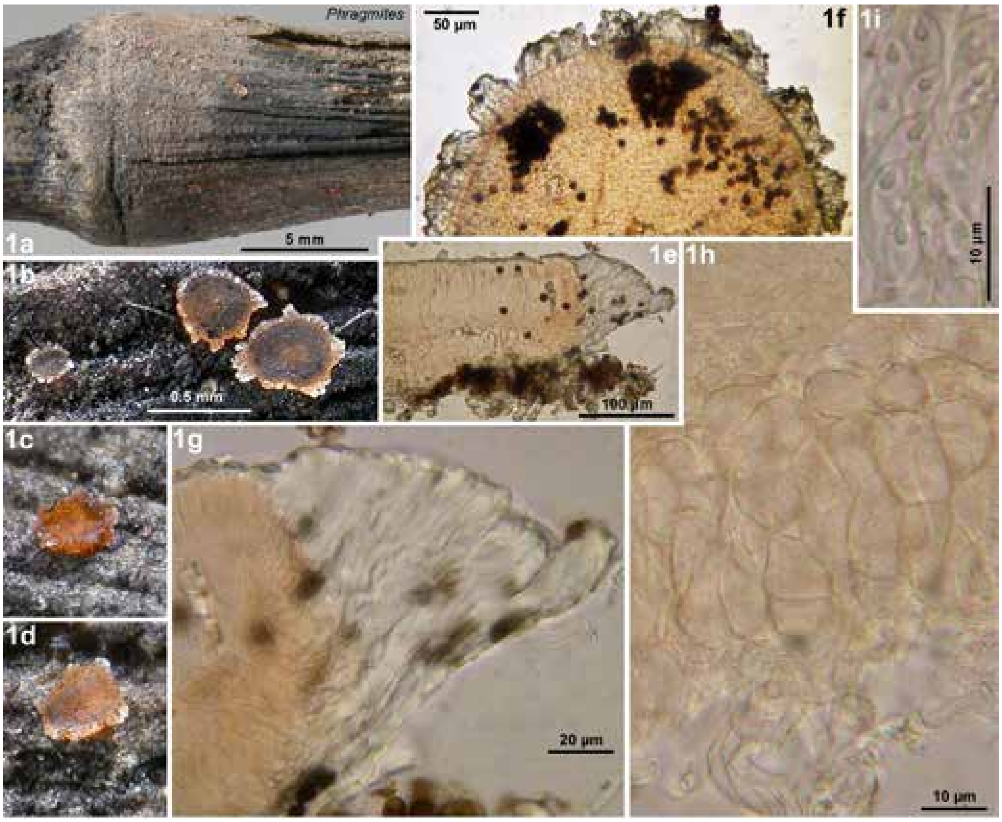


Plate 350. **1**: *Orbilia* cf. *breviaristata*. – **1a**. dead xeric culm of *Phragmites australis* blackened by *Arthrinium arundinis*; **1b–d**. rehydrated apothecia; **1e**. apothecium in median section (with dark brown conidia of *Arthrinium*); **1f**. apothecium in top view; **1g**. marginal ectal excipulum in median section; **1h**. id., basal ectal excipulum; **1i**. mature ascospores inside asci. – Living state, except for asci in **1i**. — **1a–i**. H.B. 8501a: Australia, Queensland, on *Phragmites*.

and geographical origin. Also here one apothecium contained broader spores without any trace of a tail.

Anamorph. The descalsia-like conidia observed on the natural substrate near apothecia of *O. breviaristata* resemble those of the similar *O. aristata* (Pl. 349: 2h). In two collections (IVV: H.B. 7171a, 8367) K-shaped, curucispora-like conidia were observed which might instead belong to the (presumed) anamorph of *Hyalorbilia subfusispora*.

Phylogeny. Two sequences comprising ITS and LSU were available of the two samples from Luxembourg. The S1506 intron is absent in both. No unequivocal differences could be observed between them in the regions without ambiguities. The ITS region was very badly sequenced but in combination of both a rather useful sequence resulted which clustered with low support sister to *O. clavuliformis* (Phyl. 12), to which it showed the lowest distance (4–4.5%), followed by *O. subaristata*, *O. aristata*, *O. subclavuliformis*, and *O. flagellispora* with 6–8% (data approximate because of ambiguous positions in *O. breviaristata*). When analysing LSU D1–D2 (not shown), *O. breviaristata* clustered strongly supported and with a 0.8% distance with *O. clavuliformis*, followed by *O. subclavuliformis* (1.5%), *O.* aff. *subaristata* (1.7%), *O. aristata* with dwayaangam-like conidia (2%), and *O. aristata* with curucispora-like conidia (2.4%).

Ecology. *O. breviaristata* was found on rotten bark and wood of xeric branches of *Ulex*, *Frangula* and *Cytisus*, somewhat woody stems of *Euphorbia*, and stems of *Rubus fruticosus* agg. The species shows an atlantic to subcontinental, cold- to warm-temperate humid distribution in western and central Europa, where it seems to prefer thermophilous hedges with *Rubus*, *Ulex* or *Cytisus*. The type locality is a rather extensively used garden in which also *O. aristata* was found at the same place, but on separate stems of *Rubus*. A collection from Spain (on *Frangula*) was from a meso-submediterranean semihumid river bank. The not included collection from northeastern Australia was in a tropical (sub)humid floodplain between savannah and rainforest on Devonian sedimentary rock, on standing, dead, xeric *Phragmites* culms being covered over large areas by a black conidial layer of *Arthrinium arundinis*.

Specimens included. **NORWAY**: **Hedmark**, 10 km NW of Hamar, 1.7 km SSE of Brumunddal, 140 m, branch of *Pinus ?nigra*, on bark, 16.VII.2012, S. Helleman (S.H. 735, doc. vid.). — **GERMANY**: **Baden-Württemberg**, Tübingen, southern Schönbuch, 5 km NE of Tübingen, 0.6 km S of Pfrondorf, Obere Mähder, 390 m, stem of *Rubus fruticosus*, on wood, 24.VII.2002, H.O. Baral (ex H.B. 7171a, M-0276444, **holotype**). – ibid., 20.XI.2006, H.O. Baral (H.B. 8367). — **LUXEMBOURG**: **Gutland**, **Remich**, Valée de Moselle, 8.5 km S of Remich, 0.6 km SSW of Schengen, N of Stréimchen, 225 m, stem of *R.* (?)*bifrons*, 11.II.2007, G. Marson (H.B. 8445i ø; sq.: MK493148). – **Luxembourg**, Luxembourg Plateau, 6 km S of Luxembourg, 1.5 km WSW of Fentange, Mierchesfeld, 283 m, stem of *R. fruticosus*, 3.XII.2006, G. Marson (H.B. 8418 ø; sq.: MK493149). — **FRANCE**: **Bretagne**, **Morbihan**, 9.5 km SE of Malestroit, 2.7 km WNW of St.-Martin-sur-Oust, Beauvais, 8 m, branch of *Cytisus scoparius*, on bark, 3.III.2009, J.P. Priou (J.P.P. 29039, doc. vid.). – ibid., stem of *Euphorbia characias*, on wood & bark, 20.IV.2014, J.P. Priou (JPP 14076, doc. vid.). – 3 km ESE of Carnac, 1 km SW of La Trinité sur Mer, W of Kervourden, 7 m, branch of *Ulex europaeus*, on wood, 24.XI.2006, J.P. Priou (J.P.P. 26204, 26210, H.B. 8376a, anam. substr.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 2.3 km NE of Mesquer, 1.3 km NE of Le Rostu, l'Île de Rostu, 2 m, branch of *U. europaeus*, on wood, 11.XI.2008, C. Lechat (J.P.P. 28217, doc. vid.). – 3 km ESE of Piriac-sur-Mer, 0.5 km E of St.-Sébastien, 20 m, branch of *U. europaeus*, on wood, 10.XI.2007, J.P. Priou (J.P.P. 27124, doc. vid.). – 13 km WSW of Nantes, 0.4 km NW of St.-Jean-de-Boiseau, W of La Rivière, 13 m, branch of *C. scoparius*, on wood, 15.XI.2009, J.P. Priou (J.P.P. 29212, doc. vid.). – **Poitou-Charentes**, **Charente-Maritime**, 8 km NW of Saintes, 3.2 km SSW of Port d'Envaux, Bois du Chail, 35 m, branch of *U. europaeus*, on wood, 13.X.2006, J.P. Priou (J.P.P. 26155, doc. vid.). — **SPAIN**: **Asturias**, 7.7 km SW of Oviedo, 1 km SSW of Las Caldas, Rio Nalón, 105 m, branch of *Frangula alnus*, on wood, 17.VI.2013, M.A. Miranda (E.R.D. 5902, doc. vid.).

Not included. **SPAIN**: **Asturias**, 17.5 km SEE of Pola de Lena, 1 km SSE of Pajares, Hayedo de Valgrande, 1058 m, stem of *Rubus fruticosus*, 5.VII.2019, E. Rubio (E.R.D. 7961, doc. vid.). — **AUSTRALIA**: **Queensland**, Einasleigh Uplands, 22 km SSW of Mossman, 2 km N of Mount Molloy, Mossman Mt. Molloy Rd, 390 m, leaf sheaths of *Phragmites australis*, 28.VIII.2006, G. Marson (H.B. 8501a).

Orbilia megaocculta Baral, **sp. nov.**, MB 813613 — Pl. 351

Etymology: named after the large ascospores similar as in species related to *O. occulta*.

Typification: Australia, New South Wales, Lithgow, branch of *Eucalyptus*, 26.X.1998, G. Marson (ex H.B. 6775, MEL 2389216, holotype).

Latin diagnosis: *Similis* Orbiliae breviaristatae *sed asci, ascosporae et cauda ascosporarum multo latiores, corpuscula refringentia multo latiora. Habitat ad corticem putridum rami sicci* Eucalypti *in zona temperata humida Australiae meridio-orientalis.*

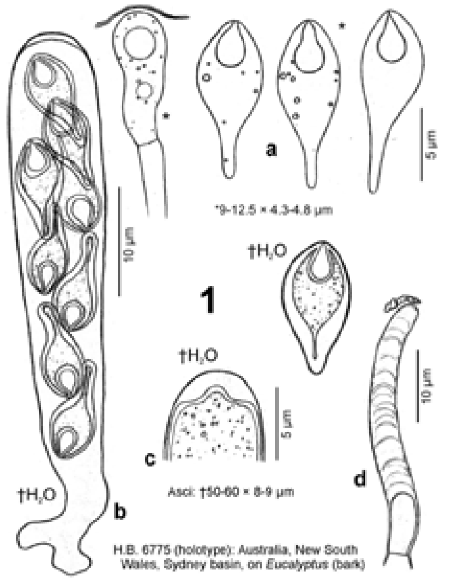


Plate 351. **1**: *Orbilia megaocculta*. – **a**. ascospores; **b**. ascus and paraphysis; **c**. ascus apex; **d**. marginal cortical cell with glassy process.

Description: — **TELEOMORPH**: **Apothecia** rehydrated ~0.2 mm diam., light orange; disc flat, margin finely crenulate. **Asci** †50–60 × 8–9 µm, 8-spored, spores ± biseriate, 3–6 lower spores inversely oriented (sometimes mixed); **apex** (†) hemispherical, dome 1.7–2.2 µm thick, with apical chamber; **base** with very short stalk, Y-shaped. **Ascospores** *9–12.5 × 4.3–4.8 µm, broadly fusoid, apex obtuse, base mostly with a short tail 2.5–4 × 0.7–0.8 µm, straight; **SBs** *3–3.5 × 2–2.2 µm, tear- to pear-shaped, apically narrowed to a small point; with some small LBs. **Paraphyses** apically uninflated to medium clavate, terminal cells */†~ 12–15 × 2.5–4.8 µm. **Medullary excipulum** not examined. **Ectal excipulum** of medium gelatinized textura globulosa (common walls †1–1.5 µm thick), cells near base †12–23 × 10–20 µm; **glassy processes** at margin 20–30 × 2.7–4 µm, stratified, coherent to form short and broad teeth. **Anchoring hyphae** not seen. **SCBs** in paraphyses globose. **Exudate** over paraphyses and glassy processes 0.3–1.5 µm thick, continuous, loosely attached. **— ANAMORPH**: unknown.

Habitat: ± corticated, 8 mm thick xeric branch of *Eucalyptus* sp., on medium decayed edge of bark in a cleft. **Associated**: none observed. **Desiccation tolerance**: some paraphyses and spores still viable after 2 years. **Altitude**: 1073 m a.s.l. **Geology**: Permian-Triassic sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia megaocculta* is characterized by rather large, broadly ellipsoid-fusoid ascospores with large, tear-shaped SBs and a short, medium thick tail, also by medium long glassy processes. The European *O. breviaristata* differs in much narrower asci and spores, much thinner spore tails, and much narrower SBs. *O. megaocculta* resembles also taxa around *O. multiaustraliensis* and *O. arizonensis* (series *Hesperidea*) in spore shape and also in the higher number of inverted spores, but these species are without glassy processes and possess crystalloid SCBs, *O. multiaustraliensis* also differs in 32-spored asci.

Ecology. *O. megaocculta* is only known from the holotype on rotten bark of a dead xeric branch of *Eucalyptus* in a warm-temperate humid eucalypt woodland at the top of a mountain in the Great Dividing Range of southeastern Australia. Only two apothecia were detected in the sample which were used up during examination.

Specimens included. **AUSTRALIA**: **New South Wales**, Sydney Basin, 95 km WNW of Sydney, 11.5 km SE of Lithgow, 1.6 km SE of Mt. York, 1073 m, branch of *Eucalyptus*, on bark, 26.X.1998, G. Marson (ex H.B. 6775, MEL 2389216, **holotype**).

Orbilia fimbriata Baral & G. Marson, **sp. nov.**, MB 813614 — Pls 352–353

Etymology: named after the long-haired apothecial margin.

Typification: Western Australia, Toolonga, trunk of *Dodonaea viscosa* subsp. *angustissima*, 8.XI.2007, G. Marson (ex H.B. 8838a, MEL 2389261, holotype; sq.: KT222369).

Latin diagnosis: *Apothecia rehydratata 0.4–1.5 mm diam., vivide (ochraceo-) aurantiaca, sessilia vel subsessilia, margine longissime albopilosa. Asci 8-spori. Ascosporae *19–21 × 3.9–4.7 µm, ellipsoideo-fusoideae, cauda basali 10–11 × 0.9–1.1 µm, basi leniter inflata praeditae, in statu vivo corpusculum refringens magnum, pyri- ad moniliformem, ad apicem affixum continentes. Cellulae vivae paraphysium corpuscula globosa continentes. Excipulum marginale pilis perlongis, copiosis, hyalinis, crassitunicatis, pauciseptatis praeditum. Exsudato nullo. Habitat ad corticem putridum siccum trunci emortui* Dodonaeae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.4–)0.5–1(–1.5) × 0.35–0.7(–1) mm diam., 0.1–0.22 mm high (receptacle near margin 0.1–0.15 mm), light to bright (yellowish-)orange(-ochraceous), non-translucent, round to often elliptical, scattered to subgregarious in small groups; disc strongly concave to finally flat, margin 70–150 µm protruding by the long, white hairs which are often somewhat teeth-like agglutinated; broadly sessile or with a broad stipe-like base, superficial; disc dry completely closed by the incurved hairs. **Asci** *65–75(–90) × 7.5–8.7 µm, †50–68 × 6–7(–8) µm, 8-spored, spores (*) biseriate, 0(–1) lower spores inverted (sometimes mixed), pars sporifera *47–55 µm long; **apex** (†) hemispherical to very slightly

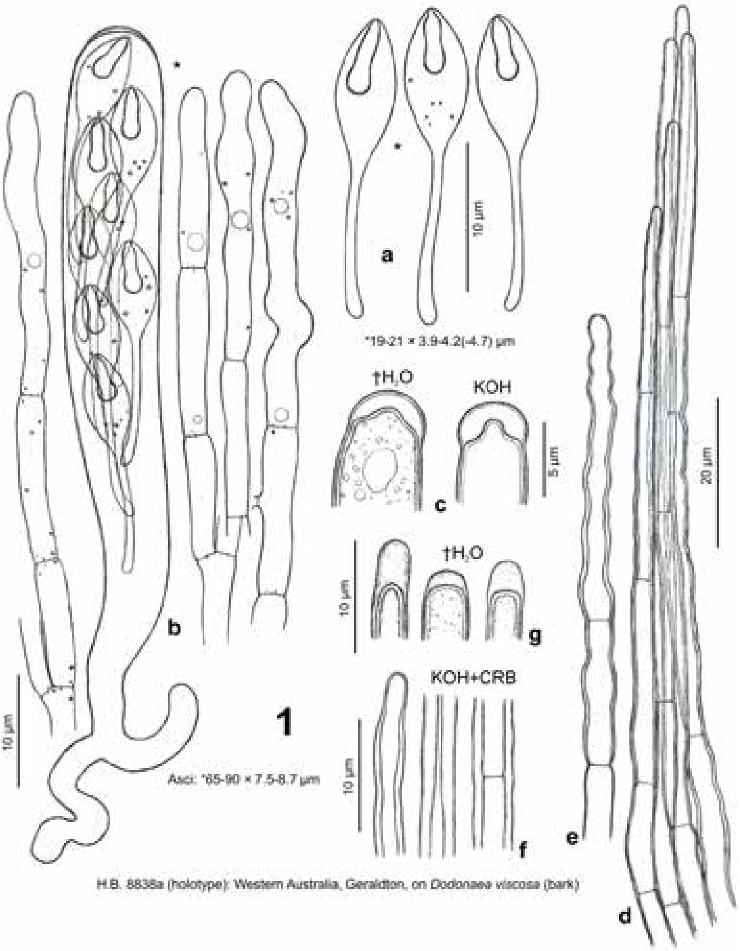


Plate 352. **1**: *Orbilia fimbriata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. agglutinated marginal hairs; **e**. non-agglutinated hair at uppermost margin; **f**. detail of hairs (tip and middle part); **g**. some hair tips with glassy caps.

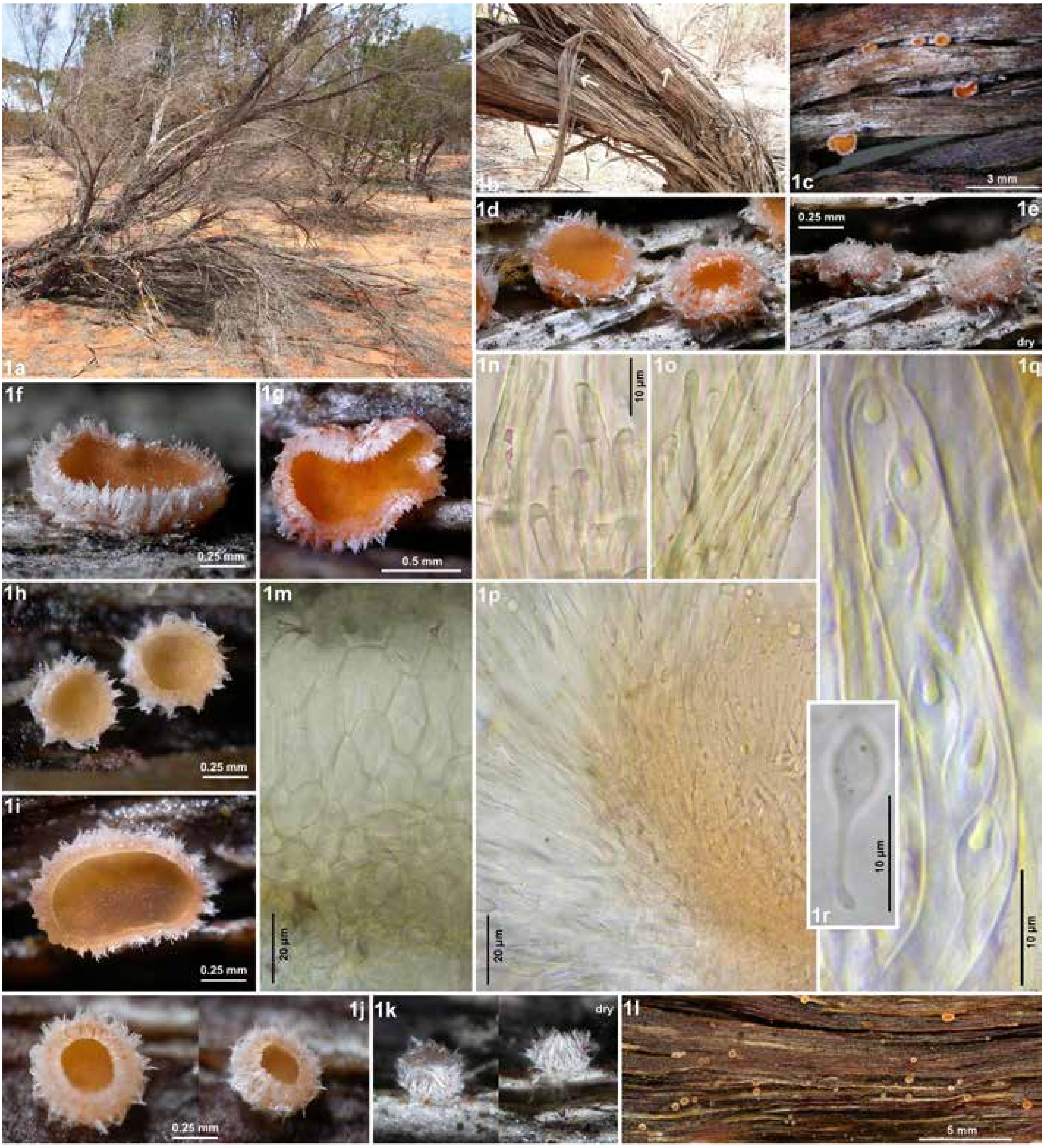


Plate 353. **1**: *Orbilia fimbriata*. – **1a**. semiarid acacia shrubland with dead *Dodonaea* shrub in front; **1b**. dead standing trunk of *Dodonaea* with detaching outer bark; **1c–d**, **f–j**, **l**. rehydrated apothecia; **1e**, **k**. dry apothecia; **1m**. median section of basal ectal excipulum; **1p**. id., marginal ectal excipulum with hairs; **1n–o**. detail of hairs; **1q**. ascus with ascospores; **1r**. ascospore. – Living state, except for **1r** (in KOH). — **1a–r**. H.B. 8838a (holotype): Western Australia, Yalgoo, on *Dodonaea*.

truncate, dome immature †1.2–1.4 µm thick (KOH 1.5–1.7 → 0.7–1.3 µm), with slight to distinct apical chamber; **base** with short to long, thin or thick, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *19–21 × 3.9–4.2(–4.7) µm, †(16–)17–19.5 × (3.5–)3.8–4.1 µm, sperm-shaped: with ellipsoid-fusoid, *9–9.5(–10) µm long head and sharply differentiated filiform tail *10–11 × 0.9–1.1 µm, apex subacute, tail slightly and gradually swollen at base, straight to slightly curved; **SBs** *4–4.5(–5) × 1.3–1.7 µm, pyriform to dumbbell-shaped, apically narrowed to a ± small point. **Paraphyses** apically uninflated to often slightly lageniform, terminal cells *16–31 × 2.2–3.5 µm, often slightly to strongly flexuous, lower cells *11–15(–20) × 1.8–3 µm; never branched at upper septum. **Medullary excipulum** subhyaline to pale orange, 25–70 µm thick, of medium dense textura intricata with some inflated cells, sharply delimited. **Ectal excipulum** hyaline to pale rose-orange, of (†) thin-walled to slightly gelatinized, vertically oriented t. globulosa-prismatica from base to mid flanks, 20–70 µm thick near base, cells *10–31 × 7–14 µm, †8–15 × 6–12 µm; 20–30 µm thick at flanks, 20–50 µm near margin, of t. porrecta oriented at a 0–10° angle to the surface, marginal cortical cells *7–15 × 3–4 µm, giving rise to hairs; **hairs** *60–210(–300) × 3–4.5 µm, ± straight, with hyaline, smooth, glassy walls *0.5–1 µm thick (in KOH 0.5–1.5 µm), gradually more thin-walled towards apex and base, here walls 0.2–0.3 µm thick, with somewhat undulating surface, sparsely septate, ± agglutinated in small groups to form very narrow teeth, towards hymenium non-agglutinated hairs *60–100 × 3.5–5 µm; wall surface CRB deep lilac; **glassy processes** mostly absent, in some apothecia present at tip of short inner hairs of upper margin, 2–4 × 3–4 µm. **Anchoring hyphae** (very) abundant, †2–4 µm wide, walls 0.2–0.4(–1) µm thick, forming a medium dense, pale yellowish t. intricata 50–80 µm thick. **SCBs** in paraphyses globose, 1–1.5 µm diam., in ectal excipulum not observed. **Exudate** over paraphyses and hairs absent, among anchoring hyphae present, thin, pale yellowish **— ANAMORPH**: unknown.

Habitat: collected 0.5–2 m above the ground, corticated, ~10–20 cm thick standing, almost dead branches and trunks of *Dodonaea viscosa* subsp. *angustissima*., on exterior of strongly detached and decayed bark, greyed, no algae. **Associated**: *Acanthostigma ?minutum*, *Mycocalicium* sp., *Orbilia ?angustoaristata*, *O. australiensis*, *O. austrocylindrica*, *O. pleiovirgula*, *O. ?pubescens*. **Desiccation tolerance**: fully viable for at least 6 months, many submature asci still alive after 20 months. **Altitude**: 190 m a.s.l. **Geology**: Cretaceous sedimentary rock (red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia fimbriata* resembles *O. aristata* and related species in ascospore shape. It differs by rather broad spore heads, paraphyses often slightly lageniform and not covered by exudate, and particularly by the very long hairs which are not agglutinated to form thick teeth but only in thin fascicles. The hairs are not solid but show a lumen up to the mostly thin-walled apex. The rather large apothecia with their orange disc and long white hairs may easily be mistaken in the field for a member of the *Helotiales*, e.g., of the family *Arachnopezizaceae*.

Phylogeny. Two sequences of almost equal length, comprising ITS and LSU, one also a short part of SSU, were obtained from apothecia of the holotype. They fully concur, and in both the S1506 intron is absent. Only the longer version was uploaded in GenBank. *O. fimbriata* clustered in the *aristata-clavuliformis* clade when analysing ITS, LSU, or both regions (Phyls 9, 12, S13). In the ITS the distance to other members of the clade lies in the range of 6–8 %, and in the LSU D1–D2 at 2.5–3.5 %, the closest taxa being *O. flagellispora* and *O. subaristata*.

Ecology. *O. fimbriata* was found on rotten, detaching bark of a dead, xeric trunk of *Dodonaea* and its branches in a subtropical semiarid acacia open shrubland in the Yalgoo ecoregion of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, branches and trunk of *Dodonaea viscosa* subsp. *angustissima*, on bark, 8.XI.2007, G. Marson (MEL 2389261, **holotype**; H.B. 8838a, **isotype**; sq.: KT222369).

Orbilia occulta (Rehm) Sacc., Syll. Fung. 8: 623 (1889) — Pls 354–355

≡ *Calloria occulta* Rehm, Hedwigia 24: 14 (1885)

Etymology: apparently referring to the apothecia growing hidden in clefts of periderm.

Typification: USA, New Jersey, Newfield, unlocalized, branch of *Vitis vinifera*, I.1882, J.B. Ellis (Rehm 770, M-0206545, lectotype, designated here, MBT382101). Georgia, Tifton, Black Shank Farm, branch of indet. angiosperm, 8.V.2015, Y.Y. Shao (GXU 1467, epitype, designated here, MBT385116, ex-epitype culture: TF018; sq.: MG742398, MG742399).

Misapplied name: J.B. Ellis (N. Amer. F. 438), as *Peziza regalis*.

Misinterpretation of *O. occulta*: Korf (1992: 510), CUP-MM-002694 = *Orbilia euphorbiae*, CUP-MM-002555 = *O. pisciformis*; Rehm (1891: 459), Velenovský (1934: 102), Kirschstein (1936: 204), Svrček (1954: 10, 1960: 16), Ellis & Ellis (1985: 12), Beyer (1998: 191), = *Orbilia aristata*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.4–0.7(–0.9) mm diam., (0.12–)0.17–0.2 mm high (receptacle 0.12–0.14 mm), light orange-rose, round, scattered, sometimes gregarious; disc flat to slightly convex, margin thin, 0–30 µm protruding, smooth or usually distinctly crenulate due to small teeth up to 30–40 × 30–50 µm; with a very short stipe 0.05 × 0.15 mm, superficial; dry bright orange. **Asci** *50–76 × (5.7–)6–6.7 µm {1}, †(37–)40–60 × (4–)4.3–5.8(–6.3) µm {4}, 8-spored, spores (*/†) subbiseriate, 1–3 lower spores inverted {2} (sometimes mixed), pars sporifera *28–38 µm long; **apex** (†) hemispherical to slightly truncate, dome †1–1.5 → 0.5–1.3 µm thick {4}, with or without apical chamber; **base** with short to medium long, thick, flexuous stalk, L-, h- (or H-)shaped. **Ascospores** *(9.5–)10–12(–13) × (2.8–)3–3.4(–3.6) µm {1}, †(7–)8–11.5(–12) × 2.7–3.3 µm {4}, sperm-shaped: with broadly ellipsoid(-fusoid) head 5–6(–7) µm long and sharply differentiated filiform tail of *(2–)2.5–6(–7) µm long × 0.3–0.4 µm thick (†0.2–0.3 µm wide), apex obtuse (to subacute), also rounded, tail not swollen at base, straight to slightly flexuous; **SBs** *1.8–2.2(–2.5) × 1.1–1.2 µm, tear- to pear-shaped, apically narrowed to a small to wide point, overmature *1.5 × 1.2 µm. **Paraphyses** apically slightly to strongly clavate-capitate (exceptionally spathulate), terminal cells *12–23 × 2.2–3.2 µm {1}, †1.5–3 {T} or 2–4.7 {1} µm wide, lower cells *6–12 × 1.5–2.4 µm {1}, †1.2–1.5 µm wide {T}; branched only towards base. **Medullary excipulum** pale orange, 30–40 µm thick, of dense or loose textura intricata with some or many inflated cells, sharply delimited. **Ectal excipulum** pale rose-orange, of (†) thin-walled to slightly gelatinized, vertically oriented t. globulosa-angularis-prismatica at base and flanks, (20–)30–70(–100) µm thick near base, cells *7–17(–21) × 7–13(–15) µm {1}, †5–11 × 3–6 µm {2}; 15–20 µm thick near margin, inner layer of t. prismatica oriented at a 40–70° angle to the surface, outer layer of t. porrecta oriented at 10–40°, marginal cortical cells †4–9 × 2–5 µm {2}; **glassy processes** (3–)10–50 × (2–)2.5–4 µm {4}, medium to high-refractive, partly stratified, ± coherent to form ± distinct small teeth. **Anchoring hyphae** abundant, */†2–3.3 µm wide, walls 0.2–0.5 µm thick {2}, sometimes forming a strongly gelatinized t. oblita up to 60 µm thick. **SCBs** in paraphyses small, globose; in ectal excipulum at flanks crystalloid, very pale yellowish-reddish, 1.8–6 × 1–2 µm {1}. **Exudate** over paraphyses (0.2–)0.5–1.5(–3) µm thick, forming a continuous layer or cloddy caps, hyaline, smooth to rough, ± firmly attached, over hairs only as small scattered granules. **— ANAMORPH**: trinacrium-like (from ascospore isolate {1}, Shao et al. 2018). **Conidiophores** forming reduced, integrated nodules or short hyphal cells of 0.5–4 × 1–1.2 µm. **Conidia** triradiate, *24–40 × 21–32 µm, stipe *14–20 × 1.5–2 µm, ~3–4-septate, arms ± straight, *13–24×1.8–2.3 µm, ~3–5-septate, gradually slightly tapered towards ends {1}.

Habitat: collected ~1 m above the ground, corticated, 3–20 mm thick, sometimes still viable twigs and branches of *Cornus* sp. {1}, *Malus domestica* {2}, *Vitis vinifera* {T}, indet. angiosperm {1}, on slightly to medium decayed bark {5} (bast), in holes or cross clefts of periderm or on periderm-free areas and on inner surface of detached bark, rarely on wood {1}, strongly greyed or not, green algae abundant or sparse. **Associated**: *Hysterographium fraxini* {1}, *Lecanora* sp. {1}, *Orbilia ?clavuliformis* {1}, *O. regalis* {1}, *Pertusaria* sp. {1}, fruticose lichen {1}. **Desiccation tolerance**: fully viable for at least 2 months. **Altitude**: 35–1200 m a.s.l. **Geology**: Miocene sedimentary rock; granite. **Phenology**: I, V (but certainly long-lived).

Taxonomic remarks. *Orbilia occulta* is characterized by sperm-like ascospores composed of a short, broadly ellipsoid head and an abrupt, thin tail of about the length of the head or slightly shorter, also by medium long glassy processes forming small teeth at the margin, and by the presence of crystalloid SCBs in the ectal excipulum. Earlier authors made no distinction between North American *O. occulta* and European *O. aristata*, which is separated here based on longer spore heads and the absence of crystalloid SCBs. Our studies revealed, however, that even within North America four

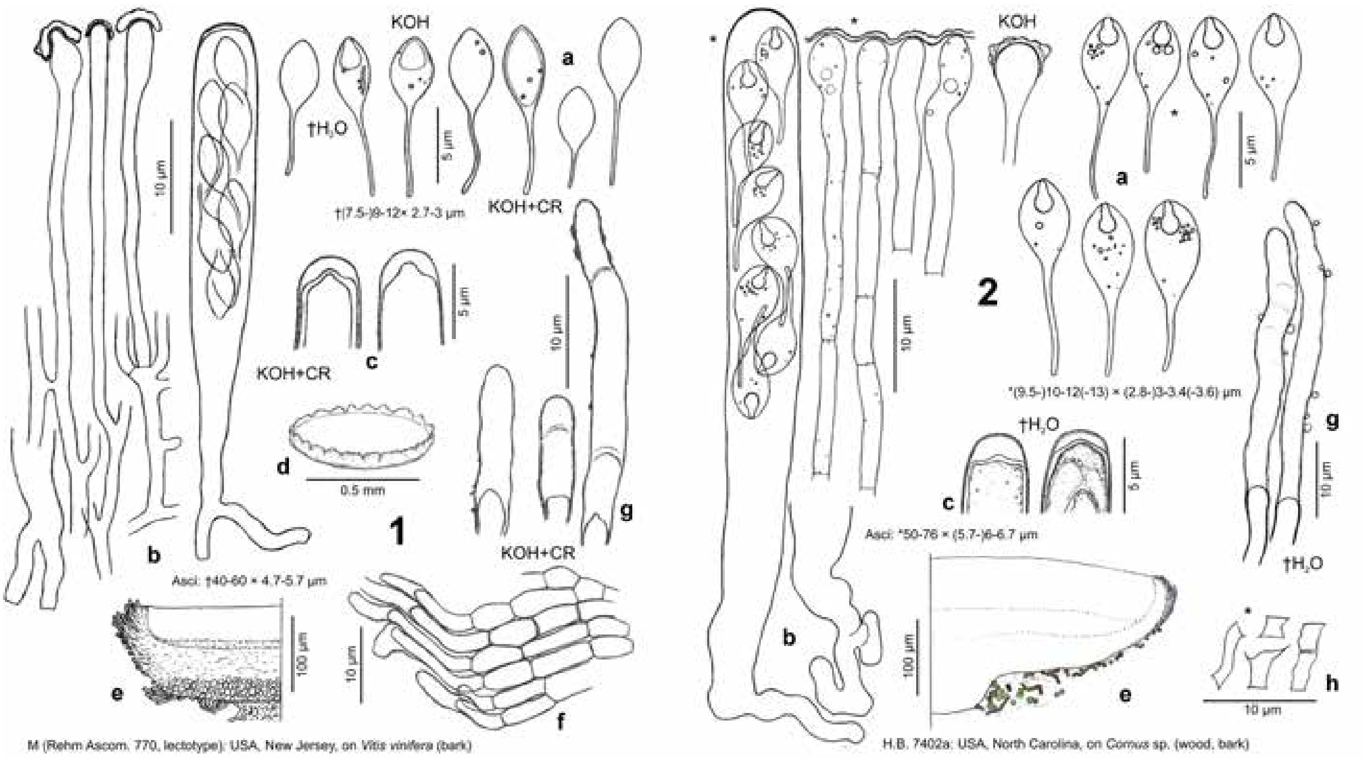


Plate 354. **1–2**: *Orbilia occulta*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium with dentate margin (rehydrated); **e**. apothecia in median section; **f**. id., ectal excipulum at mid flanks, cortical cells with glassy processes; **g**. marginal glassy processes; **h**. crystalloid SCBs in ectal excipulum at flanks.

different species with thin, basally uninflated spore tails need to be distinguished: *O. aristata*, *O. clavuliaristata*, *O. occulta*, and *O. spermoides*. The rather short spores of *O. occulta* strongly resemble those of the European (and Australian) *O. breviaristata*, which differs in slightly longer and narrower spore heads and SBs, in the absence of crystalloid SCBs, and in smaller apothecia.

To the closest relatives of *O. occulta* appear to belong the mainly North American conifericolous *O. spermoides* and the Australian *O. austroocculta*. The three species much resemble each other in spore shape, also in the comparatively short and broad SBs. *O. occulta* and *O. spermoides* further share the presence of crystalloid SCBs, which are present in noticeable abundance within series *Hemiorbilia* only here and in *O. angustoaristata* and *O. breviclava*. *O. occulta* differs from *O. spermoides* in shorter spore tails, the presence of distinct exudate over the ± swollen paraphysis apices, and in a thinner marginal excipulum composed of a less developed textura porrecta, the cortical cells of which do not form hyphoid agglutinated hairs, also in a flat hymenium. For the differences to *O. austroocculta* see p. 735.

Variation in *O. occulta* was observed in the paraphysis apices, some of which were medium to strongly inflated, but in other apothecia of the same population only slightly so. Also the length of glassy processes and the thickness of apothecia and basal ectal excipulum varied considerably. One of the two specimens on *Malus* was immature and grew as a mixture with the lectotype of *O. regalis* (M.C. Cooke 2778, see under *O. regalis*, p. 775, and IVV: H.B. 5343). In the mature specimen on *Malus* (J.B. Ellis NAF 438) and the sample from Georgia the spores were shorter (†7–10 × 2.7–3.2 µm) than in those on *Vitis* and *Cornus*.

Type studies. In the protologue of *Calloria occulta*, Rehm (1885) mentioned two collections: J.B. Ellis NAF 142 and 848, both 'on outer bark of living grape vine'. Two duplicate series of one of them (Ellis 848, Jan. 1882) were distributed as Rehm Ascomyc. 770 and J. Kunze Fungi Sel. Exs. 282. Specimens of these two series exist at M. Although Rehm mentioned besides Rehm 770 also Kunze 282 and Ellis 142, it must be assumed that his description is solely based on Rehm 770. In the present study, Rehm's specimen Ascomyc. 770 was thoroughly investigated from a specimen in M (M-0206545, Pl. 354: 1). This is designated here as **lectotype** of *O. occulta*. The specimen from Georgia (on indet. angiosperm, TF018, GXU 1467), from which a sequence was gained, is designated here as **epitype** of *O. occulta* (Pl. 355: 4).

Duplicate specimens of Rehm 770 in M-0206544, S-F9973, and S-F9974 were not studied, but a duplicate in HBG (Pl. 355: 1). This was later labelled '*Orbilia cruenta*', probably based on Seaver's (1951) opinion of a synonymy between these two taxa. Rehm (1885) described the spores as oval, with a long filiform lower part, 15 × 3 µm, whereas in the present reexamination distinctly shorter spores were found. The apothecial size stated in the protologue ('0.3–7 mm') is clearly an error for 0.3–0.7 mm.

Also NAF 142 was studied from a duplicate in M (as '*Peziza vinosa*'). This remained unidentified because no spores could be found. The strongly truncate, thin-walled ascus apex suggests that it does not belong in section *Hemiorbilia*. The asci are narrower [†47–50(–65) × 3.5–4.5 µm], the paraphyses apically hardly inflated and covered by a 1 µm thick exudate, and the glassy processes up to 20 µm long. The substrate is decorticated angiosperm wood, while the label suggests 'decaying bark and wood'.

Misapplication. Because of a strong macroscopical resemblance, J.B. Ellis (NAF 438), M.C. Cooke (nr. 2778), and later authors confused *O. occulta* and *O. regalis*, although these species have very differently shaped ascospores and paraphyses. In the two specimens preserved at K and issued as *Peziza regalis*, both species grew in association in Cooke 2778 (lectotype of *O.*

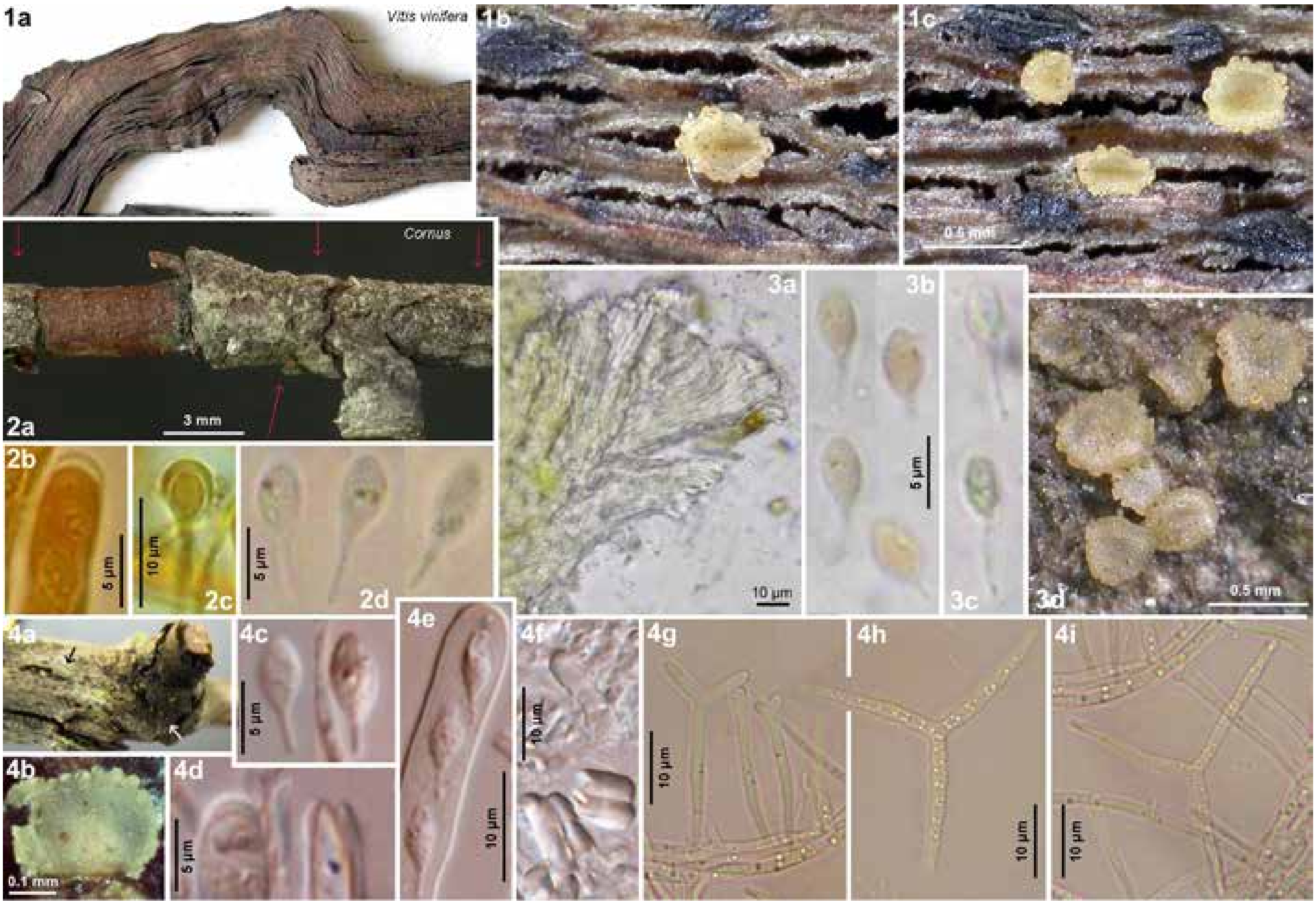


Plate 355. **1–4**: *Orbilia occulta*. – **1a**. detached bark of *Vitis vinifera* (inner surface); **2a**. dead corticated xeric branch of *Cornus*; **4a**. corticated twig of indet. angiosperm; **1b–c**, **3d**, **4b**. rehydrated apothecia; **3a**. marginal ectal excipulum in median section; **4f**. glassy processes; **2b**, **4d**. ascus apices; **4d** right: apex of emptied ascus with slit-like opening; **2c**. paraphysis apex; **2d**, **3b–c**, **4c**, **e**. ascospores; **4g–i**. conidia on reduced conidiophores (from culture). – Dead state (**2b–c** in KOH+IKI, **2d**, **3a** in KOH, **3b** in KOH+CR, **3c**, **4c–f** in H_2O). – **4**: phot. Y.Y. Shao. — **1a–c**. Rehm 770 (isolectotype, HBG): USA, New Jersey, on *Vitis*; **2a–d**. H.B. 7402a: North Carolina, on *Cornus*; **3a–d**. N. Amer. F. 438 (K(M) 180561): unlocalized (?New Jersey), on *Malus*; **4a–i**. GXU 1467 (epitype): Georgia, Tifton, on indet. angiosperm.

regalis), while only *O. occulta* could be detected in Ellis NAF 438. In Cooke 2778 the identity of the *O. occulta* population is somewhat uncertain because no spores could be found, but its affiliation in section *Hemiorbilia* is beyond doubt.

Rehm (1891: 459) referred German collections from Mittelfranken and Thüringen on detaching bark of *Malus* to *O. occulta*. Two from Mittelfranken exist in S (VIII.1866, Neuhof and Sugenheim, S-F9975, 9976, as *O. cruenta*) and carry the note '*Calloria occulta* mihi, spec. nov.', but were not cited in the protologue and were not examined by us. Several later authors used the name *O. occulta* for European collections which possibly all represent *O. aristata*. Seaver (1951: 158) referred *O. occulta* to synonymy with *O. cruenta* Schwein., however, the identity of *O. cruenta* is unclear (see p. 1668), as is the origin of Seaver's description of *O. cruenta* which does not mention any spore tails.

Reexamination of the two Macaronesian collections reported by Korf (1992) under the name *O. occulta* revealed distinct differences in spore shape between them, which is already obvious from his sketches. Ascus apical thickenings are absent in both collections, which are treated here as members of two different series of section *Aurantiorubrae*: *O. euphorbiae* in series *Regales* (Pl. 401: 3) and *O. pisciformis* in series *Commatoideae* (Pl. 419: 2).

Anamorph. The conidia obtained by Y.Y. Shao in pure culture resemble those of *Trinacrium subtile* but are smaller and with narrower stipe and arms (Shao et al. 2018; Pl. 355: 4g–i). In this culture also small, subglobose, light brown conidia-like structures developed singly on short hyaline side branches, which where tentatively classified in Shao et al. (l.c.: fig. 1: 4c) as chlamydospore-like bodies. Although brown-walled cells have so far never been seen in pure culture of *Orbiliomycetes*, it appears from the single available photo that these structures emerged from the hyphae of the *Orbilia*.

Phylogeny. An ITS sequence was gained by Y.Y. Shao (Shao et al. 2018) from pure culture of the sample from Georgia. In our phylogenetic analysis it clustered strongly (ITS) or medium supported (ITS+LSU) in a clade with *O. spermoides* (Phyls 9, 13), here called *occulta-spermoides* clade, though with an ITS distance of 9%. A short piece of LSU (~150 nt) comprising the partial D1 region shows a 4.5% distance (7 deviating nt). No chromatograms were available for this isolate to verify the two sequences.

The *occulta-spermoides* clade consistently clustered as a sister group of the *aristata-clavuliformis* clade. This placement received strong support in our ITS analysis (Phyl. 12) or the combined analysis of SSU+ITS+LSU in Baral et al. (2017b), medium support in the present combined analysis of ITS+LSU (Phyl. 9), or no support based on LSU (S13).

Ecology. *O. occulta* is so far only known from three sites in eastern North America, growing on slightly to medium decayed bark (also wood) of xeric twigs and branches of *Cornus*, *Malus*, and *Vitis*. Two sites are located in the warm-temperate humid lowlands of New Jersey and cold-temperate humid highlands of southern Appalachian Mountains, and one in the subtropical humid lowlands of Georgia.

Specimens included. **USA**: **New Jersey**, Newfield, unlocalized, branch of *Vitis vinifera*, on bark, I.1882, J.B. Ellis (NAF 848, Rehm 770, M-0206545, **lectotype**; H.B. 5054a ø; M-0206544, HBG, **isolectotypes**). – ibid., branch of *Malus domestica*, on bark, undated, J.B. Ellis (Cooke 2778, K(M), immature [mixture with *O. regalis*], H.B. 5344 ø). – Unlocalized, branch of *M. domestica*, on bark, undated, J.B. Ellis (N. Amer. F. 438, as *Peziza regalis*; K(M) 180561, as *Orbilia regalis*; H.B. 9769 ø). – **North Carolina**, Appalachian Mts., Blue Ridge Mts., 31 km E of Franklin, 8 km NE of Cashiers, Big Green Mt., Panthertown Valley, 1200 m, twig of *Cornus*, on bark & wood, 20.V.2003, W. Jaklitsch (W.J. 2174 ø, H.B. 7402a). – **Georgia**, 7 km NNW of Tifton, Black Shank Farm, 105 m, branch of indet. angiosperm, on bark, 8.V.2015, Y.Y. Shao (GXU 1467, **epitype**, TF018, anam. cult., doc. vid., sq.: MG742398, MG742399).

Orbilia austroocculta Baral & G. Marson, **sp. nov.**, MB 813615 — Pls 356–357

Etymology: named after the occurrence in Australia and the similarity with *O. occulta*.

Typification: Western Australia, Wannamal, branch of *Acacia*, 4.IX.2006, G. Marson (ex H.B. 8582a, MEL 2389241, holotype).

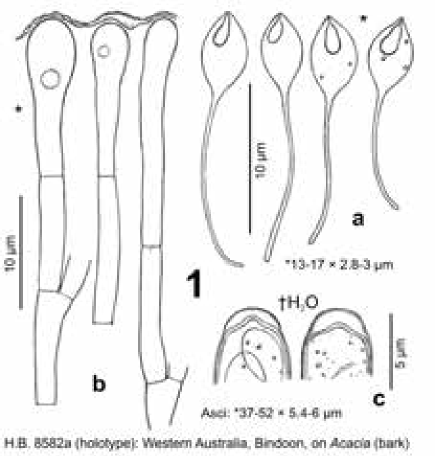


Plate 356. **1**: *Orbilia austroocculta*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices.

Latin diagnosis: *Similis* Orbiliae occultae *sed ascosporae apice magis acutae, cauda multo longiore, cellulae vivae excipuli marginalis absque corpusculis crystalloideis. Habitat ad corticem putridum rami sicci* Acaciae *in zona subtropica semihumida Australiae meridio-occidentalis.*

Plate 357. **1**: *Orbilia austroocculta*. – **1a**. semihumid Eucalypt open woodland, fallen *Acacia* tree; **1b**. dead corticated xeric branch of *Acacia* (rehydrated); **1c–f**. rehydrated apothecia; **1g**. median section of ectal excipulum near margin; **1h**. id., marginal glassy processes agglutinated as teeth; **1i–k**. mature asci; **1l**. ascus apex; **1m**. ascospores; **1n**. conidium from substrate. – Living state, except for **1j–k** (in KOH+IKI), **1l** (in H_2O), right ascus in **1i**, upper spore in **1m**. — **1a–n**. H.B. 8582a (holotype): Western Australia, Bindoon, on *Acacia*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.28–0.75(–1) mm diam., 0.15–0.2 mm high (receptacle 0.09–0.11 mm), bright orange, hardly translucent, round to elliptical, scattered; disc slightly concave to flat, margin distinct, 0–40 µm protruding (including teeth), with prominent white teeth; with a hidden stipe 0.1 × 0.1 mm, erumpent from holes or cracks in periderm; dry ± hysterioid. **Asci** *37–52 × 5.4–6 µm, †33–40 or 46–60 × 4.5–5.3 µm, 8-spored, spores *1–2-seriate, 1(–2) lower spores inverted (not mixed), pars sporifera *27 µm long; **apex** (†) ± hemispherical, dome †1.1–1.4 → 0.7–0.8 µm thick, with small apical chamber; **base** with short to medium long, ± thick, flexuous stalk, L-shaped. **Ascospores** */†13–17 × 2.8–3 µm, with 5–5.5 µm long, broadly fusoid head and sharply differentiated, long and very narrow, basally uninflated tail *(6–)7.5–11.5(–12.5) × 0.3 µm (†0.2 µm), apex subacute to acute or almost acuminate († acute to acuminate), tail straight to often slightly or medium curved; **SBs** *2–2.5 × 0.7–1.1 µm, tear- to pear-shaped, apically narrowed to a small point, with or without very short filum. **Paraphyses** apically slightly to medium clavate, terminal cells *12–20 × 2.5–4.3 µm, lower cells *10–14 × 1.7–2.1 µm; unbranched at upper septum, hymenium pale orange. **Medullary excipulum** hyaline to light orange, 40 µm thick, of dense, horizontally oriented textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** hyaline, light orange towards margin, of thin-walled, vertically oriented t. angularis-globulosa from base to submargin, 50 µm thick near base, cells *(7–)10–16(–25) × (6–)8–13(–16.5) µm; 15–20 µm thick near margin, outer part of t. prismatica-porrecta oriented at a 10–20° angle to the surface, marginal cortical cells *6–13 × 2.5–4 µm; **glassy processes** 30–100 × 2–3 µm, high-refractive, stratified, curved inwards, coherent to form distinct teeth. **Anchoring hyphae** sparse, ~2 µm wide. **SCBs** in paraphyses globose, inconspicuous, 1–1.5 µm diam., in ectal excipulum 2–2.5 µm diam. **Exudate** over paraphyses and glassy processes 0.3–1(–1.7) µm thick, granular-cloddy to continuous, subhyaline, ± firmly attached. — **ANAMORPH**: unknown (but see below).

Habitat: collected 0.5–1.5 m above the ground, ± corticated, 10–11 mm thick branch of *Acacia* sp., on very decayed bark (bast), strongly greyed, quite many green algae. **Associated**: *Orbilia albidorosea*, *O. austroregalis*, *O. pleiocrescens*, crustose lichens. **Desiccation tolerance**: fully viable for at least 2 months, some immature asci and many paraphysis and excipular cells still alive after 11 months. **Altitude**: 272 m a.s.l. **Geology**: Archean granulite with granitic gneiss (red-brown soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia austroocculta* closely resembles the North American *O. occulta* and *O. spermoides* in the ascospores having short and broad heads and abrupt, very narrow tails. From *O. occulta* it differs in more acute spore apices and much longer tails, and from *O. spermoides* in clavate paraphyses covered by exudate and in narrower spore heads. From both species *O. austroocculta* further differs in the absence of crystalloid SCBs.

Anamorph. On the substrate three different kinds of conidia were observed: a trinacrium-like conidium with slightly upwards curved arms, a multiarmed dicranidion-like conidium, and K-shaped, curucispora-like conidia with curved arms (the latter probably belonging to a *Hyalorbilia*). The trinacrium-like conidium would best fit the known anamorphs of series *Hemiorbilia*.

Ecology. *O. austroocculta* is only known from a single collection on rotten bark of a xeric branch of *Acacia* in a subtropical semihumid eucalypt woodland (with *Macrozamia*) in southwestern Australia (Jarrah Forest ecoregion).

Specimens included. **AUSTRALIA**: **Western Australia**, Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 271 m, branch of *Acacia*, on bark, 4.IX.2006, G. Marson (ex H.B. 8582a, MEL 2389241, **holotype**, anam. substr.)

Orbilia spermoides Baral & G. Marson, **sp. nov.**, MB 813616 — Pls 358–359, Map 61

Etymology: named according to the sperm-shaped ascospores.

Typification: USA, Arizona, Grand Canyon, Tusayan, branch of *Pinus edulis*, 28.VIII.1994, G. Marson (ex H.B. 5227a, M-0276588, holotype).

Latin diagnosis: *Similis* Orbiliae occultae *sed exsudato paraphysium absente vel minute granuloso, cellulae vivae paraphysium corpuscula crystalloidea continentes, ascosporae cauda longiore, corpuscula refringentia majora, apothecia majora. Habitat ad corticem leniter vel valde putridum ramorum siccorum coniferarum in zona temperata ad boreale subhumida ad humida Americae septentrionalis et orosubmediterranea Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1.5(–2.8) × (0.35–)0.5–1 mm, (0.15–)0.2–0.25(–0.3) mm high (receptacle 0.12–0.14 mm), (pale to) light to bright orange-rose, round or broadly to narrowly elliptical if growing in clefts, scattered to ± gregarious; disc strongly concave to flat, margin with prominent, white, pubescent teeth 50–130 × 50–100 µm, rising 30–120 µm above disc, rarely smooth; stipe absent or ± distinct, obconical, 0.1–0.2 × 0.2–0.35 mm, superficial or often distinctly erumpent from outer layers of bark; disc dry nearly closed, large apothecia then ± hysteriform, bright to deep orange. **Asci** *(58–)65–80(–103) × (5–)5.5–6.7(–7.3) µm {5}, †(46–)50–70(–74) × (4.2–)5–5.5(–6.5) µm {2}, 8-spored, spores (*) subbiseriate, (0–)1–2(–3) lower spores inversely oriented {5} (not or sometimes mixed), pars sporifera *30–35(–45) µm long; **apex** (†) hemispherical to slightly truncate, dome †0.7–1.3 → 0.4–0.8 µm thick {4}, with ± indistinct apical chamber; **base** with short to long, medium thick, flexuous stalk, T-, L- or h-shaped. **Ascospores** *(9–)12–17(–18.5) × 3.2–3.8(–4) µm {4}, *15–18.5 × 3.2–3.5 µm {France}, †10–13 × 2.8–3.2 µm wide {2}, sperm-shaped: with broadly ellipsoid-fusoid head 5–6(–7) {4} or 6–7(–8) {France} µm long and sharply diffenentiated filiform tail ((3–))(5–)7–9.5(–11) × 0.2–0.5 µm (†0.2–0.3 µm), apex obtuse, also rounded or subacute, base of tail not or only slightly inflated to *0.5(–0.7) µm, head sometimes slightly inequilateral, tail straight or slightly curved; **SBs** *(1.8–)2–2.5(–2.8) × 1.2–1.6(–1.7) µm {5}, broadly tear- to pear-shaped, apically narrowed to a ± small point. **Paraphyses** apically uninflated, also slightly to medium clavate or spathulate-lageniform, straight or often slightly to strongly flexuous, terminal cells *(11–)13–25(–28) × (1.7–)2–3(–3.5) µm {4}, lower cells *8–15.5(–17.5) × 1.7–2.6 µm {4}, †1.2–1.6 µm wide; not or rarely branched at upper septum (exceptionally below apex); hymenium light orange-rose. **Medullary excipulum** in total 50–130 µm thick, usually 2-layered: upper layer 20–40 µm thick, of light orange-rose, ± horizontally oriented, dense textura porrecta-intricata with a few inflated cells; lower layer 30–100 µm thick, of hyaline, dense to rather loose t. intricata with many inflated cells, medium to very sharply delimited. **Ectal excipulum** towards margin pale to light orange-rose, from base to mid flanks of thin-walled († slightly gelatinized), vertically oriented t. angularis(-prismatica), (35–)50–70 µm thick near base, cells *9–24 × 7.5–16 µm {4}; 20–40 µm thick at mid flanks, 20–70 µm at margin, at mid flanks or margin of a thick t. porrecta oriented at a 0–45° angle to the surface {5}, forming fascicles of agglutinated cell rows or sometimes free **hairs** ~30–60 µm long, 1–4-septate, individual cells *(9–)12–20(–25) × 3–4.5(–6) µm {3}, **glassy processes** 10–70 × (2.5–)3–4(–5) µm {5}, rarely only 3–6 µm long (exceptionally absent), high-refractive, stratified or not, slightly to strongly outwards curved, sometimes hooked, cell rows and glassy processes coherent to form hairy teeth at mid flanks and margin. **Anchoring hyphae** sparse to abundant, */†2–3.7 µm wide, walls 0.2–0.3(–0.5) µm thick {2}, gelatinized or not. **SCBs** in paraphyses and excipular cells from base to margin crystalloid, hyaline to pale orange, 2.8–7 × (1.5–)2–3(–4) µm {5}, also globose. **Exudate** absent or finely granular, 0.1–0.3 µm thick {5}. — **ANAMORPH**: trinacrium-like (from ascospore isolate {1} and natural substrate {5}). **Conidiophores** not seen. **Conidia** 2-armed (T-shaped), total size *20.5–32 × 18–33 µm (†21–23 × 19.5–26.5 µm) {4}, stipe *16–26 × 3.1–4.5 µm (†14–17.5 × 3.5–4 µm), (3–)4–5(–6)-septate, arms ± tapering, distinctly bent downwards, */†8–15 × 3.5–4.2 µm, (1–)2–3(–4)-septate, 1 unbranched phragmoconidium seen in pure culture: *30 × 4 µm, 5-septate.

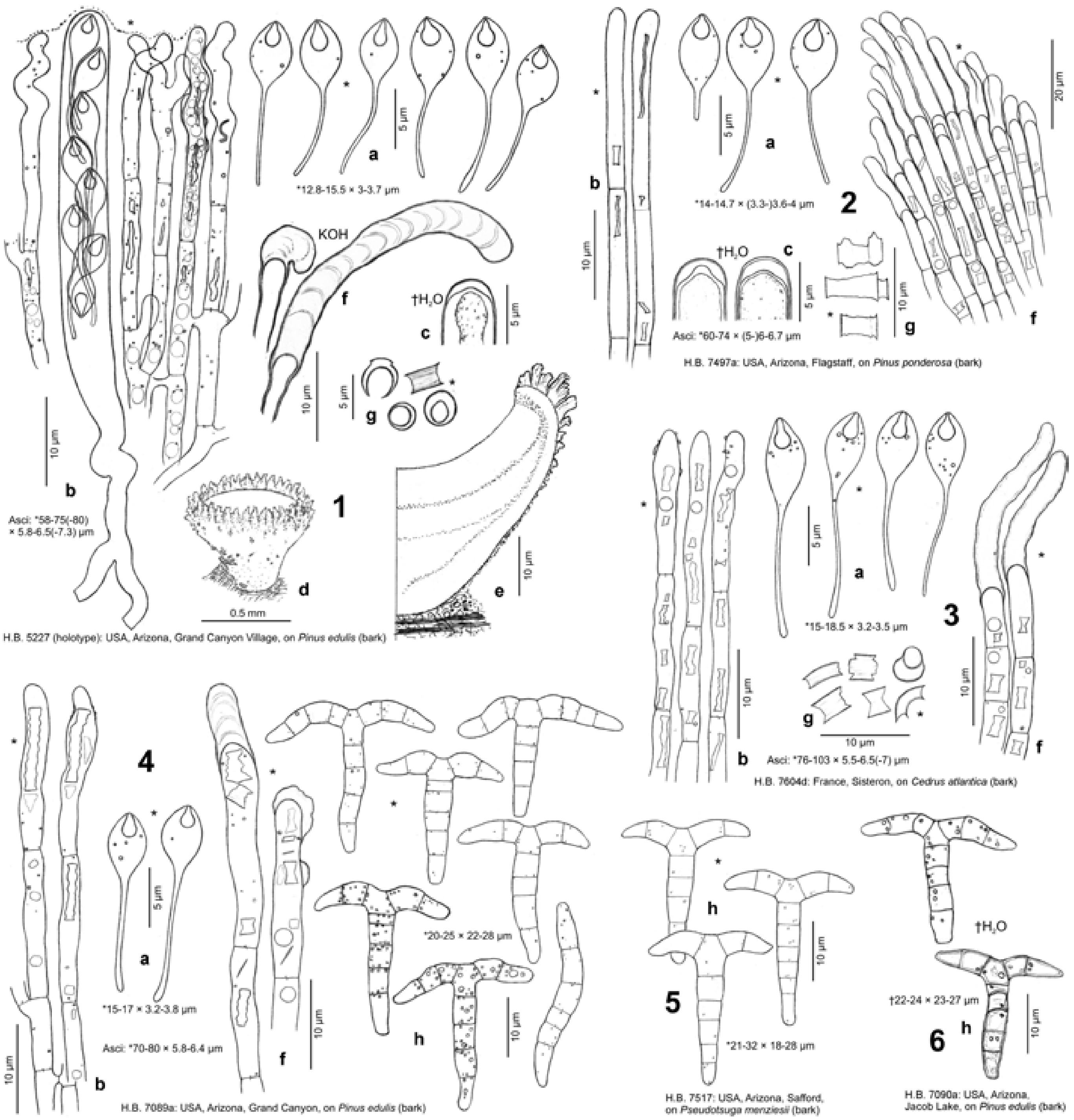


Plate 358. **1–6**: *Orbilia spermoides*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium (rehydrated); **e**. apothecium in median section; **f**. id., marginal ectal excipulum, cortical cells with glassy processes; **g**. crystalloid SCBs in lower parts of ectal excipulum; **h**. conidia from substrate (**4h**, **6h**) and pure culture (**5h**).

Habitat: collected 0.5–5 m above the ground on still-attached, corticated or sometimes nearly decorticated, 6–23 mm thick twigs and branches of living or recently dead young or old trees of *Cedrus atlantica* {1}, *Pinus edulis* {3}, *P. ponderosa* {2}, *Pseudotsuga menziesii* {2}, branches often curved down towards ground, on slightly to strongly decayed, partly loosely attached bark {8} (periderm & bast), usually growing in cross clefts of bark, often in large numbers, exceptionally a few apothecia on wood {2} in cracks through bark, more or less greyed, sometimes covered by green algae. **Associated**: *Caloplaca holocarpa* {1}, *Carestiella ?schizoxyloides* {1}, *Claussenomyces pseudotsugae* {1}, *Cryptodiscus muriformis* {1}, ?*Flavoparmelia* {1}, *Hyalorbilia orbilicola* (parasitic on *O. flagellispora*) {1}, ?*Lecidea* sp. {3}, *Melanohalea* sp. {1}, *Orbilia ?clavuliformis* {1}, *O. flagellispora* {1}, *O. multimacroasca* {1}, *O. phanosoma* {1}, *O. subclavuliformis* {1}, *Parmelia sulcata* {1}, '*Patinella*' *abietina* {1}, *Propolis ?strobilina* {1}, *Pseudevernia intensa* {1}, *Sclerococcum* sp. {4}, *Usnea ?parvula* {2}. **Desiccation tolerance**: fully viable for 19 months, conidia still alive after 2 years. **Altitude**: 2068–2820 m a.s.l. (North America), 1447 m (Europe). **Geology**: Permian lime- & sandstone; granite, andesite, rhyolite, gneiss, basalt. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia spermoides* strongly resembles the angiosperm-inhabiting *O. occulta* in spore shape and glassy processes, but is readily separated by the paucity of exudate, the uninflated paraphysis apices, the hyphoid agglutinated cell rows at the margin, larger and thicker apothecia, longer spore tails, larger SBs, and particularly by the presence of crystalloid SCBs in paraphyses and excipular cells. For the delimitation from *O.*

Plate 359. **1–3**: *Orbilia spermoides*. – **2a**. Douglas fir mixed forest in Pinaleno Mts.; **1a–b**, **2b**, **d**, **3a–b**. rehydrated apothecia; **1c–d**, **2c**. dry apothecia; **1e**. apothecium in median section; **3d**, f. id., marginal region with glassy processes; **3c**. id., basal ectal excipulum, cells with crystalloid SCBs; **1f**, **3e**. asci with mature ascospores; **1g**. conidia from substrate. – Living state, except for ascus in **3e**. — **1a–g**. H.B. 7497a: USA, Arizona, Flagstaff, on *Pinus*; **2a–d**. H.B. 7517: ibid., Safford, on *Pseudotsuga*; **3a–f**. H.B. 7604d: France, Sisteron, on *Cedrus*.

aristata (p. 709) and *O. austroocculta* (p. 733) see under these species. In the hyphoid cell rows forming a thick t. porrecta at the margin the species resembles *O. fimbriata*, while other members of series *Hemiorbilia* show usually only a thin outer layer of t. porrecta.

Variation. In *O. spermoides* the glassy processes are remarkably variable in length. They are sometimes completely absent on most of the marginal cortical cells, or form very short caps on the agglutinated marginal cell rows. Possibly the processes got lost as they easily break at their base. The single

Map 61. Known distribution of *O. spermoides* in North America.

European collection differs from the North American merely in slightly longer spore heads and slightly longer asci.

Anamorph. *O. spermoides* formed trinacrium incurvum-like conidia in pure culture and on the natural substrate, in contrast to species related to *O. aristata* which have larger trinacrium subtile-like conidia and higher-branched conidial types.

Phylogeny. Two sequences obtained from the same sample from Pinaleno Mts. on *Pseudotsuga*, one from an ascospore isolate and one from apothecia, comprise the S1506 intron, ITS, and LSU, one also SSU. The two sequences surprisingly differ in the ITS region by 4 nt, in the intron by 1 nt, and in the LSU by 1 nt.

In our phylogenetic analyses, *O. spermoides* formed with *O. occulta* with rather high distance a supported clade (for details see under *O. occulta*, p. 732). The species is rather distant from the *aristata-clavuliformis* clade (11–15 % in ITS, 3.3–4.7 % in LSU D1–D2), also the intron shows a very high distance to all other members of section *Hemiorbilia* which have it (> 20 %).

Ecology. *O. spermoides* inhabits slightly to strongly rotten bark of xeric twigs and branches of gymnosperms. In western North America it was found on *Pinus* and *Pseudotsuga* in cold-temperate subhumid pinyon-juniper woodlands and cold-temperate to boreal humid ponderosa pine, Douglas fir, and Engelmann spruce forests of the Colorado Plateau (Grand Canyon, Mogollon Rim) and Chihuahuan Desert (Pinaleno Mountains). The single record from southern Europe on *Cedrus* was in an orosubmediterranean humid open mixed forest on the south-exposed slope of the Lure mountain range in calcarean Southern French Prealps.

Specimens included. **USA**: **Arizona**, Grand Canyon, Kaibab Plateau, 28 km ESE of Fredonia, 13 km NNW of Jacob Lake, 2115 m, branch of *Pinus edulis*, on bark, 17.V.1995, G. Marson (H.B. 7090a, anam. substr.). – Coconino Plateau, 8.5 km NNE of Tusayan, Mather Point, 2177 m, branch of *P. edulis*, on bark, 13.VI.2000, G. Marson (H.B. 7089a, anam. substr.). – 3 km N of Tusayan, 2068 m, branch of *P. ponderosa*, on bark, 28.VIII.1994, G. Marson (ø). – ibid., branch of *P. edulis*, on bark, 28.VIII.1994, G. Marson (M-0276588, **holotype**; H.B. 5227a, **isotype**). – Mogollon Rim, 16 km NW of Flagstaff, San Francisco Peaks, 6 km WSW of Humphreys Peak, 2550 m, branch of *P. ponderosa*, on bark, 17.VI.2003, G. Marson (H.B. 7497a, anam. substr.). – 80 km SSE of Vernon, 8 km SW of Hannagan Meadow, Coronado Trail, 2820 m, branch of *Pseudotsuga menziesii*, on bark, 2.VI.2003, G. Marson (H.B. 9576e ø). – Chihuahuan Desert, 24 km SSW of Safford, Pinaleno Mts., 2.8 km SE of Mt. Graham, 2285 m, branch of *P. menziesii*, on bark, 31.V.2003, G. Marson (H.B. 7517, anam. cult., anam. substr., CBS 140833; sq.: KT215269, KT380068). — **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Alpes-de-Haute-Provence**, 16 km SW of Sisteron, 6.5 N of St.-Étienne-les-Orgues, 2.7 km SW of montagne de Lure, 1447 m, branch of *Cedrus atlantica*, on bark, 8.VIII.2003, G. Marson (H.B. 7604d, anam. substr.).

Orbilia nanosperma Baral & G. Marson, **sp. nov.**, MB 813617 — Pls 360–361

Etymology: named after the small sperm-shaped spores.

Typification: Western Australia, Northcliffe, bark of *Eucalyptus jacksonii*, 16.XII.2001, G. Marson (ex H.B. 7201b, MEL 2389220, holotype).

Latin diagnosis: *Apothecia rehydratata 0.15–0.5 mm diam. (sine dentibus), aurantiaca, sessilia, margine exigue albido-dentata. Asci 8-spori. Ascosporae *5.5–7 × 1.6–1.9 µm, ellipsoideo-fusoideae, cauda basali 2–3.2 × 0.2–0.3 µm praeditae, in statu vivo corpusculum refringens lacrimiformem, ad apicem affixum continentes. Excipulum marginale processis vitreis perlongis, dentes conspicuos formantibus praeditum. Habitat ad corticem separatum, leniter putridum rami sicci* Eucalypti jacksonii *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.4(–0.5) mm diam. (excl. teeth), 0.06–0.16 mm high (receptacle 0.06–0.09 mm), pale to light orange(-rose), round, scattered; disc flat, margin not or scarcely protruding, with 6–13 very prominent whitish teeth (20–)50–100 × (20–)30–70(–100) µm; sessile, superficial; dry with strongly incurved teeth partially or entirely covering the disc. **Asci** *~25–33 × 3.5–4.3 µm, †22–33 × 3–3.7 µm, 8-spored, spores (*) biseriate, 1(–2) lower spores inverted (not mixed), pars sporifera *12–16 µm long (†10–12 µm); **apex** (†) conico-hemispherical, dome †0.8–1 → 0.6 µm thick, in KOH mature 1–1.9 µm, without or sometimes with apical chamber; **base** with short to long, thin, flexuous stalk, L-shaped. **Ascospores** *5.5–7 × 1.6–1.7(–1.9) µm, †5–6.5(–7) × 1.4–1.6 µm, sperm-shaped: with ellipsoid-fusoid head and sharply differentiated filiform tail, head 3.3–4 µm long, apex obtuse to subacute, tail *2–3.2 × 0.2–0.3 µm, not swollen at base, straight or sometimes flexuous, often slightly to strongly geniculate near head; **SBs** *1.3–1.5 × 0.5–0.7 µm, tear- to pear-shaped, apically narrowed to a small point. **Paraphyses** apically uninflated or slightly to medium capitate, terminal cells †(3.5–)8–15 × 1.8–3.5 µm, lower cells †4–7 × 1.8–2.2 µm; unbranched at upper septum. **Medullary excipulum** hyaline, 10–40 µm thick, of medium dense textura globulosa forming horizontal chains, indistinctly to sharply delimited. **Ectal excipulum** of (†) distinctly thick-walled, ± vertically oriented t. globulosa-angularis from base to margin, 20–70 µm thick near base, cells †8–24 × 6–19 µm; 15 µm thick near margin, outermost margin of t. porrecta oriented at a 70–80° angle to the surface, marginal cortical cells †5–9 × 2–2.5 µm; **glassy processes** 10–100 × 2.5–4 µm, high-refractive, brittle, frequently stratified, ends curved inwards, agglutinated to form very prominent teeth. **Anchoring hyphae** medium abundant, †1.7–3.3 µm wide, walls 0.2–0.8 µm thick. **SCBs** in paraphyses globose, ~0.7–1.5 µm diam. **LBs** light yellow-orange

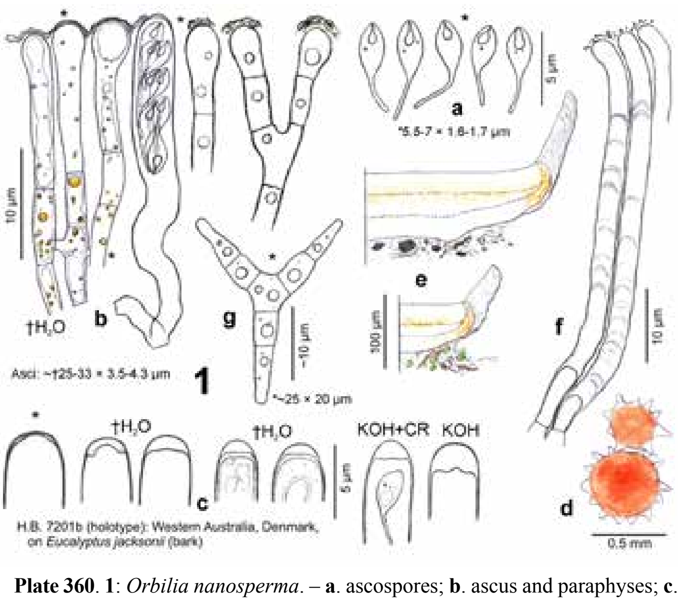


Plate 360. **1**: *Orbilia nanosperma*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. glassy processes on marginal cortical cells; **g**. conidium from substrate.

Plate 361. **1**: *Orbilia nanosperma*. – **1a**. Eucalypt tall open forest (karri tingle), hanging xeric bark of *Eucalyptus jacksonii*; **1b**. outer surface of bark; **1d**, **f**, **h–k**. rehydrated apothecia; **1c**, **e**. dry apothecia; 1l. apothecium in external view; **1g**. asci and paraphyses (in KOH+IKI). — **1a–l**. H.B. 7201b (holotype): Western Australia, Warren, on *Eucalyptus*.

(carotenoids), abundant in lower part of paraphyses and in marginal excipulum, (†) up to 2 µm diam., IKI pale blue-green. **Exudate** over paraphyses 0.2–0.8 µm thick, continuous, finely rough, hyaline, firmly attached; over teeth granular. **— ANAMORPH**: trinacrium-like (presumed, from natural substrate). **Conidiophores** not seen. **Conidia** *~25 × 20 µm, stipe *13 × 3.3 µm, 2-septate, arms *12 × 3.5 µm, 2-septate, straight, distinctly tapering.

Habitat: collected 2–4 m above the ground, on large thin pieces of bark detached from ~60 m tall trees of *Eucalyptus jacksonii*, fallen from high above the canopy, on slightly decayed bast, on outer surface (very exceptionally on inner surface), slightly greyed, covered by a few algae (?*Gloeocapsa*). **Associated**: *Lachnum eucalypticola*, *Orbilia aviaristata, O. lilacina*, *O.* ?*pseudoflagellispora*. **Desiccation tolerance**: mature asci viable after 3 months (a few still after 9 months), ascospores survived for 9 months. **Altitude**: 195 m a.s.l. **Geology**: granite with alkali feldspar, migmatite, diorite, gabbro. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia nanosperma* is easily recognized by its small sperm-shaped ascospores and long triangular marginal teeth, also by comparatively small apothecia. The spores are similar as in *O. aristata* or *O. breviaristata* but much smaller. They also resemble those of *O. saccharifera* (section *Aurantiorubrae*) even in size, but that species differs in lacking an apical dome, longer asci (†33–47 µm), different paraphyses, and in much shorter glassy processes which emerge from thicker, septate cortical cells and which do not form teeth.

Anamorph. Only two rather small trinacrium-like conidia were seen on the natural substrate.

Ecology. *O. nanosperma* was collected on detached, slightly decayed, xeric bark of *Eucalyptus jacksonii* (Red Tingle) in a subtropical semihumid (summer-dry) open (though rather dense) eucalypt (karri-tingle) forest in the Warren ecoregion at the southern end of Darling Range in southwestern Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Warren, 30 km SE of Pemberton, 14 km ENE of Northcliffe, W of Shannon, Middleton Road, 195 m, *Eucalyptus jacksonii*, on bark detached from branches, 16.XII.2001, G. Marson (ex H.B. 7201b, MEL 2389220, **holotype**; MEL 2389282, **isotype**, anam. substr.).

Orbilia aviflagellata Baral & G. Marson, **sp. nov.**, MB 813618 — Pls 362–363

Etymology: named after the ascospores having an inflated apex like a bird's head, but otherwise similar to *O. flagellispora*.

Typification: Western Australia, Mt. Singleton, twig and branch of *Acacia*, 24.XI.2001, G. Marson (ex H.B. 7204b, MEL 2389223, holotype).

Latin diagnosis: *Apothecia rehydratata 0.2–1 mm diam.*, *roseo-aurantiaca*, *sessilia*, *margine exigue albido-dentata. Asci 8-spori. Ascosporae *18.5–25 × 2.8–3.6 µm*, *triangulare-fusoideae*, *asymmetricae*, *cauda basali 13–17 × 0.3–0.4 µm*, *basi valde inflata praeditae*, *in statu vivo corpusculum refringens lacrimiformem*, *ad apicem affixum continentes. Excipulum marginale processis vitreis*, *dentes conspicuos formantibus praeditum. Habitat ad corticem vel lignum putridum ramuli et rami sicci* Acaciae *in zona subtropica semiarida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.25–0.6(–1) mm diam., 0.12–0.17 mm high, pale to light dirty orange-rose, slightly translucent, round, medium to very scattered; disc flat, margin 0–10 µm protruding, with ~15–22 prominent whitish teeth 30–90 × 20–80 µm, these sometimes short or absent; broadly sessile, superficial, dry ± contracted, disc partly closed by the incurved hairs. **Asci** *58–75 × 6.5–7.5 µm, †49–67 × 6–6.6 µm, 8-spored, spores (*) biseriate, 0–2(–3) lower spores inverted (± not mixed), pars sporifera *30–38 µm long; **apex** (†) hemispherical to slightly truncate, dome †1.5–1.8 → 1–1.2 µm thick (KOH 2.5–3 → 1.5–2 µm), with distinct apical chamber; **base** with short to medium long, ± thick, flexuous stalk, L- to Y-shaped. **Ascospores** *(18.5–)20–25 × 2.8–3.3(–3.6) µm, †20–25 × 3–3.4 µm, sperm-shaped: with fusoid to fusiform head and sharply edifferentiated filiform tail, head 5.5–7 µm long, apex obtuse to subacute-acuminate, tail 13–17 × 0.3–0.4 µm, always with distinctly swollen, bulbous base */†1.1–1.5 µm thick, head in profile view strongly inequilateral (triangular), tail straight to slightly (sometimes medium) curved; **SBs** *(2.2–)2.7–3.2(–3.5) × 1.3–1.5(–1.7) µm, tear- to pear-shaped, apically narrowed to a ± small point. **Paraphyses** apically uninflated to slightly clavate-capitate, rarely lageniform, terminal cells *(6–)11–20(–25) × 2.2–3(–3.5) µm, lower cells *10–18 × 1.6–2 µm (up to 2.5 µm wide near base); branched only near base. **Medullary excipulum** ± hyaline, 30–50 µm thick, of dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a 5–8 µm thick layer of t. porrecta. **Ectal excipulum** hyaline, towards margin pale orange, of (†) thin-walled to slightly gelatinized, vertically oriented t. globulosa-angularis from base to mid flanks, 30–60 µm thick near base, cells *8–24 × 6–16 µm; 20–35 µm thick at flanks and margin, at margin inner part of t. prismatica-angularis oriented at a 45–90° angle to the surface, outer part of t. porrecta oriented at 30–70°, marginal cortical cells *10–15 × 2.7–3.2 µm, †8–13 × 2–3 µm; **glassy processes** (5–)10–60(–100) × (2–)2.5–3(–3.5) µm, high-refractive, often stratified, straight or partly curved inwards towards end, easily breaking, coherent to form distinct teeth. **Anchoring hyphae** sparse to abundant, *1.8–3.5 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose, (0.7–)1.5–2.5 µm diam. **Exudate** over paraphyses (0.5–)1–3(–4) µm thick, cloddy, hyaline to very pale chlorinaceous, loosely attached; over margin and flanks 1–3 µm thick. — **ANAMORPH**: unknown.

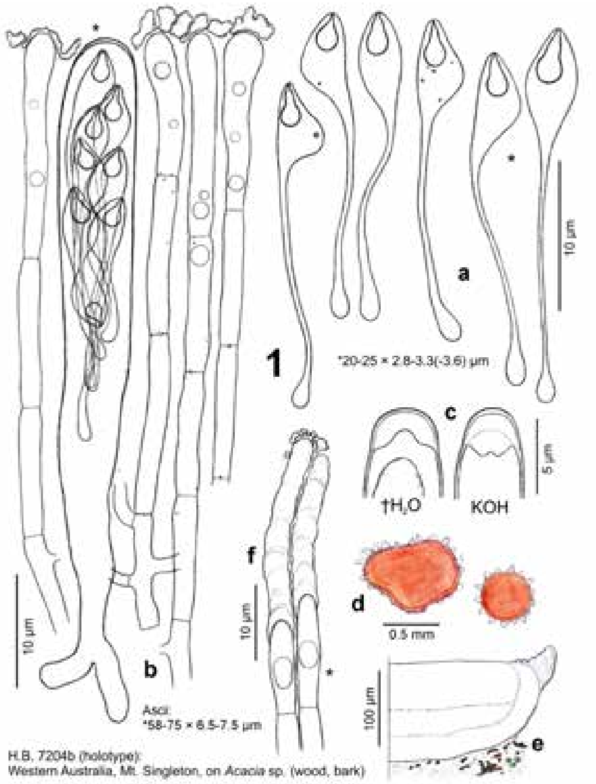


Plate 362. **1**: *Orbilia aviflagellata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. glassy processes on marginal cortical cells.

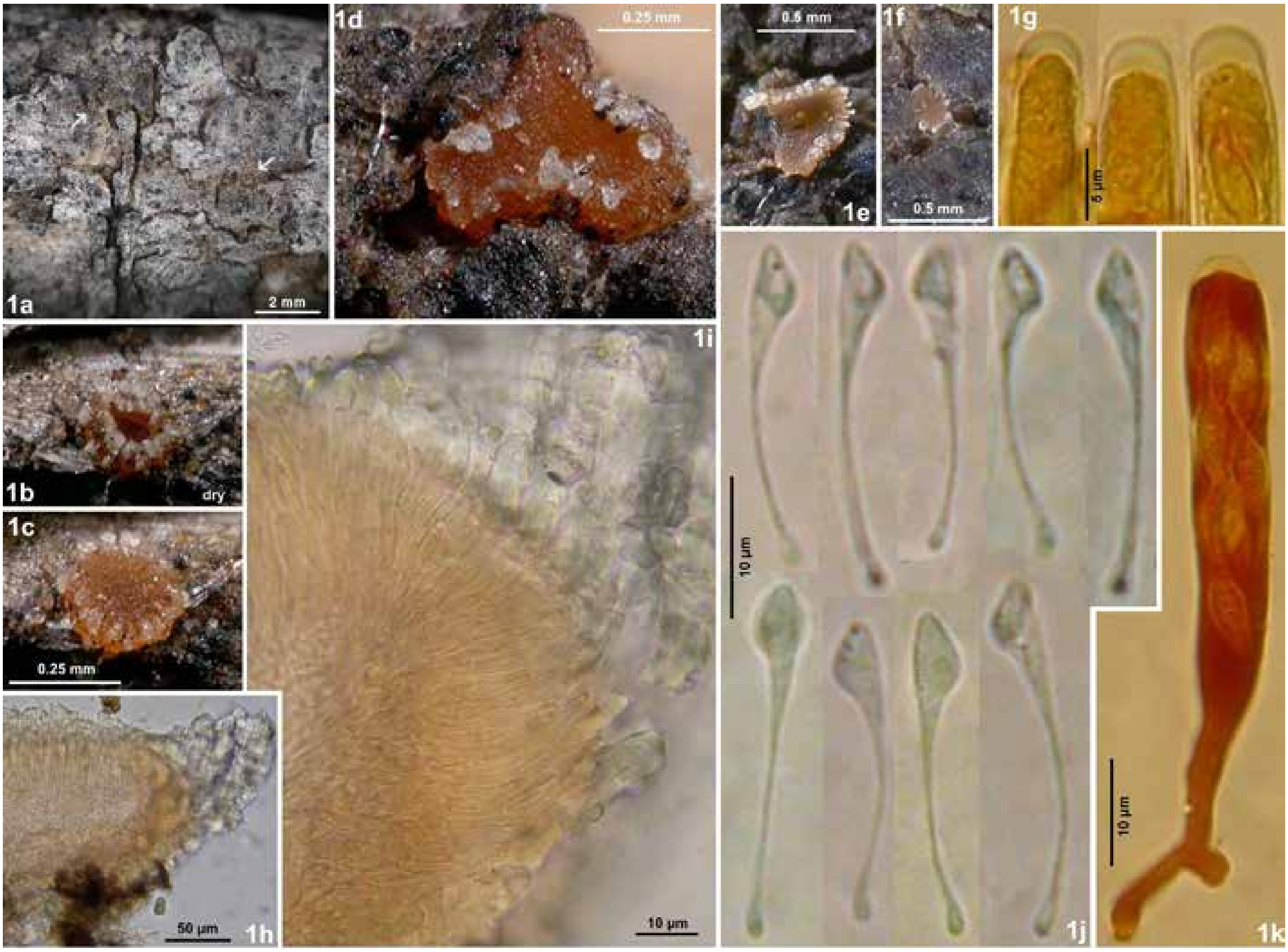


Plate 363. **1**: *Orbilia aviflagellata*. – **1a**. dead corticated xeric branch of *Acacia*; **1b**. dry apothecium; **1c–f**. rehydrated apothecia; **1h**. apothecium in median section; **1i**. id., marginal ectal excipulum with glassy processes; **1g**. ascus apices; **1k**. ascus; **1j**. ascospores. – Dead state (**1g**, **k** in KOH+IKI; **1h–j** in H_2O, lower left 3 spores in KOH). — **1a–k**. H.B. 7204b (holotype): Western Australia, Mt. Singleton.

Habitat: collected 0.5–2 m above the ground, partially to almost entirely decorticated, 2 and 11 mm thick twig and branch of *Acacia* sp., on bark (bast), more rarely on wood, medium to strongly decayed, greyed, algae absent or sparse. **Associated**: *Caloplaca* sp., *Orbilia amberina*, *O. australiensis*, *O. austroobtusispora*, *O. helicoobliqua*, *O. hesperidea*, *O. microserpens*, *O. multiserpens*, *O. myriolilacina*, *O. myriooblique*, *O. nothovinosa*, *O. paraobliqua*, *O. pleioaustraliensis*, *O. pleioaustrocylindrica*, *Ostropales*, ?*Parmelia* sp., *Patellaria* ?*andina*, *Symbiotaphrina* ?*desertorum*, ?*Triblidium* sp. **Desiccation tolerance**: fully viable for at least 18 months. **Altitude**: 380 m a.s.l. **Geology**: Archean sedimentary rock (light ochre soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia aviflagellata* closely resembles the predominantly mediterranean *O. subaristata*, from which it differs in the ascospores having consistently asymmetrical heads. The strongly inequilateral shape of the spore heads is only visible in profile view, whereas in front view the spores perfectly fit those of *O. subaristata*. This peculiar 3-dimensional spore shape was observed in all ~12 apothecia tested. Likewise, the spore length of 19–25 µm was found to be rather constant within the holotype collection. For the similar *O. aviaristata* see below.

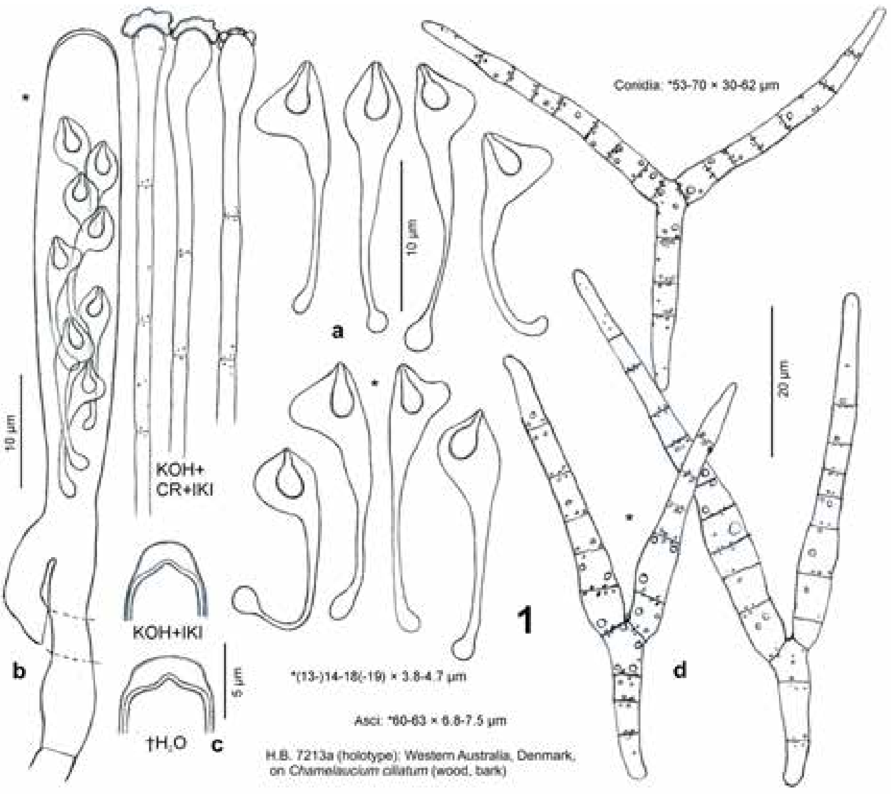


Plate 364. **1**: *Orbilia aviaristata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. conidia from substrate.

Ecology. *O. aviflagellata* grew on ± rotten bark and wood of xeric twigs and branches of *Acacia* in a subtropical semiarid eucalypt open woodland in the Darling Plateau of southwestern Australia, at the border between Avon Wheatbelt and Yalgoo ecoregion.

Specimens included. **AUSTRALIA**: **Western Australia**, Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, W of Lake Moore, 380 m, twig & branch of *Acacia*, on bark & wood, 24.XI.2001, G. Marson (ex H.B. 7204b, MEL 2389223, **holotype**).

Orbilia aviaristata Baral & G. Marson, **sp. nov.**, MB 813619 — Pls 364–365

Etymology: named after the ascospores being similar as in *O. aristata* but with the inflated apex resembling a bird's head.

Typification: Western Australia, Denmark, branch of *Chamelaucium ciliatum*, 15.XII.2001, G. Marson (H.B. 7213a, MEL 2389228, holotype).

Latin diagnosis: *Similis* Orbiliae aviflagellatae *sed ascosporae distincte breviores*, *capitibus magis triangularibus*, *distincte latioribus*, *caudis subapicaliter saepe inflatis*, *dentes apotheciorum pauces*, *latiores*. *Habitat ad corticem vel lignum putridum ramorum siccorum* Chamelaucii *et* Eucalypti *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.6 mm diam. (0.2–0.45 mm excl. teeth), 0.15 mm high (receptacle 0.09–0.1 mm), light orange-rose, not or slightly translucent, ± round, medium to very scattered; disc flat, margin 10 µm protruding, with ~7–10 prominent whitish, ± triangular teeth 60–100 × 60–100 µm; sessile on a stalk-like base 0.05 × 0.22 mm, superficial; disc dry deep orange-red, somewhat contracted but teeth still projecting outwards. **Asci** *60–63 × 6.8–7.5 µm {T}, †38–55(–60) × 5.5–6.8(–7.5) µm {2}, 8-spored, spores (*) biseriate, 0–2 lower spores inverted (not mixed) {2}, pars sporifera *35 µm long, †27–32 µm; **apex** (†) hemispherical to slightly conico-truncate, dome †1.5–2 → 0.7–1.5 µm thick (H_2O or KOH) {2}, with small apical chamber; **base** with short to medium long, ± thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(13–)14–18(–19) × 3.8–4.7 µm (3.5–3.8 µm in front view) {T}, †(11.5–)12.5–16.5 × 3.4–4(–4.3) µm (2.8–3.2 µm in front view) {2}, sperm-shaped: with broadly fusiform head and sharply edifferentiated, filiform to subulate tail, head 4.5–5.5 µm long, apex obtuse to subacute-acuminate, tail 10–14 µm long, upper half or third usually ± widened, base always distinctly swollen (bulbous), */†(1–)1.3–1.6(–1.9) µm thick, head in profile view very strongly inequilateral (triangular), tail straight to often slightly to medium (rarely strongly) curved, 0.3–0.6 µm thick at narrowest part; **SBs** *3–3.5 × 1.3–1.6 µm {T}, tear- (to pear-)shaped, apically narrowed to a small to wide point. **Paraphyses** apically slightly to medium clavate(-capitate), terminal cells †12–19(–23) × (2–)2.5–3(–3.5) µm {T}, lower cells †8–13 × 1.3–1.8 µm {T}; unbranched. **Medullary excipulum** hyaline, 30 µm thick, of medium dense, horizontally oriented textura intricata with many large inflated cells (t. globulosa), medium sharply delimited. **Ectal excipulum** hyaline, of (†) slightly to medium gelatinized (common walls 1–1.5 µm), indistinctly vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 50–60 µm thick near base, cells †9–15 × 7–10 µm {T}; 15–20 µm thick at margin, inner part of t. angularis oriented at a high angle to the surface, outer part of t. prismatica-porrecta oriented at 70–80° (submargin) or 40–60° (upper margin), marginal cortical cells †6–10 × 2.5–3.5 µm {T}; **glassy processes** 10–100 × 2–3.7 µm {T}, high-refractive, stratified or not, ± straight but curved inwards at the end, coherent to form distinct teeth. **Anchoring hyphae** sparse, †1.5–3 µm wide, walls 0.2–0.5 µm thick. **SCBs**: no data available. **Exudate** over paraphyses (0.2–)1–2(–4) µm thick, cloddy, hyaline, firmly attached; over marginal teeth 2–3 µm thick. — **ANAMORPH**: trinacrium-like (presumed, from natural substrate {T}). **Conidiophores** not seen. **Conidia** Y-shaped, total size *53–70 × 30–62 µm, stipe *17.5–25 × 3.5–4.5 µm, 2–3-septate, arms *35–57 × 4–5.5 µm, 6–10 septate, tapering, slightly to strongly diverging, ± straight {T}.

Habitat: collected 0–4 m above the ground, corticated to partially decorticated, 5–12 mm thick branches of *Chamelaucium ciliatum* {T}, trunk of *Eucalyptus jacksonii* {1}, on bark (bast) {2} and wood {T}, at edges of detaching bark {T} or on outer surface of entirely detached

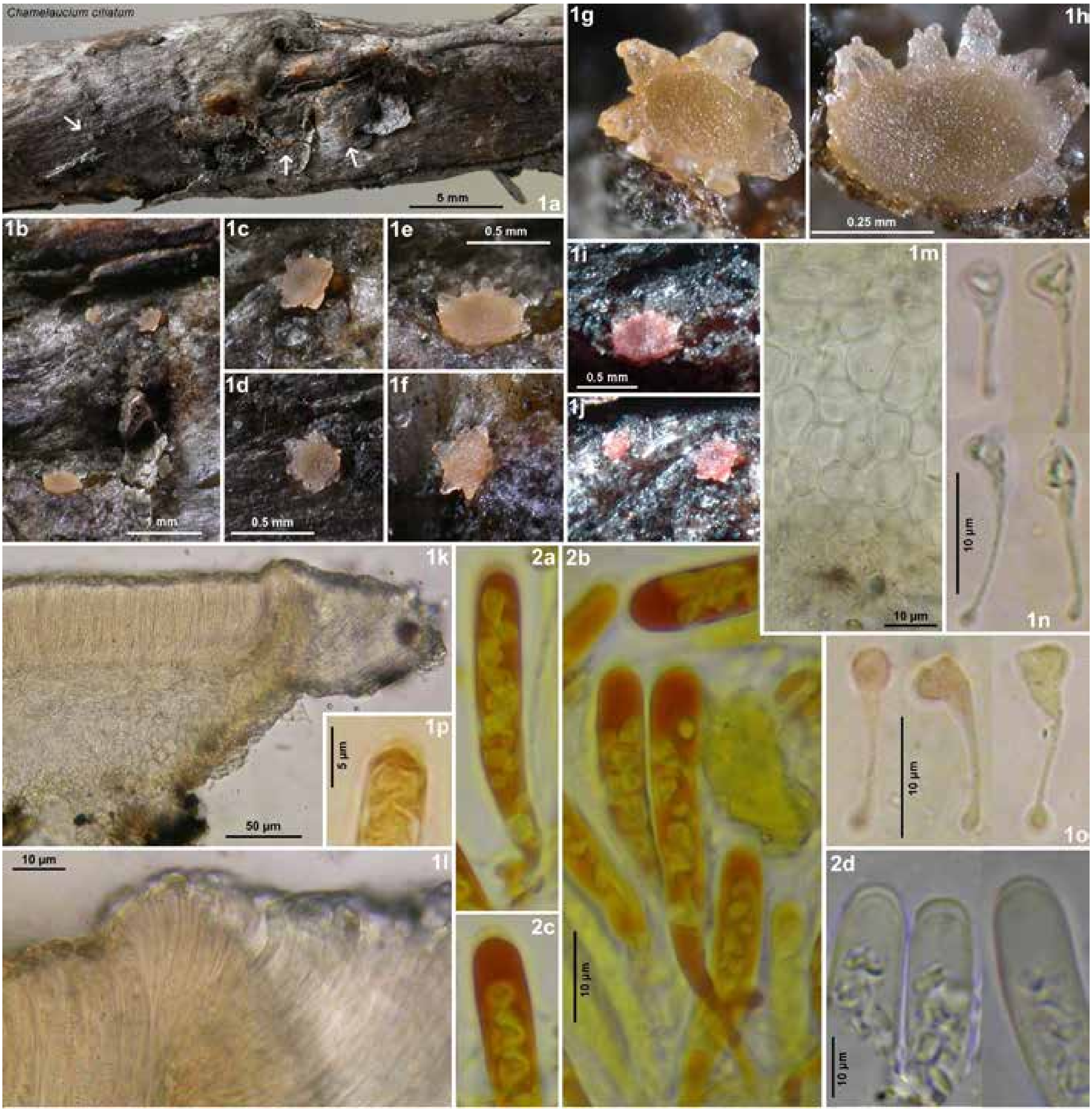


Plate 365. **1–2**: *Orbilia aviaristata*. – **1a**. dead, partially decorticated, xeric branch of *Chamelaucium ciliatum*; **1b–j**. rehydrated apothecia (**i–j**: phot. 2002, **b–h**: phot. 2006); **1k**. apothecium in median section; **1l**. id., marginal ectal excipulum with glassy processes; **1m**. id., basal ectal excipulum; **1n–o**. ascospores; **1p**, **2c–d**. ascus apices; **2a–b**. asci. – Dead state (**1n**, **2d** in H_2O; **1k–m** in KOH; **1o** in KOH+CR, **1p**, **2a–c** in KOH+IKI). — **1a–p**. H.B. 7213a (holotype): Western Australia, Denmark, on *Chamelaucium*; **2a–d**. H.B. 7201e: ibid., Northcliffe, on *Eucalyptus*.

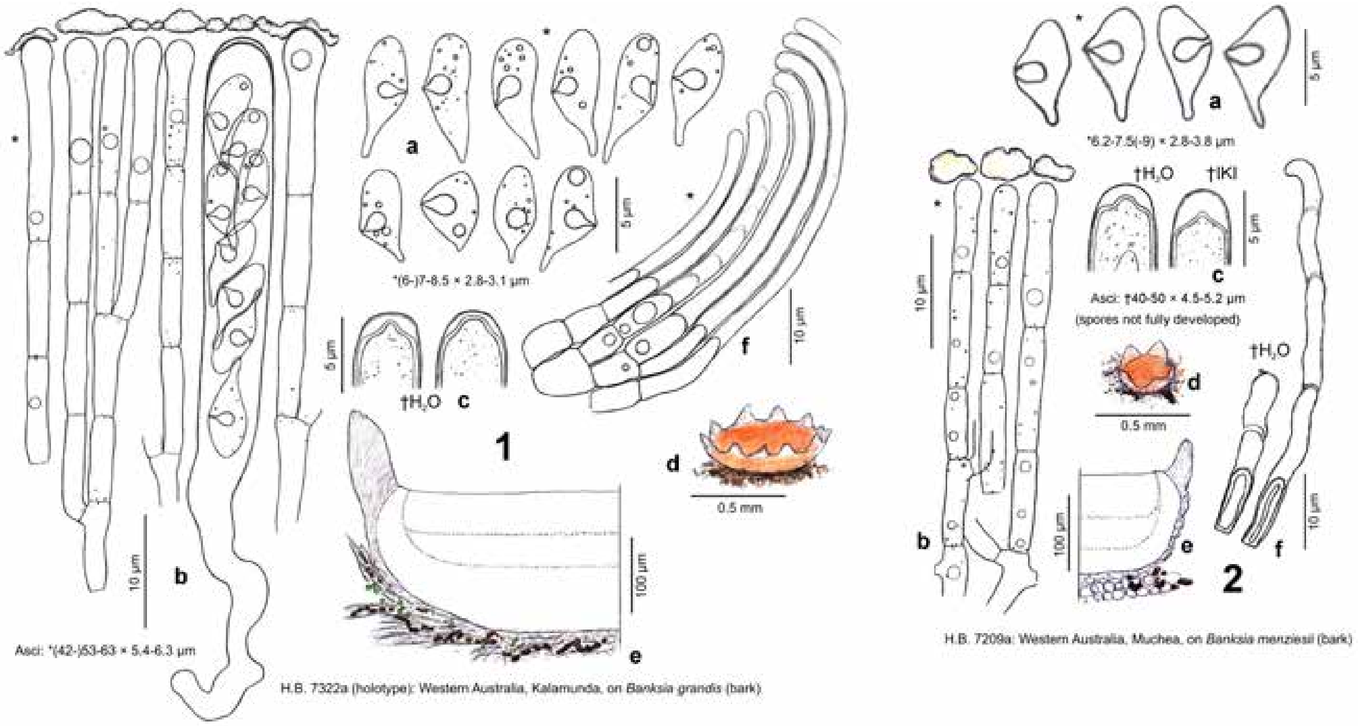
trunk bark fallen from high above (1), 0.1 mm deep slightly to strongly rotten, partly over cracks of periderm, ± greyed, green algae absent or abundant (?*Gloeocapsa*). **Associated**: *Orbilia ?multiaustrocylindrica* {1}, *O. ?subclavuliformis* {1}, *O. triangulispora* {1}. **Desiccation tolerance**: fully viable for at least some weeks, dead in all parts after 9.5 months. **Altitude**: 75–195 m a.s.l. **Geology**: felsic granitic rocks with alkali feldspar, diorite, migmatite, gabbro. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia aviaristata* closely resembles *O. aviflagellata*, from which it is tentatively separated by much shorter ascospores with distinctly wider, more triangular and asymmetrical heads, which often show a craw-like swelling at the transition to the spore tails, also by fewer and more triangular marginal teeth.

Anamorph. Only three conidia were detected on the natural substrate (Pl. 364: 1d). One of them resembles the type of *Trinacrium subtile* but the other two had less divergent arms.

Ecology. *O. aviaristata* was found on rotten bark and wood of xeric branches of *Chamelaucium ciliatum* and on detached fallen bark of *Eucalyptus jacksonii* (Red Tingle) at two distant (100 km) sites in subtropical semihumid eucalypt (karri-tingle) tall and low open forests in the Jarrah Forest and Warren ecoregions in the southern Darling Range and Plateau of southwestern Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Jarrah Forest, 47 km WNW of Albany, 13 km NNE of Denmark, NE of Mt. Lindesay, 75 m, branch of *Chamelaucium ciliatum*, on bark & wood, 15.XII.2001, G. Marson



H.B. 7322a (holotype): Western Australia, Kalamunda, on *Banksia grandis* (bark).

H.B. 7209a: Western Australia, Muchea, on *Banksia menziesii* (bark)

Plate 366. **1–2**: *Orbilia aviceps*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., marginal cortical cells with glassy processes.

(ex H.B. 7213a, MEL 2389228, **holotype**, anam. substr.). – Warren, 30 km SE of Pemberton, 14 km ENE of Northcliffe, W of Shannon, Middleton Road, 195 m, *Eucalyptus jacksonii*, on bark detached from branches, 16.XII.2001, G. Marson (H.B. 7201e ø).

Orbilia aviceps Baral & G. Marson, **sp. nov.**, MB 813620 — Pls 366–367, Map 62

Etymology: named after the ascospores resembling a bird's head.

Typification: Western Australia, Kalamunda, branches of *Banksia grandis*, 13.XII.2001, G. Marson (ex H.B. 7322a, MEL 2389235, holotype).

Latin diagnosis: *Apothecia rehydratata 0.2–0.9 mm diam. (cum dentibus), aurantiaca vel rosea, sessilia vel substipitata, margine exigue albido-dentata. Asci 8-spori. Ascosporae *6–9 × 2.8–3.8 µm, valde clavatae, ex uno latere leniter vel modice protrudentes, asymmetricae, saepe cauda basali 1–1.5 × 0.3–0.5 µm praeditae, corpusculum refringens lacrimiformem, ad protrusionem lateralem affixum continentes. Excipulum marginale processis vitreis, dentes conspicuos formantibus praeditum. Habitat ad corticem putridum siccum ramorum partim vivorum plerumque* Banksiae *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–0.7(–0.9) mm diam. (incl. teeth), 0.1–0.21 mm high (receptacle 0.1–0.15 mm), light to bright orange or rose, ± translucent, round, very scattered or subgregarious in small groups; disc flat, margin 0–10 µm protruding (excl. teeth, 10–100 µm incl. teeth), with 5–16 prominent whitish teeth 20–100 × 30–120 µm; ± broadly sessile or with a distinct stipe 0.07–0.1 × 0.16 mm, superficial to slightly erumpent; disc dry partially to entirely covered by the incurved teeth, bright orange(-rose). **Asci** *(42–)48–56(–63) × 5.4–6.5 µm {2}, †38–50 × 4.5–5.5 µm {3}, 8-spored, spores *1–2-seriate, (0–)1–3(–4) lower spores inverted {2} (rarely mixed), pars sporifera *30–33 µm long; **apex** (†) hemispherical to very slightly truncate, dome †0.8–1 → 0.5–0.8 {1} or 1.2–1.7 → 0.8–1 {1} µm thick, with or without distinct apical chamber; **base** with short to medium long, thick, flexuous stalk, L- to Y-shaped. **Ascospores** *(6–)7–8(–9) × 2.8–3.3(–3.8) µm {3}, †5.5–7 × 2.3–3.2 µm {2}, strongly clavate, rarely fusoid, with slight to distinct, obtuse to subacute lateral protrusion, apical end rounded to obtuse, base strongly attenuated, tail-like or often with a distinct short tail 1–1.5 × 0.3–0.5 µm, head slightly to strongly inequilateral, tail straight or slightly curved; **SBs** attached at the lateral protrusion, *1.8–2.6 × 1.2–1.5 µm {2}, (broadly) tear-shaped, apically narrowed to a small point, pointing with the acute end laterally or obliquely downwards. **Paraphyses** apically uninflated to slightly (rarely medium) capitate-clavate, terminal cells *(8.5–)11–20(–23) × (2–)2.5–3.5(–4)((–4.5)) µm {3}, lower cells *(6.5–)7.5–11 × 1.8–2.7 µm {3}; unbranched at upper septum. **Medullary excipulum** hyaline to pale rose, 20–70 µm thick, of medium dense textura intricata with many inflated cells, rather sharply delimited from ectal excipulum, at flanks by a t. porrecta. **Ectal excipulum** hyaline, pale reddish towards margin, of (†) slightly to medium gelatinized, vertically oriented t. (globulosa-)angularis(-prismatica) from base to margin, 25–110 µm thick near base, cells *10–25 × 9–17 µm {2}, †10–17 × 8–11 µm {1}, common walls †0.3–1(–1.5) µm thick; 20–30 µm thick near margin, inner part of t. prismatica oriented at a 60–90° angle to the surface, outer part of t. porrecta oriented at 10–40°, marginal cortical cells *8–12 × 3–3.5 µm {1}, †7–10 × 2–3 µm {1}; **glassy processes** 10–100 × 2–3.5 µm {2} (2–10 µm long at innermost margin), high-refractive, slightly stratified, brittle, straight or inwards curved, coherent to form compact teeth. **Anchoring hyphae** medium to very abundant, */†(1.7–)2–3(–4) µm wide, walls 0.2–0.5(–1) µm thick {2}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1–2.2 µm diam. **Exudate** over paraphyses (0.5–)1–2(–3) µm thick, cloddy, hyaline to pale yellowish, loosely attached; on glassy processes absent or sparse and thin. **— ANAMORPH**: unknown.

Habitat: collected (0–)1–3 m above the ground, on corticated, (4–)7–16 mm thick still-attached branches (especially towards their ends) or on up to 15–20 cm thick standing, partly still-living trunks, of *Acacia* sp. {1}, *Banksia grandis* {3}, *B. menziesii* {2}, on attached or partially detached, medium to strongly decayed bark {5} (periderm {3} and bast {2}), partly on scars where leaves or fruits were attached, slightly to strongly greyed, green algae sparse or abundant. **Associated**: *Cosmospora* sp. {1}, *Gloniopsis* sp. {1}, *G. praelonga* {3}, *Mellitiosporiella* sp. {1}, *Nitschkia* cf. *broomeana* {1}, *Orbilia amberina* {1}, *O. austrocylindrica* {1}, *O. curvatinavajoana* {2}, *O. eucalypti* {3}, *O. microserpens* {1}, *O.* ?*nothovinosa* {1}, *O. pleioserpens* {1}, *Patellaria* '*andina*' {1}, *Proliferodiscus griseoviolaceus* {1}, ?*Stilbella* sp. {1}, ?*Teichospora* sp. {1}. **Desiccation tolerance**: fully viable for at least 16 months. **Altitude**: 65–370 m a.s.l. **Geology**: Cretaceous sedimentary rock; Archean granite, granulite, feldspar, migmatite. **Phenology**: long-lived.

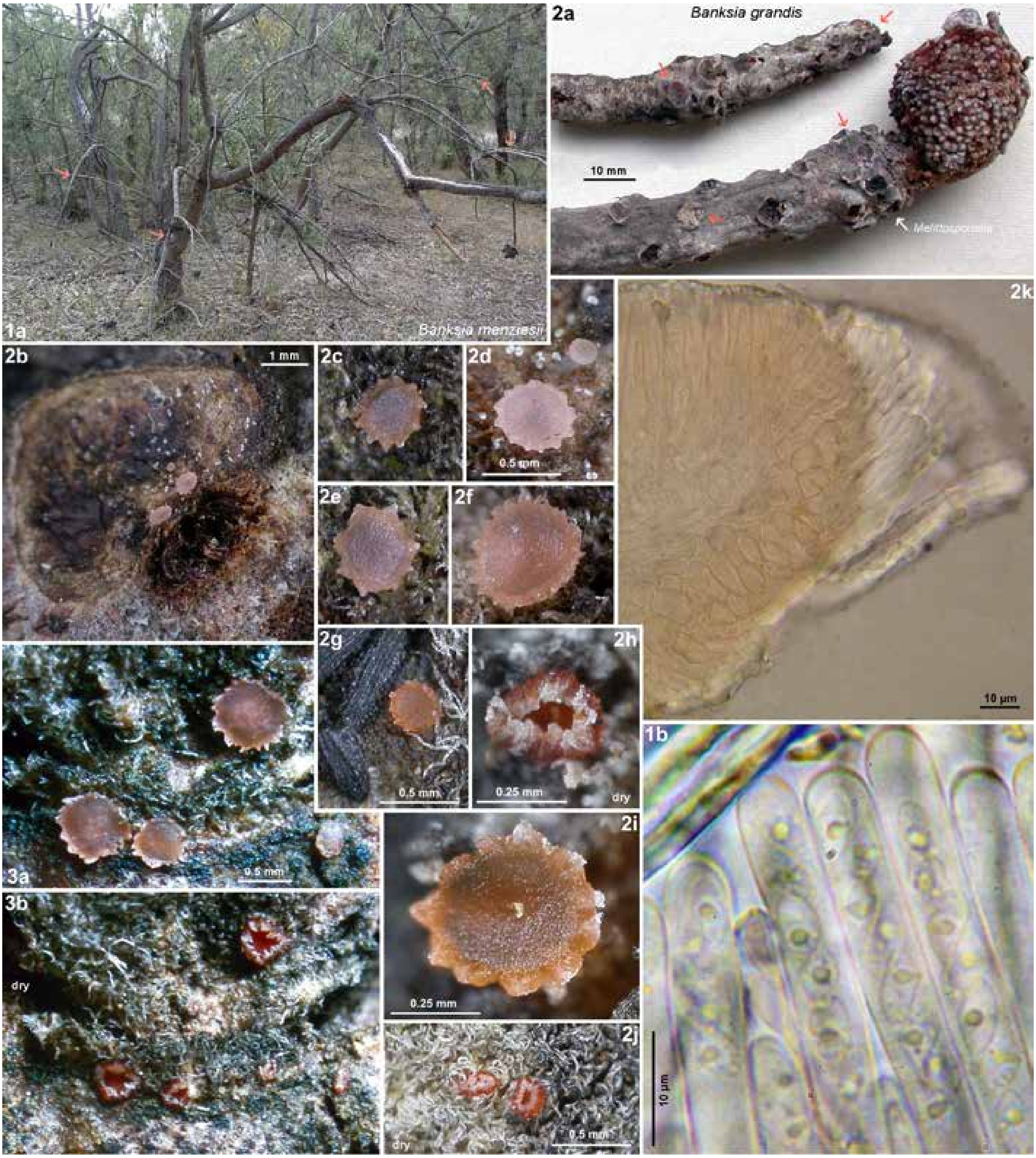


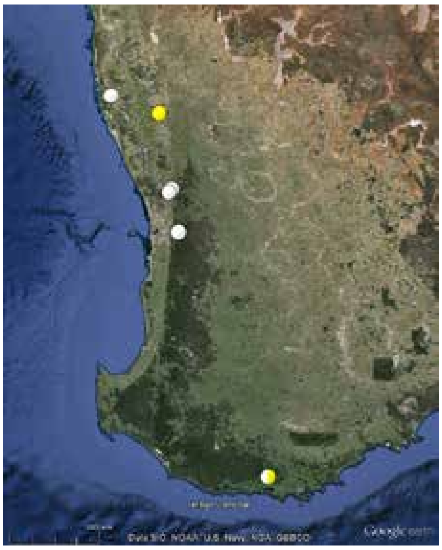
Plate 367. **1–3**: *Orbilia aviceps*. – **1a**. *Banksia menziesii* in semihumid banksia-eucalypt open woodland; **2a**. dead corticated xeric branches of *B. grandis*; **2b–g**, **i**, **3a**. rehydrated apothecia (**2g** with *Gloniopsis praelonga*); **2h**, **j**, **3b**. dry apothecia; **2k**. marginal ectal excipulum in median section, with glassy processes; **1b**. mature asci with ascospores. – Living state. — **1a–b**. H.B. 7209a: Western Australia, Muchea, on *Banksia*; **2a–k**. H.B. 8659a: ibid., Kalamunda, on *Banksia*; **3a–b**. H.B. 7322a (holotype): ibid., on *Banksia*.

Taxonomic remarks. *Orbilia aviceps* is well characterized by its strongly asymmetrical ascospores with a lateral protrusion and a short basal tail, somewhat resembling a bird's head, or the flowers of *Aconitum*. The tear-shaped spored body is attached to the lateral protrusion, similar as in *O. corculispora* (concerning the peculiar feature of lateral insertion of SBs see also p. 72). For the similar *O. triangulispora* see below.

Although the spores resemble those of *O. corculispora*, *O. aviceps* is placed in series *Hemiorbilia* because of the similarity with the two preceding species regarding spore shape, long glassy processes, and paucity of inverted lower spores. Molecular data were not available from this and the very similar *O. triangulispora*.

Variation. The apothecia varied in size from 0.2–0.3 up to 0.3–0.9 mm, including their teeth, also in the number of teeth. The distinct though short spore tails, which are the main difference to *O. triangulispora*, were only very exceptionally absent.

Ecology. *O. aviceps* was found on ± rotten bark of xeric branches of two species of *Banksia*, once also on *Acacia*, in



Map 62. Known distribution of *O. aviceps* (white) and *O. triangulispora* (yellow) in southwestern Australia.

subtropical semihumid southwestern Australia: in banksia-eucalypt open woodlands in the coastal Geraldton Sandplains and at the northern end of Darling Range, here also in a eucalypt open forest (jarrah-marri), and at the southern end of Darling Range/Plateau in a eucalypt low open forest (karri-tingle).

Specimens included. **AUSTRALIA**: **Western Australia**, Geraldton Sandplains, 20 km SE of Jurien Bay, 18 km NE of Cervantes, Cervantes Rd, 65 m, branch of *Acacia*, on bark, 11.XI.2007, G. Marson (H.B. 8954e). – Swan Coastal Plain, 48 km NNE of Perth, 4.5 km NE of Muchea, Reserve Road, 800m 97 m, branch of *Banksia menziesii*, 3.IX.2006, G. Marson (G.M. 2006-09-03.1 ø). – Jarrah Forest, 54 km NNE of Perth, 11 km NE of Muchea, 187 m, trunk of *B. menziesii*, on bark, 23.XI.2001, G. Marson (H.B. 7209a). – 28 km E of Perth, 8 km ESE of Kalamunda, 4 km E of Bickley, junction of Lockwood and Gunjin Road, 370 m, branches of *B. grandis*, on bark, 13.XII.2001, G. Marson (ex H.B. 7322a, MEL 2389235, **holotype**). – ibid., 7.IX.2006, G. Marson (H.B. 8659a). – 7 km WNW of Albany, 13 km NNE of Denmark, NE of Mt. Lindesay, 75 m, branch of *B. grandis*, on bark, 15.XII.2001, G. Marson (ø).

Orbilia triangulispora Baral, **sp. nov.**, MB 813621 — Pls 368–369, Map 62

Etymology: referring to the nearly triangular shape of the ascospores.

Typification: Western Australia, Denmark, branch of *Chamelaucium ciliatum*, 15.XII.2001, G. Marson (ex H.B. 7213b, MEL 2389229, holotype).

Latin diagnosis: *Similis* Orbiliae avicipiti *sed ascosporae distincte breviores et latiores, absque cauda. Habitat ad corticem et lignum putridum siccum ramorum* Chamelaucii *et* Verreauxiae *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.6 mm diam., 0.1–0.2 mm high (receptacle 0.1–0.15 mm), bright orange to (rose-)orange, slightly translucent, round, scattered to subgregarious; disc flat, margin distinct, 5–15 µm protruding (30–100 µm incl. teeth), with prominent ± whitish teeth of 40–120 × 30–100 µm (varying in size between apothecia); sessile or with distinct, 0.05 mm high stipe, superficial; dry deep apricot-red. **Asci** *50–58 × 5.3–6 µm {1}, †(37–)42–53 × 4.5–5.3 µm {2}, 8-spored, spores (†) uniseriate, orientation irregular {T} or basal 2–5 spores inverted {1}, pars sporifera *29–33 µm; **apex** (†) hemispherical to slightly truncate, dome †1–1.3 → 0.8–1 µm thick {2}, apical chamber partly distinct; **base** with short to medium long, thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(3.5–)4–4.7 {T} or 5–6(–7) {1} × (3.3–)3.5–4 {2} µm, triangular in profile view (in front view probably ellipsoid-fusoid), with ± pronounced, obtuse to subacute lateral protrusion, apical end mostly obtuse, basal end ± attenuated, rarely tail-like; **SBs** attached at lateral protrusion, *(1.8–)2–2.5(–3) × (1–)1.2–1.4(–1.6) µm {2}, tear- to pear-shaped, also subglobose, apically narrowed to a small point, with or without a very short filum, acute end pointing laterally or sometimes slightly downwards. **Paraphyses** apically slightly clavate-capitate, terminal cells *12–20 × (2–)2.5–3.5 µm {1}, †12–19 × 2.2–3 µm {T}, lower cells *8–12.5(–14) × 1.8–2.4 µm {1}, †6–9 × 1.3–1.7 µm {T}; frequently branched in middle and lower part. **Medullary excipulum** very pale to light orange, 30–60 µm thick, of medium dense textura intricata or t. globulosa, with some or many inflated cells, indistinctly to sharply delimited. **Ectal excipulum** pale to light orange, of (†) not or slightly to medium gelatinized, ± vertically oriented t. globulosa-angularis-prismatica from base to mid flanks, 25–60 µm thick near base (up to 100 µm in stipe), cells *10–24(–28) × 8–16(–18) µm {1}, †8–15 × 6–8 µm {T}, common walls up to †0.5–1 µm thick; 20–30 µm thick near margin, inner layer of t. angularis, outer layer of t. prismatica-porrecta oriented at a 20–45° angle to the surface, marginal cortical cells *10–12 × 4–5 µm {1}, †8–11 × 2.5–3.5 µm {T}; **glassy processes** 5–100 × 2–3 µm {T}, high-refractive, not stratified (in KOH slightly so), brittle, partly curved inwards near apex (sometimes uncinate), coherent to form large distinct teeth. **Anchoring hyphae** abundant, †1.5–3 µm wide, walls 0.2–0.4(–1) µm thick {2}, forming a 5–10 µm thick hyaline layer on flanks. **SCBs** in paraphyses and marginal excipulum globose, (0.8–)1.5–2 µm diam. {1}. **Exudate** over paraphyses (0.3–)1–2.5(–3) µm thick, thin and rough or large and cloddy, loosely attached; over teeth absent or 1–2 µm thick, firmly attached. **— ANAMORPH**: unknown.

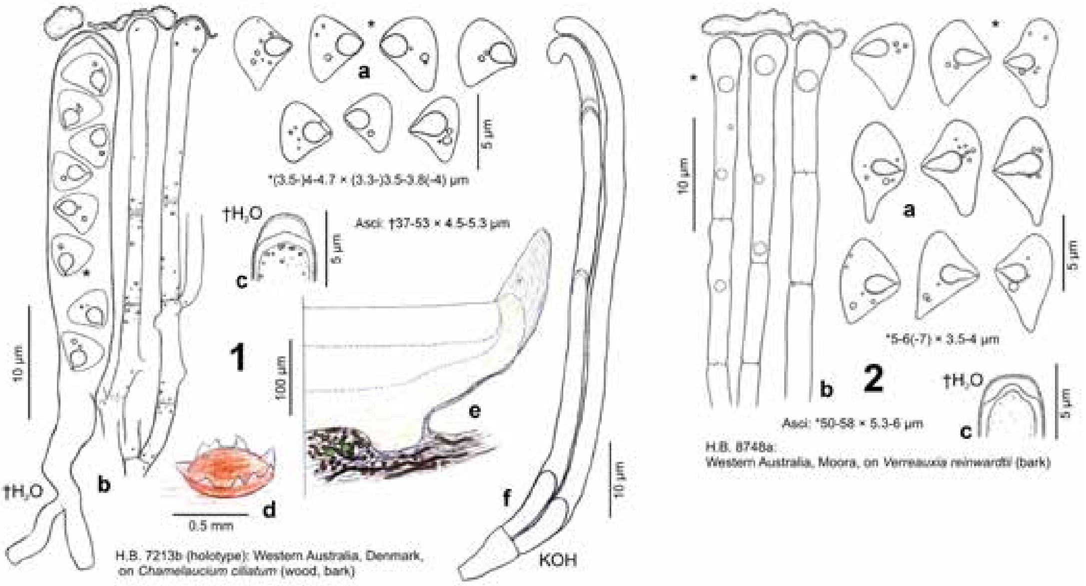


Plate 368. **1–2**: *Orbilia triangulispora*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium (rehydrated); **e**. apothecium in median section; **f**. id., marginal cortical cells with long agglutinated glassy processes.

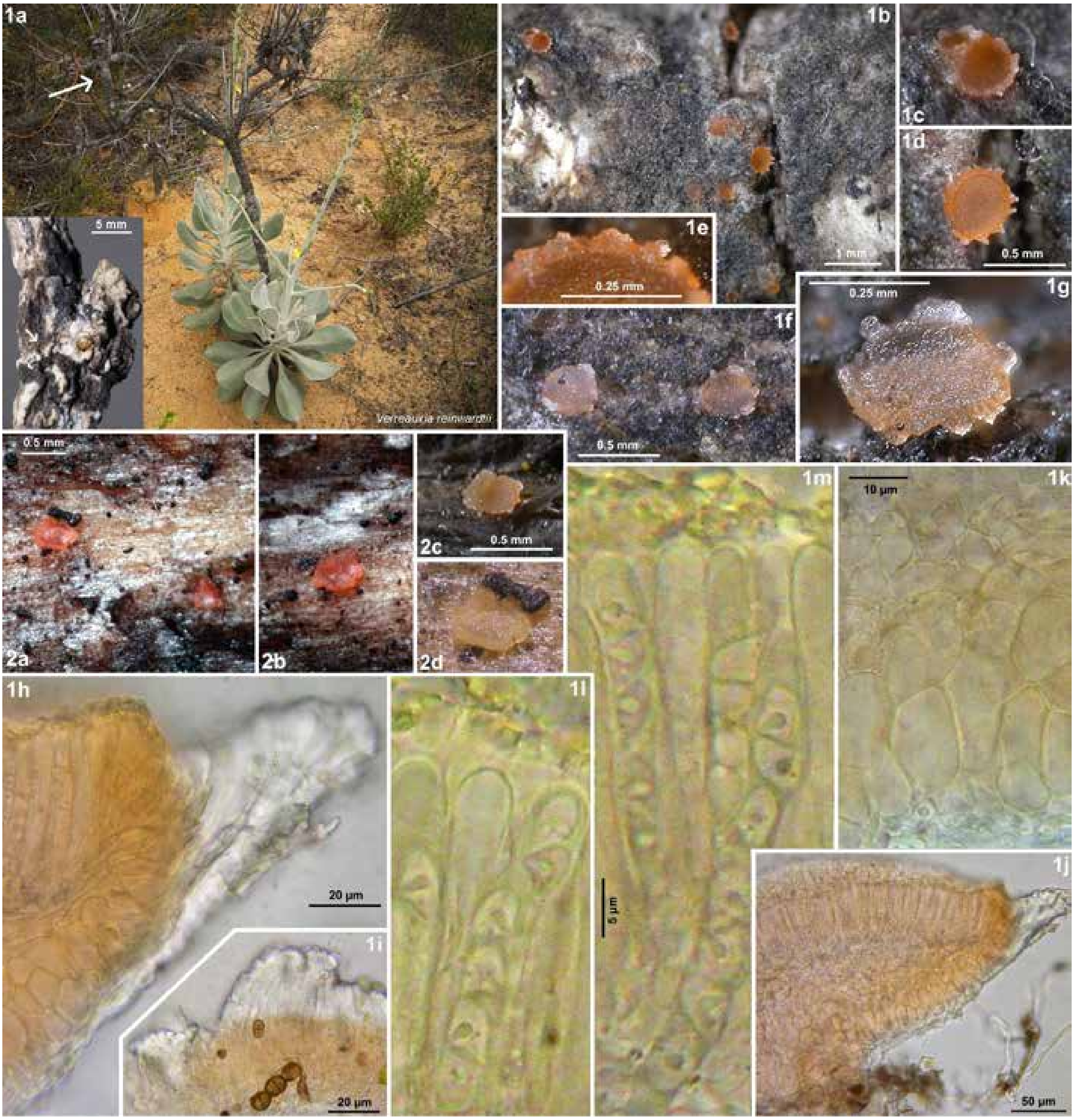


Plate 369. **1–2**: *Orbilia triangulispora*. – **1a**. acacia shrubland, *Verreauxia reinwardtii* with dead, corticated, xeric branch (arrow); **1b–g**, **2a–d**. rehydrated apothecia (phot. **2a–b** after 10 months, **2c** after 4.5 years, **2d** after 10 years); **1j**. apothecium in median section; **1h**. id., marginal ectal excipulum with glassy processes; **1i**, marginal teeth in top view; **1k**. basal ectal excipulum in median section; **1l–m**. mature asci with ascospores. – Living state (except for mature asci in **1l–m**). — **1a–m**. H.B. 8748a: Western Australia, Moora, on *Verreauxia*; **2a–d**. H.B. 7213b (holotype): ibid., Denmark, on *Chamelaucium*.

Habitat: collected 0–1 m above the ground, partially to entirely decorticated, 8–11 mm thick branches of *Chamelaucium ciliatum* {1}, *Verreauxia reinwardtii* {1}, on 0.1 mm deep strongly decayed bark {2} and wood {1}, slightly to strongly greyed, green algae sparse. **Associated**: *Orbilia amberina* {1}, *O. aviaristata* {1}, *O. curvativitalbae* {1}, *O. lilacina* {1}, *O. ?multiaustrocylindrica* {1}, *O. plurililacina* {1}, *O. ?subclavuliformis* {1}, *Ostropales* {1}, ?*Parmelia* sp. {1}, *Proliferodiscus olivaceoviridis* {1}. **Desiccation tolerance**: viable in all parts after 3 months, some spores still alive after 9.5 months. **Altitude**: 75–235 m a.s.l. **Geology**: Cretaceous sedimentary rock (ochre sandy soil); granite. **Phenology**: long-lived.

Taxonomic remarks. The ascospores of *O. triangulispora* resemble *O. aviceps* in shape, but are shorter and wider and never possess a distinct tail. The basal spore end is only sometimes tail-like, otherwise it is still recognizable in being often more attenuated than the upper end. In combination with the occurrence on different host plants, *O. triangulispora* is believed to represent a species of its own.

Variation. The spores and SBs in the paratype are longer than in the holotype and some spores resemble *O. aviceps* in their attenuated base.

Ecology. *O. triangulispora* grew on rotten wood and bark of xeric branches of *Verreauxia* and *Chamelaucium* at two very distant (500 km) sites in southwestern Australia: in a subtropical semihumid eucalypt open woodland in the Swan Coastal

Plain ecoregion at the northern part of Darling Plateau and in a eucalypt low open forest (karri-tingle) in the Jarrah Forest ecoregion at the southern end of Darling Range.

Specimens included. **AUSTRALIA**: **Western Australia**, Swan Coastal Plain, 150 km N of Perth, 13 km WNW of Moora, Dandaragan Road, 235 m, branch of *Verreauxia reinwardtii*, on bark, 24.X.2007, G. Marson (H.B. 8748a). – Jarrah Forest, 47 km WNW of Albany, 13 km NNE of Denmark, NE of Mt. Lindesay, 75 m, branch of *Chamelaucium ciliatum*, on wood & bark, 15.XII.2001, G. Marson (ex H.B. 7213b, MEL 2389229, **holotype**).

Series *Vibrioides*

Orbilia subgenus ***Hemiorbilia*** section ***Hemiorbilia*** series ***Vibrioides*** Baral, E.Weber & G. Marson, **ser. nov.**, MB 829071 – Type species: *Orbilia vibrioides* Baral, Priou & G. Marson

Etymology: named according to the ascospores resembling bacteria of the genus *Vibrio* in some of the species, including the type.

Latin diagnosis: *Apothecia sessilia, disciformia, aurantio-ochracea vel roseo-rubra, disco et margine glabro vel saepe albido- ad luteo-pulveraceo, margine parum crenulato vel costato. Asci 8- ad 128-spori, apice in statu emortuo hemisphaerico, valde crassitunicato. Ascosporae ovoideae, cylindricae vel clavatae, apice rotundato vel obtuso, rectae vel valde curvatae, in statu vivo corpusculum refringens bacilliformem, lacrimiformem vel globosum, ad apicem vel subapicem affixum continentes. Paraphyses ad apicem non vel parum inflatae, exsudato crasso, hyalino vel fortiter sulphureo tectae. Excipulum marginale absque processis vitreis. Habitat ad lignum vel plerumque corticem putridum ramorum in aere prominentium,* etiam ad culmos vel folios Poacearum, *in zona temperata vel subtropica ad tropica, humida ad arida.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.15–0.5(–0.9) mm diam., pale to bright ochraceous- to rose-orange, rarely pale cream, disc and exterior smooth or slightly to strongly pruinose to warted by whitish to mostly yellow exudate, margin in some taxa crenulate or ribbed, sessile. **Asci** *27–60 × 4.7–6.8 µm when 8-spored, *(46–)55–80(–120) × (8.5–)9.5–13(–15) µm when 32–128-spored, ± half of spores inverted (strongly mixed); **apex** (†) hemispherical, with very thick dome: immature 1.5–2.5(–3.5) µm when 8-spored, (2–)3–4(–6) µm when 32–128-spored, often with small apical chamber; **base** T-, L-, Y- or h-shaped. **Ascospores** *(3.4–)3.8–5(–5.3) µm long when 8-spored, *(4.3–)5–15(–17) µm when 32–128-spored, (1.4–)1.6–2.6(–3.2) µm wide, cylindrical to clavate, apex rounded to obtuse, base rarely with a tail, straight to ± strongly curved (cashew- to L-shaped or helicoid); **SBs** attached to apical or subapical (to lateral) spore wall, (1–)1.5–3.5(–4.5) × (0.2–)0.3–1.3 µm, rod-shaped to ampulliform or tear-shaped to globose, straight, sometimes geniculate, apically narrowed to a wide or sometimes very narrow point. **Paraphyses** uninflated or slightly clavate-capitate at the apex, terminal cells 0.6–1.3(–2.2)× as long as lower cells, unbranched or sometimes branched near apex. **Ectal excipulum** cells near base *(5–)7–15(–18) × (4–)5–13(–16) µm, near margin of t. angularis to mostly t. prismatica-porrecta, outer part oriented at a high to often medium or low angle, without **glassy processes**. **SCBs** globose or absent; **VBs** consistently absent; **carotenoids** in LBs not observed. **Exudate** (0.2–)1–3(–8) µm thick, coarsely cloddy, loosely to firmly attached, hyaline to bright sulphur-yellow. **— ANAMORPH**: unknown.

Habitat: on bark and wood of corticated to decorticated, dead, still-attached twigs and branches of angio- rarely gymnosperms, rarely on *Poaceae*; temperate humid or subtropical to tropical semihumid to arid; all species desiccation-tolerant.

Recognized species: 10.

Taxonomic remarks. Series *Vibrioides* represents a somewhat isolated lineage characterized by a series of partly plesiomorphic traits, including a strong wall thickening of the hemispherical apex of the predominantly multispored asci, straight to strongly curved ascospores with apically or obliquely attached spore bodies, ± uninflated paraphyses with short terminal cells, and abundant external exudate.

The multispored members of this series are already macroscopically rather easily recognizable by apothecia with a pruinose to prominently warted hymenium. The rough to cloddy, pale to bright sulphur-yellow exudate covers the tips of paraphyses and the often ribbed margin. It is predominantly firmly attached to the paraphyses, at least its innermost part, for the case that it consists of several layers. The exudate shows a striking autofluorescence under UV-illumination (365 nm, yellow to orange, Fig. 97), in contrast to other members of section *Hemiorbilia* in which the fluorescence is comparatively weak. Because the autofluorescence of the surrounding substrate is usually low, the mostly scattered apothecia can easily be detected under UV, even in the dry state. The paraphyses project either singly or in fascicles about 5–15 µm beyond the hymenium and provoke a warted surface, reminiscent of a crumble cake.

The very thick apical domes of the asci are characteristic of the whole group, also the rod-shaped to ampulliform to globose SBs which are subapically inserted in some of the multispored species and then partly geniculate. A faintly yellowish-reddish (dextrinoid) iodine reaction of the thick inner part of the apical dome was inconsistently obtained in *O. vibrioides*, *O. junci*, *O. myrioobliqua*, *O. helicoobliqua*, *O. angustoobliqua*, and *O. paraobliqua* (in IKI or MLZ, with or without KOH-treatment). This inner part stains distinctly pinkish-red in CR_{SDS}, but this congophilous reaction is also observed in other members of section *Hemiorbilia*. *O. junci* is tentatively placed in series *Vibrioides* here because of its strongly thickened apical dome, but otherwise it shares also characteristics of series *Hesperideae*.

Species delimitation. Some infraspecific variability was noted in most of the included species, sometimes within a population or even a single apothecium. Due to this variation and the often only slight interspecific differences, together with the frequently observed coexistence of two or up to five of the multispored taxa of series *Vibrioides* within the same collection, the present species concept needs further investigation. Particularly three species were problematic: *O. anguliobliqua*, *O. helicoobliqua*, and *O. curvatiobliqua*. They are only known from a single mixed collection on *Acacia*, in which they grew in separate populations on different twig fragments, though in close association with two further species of this series, *O. myrioobliqua* and *O. pleistoobliqua*. During documentation, the three populations were thought at first to belong to a single species, but finally we preferred to separate them as different species.

Anamorph. We have rarely seen conidia on the natural substrate in association with members of series *Vibrioides*: tridentaria-like in *O. vibrioides* and *O. graminis*, dwayaangam-like and trinacrium-like in the multispored Australian species. However, their connection to a teleomorph remained uncertain. *O. junci* possesses a dwayaangam-like anamorph, but its affiliation in series *Vibrioides* is uncertain because DNA data were unavailable.

Phylogeny. Sequences comprising ITS and LSU were available for *O. myrioobliqua*, *O. helicoobliqua*, *O. graminis*, and two different genotypes of *O. vibrioides*. When analysing ITS+LSU (Phyl. 9), ITS (Phyl. 10), or LSU (Phyl. S13), the four species clustered in a strongly (ITS+LSU, ITS, LSU)

Table 67. Positions in the LSU (D1–D2) found to be more or less specific to series *Vibrioides* (yellow), in comparison with series *Hesperideae* (green) and series *Hemiorbilia* (blue). Y = C/T, R = A/G. Position numbers starting with TGACCT by omitting predominant gaps in alignment of all groups of *Orbiliomycetes*.

Taxa	159–163	167–170	223–228	240–244	252–256	522–526	559–565
O. vibrioides	ATGTT	GTAG	GTGTAC	TGCCT	TAACT	CTGTG	CCACTGT
O. graminis	ATGTT	GTAG	GTGCAC	TGCCA	TAACT	CTGCG	CCGCTGC
O. myrioobliqua	ATGTT	GTAG	GTGTAC	TGCCT	TAACT	CTGCG	CCGCTGC
O. helicoobliqua	ATGTT	GTAG	GTGTAC	TGCCT	TAACT	CTGCG	CCGCTGC
O. sarothamni	ATGCT	GTTG	GTACGC	TACTT	TAGCT	CTGTG	CCACTGT
O. corculispora	ATGTT	GTTG	GTACGC	TACTT	TAACT	CTCCA	CTGGTGY
O. octocorcorculispora	ATGCT	GTTG	GTACGC	TACTT	TAGCT	CTCCG	TCGGTGC
O. australiensis	ATGCT	GCGG	GTCTTT	TGCTT	TAGCT	CTCCG	CCGGTGY
O. pleioaustraliensis	ATTCT	GATR	GTCTTT	TGCTT	TAGTT	CTCTR	CCAGTGT
O. adenocarpi	ATGCT	GTTG	GTACGC	TGCTT	TAGCT	?	?
O. myriofusiclava	ATGCT	GTTG	GTACGC	TGCTT	TAGCT	CTCCG	CCGGTGC
O. aprilis	ATGCT	GTTG	GTACGC	TRCTT	TAGCT	CCTCG	CCGTGGT
O. crenatovinosa	ATGCT	GTTG	GTACGC	TGCTT	TAGCT	CTCCG	CCGGTGT
O. cryptogena	ATGCC	GTTG	GTACGC	TGCTT	TGGCT	CTCCA	CTGGTGC
O. hesperidea	ATGCC	GTTG	GTCTTT	TGCTT	TGGCT	CTYCG	CCGGTGC
O. alpigena	ATGCC	GTTG	GTACGC	TGCTT	TGGTT	CTCCG	CCGGTGC
O. multicurvula	ATGCC	GTTG	GTACGC	TGCTT	TGGCT	CGAAC	?
O. subulivinosa s.l.	ATGCC	GTTG	GTACGC	TGCTT	TGGCT	YTCCG	CCGGTGC
O. (*sub*)*vinosa/arachnovinosa/nothoaprilis/ angustoaristata/velutina*	ATGCC	GTTG	GTACGC	TGCTT	TGGCT	CTCCG	CCGGCGC
O. georgiana	ATGCC	GTTG	GTACGC	TGCTT	TGGCT	CTCCG	CCGGTGC
O. *spermoides/fimbriata*	ATGCT	GTTG	GTACGC	TGCTT	TAGCT	CTCCG	CCGGTGC
O. (*sub*)*clavuliformis*/*flagellispora*/(*brevi*)*aristata*	ATGCT	GTTG	GTACGC	TACTT	TAGCT	CTCYG	CCAGTGT
O. subaristata	ATGCT	GTTG	GTACGC	TACTT	TAGCT	CTCCG	CCGGTGT

supported clade that stands rather isolated from other groups of section *Hemiorbilia*. A distance of 16.5–23.5 % (S1506 intron), 12–13.5 % (ITS), and 2–3 % (LSU D1–D2) is noted between the 64-spored and the 8-spored taxa, but between *O. vibrioides* s.l. and *O. graminis* the distance is even higher (21 % in intron, 16.5–19 % in ITS, 4 % in LSU), while between *O. myrioobliqua* and *O. helicoobliqua* it is only 1.3 % (ITS) and 0.2–0.4 % (LSU).

Further DNA data from multispored members of series *Vibrioides* are required to substantiate the above result which places the multispored Australian taxa with strongly fluorescent exudate in close relationship with 8-spored taxa from outside Australasia in which the exudate is less fluorescent. The morphological similarity in spore shape between *O. vibrioides*/*graminis* and *O. curvatiobliqua* and the thick-walled ascus apex in all members of this group support the close relationship between 8- and multispored taxa.

Specific nucleotide positions. The entire series *Vibrioides* shares a few positions with two members of the *cryptogena-sarothamni* clade: at pos. 162 and 254 of LSU D1 with *O. corculispora* and at pos. 524 and 562 of LSU D2 with *O. sarothamni* (Tab. 67). However, it differs from the *cryptogena-sarothamni* clade in the motif ATTA (vs. ATTG) at the 5'-end of ITS2 (Tab. 20) and also lacks the large gap region downstream of it, mentioned under series *Hesperideae*.

The two available sequences of *O. vibrioides* s.l. differ in the SSU V8 at pos. 66 by CGA**A**AG (as in the *Lecophagus* and *Hyalorbilia* clade and some *Dactylellina* spp.) from all other *Orbilia* spp. which here have CGA**G**AG. Only short parts of SSU were available for *O. graminis*, *O. myrioobliqua*, and *O. helicoobliqua* which do not cover this region.

Ecology. The three species with 8–16-spored asci occur in temperate humid to subtropical semihumid areas of Europe, North America, and Macaronesia. Two inhabit xeric culms and leaves of monocots whereas *O. vibrioides* s.l. was found on both angio- and gymnosperm wood and bark. The as yet known distribution of the eight multispored species is confined to the west and southwest of Australia, where the sites extend from subtropical semihumid at the northern border of Darling Range to tropical arid at the Pilbara semidesert. The inhabited hosts include *Fabales*, *Myrtales*, *Proteales*, and *Santalales*. Most of the collections were on *Acacia*, and the majority of apothecia grew on bark of corticated branches, often in association with other species of *Orbilia*, mainly of section *Hemiorbilia*, but also with *Hysteriales*, *Ostropales*, *Patellariales*, and lichens.

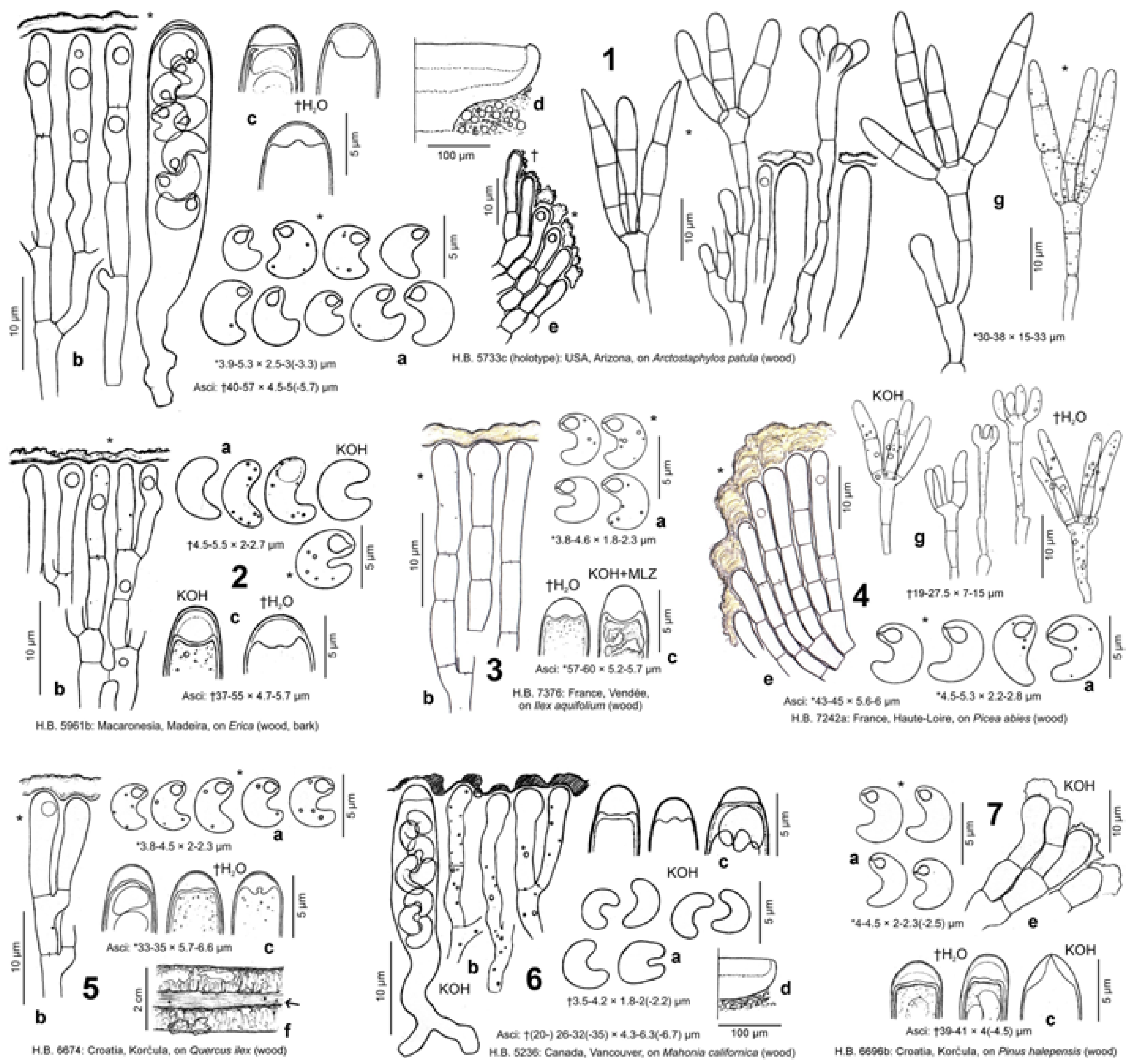
Orbilia vibrioides Baral, Priou & G. Marson, **sp. nov.**, MB 813536 — Pls 370–371, Map 63

Etymology: named after the ascospores which resemble bacteria of the genus *Vibrio*.

Typification: USA, Arizona, Sedona, branch of *Arctostaphylos patula*, 8.V.1995, G. Marson (ex H.B. 5733c, M-0276606, holotype).

Latin diagnosis: *Apothecia rehydratata 0.14–0.9 mm diam., aurantiaca vel roseo-rubra, sessilia, margine laevi. Asci 8-spori, apice in statu emortuo valde crassitunicati. Ascosporae *3.5–5.3 × 1.8–3.3 µm, valde curvatae (botuliformes), apice rotundatae vel obtusae, basi leniter attenuatae, in statu vivo corpusculum refringens magnum, globosum vel lacrimiformem, ad apicem cuspide brevi affixum continentes. Cellulae vivae excipuli marginalis et paraphysium corpuscula globosa continentes. Habitat ad lignum vel corticem modice vel valde putridum ramulorum et ramorum siccorum fruticum et arborum angiospermarum vel coniferarum in zona temperate humida ad subtropica sub- vel semihumida Europae, Macaronesiae et Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.14–0.2 up to 0.2–0.5(–0.9) mm diam., 0.07–0.18 mm high (receptacle 0.07–0.13 mm), pale to bright orange to rose-red, translucent, round, slightly undulating when large, scattered to densely gregarious in small groups; disc flat, margin ± distinct, 0–5 µm rising above disc, smooth; sessile, rarely with hidden stipe 0.09 × 0.1 mm, slightly immersed in algal layer; dry bright to deep (pink-)orange to brick-red. **Asci** *33–35 {1} or 42–45 {1} or 57–60 {1} × (5.2–)5.5–6(–6.8) {3} µm, †(20–)26–57 × (4–)4.5–5.5(–6.7) µm {7}, 8-spored, orientation irregular, pars sporifera *20–22 µm; **apex** (†) hemispherical to very slightly conical or truncate, dome †1.5–2.5(–3.5) → 1–2.5 µm thick {9} (in KOH thicker than in H_2O), with small apical chamber, endotunica in CR_{SDS} light rose-red, IKI very pale reddish-grey (dextrinoid); **base** with short to long, thick to thin, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(3.5–)3.8–5(–5.3) × (1.8–)2–2.5(–3.3) µm {11}, †3.5–5.5 × 1.8–2.7 µm {3}, cashew-shaped, apex rounded to obtuse, base partly slightly



H.B. 5733c (holotype): USA, Arizona, on *Arctostaphylos patula* (wood)

H.B. 5961b: Macaronesia, Madeira, on *Erica* (wood, bark)

H.B. 7376: France, Vendée, on *Ilex aquifolium* (wood)

H.B. 7242a: France, Haute-Loire, on *Picea abies* (wood)

H.B. 6674: Croatia, Korčula, on *Quercus ilex* (wood)

H.B. 5236: Canada, Vancouver, on *Mahonia californica* (wood)

H.B. 6696b: Croatia, Korčula, on *Pinus halepensis* (wood)

Plate 370. **1–7**: *Orbilia vibrioides*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices (**7c** right: after ejection); **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. corticated xeric branch with narrow decorticated old wound; **g**. conidia emerging from hymenium of *O. vibrioides* (**1g**) or the associated *O. cylindrospora* (**4g**).

attenuated, (very) strongly curved by (90–)120–180°, sometimes very slightly helicoid; **SBs** apically attached to spore wall, *1–2(–2.2) × 0.7–1.3 µm {5}, broadly tear-shaped to globose {11}, apically narrowed to small point, mostly with a very short filum; with a few minute LBs. **Paraphyses** apically uninflated to slightly clavate-capitate, terminal cells *(6–)8–12(–15) × (1.7–)2–3(–3.3) µm {3}, †1.5–3 µm wide {2}, straight, sometimes ± flexuous, lower cells *(4–)5–12 × 1.8–3.2 µm {4}; never or sometimes branched at upper septum. **Medullary excipulum** (very) pale rose, ~10–50 µm thick, of dense textura angularis(-intricata), medium sharply delimited. **Ectal excipulum** very pale rose, sometimes pale orange near margin, of thin-walled, ± vertically oriented t. angularis-globulosa from base to mid flanks or margin, 30–40(–80) µm thick near base, cells *5–15(–18) × 5–13(–16) µm {4}; 15–25 µm thick near margin, of t. prismatica-porrecta oriented at a 30–80° angle to the surface, outer part also at 10–30°, marginal cortical cells cylindric-clavate, (†) somewhat thick-walled, */†(5–)6–12(–16) × 2.5–3.5(–5) µm {3}, **glassy processes** absent. **Anchoring hyphae** ± abundant, *1.8–3 µm wide (up to 5 µm near insertion), walls 0.2(–0.3) µm thick {3}. **SCBs** in paraphyses and excipulum absent or often present, globose. **Exudate** very pale to light chlorinaceous- or sulphur-yellow, over paraphyses (0.3–)1–2(–4) µm thick, continuous to coarsely cloddy, ± loosely attached; over margin rough-cloddy, (0–)1–5(–8) µm thick. **— ANAMORPH**: unknown (but see below).

Habitat: collected 0.1–3 m above the ground, corticated to decorticated, 2.5–45 mm thick twigs and branches of *Arbutus andrachne A. menziesii* {1}, *Arctostaphylos patula* {1}, *Buxus sempervirens* {1}, *Corylus avellana* {1}, *Erica* sp. {1}, *E. scoparia* {1}, *Ilex aquifolium* {1}, *Laurus novocanariensis* {1}, *Mahonia dictyota* {1}, *Malus × scheideckeri* {1}, *Picea abies* {4}, *Pinus halepensis* {1}, *Quercus ilex* {1}, *Salix* sp. {1}, *Sambucus* sp. {1}, *Taxus baccata* {1}, *Ulex europaeus* {3}, partly on or close to long decorticated old wounds, on 0.1–1 mm deep slightly to strongly decayed wood {20} and bark {4}, greyed, covered by green algae. **Associated**: *Claussenomyces* sp. {1}, *Chrysodisca peziculoides* {1}, *Cryptodiscus foveolaris* {1}, *C. tabularum* {1}, *Dacrymyces* sp. {1}, *Diplolaeviopsis* sp. {1}, *Durella* sp. {2/1}, *D. ?connivens* {1}, *Gloniella* sp. {1}, *Hysterium* sp. {1}, *?Hysteropatella* sp. {1}, *Mellitiosporiella pulchella* {1}, *M. macrospora* {1}, *Mollisia ?melaleuca* {1}, *M. obscura* {1}, *Neodasyscypha cerina* {1}, *Orbilia aprilis* {1}, *O. cylindrospora* {4}, *O. ?dixiensis* {1}, *O. eucalypti* {1}, *O. euonymi* {2}, *O. flavida* {1}, *O. hesperidea* {1}, *O. pleionavajoana* {1}, *O. vinosa* {2}, *O. ?subulivinosa* {1}, *Parmelia sulcata* {1}, *Perrotia flammea* {1}, *Phragmiticola* sp. {1}, *Pragmopora* sp. {1}, *Propolis viridis* {2}, *Sarea difformis* {1}, *Stictis friabilis* {1}, *Trentepohlia* sp. {1}, *Triblidium calyciiforme* {1}, *Usnea* sp. {1}. **Desiccation tolerance**: fully viable for at least 6 weeks, paraphyses and excipular cells still alive after 22 months. **Altitude**: 3–510 m a.s.l. (central and atlantic Europe), 12–1275 m (southern Europe), 90–180 m (northern North America), 1320 m (southern North America). **Geology**: Cambrian, Ordovician, Silurian & Devonian silt- & sandstone, Pennsylvanian-Permian red sandstone, Muschelkalk, Cretaceous sand-, silt- & limestone, dolomite, Pleistocene sand; granite, diorite, gabbro, basalt, mica schist & gneiss. **Phenology**: V–VI, VIII–III (throughout the year, long-lived).

Taxonomic remarks. *Orbilia vibrioides* is well characterized by its small, strongly curved (cashew-shaped) ascospores and thick apical domes. The inner part of the apical dome reacts very pale reddish-grey (dextrinoid) in IKI (KOH-pretreated, negative in MLZ, observed in H.B. 5961b and 6696b). In those species of section *Orbilia* with similar cashew-shaped spores the dead asci have thin-walled truncate apices.

For the very closely related *O. graminis* on herbaceous monocots see p. 750. Two samples on *Pinus sylvestris* from southern France (Pl. 372: 5) are intermediate to *O. graminis* in having subulate SBs and are mentioned under that species.

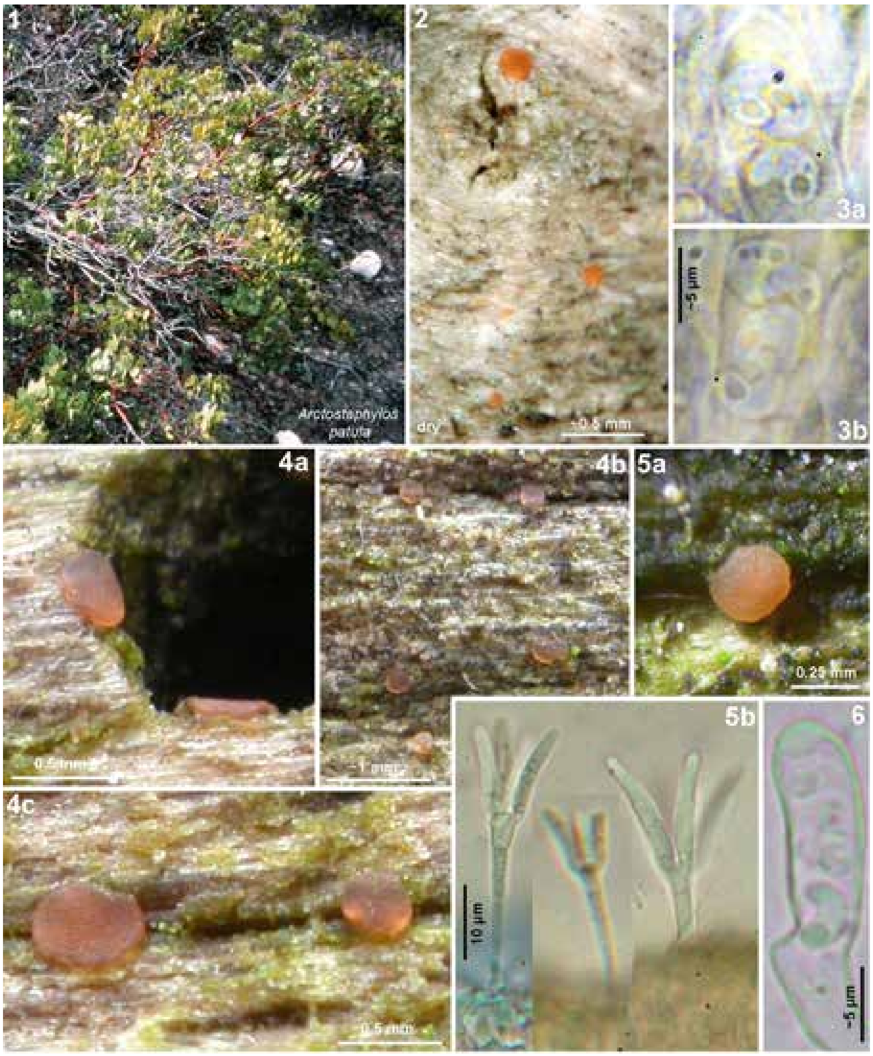


Plate 371. **1–6**: *Orbilia vibrioides*. – **1a**. montane Chaparral scrubland with *Arctostaphylos patula*; **4a–c**, **5a**. rehydrated apothecia; **2**. dry apothecia; **3a–b**, **6**. mature ascospores inside asci (**6**: thick-walled ascus apex); **5b**. conidia emerging from hymenium of *O. cylindrospora*. – Living state, except for asci, some spores in **6**, some cells of conidia. – **2**, **6**: phot. J.P. Priou, **5a–b**: phot. S. Helleman. — **1**. H.B. 5733c (holotype): USA, Arizona, on *Arctostaphylos*; **2**. J.P.P. 25021: France, Bretagne, on *Ulex*; **3a–b**. H.B. 7242a: France, Haute-Loire, on *Picea*; **4a–c**. H.B. 7376: France, Vendée, on *Ilex*; **5a–b**. 20.IX.2010: Germany, Thüringen, on *Picea*. **6**. J.P.P. 11207. France, Gironde, on *Erica*.

Variation. There is considerable variation in spore and ascus size, and especially in the size of the spore body, but without apparent ecological correlation. The collections from Madeira and Arizona showed the largest dimensions (ascus length, apical thickening, spore length and width). The exudate on the apothecial margin is often rather thick and layered, resembling stratified glassy caps. However, its yellow colour in water and the lilac stain in CRB suggest that there is only exudate present.

Anamorph. Tridentaria-like conidia emerged in great number from the hymenium of a mature apothecium of *O. vibrioides* (Pl. 370: 1g). However, a parasitic infestation is imaginable since we found two times very similar conidia emerging from the apothecia of *O. cylindrospora* (section *Orbilia*; Pls 370: 4g; 371: 5b). Yet, in these two collections *O. vibrioides* grew in association. It remains open whether the tridentaria-like conidia belong to any of the two species (see also under *Hyalorbilia hergiswiliana*, p. 433, for which a parasitic growth in hymenia of *Orbilia vinosa* and perhaps *O. montigena* is considered). The conidia in the three samples associated with *O. vibrioides* were 3–4-armed, total size †/*19–38 × (5–)13–33 µm, stipe 8–12.5 × 2–3.3 µm, 0–1-septate, arms (6.5–)10–27(–36) × 2.3–4 µm, 1–2 or (2–)3–4(–6)-septate, slightly to strongly tapering, ± diverging; conidiophores short, */†~2–10 × 1.5–2.2 µm. In a further collection of *O. vibrioides* (H.B. 9822b), a similar 3-armed conidium was seen on the natural substrate. Comparable conidia but with more than 3–4 arms were observed in association with *O. pleiomicrosoma* (Pls 813–814), partly also ermerging from the apothecia.

In two further collections of *O. vibrioides* trinacrium-like (Y-shaped) conidia were observed on the natural substrate near the apothecia (see IVV): in H.B. 7376 with two arms, total size †27–36(–51) × 27–48 µm, stipe 13–15 × 2–2.6 µm, 1–3-septate, arms only slightly tapering, 16–27 × 2–3 µm, 2–4(–7)-septate; in J.P.P. 11207 with larger conidia, one of the two conidia with one arm branched again (similar as in *H. hergiswiliana*).

Phylogeny. Sequences gained from apothecia collected in the departments Ardèche (on *Picea*) and Var (on *Arbutus*) comprise SSU, ITS, and LSU. The S943 and S1506 introns are present in the former but absent in the latter sample. In addition, a distance of 8 % in the ITS is observed between the two samples, but only 0.8 % (5 nt) in the LSU D1–D2, and 0 % in LSU D3–D5 and SSU V8–V9.

An uncultured DNA isolate from *Picea* shoots and needles in Lithuania (KP897546, clone 2168_426, Menkis et al. 2015), comprising partial 5.8S and entire ITS2, shows in the ITS2 region a perfect match to *O. vibrioides* on *Picea* (except for 2 inserts), though differing by 4 nt in the 5.8S, probably by mistake. A total of nine sequences of *O. vibrioides* from two remote sites in Lithuania were obtained by Menkis et al., all from shoots of *Picea* damaged by the spruce bud scale, showing a variation of 0–2.5 % in the ITS2 region (A. Menkis pers. comm.). No doubt, all these conifericolous strains are conspecific, and it might be interpreted as a hint that samples on coniferous substrate here referred to *O. vibrioides* belong to a species of their own.

Our analyses place *O. vibrioides* and *O. graminis* in a strongly (ITS+LSU, LSU) or medium (SSU+ITS+LSU, ITS, S1506 intron) supported clade (Phyls 7, 9–10, S12, S13), but with a distance of 15.5–17 % in the ITS, 21.5 % in the intron, and 4 % in the LSU D1–D2. This clade, which also includes *O. myrioobliqua* and *O. helicoobliqua* (shown in Phyls 9–10), clustered in all these analyses unresolved among the other clades of section *Hemiorbilia*. BLAST searches in GenBank for LSU D1–D2 yielded species of series *Hesperideae* and *Hemiorbilia* with a 95 % similarity. Also the ITS region best matches members of section *Hemiorbilia*, though with high distance and ambiguous alignment. BLAST searches for the intron yielded members of various groups of *Orbilia* with a distance of ~22–25 %, and for the SSU V8–V9 region members of section *Hemiorbilia*.

Ecology. Contrary to the similar *O. graminis*, *O. vibrioides* was so far only found on woody substrates: slightly to strongly decayed wood and bark of xeric twigs and branches of both coniferous and angiosperm trees and shrubs. The collections are mainly from humid to semihumid regions of Europe, especially from the supra- to mesotemperate or supra- to mesosubmediterranean atlantic west (Great Britain, France, Spain), also from subcontinental central Europe (Thüringen), orotemperate southern France (Massif central), hemiboreal Lithuania (DNA extract), and mesomediterranean France and Dalmatia. One record was from mesosubmediterranean (sub)humid laurel forests in Madeira (Macaronesia). Three samples from western North America include the mild-maritime humid Pacific northwest (southern end of Coast Mountains) and warm-continental subhumid west (manzanita chaparral scrubland at Mogollon Rim adjacent to Sonoran Desert). The vegetation includes different laurel forests (*Lauro novocanariensis-Perseetum indicae*, *Ilici canariensis-Ericetum platycodonis*), *Ulex* shrubs, a *Quercus*-*Castanea* forest, and a submediterranean *Quercus ilex* forest, and in Thüringen a cold-temperate montane *Picea* plantation.

Map 63. Known distribution of *O. vibrioides* in Europe and Macaronesia.

Specimens included. **GREAT BRITAIN**: **Wales**, **Ceredigion**, 17.5 km NE of Lampeter, 4.5 km ESE of Tregaron, 322 m, branch of *Salix*, on bark, 2.X.2011, J.P. Priou (H.B. 9613 ø, J.P.P. 11123). – **Powys**, 12 km W of Crickhowell, 1.8 km S of Aber Village, 196 m, branch of *Sambucus*, on bark, 3.X.2011, J.P. Priou (J.P.P. 11136, doc. vid.). – **Swansea**, 20 km W of Swansea, 8 km S of Burry Port, ESE of Llanmadoc, 58 m, branch of *Ulex europaeus*, on wood, 29.IX.2011, J.P. Priou (J.P.P. 11100, doc. vid.). – **South East England**, **West Sussex**, 2 km SSE of Crawley, 1 km SE of Tilgate, Tilgate Park, 100 m, branch of *Malus* × *scheideckeri*, on wood, 17.I.2014, N. Aplin (ø, doc. vid.). — **LITHUANIA**: **Kaunas**, 11.5 km SE of Kaunas, 2.5 km S of Vaišvydava, 77 m, shoots/needles of *Picea abies*, VII.2013 (Menkis et al. 2015, mol. extr.; sq.: ined.). – **Šiauliai**, 35 km WNW of Šiauliai, 10.5 km WNW of Kuršėnai, 100 m, shoots/needles of *P. abies* VII.2013 (Menkis et al. 2015, mol. extr.; sq.: KP897546). — **GERMANY**: **Thüringen**, Thüringer Wald, 8 km NW of Sonneberg, 1.2 km SW of Rabenäußig, Langeberg, 510 m, branch of *Picea abies*, on wood, 20.IX.2010, S. Helleman (S.H. 668 ø, doc. vid., anam. substr.). — **FRANCE**: **Bretagne**, **Morbihan**, 3.3 km SE of Malestroit, N of Nazareth, 67 m, branch of *Buxus sempervirens*, on bark, 1.III.2012, J.P. Priou (J.P.P. 12057, doc. vid.). – 3.8 km WNW of La Gacilly, N of St.-Jugon, 80 m, branch of *Taxus baccata*, on wood, 17.II.2012, J.P. Priou (J.P.P. 12047, doc. vid.). – 13 km W of Herbignac, 2 km SW of Pénestin, la Poudrantais, 3 m, branch of *Ulex europaeus*, on wood, 9.XII.2005, J.P. Priou (J.P.P. 25161, doc. vid.). – 5.5 km SW of Auray, 1.5 km NW of Crac'h, Baie St.-Jean, 10 m, twig of *Ulex europaeus*, on wood, 25.I.2005, J.P. Priou (J.P.P. 25021, doc. vid.). – **Pays-de-la-Loire**, **Vendée**, 21 km SSW of La Roche-sur-Yon, 2.3 km NNW of Avrillé, Bois de la Garde, 35 m, branch of *Ilex aquifolium*, on wood, 5.VI.2003, H.O. Baral (H.B. 7376). – **Aquitaine**, **Gironde**, 20 km SW of Royan, 6 km SSW of Soulac-sur-Mer, l'Amélie, Arrière dune, 12 m, twig of *Erica scoparia*, on wood, 20.XI.2011, J.P. Priou (J.P.P. 11207, doc. vid.). – **Auvergne**, **Haute-Loire**, Massif central, 15 km SSW of Le-Puy-en-Velay, 2.7 km WNW of Cayres, 1275 m, branch of *Picea abies*, on wood, 4.X.2002, G. Marson (H.B. 7242a, anam. substr.). – ibid., branch of *P. abies*, on wood, 28.VIII.2015, G. Marson (ø). – **Ardèche**, 8 km ENE of Le Cheylard, 1.5 km NE of St.-Julien-Labrousse, 812 m, twigs and branches of *P. abies*, on wood, 11.X.2016, G. Marson (G.M. 2016-10-11.1; sq.: MG372374). – **Provence-Alpes-Côte d'Azur**, **Var**, 10 km W of Cogolin, 5 km NW of Gorbière, SW of Capelude, 380 m, twigs and branches of *Arbutus andrachne*, on wood, 4.IX.2017, G. Marson (G.M. 2017-09-04.2; sq.: MH221062). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 8 km W of Korčula, Pupnat, south-slope of Veli vrh, 400 m, branch of *Pinus halepensis*, on wood, 11.VI.2000, H.O. Baral (H.B. 6696b). – 3.5 km WSW of Korčula, 1.8 km NW of Žrnovo, Kočje, 190 m, branch of *Quercus ilex*, on wood, 3.VI.2000, H.O. Baral & N. Matočec (H.B. 6674). — **SPAIN**: **Asturias**, 2.4 km N of Pola de Somiedo, 2 km S of Castro, 703 m, branch of *Corylus avellana*, on wood, 7.VI.2013, H.O. Baral (H.B. 9822b, anam. substr.). — **MACARONESIA**: **Madeira**, 8 km SSW of Ponta Delgada, 1.8 km N of Lombo do Moleiro, W of Boca da Encumeada, 990 m, twig & branch of *Erica*, on bark & wood, 29.VI.1997, R. Reuter (H.B. 5961b). – 4.5 km W of Seixal, 2.5 km S of Ribeira da Janela, 885 m, branch of *Laurus novocanariensis*, on wood, 13.X.2009, J.P. Priou (J.P.P. 29180, doc. vid.). — **CANADA**: **British Columbia**, 10 km W of Vancouver, University of British Columbia, west side of Walter Gage building, 90 m, branch of *Mahonia dictyota*, on wood, 20.VIII.1994, G. Marson (H.B. 5236). – 11 km NNW of Victoria, Observatory Hill, NW of planetarium, 218 m, twigs and branches of *Arbutus menziesii*, on wood, 28.I.2017, O. & A. Ceska (O.C. 2170126, doc. vid.). — **USA**: **Arizona**, Mogollon Rim, 37 km SSW of Flagstaff, NE of Sedona, 1320 m, branch of *Arctostaphylos patula*, on wood, 8.V.1995, G. Marson (ex H.B. 5733c, M-0276606, **holotype**, anam. substr.).

Orbilia graminis Baral & G. Marson, **sp. nov.**, MB 813537 — Pls 372–373, Map 64

Etymology: referring to the substrate, leaves of *Poaceae*.

Typification: Luxembourg, Koedange, leaves of *Phragmites australis*, 23.V.1994, G. Marson (ex H.B. 5084a, M-0276489, holotype).

Latin diagnosis: *Similis* Orbiliae vibrioidi *sed ascosporae leniter angustiores, corpusculum refringens bacilliforme vel subulatum, cellulae terminales paraphysium leniter longiores. Habitat ad culmos vel folios putridos siccos* Poacearum, *plerumque* Phragmitis australis, *in zona temperata atlantica vel subcontinentali Europae.*

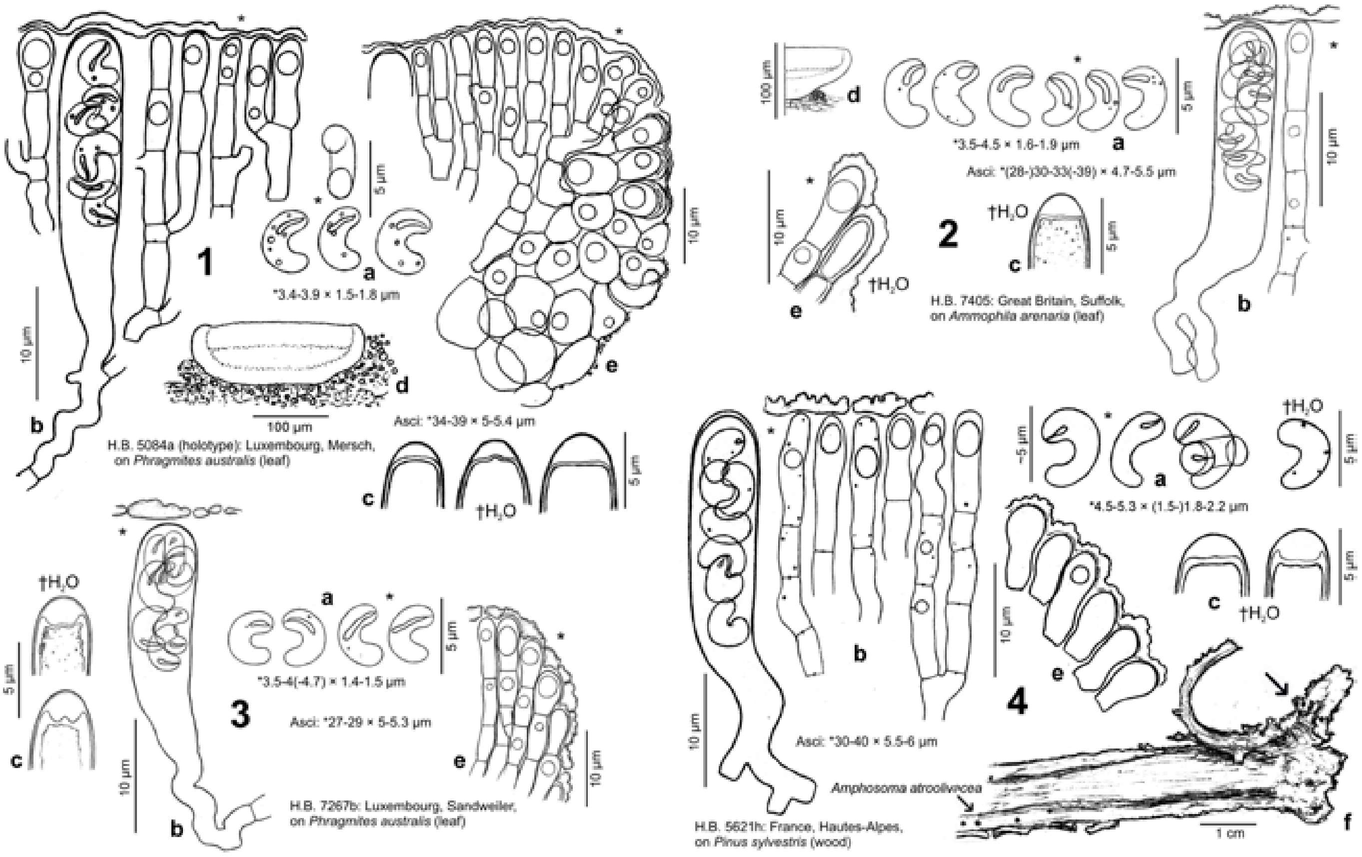


Plate 372. **1–3**: *Orbilia graminis*; **4**: *O.* cf. *graminis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. partially decorticated xeric branch of *Pinus*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.1–0.3(–0.4) mm diam., 0.06–0.1 mm high, pale to light cream or usually pure rose(-orange), round or very slightly lobate, scattered to gregarious; disc flat, margin indistinct or distinct, 0–5 µm rising above disc, smooth; broadly sessile or with ill-defined stipe, superficial or immersed in algal layer; dry pale to bright orange-rose-red. **Asci** *27–39 × (4.7–)5–5.5 µm {3}, †(21–)24–35 × 3.8–4.5(–4.8) µm {4}, (6–)8-spored, spores ± 2–3-seriate, ~3–4 lower spores inversely oriented (upper spores partly crosswise), pars sporifera *13–17 µm long; **apex** (†) hemispherical to slightly conical(-truncate), dome †1.5–2.3 → 1–1.5(–2) µm thick {5}, with or without small apical chamber; **base** with short to long, ± thin, flexuous stalk, L- or h-shaped. **Ascospores** *3.4–4.2(–4.7) × (1.4–)1.5–1.8(–1.9) µm {4}, cashew-shaped, both ends rounded, very strongly curved by (100–)140–180°; **SBs** apically attached to spore wall, *1.8–2.8(–3) × (0.2–)0.3–0.4(–0.5) µm {4}, rod-shaped to vermiform-subulate {5}, straight to medium flexuous, apically narrowed to a ± small point, overmature *1.5 × 0.8 µm, tear-shaped. **Paraphyses** apically uninflated to slightly (to medium) clavate (sometimes spathulate to sublageniform), terminal cells *4–9.5 × 1.5–2.7(–3.2) µm {2}, †1.3–2 µm wide, lower cells *(1.7–)4–7.5 × 1.8–2.5 µm {2}; sometimes branched near apex. **Medullary excipulum** very pale rose, 10–30 µm thick, of dense textura angularis-intricata, medium sharply delimited. **Ectal excipulum** hyaline to very pale rose, of thin-walled († slightly gelatinized) t. globulosa-angularis from base to mid flanks or margin, 20–30 µm thick near base, cells *(5–)7–13(–15) × 5–12 µm {4}, irregularly vertically oriented; 10–20 µm thick near margin, marginal cortical cells *6–10 × 2.5–5.2 µm {4}, thin or firm walls without {2} or with very thin (0.3–1 µm thick) glassy caps {1}, oriented at 20–80°. **Anchoring hyphae** medium abundant, */†(1.7–)2–2.5(–3) µm wide, walls 0.2(–0.4) µm thick {3}. **SCBs** globose, in paraphyses 1–2 per cell, large; in excipulum 1.5–3.5 µm diam. **Exudate** over paraphyses 0.3–1.7 µm thick, continuous to cloddy, rough, ± loosely attached; over margin 0.5–2.5 µm thick, hyaline. **— ANAMORPH**: unknown (but see below).

Habitat: collected 0.1–0.8 m above the ground, on standing, ~1–2 year old leaves or leaf sheaths of *Ammophila arenaria* {1}, *Phragmites australis* {8}, leaf sheaths ± attached to culm, on medium to strongly decayed epidermis or in furrows or longitudinal clefts on epidermis-free areas (*Phragmites*), mainly on ribbed upperside of leaf (*Ammophila*), greyed, medium to strongly covered by green algae. **Associated**: *Albotricha acutipila* {1}, ?*Cryptodiscus* sp. {1}, *Orbilia septispora* {2}, '*Pezizella*' *nigrocorticata* {1}, *Unguiculariopsis* sp. {1}, crustose lichens. **Desiccation tolerance**: ± fully viable for at least 4 months. **Altitude**: 7–565 m a.s.l. **Geology**: fluviatile deposits from Keuper (marl & sandstone) and Lower Jurassic sandstone, Quaternary sand, silt & gravel. **Phenology**: IV–VII, XII–I (probably throughout the year, long-lived).

Taxonomic remarks. The ascospores of *O. graminis* strongly resemble those of the lignicolous *O. vibrioides*, but markedly differ in containing narrow, elongated instead of broadly tear-shaped SBs, and in occurring on *Poaceae*. *O. graminis* further differs in slightly narrower spores and slightly shorter terminal cells of paraphyses.

Variation. *O. graminis* apears to be rather constant and easily recognizable. It shows distinct variation in ascus length among the few studied specimens but deviates only slightly in size and shape of spores and spore bodies. However, the SBs turn tear-shaped in overmature spores which obscures the difference to the otherwise very similar *O. vibrioides*.

Not included collections. Two samples on bark and wood of *Pinus sylvestris* from southern France (Pl. 372: 4) deviate from *O. vibrioides* in slightly narrower spores containing subulate SBs ~1.5–2 × 0.3–0.4 µm (one of them was only studied in the dead state). The spores strongly resemble *O. graminis*,

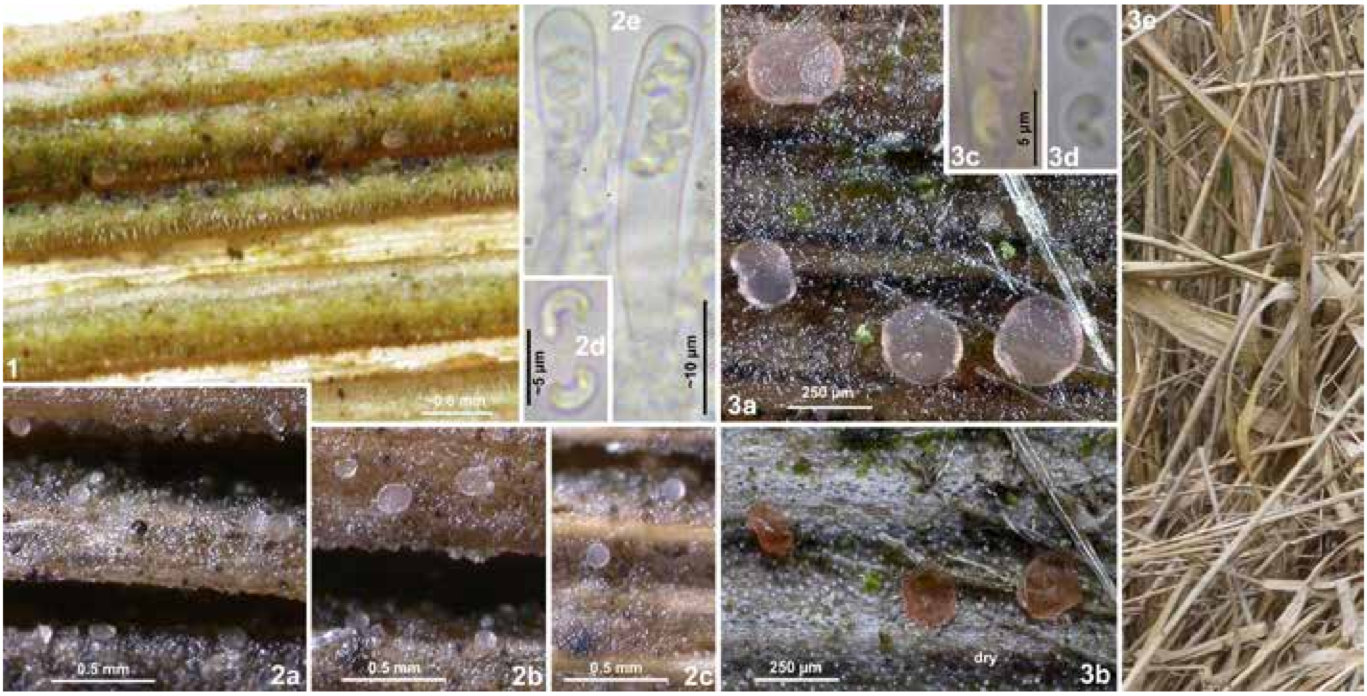


Plate 373. **1–3**: *Orbilia graminis*. – **3e**. *Phragmites* stand; **1**, **2a–c**, **3a**. rehydrated apothecia (**2**: after almost 4 years, originally light rose); **3b**. dry apothecia; **2e**. asci (fully turgescent); **2d**, **3c–d**. ascospores. – Living state. — **1**. H.B. 7405: Great Britain, Suffolk, on *Ammophila*; **2a–e**. H.B. 7267b: Luxembourg, Sandweiler, on *Phragmites*; **3a–e**. G.M. 2017-05-20.1: Luxembourg, Koedange, on *Phragmites*.

but due to the lignicolous habitat they are not included in either description. The apothecia were light rose-pink, and the terminal cells of paraphyses are with *7.5–12 µm slightly longer than in *O. graminis*.

Anamorph. In two collections of *O. graminis* (IVV: H.B. 5087, 7267b) a few 3-armed tridentaria-like conidia were found near the apothecia which resemble those observed in *O. vibrioides*. Yet, in H.B. 7267b *O. septispora* (section *Habrostictis*, IVV: H.B. 7267a) grew in association and the observed conidia might rather belong to this species, for which such an anamorph was obtained in culture.

Phylogeny. A sequence gained from apothecia of a specimen from Koedange comprises ITS (with S1506 intron) and LSU. *O. graminis* clustered with *O. vibrioides*, *O. myrioobliqua*, and *O. helicoobliqua* in a highly or medium supported clade, but with a very high distance (see under *O. vibrioides*, p. 750, and series *Vibrioides*, p. 746).

Map 64. Known distribution of *O. graminis* in Europe.

Ecology. *O. graminis* was collected on ± rotten, still standing xeric culms (leaf sheaths), mainly of *Phragmites*, in cold-temperate subcontinental humid areas of Europe, including a small hemiboreal area in Denmark, but also in atlantic mesotemperate humid southeastern Europe. A single record on *Ammophila* in the atlantic lowlands of Suffolk (Great Britain) indicates that *O. graminis* has a wider amplitude. The *Phragmites* stands in Luxembourg were rather undisturbed swampy areas with *Salix*, that in Suffolk a treeless dyke at the sea shore close to a large *Phragmitetum*. Olariaga et al. (2015: 7) reported *O. graminis* in their study of *Phragmitetum* formations in Gipuzkoa (País Vasco). The two not included collections on *Pinus* are on Middle Jurassic calcareous marl from orosubmediterranean humid Southern French Prealps.

Specimens included. **GREAT BRITAIN**: **East England**, **Suffolk**, 10 km SSW of Southwold, 5 km NNE of Leiston, Minsmere Haven, 5 m, leaves of *Ammophila arenaria*, 5.VII.2003, S.M. Francis (E.B. 4431, K(M) 145649, H.B. 7405). — **DENMARK**: **Midtjylland**, 8 km SW of Viborg, 1 km SE of Hald Hovedgard, Hald Sø, Niels Bugges Kro, 10 m, culm of *Phragmites australis*, 15.V.2005, H.O. Baral (ø). — **LUXEMBOURG**: **Gutland**, **Mersch**, Luxembourg Plateau, 4.3 km S of Larochette, 1.2 km N of Koedange, below Folkend, Mäschpesch, 300 m, leaf sheaths of *P. australis*, 23.V.1994, G. Marson (ex H.B. 5084a, M-0276489, **holotype**; G.M. 5176, **isotype**). – ibid., leaf sheaths of *P. australis*, 25.IV.1994, G. Marson (H.B. 5087, G.M. 5162). – ibid., 0.5 km NNE of Koedange, 297 m, 1.XII.2016, G. Marson (G.M. 2016-12-01.1). – ibid., 20.V.2017 (G.M. 2017-05-20.1; sq.: MH221061). – **Luxembourg**, 7.5 km E of Luxembourg, 1.2 km ENE of Sandweiler, Neimillen, 305 m, culms & leaf sheaths of *P. australis*, 1.XII.2002, G. Marson (H.B. 7267b). — **GERMANY**: **Baden-Württemberg**, Oberschwäbisches Hügelland, 13 km NNW of Ravensburg, 4.8 km SSE of Altshausen, Schreckensee, 565 m, leaf sheaths of *P. australis*, 26.VI.1994, G. Marson (H.B. 5128, G.M. 5199). — **SPAIN**: **País Vasco**, **Gipuzkoa**, 10.5 km WSW of San Sebastián, 6 km E of Zarautz, Itzao, 7 m, culms of *P. australis*, 7.I.2013, I. Olariaga (ARAN-F A3025083, doc. vid.).

Not included. **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, Alpes de Provence, 24 km SE of Gap, 5 km E of Turriers, 0.6 km SW of Col des Garcinets, 1147 m, branch of *Pinus sylvestris*, on bark, 25.VIII.1996, G.

Marson (H.B. 5621h ø). – 17 km NE of Digne-les-Bains, 5 km SSW of Prads-Haute-Bléone, WSW of Blégier, 970 m, branch of *Pinus sylvestris*, on wood, 24.VIII.1996, G. Marson (ø)

Orbilia myrioobliqua Baral & G. Marson, **sp. nov.**, MB 813510 — Pls 374–375, Map 65

Etymology: referring to the 64-spored asci and obliquely inserted spore bodies. **Typification**: Western Australia, Pithara, twigs of *Acacia*, 24.XI.2001, G. Marson (ex H.B. 7208a, MEL 2389226, holotype).

Latin diagnosis: *Apothecia 0.15–0.33 mm diam., sessilia, erumpentia, aurantio-ochracea, margine albido- vel pallide luteo-pulveracea. Asci 64-spori, apice in statu emortuo rotundati, fortiter crassitunicati. Ascosporae *4.3–7 × 2–3.2 µm, subcylindricae vel clavatae, in statu vivo corpusculum refringens cylindricum vel subclavatum, obliquum vel geniculatum, ad subapicem affixum continentes. Paraphyses ad apicem leniter clavato-capitatae. Excipulum et paraphyses exsudato valido aspero sulphureo tectae. Habitat ad corticem, etiam lignum putridum ramulorum et ramorum in aere prominentium fruticum vel arborum angiospermarum* (Fabales, Myrtales, Santalales), *etiam in petiolis* Macrozamiae, *in zona tropica et subtropica arida ad semihumida Australiae occidentalis et meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.33(–0.4) mm diam., 0.1–0.15 mm high, pale to bright (dirty) ochre- to brick-orange, non-translucent, round, rarely elliptical, scattered; disc slightly concave to flat, with whitish to yellowish pruina or warts, margin thick, 0–20 µm protruding, often distinctly whitish to pale or light yellow pruinose, finely crenulate or with ± prominent radial ribs; broadly sessile, slightly to strongly immersed in cracks, partly almost superficial; dry with small cupulate disc, bright yellow to (ochre-)orange. **Asci** *(46–)60–75(–90) {6} × 8.5–9.5 {2} or 9.5–10.3 {2} or 10.7–12(–12.5) {3}, †(47–)55–75(–82) {6} or (60–)75–100(–118) {1} × (7–)8–8.5 {2} or (9–)9.5–11.5(–13) {4}, 64-spored [~(38–)48–64 spores counted], spores multiseriate, lower spores often inverted (strongly mixed), pars sporifera *39–55 µm long; **apex** (†) hemispherical, dome *1–1.7 µm thick, †3–4(–5) → 1.5–3.7 µm {5} [KOH 3.5–5.5 → 1–3.5(–4.5) µm], mostly with apical chamber, KOH+MLZ negative or pale reddish; **base** unstalked or with short to medium, rarely very long, ± thick, flexuous stalk, L-, T- or Y-shaped. **Ascospores** *(4.3–)4.5–6.5(–7)((–8.5)) {8} × (1.8–)2–2.7 {7} or 2.7–3.2 {2} µm, †(4–)4.5–6.5(–7.3) × 2–2.5((–3)) µm {6}, (sub)cylindrical(-ellipsoid) or slightly to medium clavate (cuneate), both ends rounded, straight, exceptionally slightly curved; **SBs** subapically to laterally attached to spore wall, *(1.8–)2.4–3(–3.3) × (0.7–)0.9–1.1(–1.3) µm {3}, rod- to narrowly pear-shaped, apically narrowed to a wide point, always obliquely oriented within spore, straight or ± geniculate. **Paraphyses** apically uninflated to slightly (rarely medium) clavate-capitate, terminal cells *(5.5–)9–13(–15) × 2–3.5 µm {3}, †2.5–4.2 µm wide {H.B. 8684}, protruding 4–10 µm beyond living asci (5–15 µm beyond dead asci), lower cells *(3.5–)8–15 × 1.5–2.8 µm {2}; unbranched near apex. **Medullary excipulum** hyaline to very pale rose, 10–25(–40) µm thick, of dense textura globulosa-intricata, very indistinctly to sharply delimited. **Ectal excipulum** hyaline to very pale rose, of (†) thin-walled (rarely slightly gelatinized), irregularly or indistinctly horizontally oriented t. globulosa-angularis from base to mid flanks, 15–30 µm thick near base, cells */†6–12(–16) × 5–10(–15) µm {4}; 15–25 µm thick near margin, of t. angularis-prismatica or t. prismatica-porrecta oriented at a 10–50° angle to the surface, marginal cortical cells *5–12 × 3–5.3 µm {3}. **Anchoring hyphae** sparse to abundant, */†1.8–3.3 µm wide, walls 0.2 µm thick {3}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 0.8–1.7 µm diam. **Exudate** light to bright sulphur-yellow (very pale yellow in KOH), over paraphyses 0.2–2(–3) µm thick, coarsely granular-cloddy, ± firmly attached; over margin and flanks 1–4 µm thick. — **ANAMORPH**: unknown.

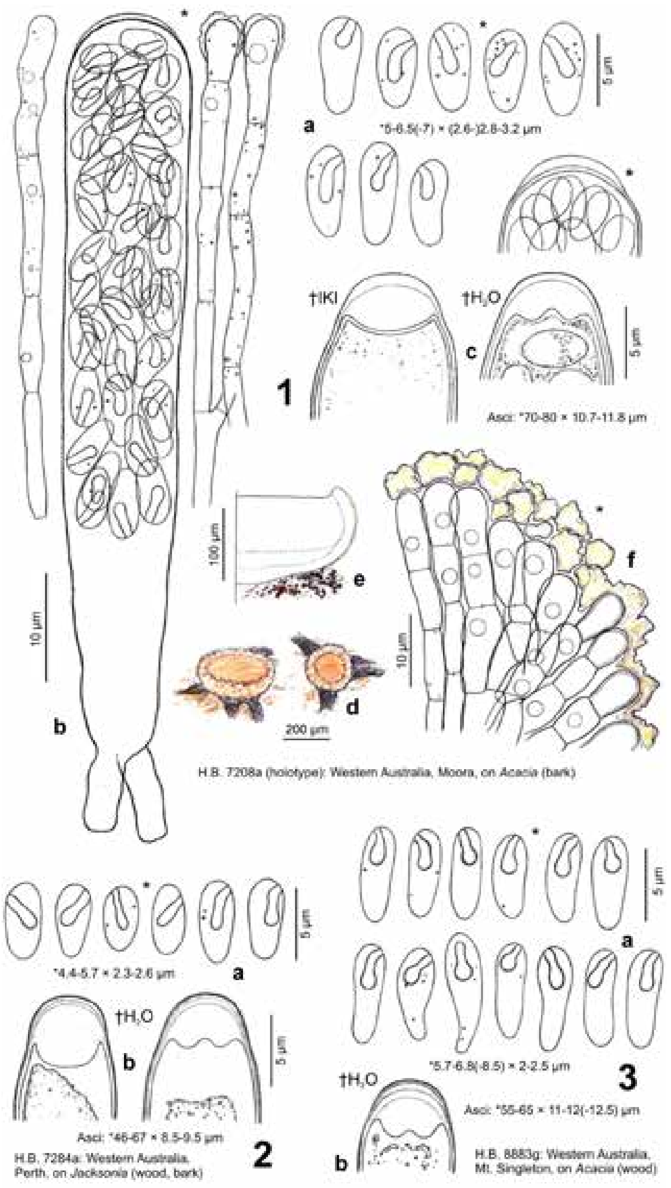


Plate 374. **1–3**: *Orbilia myrioobliqua*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., marginal ectal excipulum.

Habitat: collected 0.2–2.5 m above the ground, corticated or partially to entirely decorticated, 1.5–13(–50) mm thick twigs and branches, rarely fruits, of *Acacia* sp. {7}, *Calothamnus* sp. {1}, *Calytrix* sp. {1}, *Hakea* sp. {1}, *Jacksonia* sp. {2}, *Nuytsia floribunda* {1}, on slightly to strongly decayed bark (periderm or bast, outer surface) {13} and wood {6}, often in small holes or larger cracks in periderm, sometimes in ?beetle gallery; on petioles of *Macrozamia riedlei* {1}; ± strongly greyed, green and orange algae sparse to abundant. **Associated**: *Amandinea* sp. {1}, *Caloplaca* sp. {2}, *Claussenomyces* spp. {4}, *Durella* sp. {1}, *D.* aff. *connivens* {1}, *Gloniopsis praelonga* {4}, *Hysterium angustatum* {1}, *Hysterobrevium mori* {1}, ?*Lecidea* sp. {1}, *Orbilia albidorosea* {1}, *O. amberina* {1}, *O. anguliobliqua* {2}, *O. australiensis* {10}, *O. austroobtusispora* {1}, *O. aviflagellata* {1}, *O. curvatiobliqua* {1}, *O. curvativitalbae* {2}, *O. eucalypti* {5}, *O. helicoobliqua* {2}, *O. hesperidea* {3}, *O. kingsiana* {1}, *O. macrocarpa* {1}, *O. macrotrapeziformis* {1}, *O. microserpens* {3}, *O. multiserpens* {1/1}, *O.* ?*multivirgula* {1}, *O. myrioeuonymi* {1}, *O. myriofusiclava* {5}, *O. myriolilacina* {2}, *O. myriomuscula* {1}, *O.* ?*navajoana* {1}, *O. nothovinosa* {4/1}, *O. paraobliqua* {2}, *O. pleioaustraliensis* {2}, *O. pleioaustrocylindrica* {1}, *Patellaria* ?*andina* {1}, *P. atrata* {1}, *Proliferodiscus griseoviolaceus* {1}, *Symbiotaphrina desertorum* {1}, ?*Triblidium* sp. {3}. **Desiccation tolerance**: fully viable for at least 14 months. **Altitude**: 11–380 m a.s.l. **Geology**: Precambrian and Cretaceous sedimentary rock; granite, granitic gneiss (red-brown to whitish soil). **Phenology**: long-lived.

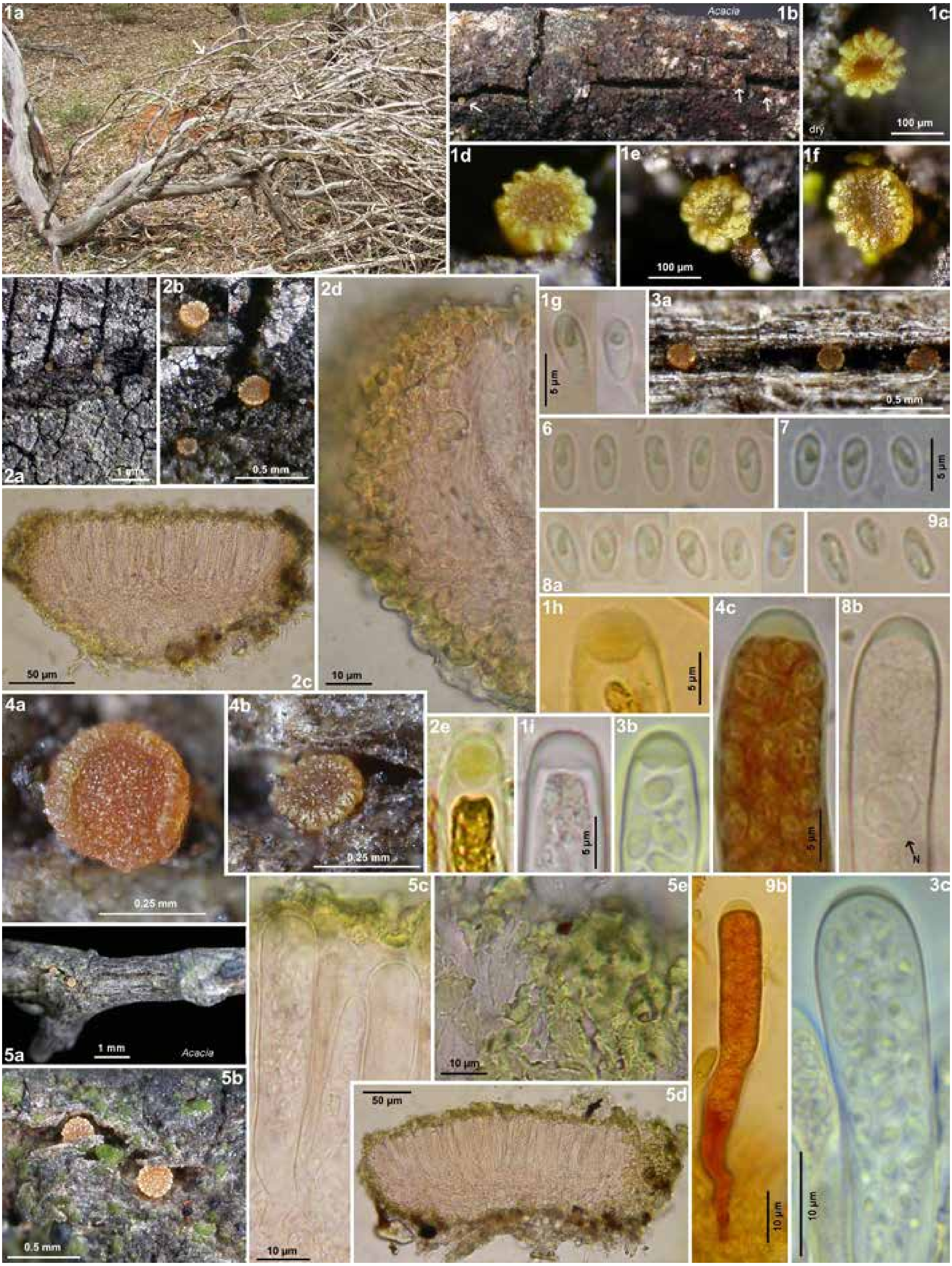


Plate 375. **1–9**: *Orbilia myriooblique.* – **1a**. Eucalypt open woodland with dead fallen *Acacia*; **1b**. dead xeric corticated branch of *Acacia*; **1f**, **2a–b**, **3a**, **4a–b**, **5a–b**. rehydrated apothecia (**1c–f**: illuminated with Luxeon-LED); **1c**. dry apothecium; **2c**, **5d**. apothecia in median section; **2d**. id., marginal ectal excipulum; **5e**. yellow exudate on margin (external view); **3c**, **5c**, **9b**. asci and paraphyses; **1h–i**, **2e**, **3b**, **4c**, **8b**. apices of immature and mature asci (**8b**: N = fusion nucleus); **1g**, **6**, **7**, **8a**, **9a**. ascospores. – Living state: **1g**, **2c–d**, **3c**, **5c–e**, **6–7**, **8a–b**; dead state: **1i**, **3b**, **9a** (in H_2O); **2e** (in KOH+MLZ); **1h**, **4c**, **9b** (in KOH+IKI). — **1a–i**. H.B. 8391a: Western Australia, Bindoon, on *Acacia*; **2a–e**. H.B. 8478a: Perth, on *Acacia*; **3a–c**. 3.IX.2006: Wannamal, on *Macrozamia*; **4a–c**. H.B. 8684: Onslow, on *Calytrix*; **5a–e**. H.B. 8883g: Mt. Singleton, on *Acacia*; **6**. H.B. 8611a: Perth, on *Jacksonia*; **7**. H.B. 8923a: Moora, on *Acacia*; **8a–b**. H.B. 8966b: ibid., on *Calothamnus*; **9a–b**. H.B. 7204s: Mt. Singleton, on *Acacia*.

Taxonomic remarks. *Orbilia myrioobliqua* is easily identified by its 64-spored asci containing small, subcylindrical to clavate ascospores with obliquely oriented SBs which are consistently subapically to almost laterally attached and often geniculate. Of course, this characteristic feature of the SBs is only visible in profile view. The similar *O. paraobliqua* differs in 128-spored asci that contain much narrower spores with apically attached SBs, whereas *O. pleistoobliqua* hardly differs in features other than spore number.

Variation. Some variation was noted among the collections, especially in ascus and spore size. Particularly in H.B. 8684 (on *Calytrix*, tropical-arid site) the asci were distinctly larger [†75–103(–118) × 11–13 µm] than in the other records. Nevertheless, the spore number never exceeded 64, and the ascus size did not depend on apothecial size which was sometimes extraordinary (up to 0.4 mm diam. and 0.15 mm thick, Pl. 375: 4). Also the spores were larger here, but this was also the case in one of the two samples near Mt. Singleton (H.B. 8883g, Pl. 374: 3). However, ascus and spore size varied between apothecia in these records. In one apothecium of the latter sparse collection the spores tend to form a tail-like base (Pl. 374: 3a) which was not seen in all the other samples, including H.B. 8684. The coexistence of the similar species *O. paraobliqua* (H.B. 8883a) and *O. anguliobliqua* (H.B. 8883i) on the same plant individuum complicated a clear identification of the populations.

In most collections the spore number seemed to lie quite consistently at ca. 64, but in some it appeared to range more around 40 (H.B. 8923a, 8966b, 8478a), at least in some asci. A few observations (e.g., in H.B. 8391a) suggest that also 32-spored asci sometimes occur.

Phylogeny. Two sequences of *O. myrioobliqua* (H.B. 7204s H.B. 8391a, both on *Acacia*) were obtained, comprising S1506 intron (badly sequenced in the latter strain), ITS, and LSU. From *O. helicoobliqua* they differ in possessing the intron, besides a 1.3–1.5 % ITS distance (3–4 nt in ITS1, 4 nt and 1 gap in ITS2) and 1–2 nt in the LSU D2 (pos. 579: G**C**CCC, 600; TT**C**TG or TT**T**TG). However, also the two *O. myrioobliqua* sequences differ by ~5 % in the intron, 1 % in the ITS (5 nt in ITS1), and by 1 nt (pos. 600) in the LSU D2 (in the D1 and D3 the three sequences are identical).

Ecology. *O. myrioobliqua* grew on ± rotten bark (rarely wood) of mostly corticated, xeric twigs and branches of trees, mainly of the order *Fabales*, but also *Myrtales*, *Proteales*, and *Santalales*. Two collection sites are located in Western Australia, in tropical arid to subtropical semiarid acacia shrublands and hummock grasslands (Pilbara, Carnarvon and Yalgoo ecoregion), the remaining are in southwestern Australia at the northern end of Darling Range, in subtropical semihumid (banksia-)eucalypt (open) woodlands (Geraldton Sandplains, Avon Wheatbelt, Jarrah Forest and Swan Coastal Plain ecoregions).

Specimens included. **AUSTRALIA**: **Western Australia**, Pilbara, 84 km SE of Onslow, 25 km N of Nanutarra Roadhouse, 120 m, branch of *Calytrix*, on bark, 5.XII.2001, G. Marson (H.B. 8684). – Yalgoo, W of Toolonga, 200 km N of Geraldton, 15 km SSE of Wannoo Billabong Roadhouse, 157 m, twig of *Acacia*, on bark, 8.XII.2001, G. Marson (H.B. 9033e). – Geraldton Sandplains, 67 km N of Geraldton, 19 km N of Northampton, 273 m, bark and fruit of *Hakea*, 9.XI.2007, G. Marson (ø). – 54 km N of Moora, 16.5 km N of Watheroo, Midlands Road, 292 m, branch of *Calothamnus*, on wood & bark, 25.X.2007, G. Marson (H.B. 8966b ø). – Avon Wheatbelt, 68 km NE of Moora, 14 km S of Dalwallinu, 1.5 km S of Pithara, 327 m, twigs of *Acacia*, on bark, 24.XI.2001, G. Marson (ex H.B. 7208a, MEL 2389226, **holotype**). – 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, branch of *Acacia*, on bark & wood, 24.XI.2001, G. Marson (H.B. 7204s ø; sq.: MK473438). – ibid., twig of *Acacia*, on wood & bark, 26.X.2007, G. Marson (H.B. 8883g). – Swan Coastal Plain, 150 km N of Perth, 13 km WNW of Moora, Dandaragan Road, 235 m, branch of *Acacia*, on bark, 24.X.2007, G. Marson (H.B. 8923a ø). – border to Jarrah Forest, 30 km NE of Perth, 4 km NE of Upper Swan, W of Walyunga, 76 m, branch of *Acacia*, on bark, 2.IX.2006, G. Marson (H.B. 8478a). – ibid., 37 m, twig of *Jacksonia*, on wood & bark, 23.XI.2001, G. Marson (H.B. 7284a). – ibid., twig of *Jacksonia*, on wood & bark, 2.IX.2006, G. Marson (H.B. 8611a ø). – 15 km SE of Mandurah, SW of Pinjarra Road, NE of Sir Ross McLarty Park, 11 m, branches of *Nuytsia floribunda*, on wood & bark, 17.XII.2001, G. Marson (H.B. 7087b ø). – Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 271 m, petioles of *Macrozamia riedlei*, 3.IX.2006, G. Marson (ø). – ibid., branch of *Acacia*, on bark, 4.IX.2006, G. Marson (H.B. 8391a, sq.: MK473439).

Map 65. Known distribution of *O. myrioobliqua* (white) and related species in southwestern Australia; blue: *O. pleistoobliqua*, lilac: *O. allantoobliqua*, orange: *O. anguliobliqua* + *O. angustoobliqua*, violet: *O. anguliobliqua* + *myrioobliqua*, green: *O. curvatiobliqua* + *O. paraobliqua* + *O. anguliobliqua* + *O. helicoobliqua* + *myrioobliqua*.

Orbilia pleistoobliqua Baral & G. Marson, **sp. nov.**, MB 813511 — Pls 376–377

Etymology: named after the 128-spored asci and the obliquely inserted spore bodies.

Typification: Western Australia, Hamelin Pool, branch of *Acacia*, 6.XI.2007, G. Marson (ex H.B. 8727c, MEL.2389252, holotype).

Latin diagnosis: *Similis* Orbiliae myrioobliquae *sed asci 128-spori, latiores, ascosporae paulo minores. Habitat ad corticem putridum ramulorum in aere prominentium* Acaciae *in zona subtropica arida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.14–0.23 mm diam., 0.09–0.12 mm high, light to bright brick-orange, non-translucent, ± round, scattered; disc flat, usually ± pruinose, margin thick, 0–12 µm protruding, usually distinctly whitish to yellowish pruinose, often with prominent radial ribs; broadly sessile, slightly to strongly immersed in cracks, partly almost superficial. **Asci** *64–86 × 12.5–15.7 µm, †58–81 × 11–15 µm, 128-spored (~83 spores counted), spores multiseriate, lower spores often inverted (strongly mixed), pars sporifera *54–55 µm long; **apex** (†) hemispherical, dome *1.5–1.7 → 1–1.2 µm thick, †2–2.8 → 1.5–2.5 µm (in H_2O or KOH), with distinct apical chamber, endotunica light red in CR_{SDS}; **base** with short to medium long, thick, ± flexuous stalk, Y-shaped. **Ascospores** *4.3–5.8 × 2–2.3, (sub)cylindrical or mostly only very slightly clavate or obclavate, both ends rounded, straight or very slightly inequilateral; **SBs** always subapically to laterally attached to spore wall, *2.3–3 × 0.7–0.9(–1) µm, rod-shaped to slightly subulate, apically narrowed to a ± wide point, either straight (then obliquely oriented) or distinctly geniculate in the upper part. **Paraphyses** apically uninflated to slightly clavate,

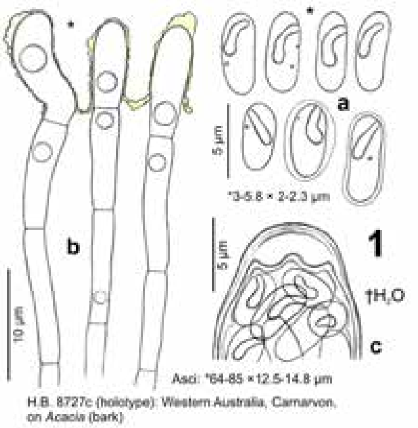


Plate 376. **1**: *Orbilia pleistoobliqua*. – **a**. ascospores (2 spores inside dead ascus seemingly ensheathed); **b**. paraphyses; **c**. ascus apex.

terminal cells *(5.5–)7–12(–18) × (2–)3–3.5(–4) µm, protruding 4–10 µm beyond dead asci, lower cells *(3.5–)7–12(–13.5) × 1.8–2.8 µm, subterminal cells *3–3.7 µm wide, unbranched near apex. **Medullary excipulum** hyaline, 20 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** hyaline, of (†) slightly gelatinized, irregularly oriented t. globulosa-angularis from base to mid flanks, 20 µm thick near base, cells *7–10 × 5.5–9 µm; 10–15 µm thick near margin, submargin of t. angularis-prismatica oriented at a 60–90° angle to the surface, upper margin of t. prismatica-porrecta oriented at 0–10°, marginal cortical cells *6–13 × 3–4 µm. **Anchoring hyphae** sparse, */†1.8–3 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.3–2.7 µm diam. **Exudate** light sulphur-yellow, over paraphyses 0.2–1(–2) µm thick, granular-cloddy, firmly attached; over margin and flanks 1–2.5 µm thick. — **ANAMORPH**: unknown.

Habitat: collected 0.5–2 m above the ground, corticated, 4–7 mm thick twigs of *Acacia* sp., on strongly decayed bark (bast), on cross clefts of periderm or bark, strongly greyed, no algae. **Associated**: *Coccomycetella* sp., *Hyalorbilia ?erythrostigma*, *Hysterobrevium mori*, *Orbilia curvatimyriella*, *O. myriella*, *O. myrioauris*, *O. myrionamibica*, *O. pleioaustraliensis*, *O. ?saguarina*, *Ostropales*, *Tryblidaria* sp. **Desiccation tolerance**: fully viable for at least 2 months, a few mature asci still alive after 40 months. **Altitude**: 67 m a.s.l. **Geology**: Cretaceous sedimentary rock (red-brown gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pleistoobliqua* is easily confused with *O. myrioobliqua*, as its main difference lies in a higher spore number. There are, however, some other characteristics which need confirmation by further collections: the spores are slightly shorter and particularly narrower, and never of distinctly clavate shape, also the SBs are slightly narrower, the asci are wider, and the apical domes not as thick as in *O. myrioobliqua*.

Ecology. *O. pleistoobliqua* is so far only known from a single collection, on rotten bark of xeric twigs of *Acacia* in Western Australia in a subtropical semiarid (almost arid) acacia shrubland (Carnarvon ecoregion).

Specimens included. **AUSTRALIA**: **Western Australia**, Carnarvon, 183 km SSE of Carnarvon, 10 km W of Overlander Roadhouse, 12 km NE of Hamelin Pool, Denham-Hamelin Road, 67 m, branch of *Acacia*, on bark, 6.XI.2007, G. Marson (ex H.B. 8727c, MEL 2389252, **holotype**).

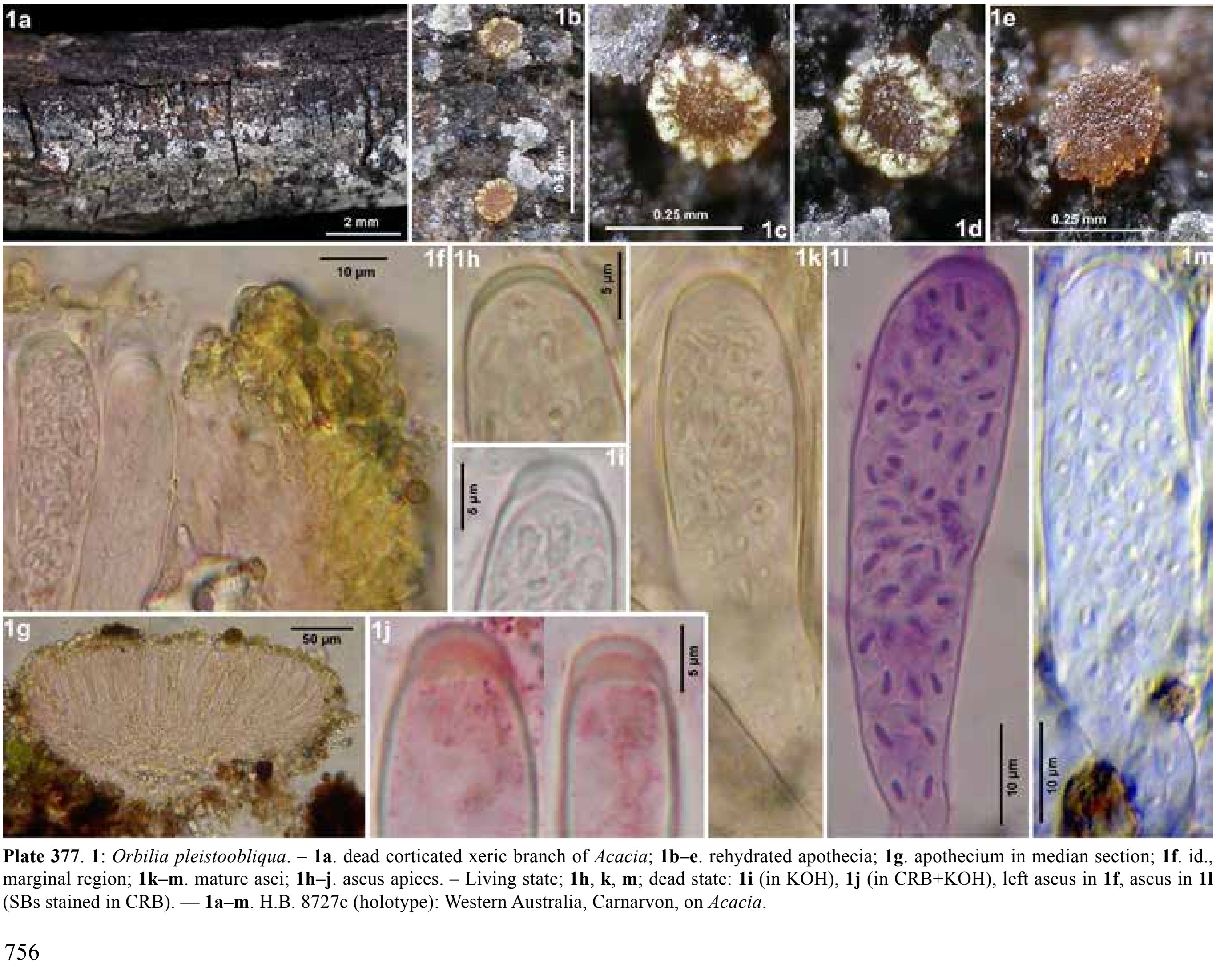


Plate 377. **1**: *Orbilia pleistoobliqua*. – **1a**. dead corticated xeric branch of *Acacia*; **1b–e**. rehydrated apothecia; **1g**. apothecium in median section; **1f**. id., marginal region; **1k–m**. mature asci; **1h–j**. ascus apices. – Living state; **1h**, **k**, **m**; dead state: **1i** (in KOH), **1j** (in CRB+KOH), left ascus in **1f**, ascus in **1l** (SBs stained in CRB). — **1a–m**. H.B. 8727c (holotype): Western Australia, Carnarvon, on *Acacia*.

Orbilia paraobliqua Baral & G. Marson, **sp. nov.**, MB 813512 — Pls 378–379

Etymology: referring to the similarity with *O. myrioobliqua* (but lacking the obliquely attached spore bodies).

Typification: Western Australia, Wubin, twig of *Acacia*, 24.XI.2001, G. Marson (ex H.B. 7204a, MEL 2389222, holotype).

Latin diagnosis: *Similis* Orbiliae myrioobliquae *sed asci 128-spori, ascosporae angustiores, corpusculum refringens ad apicem affixum. Habitat ad corticem putridum ramulorum in aere prominentium* Acaciae *in zona subtropica semiarida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.33 mm diam., 0.11–0.13 mm high, pale to bright orange-ochraceous, non-translucent, round, ± scattered; disc flat, yellowish warted-pruinose, margin thick, not protruding, whitish to yellowish pruinose, sometimes ribbed; broadly sessile, superficial. **Asci** *65–85(–92) × 10.5–13(–14) µm {2}, †60–80 × 9.3–12 µm {2}, 128-spored (75–107 spores counted), spores (*) multiseriate, lower spores somewhat more often inverted than upper spores (strongly mixed), pars sporifera *45–55 µm long; **apex** (†) hemispherical, dome *1.5 → 1 µm thick, †3–4.5(–5.5) → 1.8–2.5 (KOH 2.5–5.5) µm {2}, with or without distinct small apical chamber, KOH+IKI negative, rarely very faintly reddish; **base** with short, ± thick, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(5–)5.5–7(–8) × (1.6–)1.7–1.9(–2.2) µm {2}, (sub) cylindrical, rarely fusoid, dumbbell-shaped or slightly tapered below, ends rounded, rarely obtuse, straight to (very) slightly curved; **SBs** consistently apically attached to spore wall, *1.7–2.5(–3) × 0.6–1.1 µm {2}, tear- to pear-shaped, also rod-shaped to ampulliform, apically narrowed to a wide to small point. **Paraphyses** apically uninflated or very slightly clavate, terminal cells *7–15.5 × 2–3(–4) µm {1}, protruding 0–10 µm beyond living asci, lower cells *(4–)7–15(–18.5) × 1.8–3(–3.5) µm {2}; rarely or often branched at upper septum. **Medullary excipulum** pale rose, 10–20 µm thick, medium dense textura intricata with many small inflated cells, not sharply delimited. **Ectal excipulum** hyaline to pale rose, of (†) thin-walled, irregularly vertically oriented t. angularis-globulosa from base to mid flanks or submargin, 15–35 µm thick near base, cells *6–12(–16) × 5–8(–10) µm {2}; 15–20 µm thick near margin, (upper) margin of t. prismatica(-porrecta) oriented at a 10–40° angle to the surface, marginal cortical cells *6–10 × 2.8–5 µm {2}. **Anchoring hyphae** sparse, †2–3 µm wide, walls 0.2(–0.4) µm thick {2}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 0.7–2 µm diam. **Exudate** over paraphyses, margin and flanks (1–)2–6(–8) µm thick, cloddy, light to bright sulphur-yellow, loosely attached. **— ANAMORPH**: unknown.

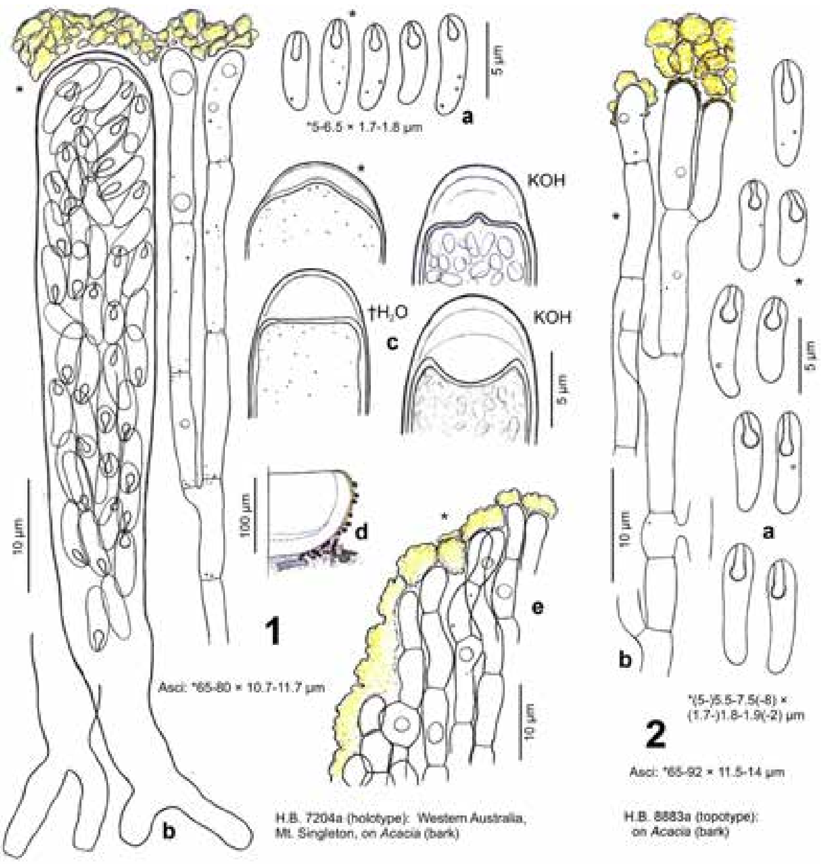


Plate 378. **1–2**: *Orbilia paraobliqua*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

Habitat: collected 1–2 m above the ground, partially to nearly entirely decorticated, 1.5–3 mm thick twigs of *Acacia* sp. {2}, on medium to very decayed bark (bast) {2}, greyed, no algae. **Associated**: *Amandinea* sp. {1}, *Caloplaca* sp. {1}, *Orbilia amberina* {1}, *O. anguliobliqua* {1}, *O. australiensis* {2}, *O. austroobtusispora* {1}, *O. aviflagellata* {1}, *O. curvatiobliqua* {1}, *O. helicoobliqua* {2}, *O. hesperidea* {2}, *O. microserpens* {1}, *O. multiserpens* {1}, *O. myriofusiclava* {1}, *O. myriolilacina* {2}, *O. myriomuscula* {1}, *O. myrioobliqua* {2}, *O. nothovinosa* {1}, *O. pleioaustraliensis* {2}, *O. pleioaustrocylindrica* {1}, *Ostropales* {1}, *Patellaria* ?*andina* {1}, ?*Triblidium* sp. {2}. **Desiccation tolerance**: submature asci still viable after 10 months. **Altitude**: 380 m a.s.l. **Geology**: Archean sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia paraobliqua* is characterized by 128-spored asci and small, cylindrical, not or only slightly allantoid ascospores. Contrary to *O. myrioobliqua*, the SBs are consistently inserted in the spore apex. The spore number of 128 was calculated from the volume of the pars sporifera, but also by counting of spores or SBs which clearly led to values much over 64. Yet, a few asci of an apothecium possibly contained only 64 spores. *O. pleistoobliqua* differs in somewhat shorter and wider spores with subapically to laterally inserted SBs, also in slightly wider asci. *O. anguliobliqua* frequently showed a similar SB-attachment but differs in curved spores and 64-spored asci.

Variation. The topotype (Pl. 378: 2) deviates in a few details from the holotype, though both originate from the same site and substrate. Its spores are larger and their SBs much more broadly attached, also the asci are wider, the paraphyses often branched at the apex (in the holotype branched only below the middle part), and the apothecia have a rougher surface.

A deviating apothecium in the topotype (Pl. 379: 2) shows an apparently reduced spore number of 64 and wider spores [*5.8–7.8(–8.5) × 2.2–2.4 µm] with longer SBs [(2.3–)2.6–3.4(–3.8) × 0.9–1.1 µm] suggesting a position intermediate to *O. myrioobliqua* but also to *O. allantoobliqua*. It cannot safely be included in *O. myrioobliqua* because of somewhat too long spores with more or less apically attached SBs, and not in *O. paraobliqua* because of too wide spores. *O. allantoobliqua* differs from this in distinctly curved spores, but some of its asci contained many inequilateral or even straight spores which do not differ from those of the deviating apothecium.

Ecology. *O. paraobliqua* grew on ± rotten bark of xeric twigs of *Acacia* sp. It is only known from a single collection site in southwestern Australia (Darling Plateau) in a subtropical semiarid eucalypt woodland (border between Yalgoo and Avon Wheatbelt ecoregion).

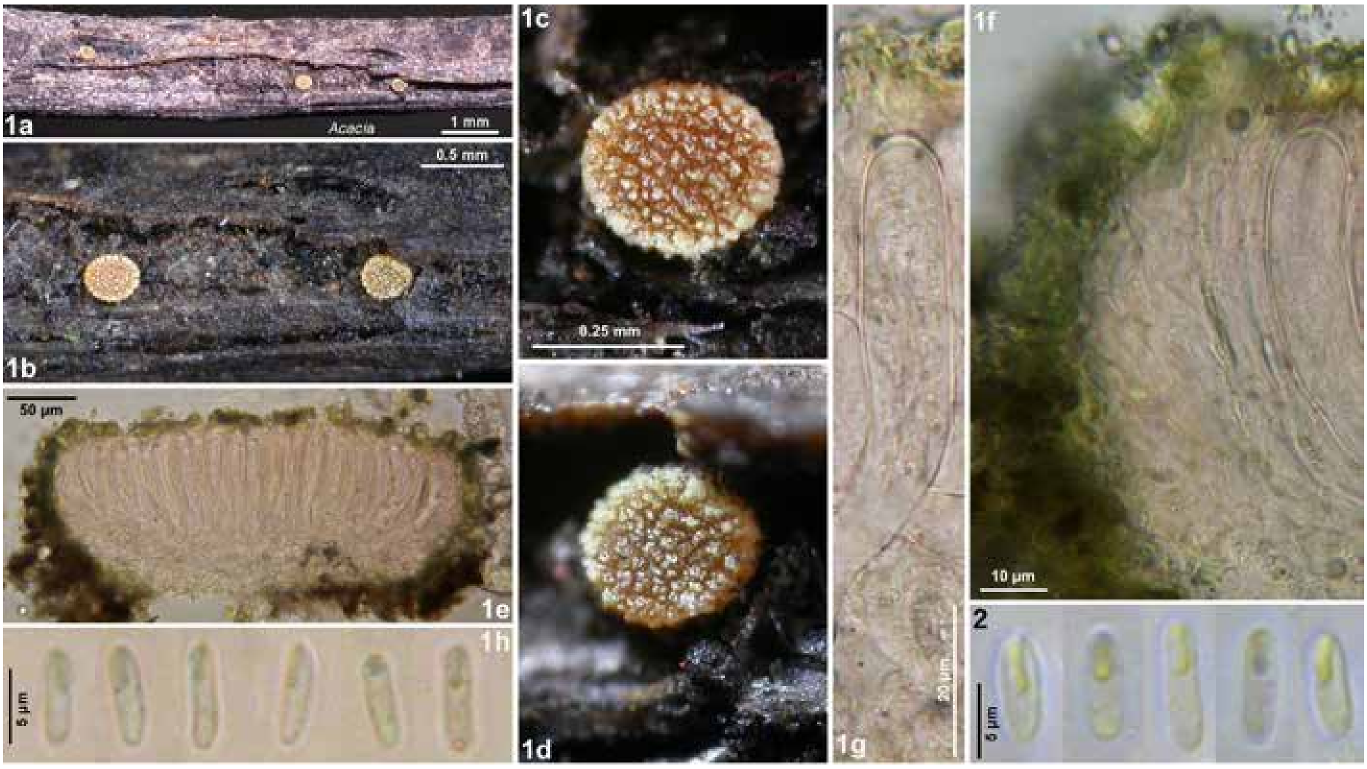


Plate 379. **1**: *Orbilia paraobliqua* (topotype); **2**. *O.* cf. *paraobliqua*. – **1a**. dead corticated xeric twig of *Acacia*; **1b–d**. rehydrated apothecia; **1e**. apothecium in median section; **1f**. id., marginal ectal excipulum; **1g**. mature ascus; **1h**, **2**. ascospores. – Living state. — **1a–h**. H.B. 8883a: Western Australia, Mt. Singleton, on *Acacia*; **2**. H.B. 8883g: ibid. (from different twig fragment, showing wider spores formed in ?64-spored asci).

Specimens included. **AUSTRALIA**: **Western Australia**, Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig of *Acacia*, on bark, 24.XI.2001, G. Marson (ex H.B. 7204a, MEL 2389222, **holotype**). – ibid., twig of *Acacia*, on bark, 26.X.2007, G. Marson (ex H.B. 8883a, mixture in MEL 2389265 [type of *O. curvatiobliqua*]).

Orbilia anguliobliqua Baral & G. Marson, **sp. nov.**, MB 813513 — Pls 380–381

Etymology: named after the basally geniculate ascospores and the obliquely inserted spore bodies.

Typification: Western Australia, Wubin, twigs of *Acacia*, 26.X.2007, G. Marson (ex H.B. 8883i, MEL 2389264, holotype).

Latin diagnosis: *Similis* Orbiliae myrioobliquae *sed ascosporae longiores et angustiores, basi saepe distincte geniculatae, supra partim constrictae. Habitat ad corticem et lignum putridum ramulorum* Acaciae *in aere prominentium in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.22–0.38 mm diam., 0.1–0.135 mm high, disc light brick-orange, non-translucent, round to broadly elliptical, laterally compressed when in clefts, scattered; disc flat, often ± strongly pruinose to warted by pale sulphur-yellow exudate, margin thin, not protruding, rough, partly ribbed, pale to light sulphur-yellow; broadly sessile, superficial to slightly erumpent between fibres. **Asci** *(55–)60–80(–88) × (10–)10.5–11.7(–12.5) µm {2}, †45–58 × 9–10.5 µm {1}, 64-spored (53–60 spores counted, exceptionally 32), spores (*) multiseriate, lower spores inverted (strongly mixed), pars sporifera *(30–)35–40(–48) or 48–57 µm long; **apex** (†) hemispherical, dome †3–4(–5) → 1.5–2.5(–4) µm thick {1}, with or without distinct apical chamber, MLZ–; **base** with short to medium long, ± thick and flexuous stalk, T-, L- or Y-shaped. **Ascospores** *6–8(–9.5) × (1.7–)1.8–2.1(–2.4) µm {2}, †(5.2–)6–8(–9.5) × (1.4–)1.6–2(–2.2) µm {2}, (sub)cylindrical to slightly clavate or dumbbell-shaped, apex rounded, sometimes obtuse, base not or only slightly attenuated, also inflated, medium to strongly curved (± L- to comma-shaped, sometimes falcate), rarely almost straight or very slightly helicoid; **SBs** apically, or often distinctly subapically (to laterally) attached to spore wall and then geniculate, *2–3.2 × (0.8–)1–1.2 µm {2}, ampulliform, apically narrowed to a wide to very wide (rarely small) point. **Paraphyses** apically uninflated or only slightly clavate, terminal cells *8–14 × 2.2–3.7 µm {1}, lower cells *5–13.5 × 2–3(–3.5) µm {1}; sometimes branched at upper septum. **Medullary excipulum** hyaline, 20–30 µm thick, of dense textura intricata-angularis, sharply delimited. **Ectal excipulum** very pale rose, of thin-walled, indistinctly oriented t. angularis-globulosa from base to mid flanks, 30–45 µm thick near base, cells *7–14 × 6–9 µm {1}; 20 µm thick near margin, of t. prismatica-

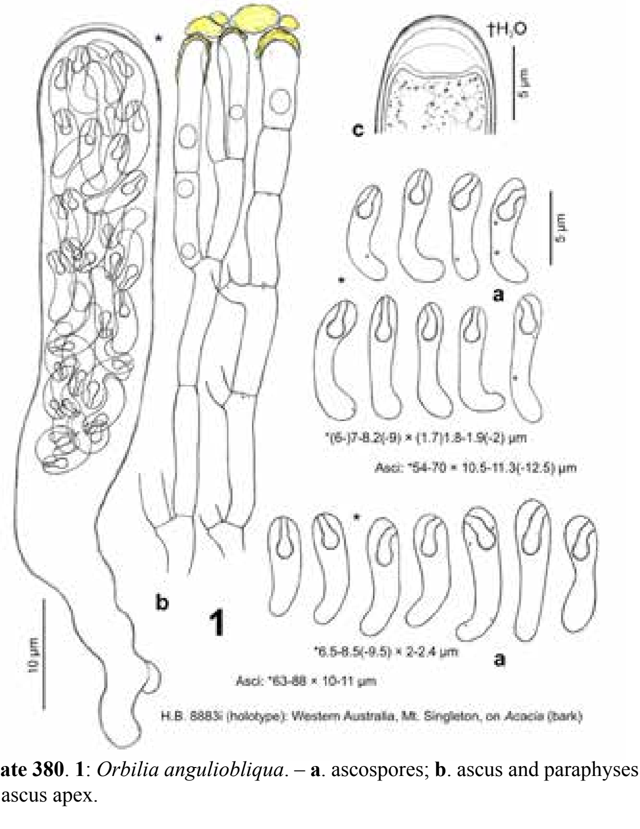


Plate 380. **1**: *Orbilia anguliobliqua*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex.

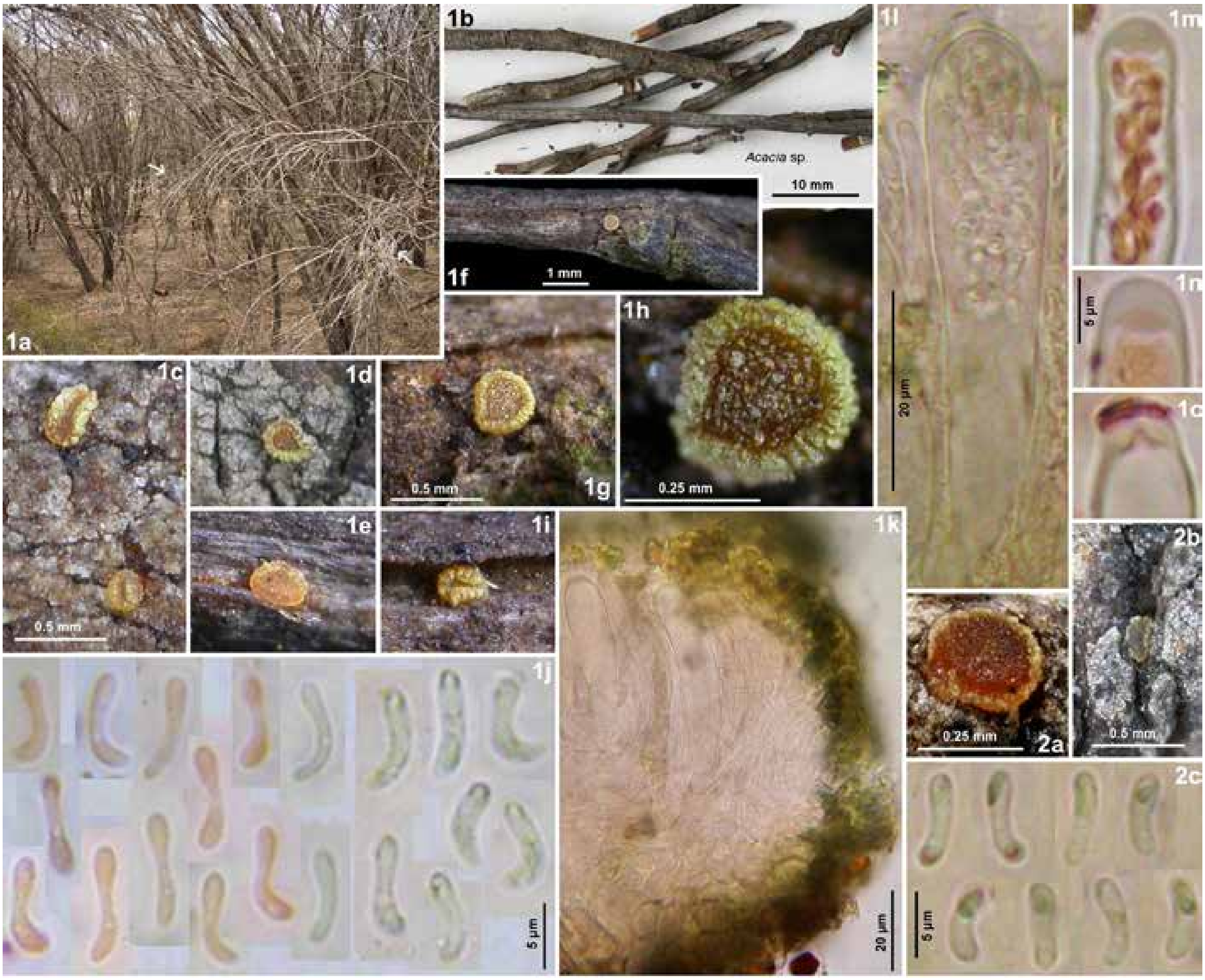


Plate 381. **1–2**: *Orbilia anguliobliqua*. – **1a**. subtropical semiarid Eucalypt woodland with *Acacia* and *Grevillea*: **1b**. xeric twigs of *Acacia* sp. taken from attached branches; **1c–i**, **2a**. rehydrated apothecia; **1k** apothecium in median section (marginal region); **1l**. mature ascus and paraphysis; **1m–o**. ascus apices; **1j**, **2c**. ascospores. – Living state, except for **1m–o** (in KOH+CR), **1j** (left in KOH+CR, 2 central spores in KOH, right in H_2O). — **1a–o**. H.B. 8883i (holotype): Western Australia, Mt. Singleton, on *Acacia*; **2a–c**. H.B. 9050f: Western Australia, Yalgoo, on *Acacia*.

porrecta oriented at a 0–40° angle to the surface, marginal cortical cells *6–8 × 2–3 µm {1}. **Anchoring hyphae** sparse, †1.5–2.5 µm wide, walls 0.2 µm thick {1}. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1–2.5 µm diam. **Exudate** over paraphyses and margin 0.2–3 µm thick, coarsely cloddy, light sulphur-yellow, firmly attached but also with loose clods. — **ANAMORPH**: unknown.

Habitat: collected 0.5–2 m above the ground, corticated to partially decorticated, 1.5–5.5 mm thick twigs of *Acacia* sp. {3}, medium to strongly decayed bark {3} (bast & periderm), also on wood {2} (close to bark), partly in cracks of bark, rarely on thallus of *Amandinea*, strongly greyed, with some green algae. **Associated**: *Amandinea* sp. {1}, *Caloplaca* sp. {1}, *Orbilia angustoobliqua* {1}, *O. ?atriplicis* {1}, *O. australiensis* {1}, *O. curvatiobliqua* {1}, *O. helicoobliqua* {1}, *O. helicovinosa* {1}, *O. hesperidea* {1}, *O. macrocarpa* {1}, *O. microserpens* {1}, *O. ?multiserpens* {1}, *O. ?multivirgula* {1}, *O. myriella* {1}, *O. myriofusiclava* {1}, *O. myriolilacina* {1}, *O. myriomuscula* {1}, *O. myrioobliqua* {2}, *O. ?navajoana* {1}, *O. paraobliqua* {1}, *O. pleioaustraliensis* {1}, *O. ?saguarina* {1}, *?Triblidium* sp. {2}. **Desiccation tolerance**: fully viable for at least 18 months. **Altitude**: 157–380 m a.s.l. **Geology**: Archean and Cretaceous sedimentary rock (ochre to red-brown sand). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia anguliobliqua* is very similar to *O. myrioobliqua* and *O. paraobliqua*, which both grew in association though on different twig fragments. The species differs from these mainly in the ascospores which are frequently basally bent (L-shaped). *O. myrioobliqua* also differs in somewhat shorter and wider spores, and *O. paraobliqua* in 128-spored asci. On different twig fragments of this collection grew also the curved-spored *O. helicoobliqua* and *O. curvatiobliqua* (for the differences see under these species).

O. angustoobliqua (Pls 387–388) is sharply separated from *O. anguliobliqua* by much longer and narrower spores with strictly apically inserted SBs. Also *O. allantoobliqua* (Pl. 386) deviates in consistently apically attached SBs, and here the spores tend to be longer and are often only slightly curved, usually allantoid (falcate) but also sometimes bent near the base. Macroscopically, no clear difference could be observed between the Australian taxa of series *Vibrioides*.

Variation. The rather small populations of *O. anguliobliqua* varied somewhat in spore size and curvature, also in ascus size, even within an apothecium. Spore shape was quite regularly L- or comma-shaped in the holotype (Pl. 380: 1a) as well as in the paratype (Pl. 381: 2c). With *6–7 × 1.7–2 µm the paratype possesses rather small spores. In a further sample (H.B. 9033f, unillustrated) the spores varied between slightly and strongly falcate and L-shaped within the single detected apothecium (spores †7–9.5 × 1.8–2.2 µm, asci ?32-spored).

Ecology. *O. anguliobliqua* grew on rotten bark (also wood) of xeric twigs of *Acacia* sp. The species is known from three subtropical semiarid sites in southwestern Australia (Darling Plateau), where it occurred in acacia open shrublands (Yalgoo coregion at border to Carnarvon) and in a eucalypt woodland (Avon Wheatbelt at border to Yalgoo).

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, twig of *Acacia*, on bark, 8.XI.2007, G. Marson (H.B. 9050f ø). – 200 km N of Geraldton, 15 km SSE of Wannoo Billabong Roadhouse, W of Toolonga, 157 m, twig of *Acacia*, on bark, 8.XII.2001, G. Marson (H.B. 9033f ø). – Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twigs of *Acacia*, on bark, 26.X.2007, G. Marson (ex H.B. 8883i, MEL 2389264, **holotype**).

Orbilia helicoobliqua Baral & G. Marson, **sp. nov.**, MB 813514 — Pls 382–383

Etymology: named after the usually helicoid ascospores and a close relationship to *O. myrioobliqua*.

Typification: Western Australia, Wubin, twigs of *Acacia*, 26.X.2007, G. Marson (ex H.B. 8883f, MEL 2389263, holotype).

Latin diagnosis: *Similis* Orbiliae myrioobliquae *et* O. anguliobliquae *sed ascosporae partim longiores, plerumque distincte helicoideae et basi attenuatae, corpuscula refringentia longiora, ad apicem affixa. Habitat ad corticem* et *lignum putridum, ramulorum et ramorum* Acaciae *in aere prominentium in zona subtropica semiarida Australiae occidentalis.*

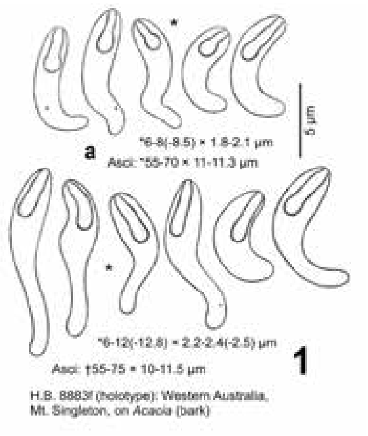


Plate 382. **1**: *Orbilia helicoobliqua*. – **a**. ascospores (2 rows from 2 different apothecia).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.3(–0.75) × 0.2–0.38 mm diam., 0.09–0.11 mm high, disc light brick-orange, non-translucent, ± round, sometimes strongly compressed when in cracks, scattered to subgregarious in small groups; disc flat, often strongly pruinose to warted by pale sulphur-yellow exudate, margin thick, 5 µm protruding, rough, partly ribbed, pale to light sulphur-yellow; broadly sessile, superficial to slightly erumpent; dry contracted, cupulate. **Asci** *55–70 × 11–11.3 µm {T}, †55–75 × (8.5–)9.5–11.5 µm {2}, 64-spored (48–60 spores

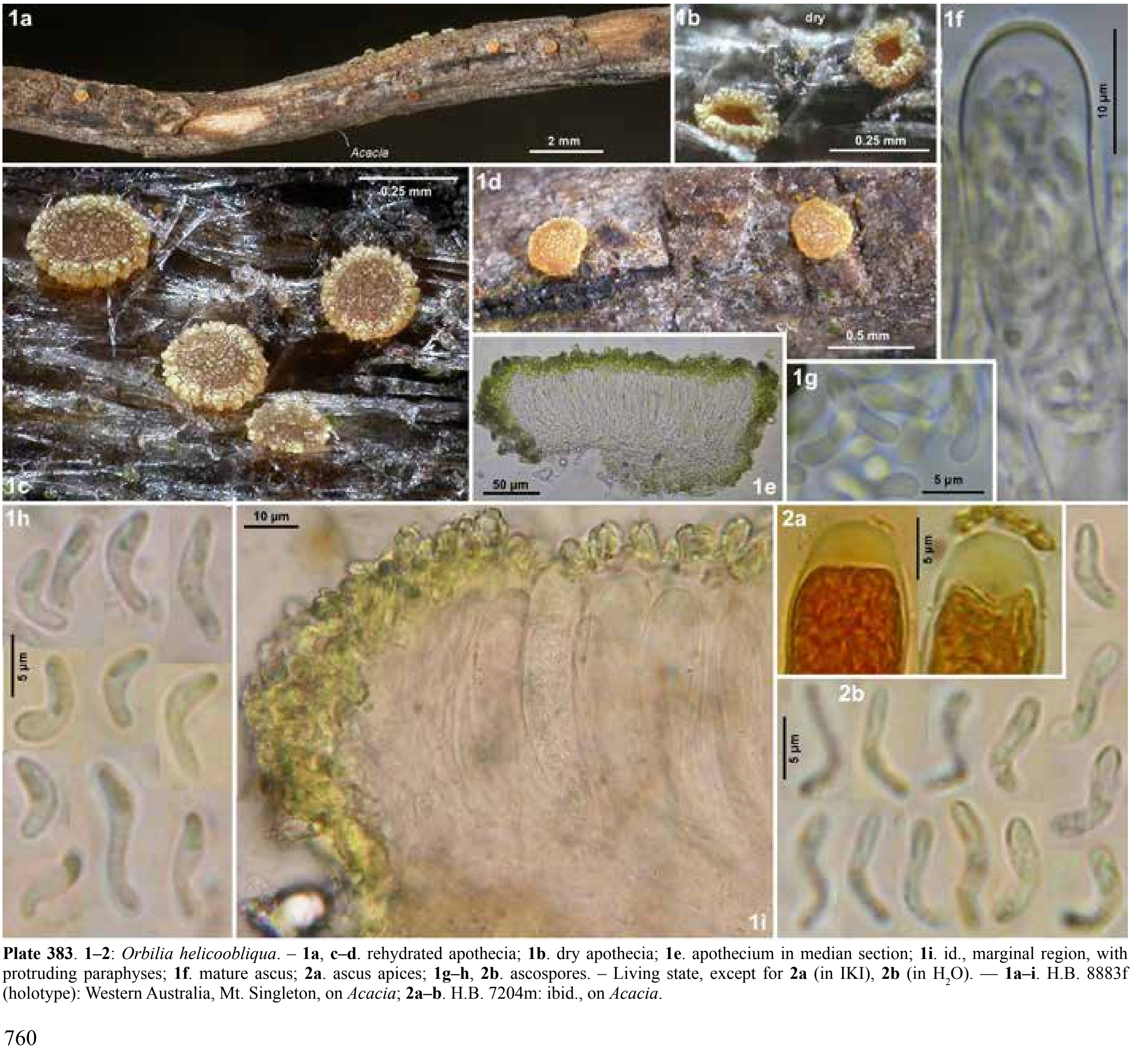


Plate 383. **1–2**: *Orbilia helicoobliqua*. – **1a**, **c–d**. rehydrated apothecia; **1b**. dry apothecia; **1e**. apothecium in median section; **1i**. id., marginal region, with protruding paraphyses; **1f**. mature ascus; **2a**. ascus apices; **1g–h**, **2b**. ascospores. – Living state, except for **2a** (in IKI), **2b** (in H_2O). — **1a–i**. H.B. 8883f (holotype): Western Australia, Mt. Singleton, on *Acacia*; **2a–b**. H.B. 7204m: ibid., on *Acacia*.

counted), spores (*) multiseriate, lower spores inverted (strongly mixed); **apex** (†) hemispherical, dome †3–4.5 → 2–2.5 µm thick, with or without distinct apical chamber, inner layer bright pink in CR_{SDS}, MLZ–; **base** with short to long, ± thick and flexuous stalk, L-shaped. **Ascospores** *(6–)6.5–10.5(–12.8) × (1.8–)2–2.3(–2.5) µm [actual length ~(6–)8–12(–14) µm] {T}, †(6.5–)7–10(–12) × (1.5–)1.8–2.1(–2.2) µm {1}, subcylindrical to clavate, apex rounded to obtuse, base slightly or usually medium attenuated, often with a distinct, sometimes very slightly swollen tail of *3–5 × 1–1.3 µm, always strongly curved, mostly distinctly helicoid (like a left-hand thread) but also falcate; **SBs** consistently apically attached to spore wall, *3–4(–4.3) × (0.9–)1–1.2 µm {T}, ± rod-shaped, partly slightly inflated at the base, apically narrowed to a wide or small point. **Paraphyses** apically slightly clavate, terminal cells *9–12.5 × 2.5–3 µm {T}, 8–15 µm longer than dead asci, lower cells *(6.5–)7.5–12 × 1.5–2 µm {T}. **Medullary excipulum** hyaline, 20 µm thick, of dense textura intricata with indistinctly inflated cells, ± sharply delimited. **Ectal excipulum** hyaline, of (†) thin-walled, indistinctly horizontally oriented t. angularis from base to mid flanks, 25 µm thick near base, cells †8–14 × 6–9 µm; 15 µm thick near margin. **Anchoring hyphae** not examined. **SCBs** in paraphyses globose, 1 µm diam. **Exudate** over paraphyses and margin 0.2–3 µm thick, coarsely cloddy, light sulphur-yellow, firmly attached. **— ANAMORPH**: unknown.

Habitat: collected 0.5–2 m above the ground, corticated to partially decorticated, 1–11 mm thick twigs and branches of *Acacia* sp. {2}, medium to strongly decayed bark {2} (bast & periderm) or wood {2}, in small cracks or holes of bark, also at edge of deep cleft in wood, strongly greyed, no algae. Associated: *Amandinea* sp. {1}, *Caloplaca* sp. {1}, *Orbilia amberina* {1}, *O. anguliobliqua* {1}, *O. australiensis* {2}, *O. austroobtusispora* {1}, *O. aviflagellata* {1}, *O. curvatiobliqua* {1}, *O. hesperidea* {2}, *O. microserpens* {1}, *O. multiserpens* {1}, *O. myriofusiclava* {1}, *O. myriolilacina* {2}, *O. myriomuscula* {1}, *O. myrioobliqua* {2}, *O. nothovinosa* {1}, *O. paraobliqua* {2}, *O. pleioaustraliensis* {2}, *O. pleioaustrocylindrica* {1}, *Ostropales* {1}, *Patellaria ?andina* {1}, ?*Triblidium* sp. {2}. **Desiccation tolerance**: fully viable for at least 18 months. **Altitude**: 380 m a.s.l. **Geology**: Archean sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia helicoobliqua* is tentatively separated from *O. anguliobliqua* by having predominantly clavate-tailed, distinctly helicoid ascospores which attain a larger length, also by longer SBs which are consistently apically attached. For the similar *O. curvatiobliqua* see below.

Variation. Within a given apothecium the sparse holotype of *O. helicoobliqua* showed a rather great variability in spore size and curvature (helicoid vs. falcate), whereas SB size was quite constant. Yet, spores from different apothecia on apparently different twig fragments of the holotype differed also markedly in spore width and SB length (Pl. 382: 1), and we consider those apothecia with larger spores (lower row in Fig. 1, Pl. 383: 1h) as typical. Also in the few apothecia of the paratype the spores varied in size (Pl. 383: 2b), being narrower and slightly longer in one apothecium (left 6 spores) compared to another (right).

Phylogeny. A sequence of H.B. 7204m comprises ITS and LSU (the S1506 intron is absent). For the differences to *O. myrioobliqua* see p. 755. One of the two *O. myrioobliqua* sequences (H.B. 7204s) was gained from the same collection, in which a total of three multispored species of series *Vibrioides* occurred, including *O. paraobliqua*. Despite a low distance between the two species, their sequences appear to be trustworthy since the morphological identity of the small group of apothecia from which each sequence was gained was tested beforehand.

Ecology. *O. helicoobliqua* grew on rotten bark and wood of xeric twigs and branches of *Acacia* sp. The species is only known from one collection site in a subtropical semiarid eucalypt woodland (border between Yalgoo and Avon Wheatbelt ecoregion) in southwestern Australia (Darling Plateau).

Specimens included. **AUSTRALIA**: **Western Australia**, Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, branch of *Acacia*, on bark & wood, 24.XI.2001, G. Marson (H.B. 7204m, sq.: MK473437). – ibid., twigs of *Acacia*, on bark & wood, 26.X.2007, G. Marson (ex H.B. 8883f, MEL 2389263, **holotype**).

Orbilia curvatiobliqua Baral, **sp. nov.**, MB 813515 — Pls 384–385

Etymology: named after the falcate ascospores and a close relationship to *O. myrioobliqua*.

Typification: Western Australia, Wubin, twig of *Acacia*, 26.X.2007, G. Marson (ex H.B. 8883j, MEL 2389265, holotype).

Latin diagnosis: *Similis* Orbiliae helicoobliquae *sed ascosporae breviores et angustiores, valde falcatae vel helicoideae, basi non vel leniter attenuatae, corpuscula refringentia breviora. Habitat ad corticem putridum, ramulorum* Acaciae *in aere prominentium in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.27–0.37 mm diam., 0.11 mm high, disc light orange, non-translucent, round to elliptical, scattered; disc flat, strongly pruinose to warted by yellow exudate, margin thin, not protruding, rough; broadly sessile, superficial or in cracks of periderm. **Asci** *60–70 × 9.7–10.7 µm, †55–67(–74) × 8.5–9.5(–10) µm, 64-spored (~50 counted spores counted); **apex** (†) hemispherical, dome †3–3.5 → 1.5–2.5 µm thick, with or without apical chamber, inner layer bright pink in CR_{SDS}; **base** sessile ot with short, thick stalk, L-, Y- or h-shaped. **Ascospores** *(4–)4.5–5.5 × 1.7–1.9(–2.1) µm [actual length ~5–7(–8) µm], †4–5(–5.5)((–7)) × (1.4–)1.5–1.8 µm, cylindrical, apex rounded (to obtuse), base not or sometimes slightly attenuated, always strongly curved, falcate or often helicoid (like a left-hand thread); **SBs** consistently apically attached to spore wall, *2.2–2.8 × 0.6–0.9 µm, tear- to pear-shaped, apically narrowed to a ± small point. **Paraphyses** apically uninflated or slightly clavate, terminal cells †11–15 × 3–4 µm, 6–12 µm longer than dead asci, lower cells *10–22 × 1.5–2(–2.5) µm. **Medullary excipulum** ~20 µm thick, not examined. **Ectal excipulum** hyaline, of (†) thin-walled, indistinctly horizontally oriented t. globulosa-angularis from base to mid flanks, 20 µm thick near base, cells †8–10(–15) × 6–10(–11) µm; 10–15 µm thick near margin. **Anchoring hyphae** not examined. **SCBs** not examined. **Exudate** over paraphyses and margin 0.5–2(–3) µm thick, coarsely cloddy, light to bright sulphur-yellow, firmly attached. **— ANAMORPH**: unknown.

Habitat: collected 0.5–2 m above the ground, corticated on 1 side, 1.8 mm thick twig of *Acacia* sp., medium to strongly decayed bark (periderm), in cracks of bark, strongly greyed, no algae. **Associated**: *Amandinea* sp., *Caloplaca* sp., *Orbilia anguliobliqua*, *O. australiensis*, *O. helicoobliqua*, *O. hesperidea*, *O. myriofusiclava*, *O. myriolilacina*, *O. myriomuscula*, *O. myrioobliqua*, *O. paraobliqua*, *O. pleioaustraliensis*, ?*Triblidium* sp. **Desiccation tolerance**: fully viable for at least 18 months. **Altitude**: 380 m a.s.l. **Geology**: Archean sedimentary rock. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia curvatiobliqua* is only known from a few apothecia growing in close vicinity of *O.*

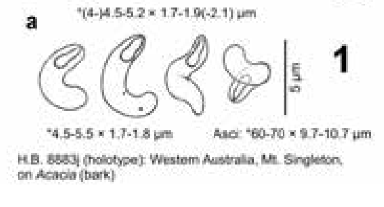


Plate 384. **1**: *Orbilia curvatiobliqua*. – **a**. ascospores.

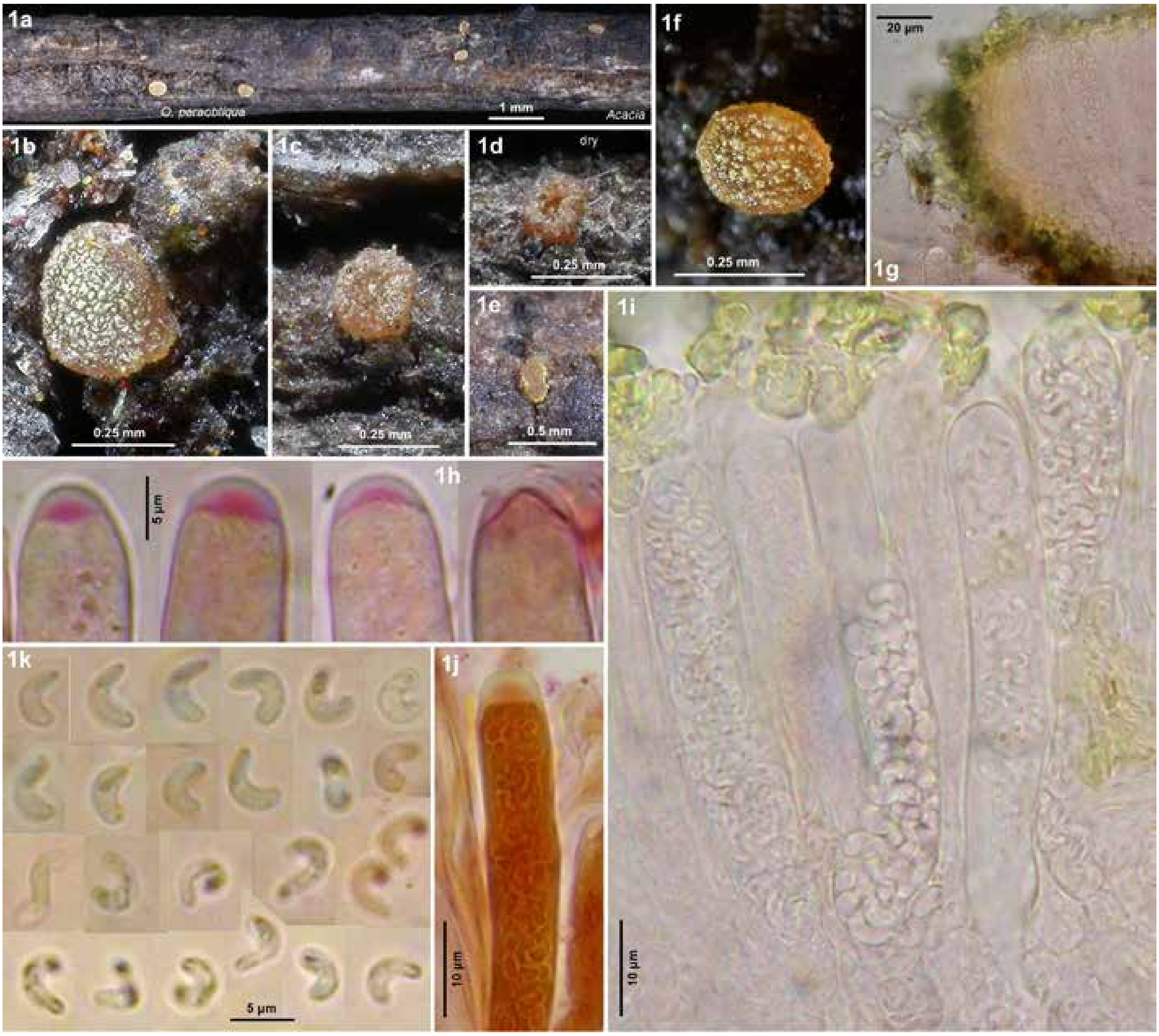


Plate 385. **1**: *Orbilia curvatiobliqua*. – **1a–c**, **e–f**. rehydrated apothecia; **1d**. dry apothecium; **1g**. apothecium in median section; **1i**. mature and immature asci; **1j–h**. ascus apices; **1k**. ascospores. – Living state, except for **1h** (in CR_{SDS}), **1k** below and right 14 spores (in H_2O, 3 right in KOH+CR), **1j** (in KOH+CR+IKI). — **1a–k**. H.B. 8883j (holotype): Western Australia, Mt. Singleton, on *Acacia*.

paraobliqua a few millimetres from each other. On different twigs of the same sample occurred the similar *O. anguliobliqua* and *O. helicoobliqua*. *O. curvatiobliqua* differs from the latter two species in smaller, especially shorter ascospores, and in SBs being usually narrowed apically to a small point, also in narrower asci. From *O. anguliobliqua* it further differs in consistently apically attached SBs and in often helicoid spores, from *O. helicoobliqua* in shorter SBs and predominantly unattenuated spore bases.

Variation. Within each of the examined apothecia the spores varied between falcate and helicoid, whereas the size of spores and SBs was rather constant.

Ecology. *O. curvatiobliqua* grew on rotten bark of a xeric twig of *Acacia* sp. in a subtropical semiarid eucalypt woodland (border between Yalgoo and Avon Wheatbelt ecoregion) in southwestern Australia (Darling Plateau).

Specimens included. **AUSTRALIA**: **Western Australia**, Avon Wheatbelt, 78 km NE of Wubin, 18 km SW of Mt. Singleton, 380 m, twig of *Acacia*, on bark, 26.X.2007, G. Marson (ex H.B. 8883j, MEL 2389265, **holotype**).

Orbilia allantoobliqua Baral & G. Marson, **sp**. **nov**., MB 813516 — Pl. 386, Map 65

Etymology: named after the slightly allantoid spores and the relationship with the Australian species of series *Vibrioides*.

Typification: Western Australia, Kumarina Roadhouse, branch of *Acacia cyperophylla*, 28.X.2007, G. Marson (ex H.B. 9695c, MEL 2389279A, holotype).

Latin diagnosis: *Similis* Orbiliae anguliobliquae *sed ascosporae leniter majores, plus minusve arcuatae, basi non distincte geniculatae, supra numquam constrictae, corpuscula refringentia longiora, semper recta et ad apicem affixa. Habitat ad lignum putridum ramuli sicci* Acaciae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.23–0.55 mm diam., 0.13–0.23 mm high (receptacle 0.18 mm), bright orange, hardly translucent, round to elliptical, scattered or in small groups; disc flat, margin ± distinct, 0–10 µm protruding, disc and margin whitish to yellowish pruinose; broadly sessile, slightly to strongly immersed in cracks; dry rather contracted, dirty orange-red. **Asci** *78–105 × (10.5–)11.5–12.5(–13) µm, †73–85 × 10–10.5(–11.5) µm, 64-spored (~50 spores counted), spores multiseriate, lower spores inverted (strongly mixed), pars sporifera *52–70 µm long; **apex** (†) hemispherical, dome †2–5 → 1.8–4.5 µm thick, with distinct apical chamber; **base** with short, thick, flexuous stalk, Y- or

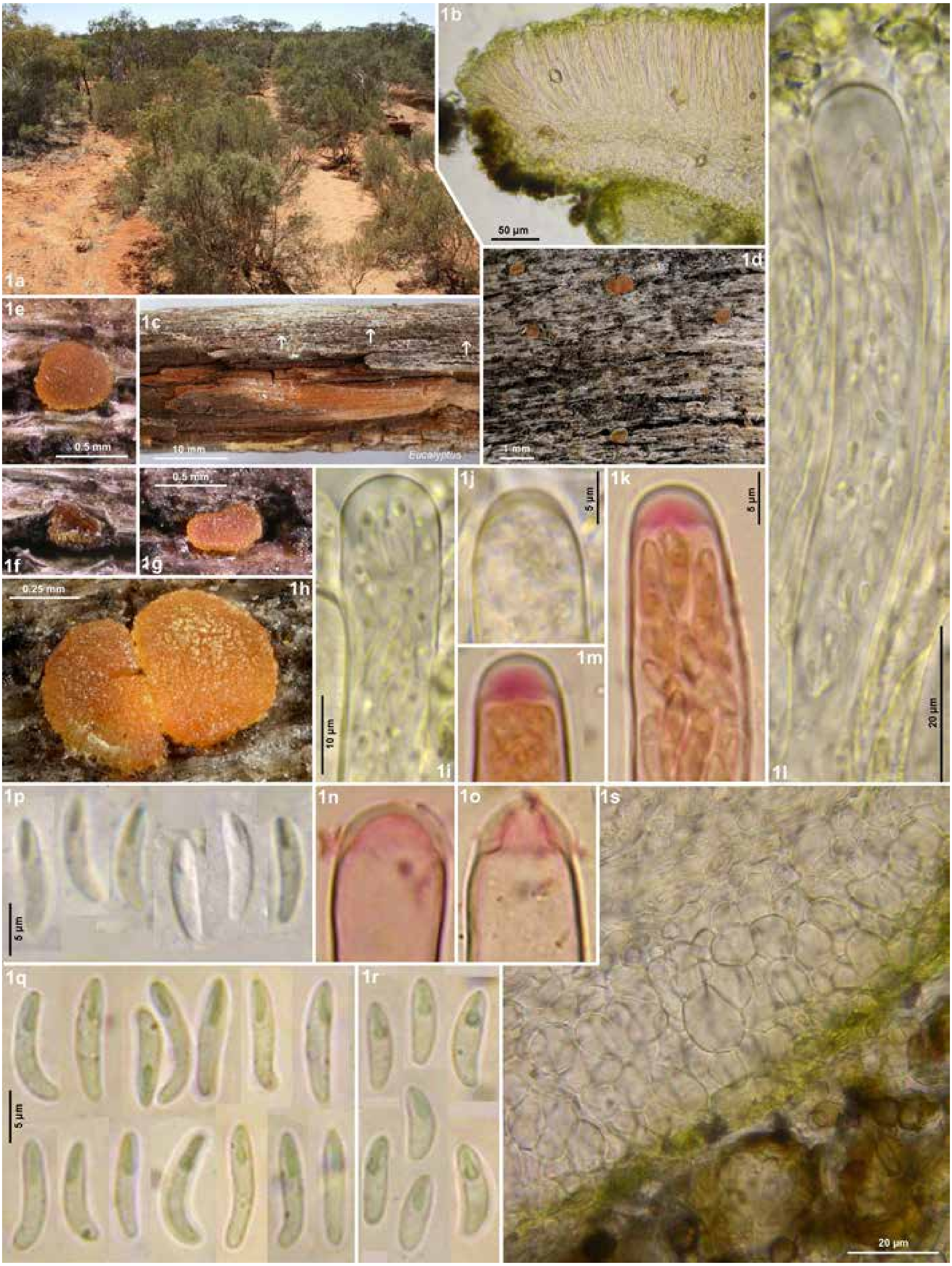


Plate 386. **1**: *Orbilia allantoobliqua*. – **1a**. subtropical arid acacia open woodland; **1b**. apothecium in median section; **1c**. decorticated xeric branch of *Eucalyptus*; **1d–e**, **g–h**. rehydrated apothecia; **1f**. dry apothecium; **1s**. ectal excipulum in median section (lower flanks); **1i**, **k–l**. asci; **1j–k**, **m–o**. ascus apices (**n–o**. basally emptied mature asci); **1p–r**. ascospores. – Living state, except for **1k**, **m–o** (CR_{SDS}). — **1a–s**. H.B. 9695c (holotype): Western Australia, Gascoyne River, on *Acacia*.

L-shaped. **Ascospores** *(6.5–)7.5–10(–11.7) × (1.8–)2–2.5(–2.6) µm, cylindrical to very slightly fusoid, ellipsoid, or clavate, never constricted, apex obtuse, base not or sometimes slightly attenuated, usually slightly to strongly curved (mainly in lower part), sometimes only inequilateral or even straight; **SBs** apically attached to spore wall, *3–4 × 0.8–1.1 µm, rod-shaped with a slight basal inflation, apically narrowed to a ± small point, straight; SBs in aged spores 2–3.3 × 1.2–1.3 µm, tear-shaped to ampulliform. **Paraphyses** apically uninflated to slightly clavate, sometimes sublageniform or moniliform, partly flexuous, terminal cells *8–18 × 2–3 µm, lower cells *11–15(–18) × 1.7–2.5 µm, at base or apex up to 3–3.3 µm wide; unbranched near apex hymenium pale orange-rose. **Medullary excipulum** pale orange-rose, 50–60 µm thick, of dense textura intricata-porrecta, horizontally oriented, partly with many inflated cells, sharply delimited. **Ectal excipulum** very pale rose, of (†) thin-walled, indistinctly oriented textura globulosa-angularis from base to mid flanks 15–70 µm thick near base, cells *(7–)9–17 × 6–12 µm; 15–20 µm thick near margin, cells, of. t. prismatica-porrecta oriented at a 10–30° angle to the surface, marginal cortical cells *4.5–10 × 2.5–4 µm. **Anchoring hyphae** very sparse, *2–2.5 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1–1.5(–2) µm diam. **Exudate** over paraphyses, margin and lower flanks 1–4 µm thick, cloddy-resinous, bright sulphur-yellow, firmly attached. — **ANAMORPH**: unknown.

Habitat: collected 2.5–3 m above the ground, decorticated, 16–17 mm thick branch of *Acacia cyperophylla*, on 0.2 mm deep very decayed wood, strongly greyed, no algae. **Associated**: *Coccomycetella* spp. {2}, *Hysterobrevium mori*, *Orbilia australiensis, O. multiaustraliensis*, *O. pleioaustraliensis*, *O. pleiocoronohesperidea, O. pleiovinosa*, *Ostropales*. **Desiccation tolerance**: fully viable after 34 months (57 months when including occasional rehydration). **Altitude**: 540 m a.s.l. **Geology**: Mesoproterozoic sedimentary rock (red-brown sand & gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia allantoobliqua* differs from *O. anguliobliqua* in slightly larger ascospores which are similarly curved though not distinctly bent below and never constricted in the middle, also in longer, always straight and apically attached SBs. Moreover, asci and pars sporifera are distinctly longer in *O. allantoobliqua*, though the spore number is the same.

Variation. Shape and curvature of the spores varied among the ca. six apothecia examined. In one of them which grew in a small group at 6–8 cm distance from the main group, the spores tend to be shorter and wider, and often rather straight (Pl. 386: 1r), reminiscent of the deviating 64-spored apothecium observed in *O. paraobliqua* (Pl. 379: 2), while in the others they were mainly of the typical size. However, such short and wide, hardly curved spores occasionally occurred also in apothecia with typical spores, which indicates that these spore variants belong to a single species. SBs were quite constant in size and shape, but get shorter and wider with age.

Ecology. *O. allantoobliqua* was found on rotten wood of a decorticated xeric branch of *Acacia* in a subtropical semiarid acacia open woodland with *Eucalyptus* in a most of the time dry riverbed in the Gascoyne ecoregion in western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Gascoyne, 171 km NE of Meekatharra, 62 km SSW of Kumarina Roadhouse, 16 km NW of Plutonic Gold Mine, 540 m, branch of *Acacia cyperophylla*, on wood, 28.X.2007, G. Marson (ex H.B. 9695c, MEL 2389279A, **holotype**).

Orbilia angustoobliqua Baral & G. Marson, **sp. nov.**, MB 813517 — Pls 387–388, Map 65

Etymology: named after the long and narrow ascospores and the similarity with *O. anguliobliqua*.

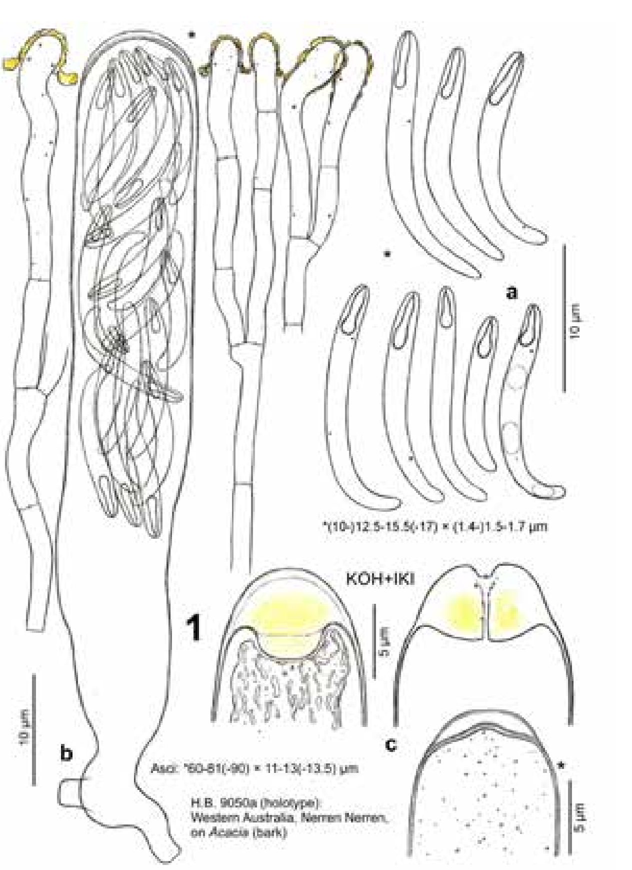


Plate 387. **1**: *Orbilia angustoobliqua*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices.

Typification: Western Australia, Toolonga, branch of *Acacia*, 8.XI.2007, G. Marson (ex H.B. 9050a, MEL 2389278A, holotype).

Latin diagnosis: *Similis* Orbiliae anguliobliquae *sed ascosporae multo longiores*, *distincte angustiores*, *corpusculum refringens ad apicem affixum. Habitat ad corticem putridum trunci vivi* Acaciae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.22–0.55(–0.65) mm diam., 0.1–0.16 mm high, light to bright orange, with partly distinct whitish-yellowish pruina, non-translucent, round to ± elliptical, scattered to subgregarious; disc flat, margin 0–10 µm protruding, ± distinctly whitish-yellowish crenulate or ribbed; broadly sessile, superficial or ± immersed in cracks; dry strongly contracted with raised margin covering most of the disc, disc bright orange-ochraceous to purplish-brown, margin whitish-yellowish powdered. **Asci** *60–81(–90) × 11–13(–13.5) µm, †54–65 × 8.5–10.5 µm, 64-spored (~50 spores counted), spores (*) multiseriate, lower spores inverted (strongly mixed), pars sporifera *(36–)40–53(–60) µm long; **apex** (†) hemispherical, dome *1.4–1.8 → 1.2–1.3 µm thick, †3.5–4.5 → 2–3 µm (KOH 4–6 → 2–4.5 µm), with or without small apical chamber, endotunica pale yellow-orange in IKI (KOH-pretreated), bright red in $\mathrm{CR}_{\mathrm{SDS}}$; **base** with short, thick stalk, T- or L-shaped. **Ascospores** *10.5–13 or mostly *(10–)13–16(–17) × (1.4–)1.5–1.7 µm, †11–15.5 × 1.4–1.7 µm, cylindric-fusoid, apex obtuse, base slightly (to medium) attenuated, medium to strongly curved near base; **SBs** apically attached to spore wall, *2.8–4(–4.5) × (0.5–)0.6–0.8(–1) µm, subulate to narrowly tear- or pear-shaped, apically narrowed to a ± small point, straight to slightly curved. **Paraphyses** apically uninflated to slightly clavate, terminal cells *(5–)10–18 × 1.8–3 µm, exceeding the hymenial surface by 2–5 µm, lower cells *7–14 × 1.7–2.2(–2.5) µm; sometimes branched at upper septum, hymenium pale rose. **Medullary excipulum** very pale rose, 20–40 µm thick, of dense textura intricata-globulosa, medium to sharply delimited. **Ectal excipulum** hyaline to very pale rose, of (†) thin-walled to slightly gelatinized, indistinctly vertically or horizontally oriented t. globulosa-angularis from base to mid flanks, 15–60 µm thick near base, cells *8–17 × 5–13 µm; 15–20 µm thick near margin, of t.

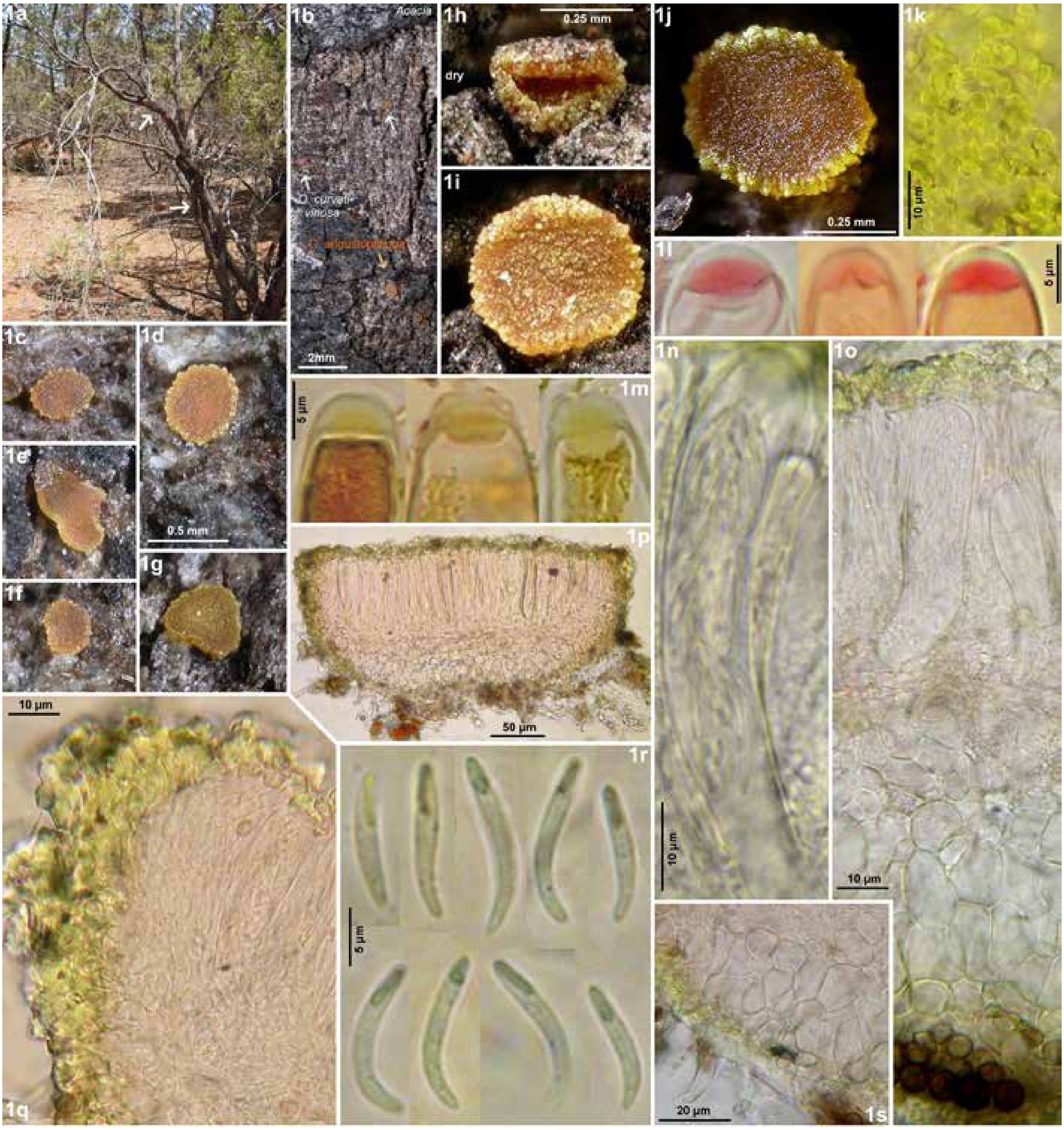


Plate 388. **1**: *Orbilia angustoobliqua*. – **1a**. acacia shrubland; **1b**. xeric bark of a dead *Acacia* shrub; **1b–g**, **i–j**. rehydrated apothecia; **1h**. dry apothecium; **1p**. apothecium in median section; **1q**. id., marginal region; **1o**. id., central part of apothecium; **1s**. id., basal ectal excipulum; **1k**. exudate on margin (external view); **1n**. mature ascus; **1l–m**. ascus apices; **1r**. ascospores. **1j–k**: illuminated by Luxeon-LED. – Living state, except for **1l** (in CR), **1m** (in KOH+IKI). — **1a–s**. H.B 9050a (holotype): Western Australia, Nerren Nerren, on *Acacia* (bark).

porrecta oriented at a 10–30° angle to the surface, marginal cortical cells *8–10 × 2.7–4 µm. **Anchoring hyphae** medium abundant, *2–3 µm wide, walls 0.2–0.4(–0.6) µm thick. **SCBs** in paraphyses absent, in ectal excipulum sparse, globose, 1.5–2 µm diam. **Exudate** over paraphyses and margin 0.3–1.5 µm thick, granular-cloddy, very rough, pale to bright sulphur-yellow, firmly attached. — **ANAMORPH**: unknown.

Habitat: collected 0.5–1.5 m above the ground, corticated, ~4 cm thick trunk of *Acacia* sp., on exterior of detached, very decayed bark (bast), partly in cracks, strongly greyed, no algae. **Associated**: *Orbilia anguliobliqua*, *O.* ?*atriplicis*, *O. helicovinosa*, *O. myriella*, *O.* ?*saguarina*. **Desiccation tolerance**: fully viable for at least 18 months. **Altitude**: 190 m a.s.l. **Geology**: Cretaceous sedimentary rock, Cenozoic regolith (red-brown sand). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia angustoobliqua* is well characterized by comparatively long and narrow, basally tapered, distinctly curved ascospores. *O. anguliobliqua* differs in much shorter, wider spores with slightly shorter and wider, partly subapically attached SBs.

Variation. In a small part of the scattered population the spores were distinctly shorter (*10.5–13 × 1.5–1.7 µm) though the other features fully concurred.

Ecology. *O. angustoobliqua* was found on rotten xeric bark detaching from the main trunk of a ca. 3 m tall *Acacia* tree in a subtropical semiarid acacia shrubland of western Australia (Yalgoo ecoregion). Some lower parts of the *Acacia* showed distinct traces of fire influence, and possibly therefore the shrub looked partially dead. *O. helicovinosa* grew intermingled with *O. angustoobliqua* but was easily recognizable by its lilaceous colour. The other associated *Orbilia* species mentioned above grew on much thinner branches and twigs (3–10 mm) of the same plant individual.

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, branch of *Acacia*, on bark, 8.XI.2007, G. Marson (ex H.B. 9050a, MEL 2389278A, **holotype**; MEL 2389277, **isotype**).

Incertae sedis

Orbilia junci Kohlm., Baral & Volkm.-Kohlm., Mycologia 90(2): 303, figs 1–14 (1998) — Pls 389–390

= *Dwayaangam junci* Kohlm., Baral & Volkm.-Kohlm., Mycologia 90(2): 304, fig. 15 (1998)

Etymology: named after the host plant, *Juncus roemerianus*.

Typification: USA, North Carolina, New Port, leaves of *Juncus roemerianus*, 20.XI.1995, J. Kohlmeyer & B. Volkmann-Kohlmeyer (IMS, holotype of teleomorph); ibid., 26.I.1997 (IMS, holotype of anamorph).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.07–0.35 mm diam., 0.06–0.1 mm high, pale to light orange-rose, translucent, round, scattered to subgregarious; disc flat or slightly convex, margin smooth, not rising above disc; broadly sessile, slightly to strongly erumpent, with an immersed obconical stipe up to 0.03 × 0.05 mm, slightly immersed in host tissue when mature; dry light orange. **Asci** *40–45 × 9–10.5 µm {1}, †35–55 × 6.8–9.3 µm {3}, 16-spored (but frequently only 8–14 spores viable) {4}, ~7–12 lower spores inversely oriented (± mixed) {4}; **apex** (†) hemispherical to broadly conico-subtruncate, dome †2.5–3.5(–4.8) → (1–)1.5–2(–2.5) µm thick {3}, with or without small apical chamber, endotunica sometimes slightly dextrinoid in MLZ (diffusely pale red), especially when pretreated by heated KOH, light rose-red in CR; **base** with short- to medium long, flexuous, thick stalk, T-, L- or Y-shaped. **Ascospores** *(6–)7–9(–10.2) × (2.3–)2.5–3.5(–4) µm {4}, †5.5–8 × 2.2–3.2 µm {2}, ± ellipsoid(-fusoid) to somewhat clavate, apex rounded to obtuse, straight, rarely distinctly curved at base; **SBs** apically attached to spore wall, 2–3 × 1–1.2(–1.5) µm {4}, tear-shaped to pyriform or ampulliform, apically narrowed to a small to wide point; with a few minute LBs. **Paraphyses** apically cylindrical or slightly clavate, sometimes curved, terminal cells *9–11 × 2–2.2 µm {1}, †4.5–8 × 1.5–2.8 µm {2}, lower cells *6.5–12 × 1.5–2.2(–3) µm {1}, †4–10 × 1.2–1.7 µm {2}, sometimes branched at upper septum. **Medullary excipulum** 15–20 µm thick, mainly present in centre, of dense t. intricata, slightly to medium sharply delimited. **Ectal excipulum** hyaline, of thin-walled, indistinctly to horizontally oriented textura angularis-prismatica from base to mid flanks, ~12–30 µm thick near base, cells *6–14 × 4.5–13 µm {2}, †6–10 × 5–6 µm {1}; 10–15 µm thick at margin, oriented at 30–70°, marginal cortical cells */†5–11 × 2.5–6 µm {3}, **glassy processes** absent. **Anchoring hyphae** very sparse, †1.5–2 µm wide, wall 0.2 µm thick. **SCBs** globose, in terminal cells of paraphyses 1–2 µm diam., in ectal excipulum 1.5–3 µm. **Exudate** over paraphyses continuous, hyaline, (0.3–)0.5–2(–3) µm thick, externally often coarsely rough, loosely attached; over margin and flanks 1–2.5 µm thick, rough. — **ANAMORPH**: dwayaangam-like (from ascospore isolate {3} and natural substrate {2}). **Conidiophores** short, *4–8.5 × 1.7–3.3 µm. **Conidia** total size *(21.5–)27–44(–50) × 18.5–26 µm; stipe *9–12 × 3–3.5 µm (main axis 10–14 µm long), 0–1-septate; twice dichotomously branched: two arms pointing upwards, two downwards, arms slightly to strongly tapered, medium to strongly curved outwards (upper arms sometimes straight), *16–24 × 2.8–3.2(–3.5) µm in situ, (1–)2(–3)-septate {2}.

Habitat: collected 0.5–1.5 m above low water level (~0.1–1 m above high tides), on dry, standing, dead since min. 1–2 years, 1.5–3 mm thick leaves of *Juncus roemerianus* {6}, very decayed, slightly greyed, green algae sparse. **Associated**: *Loratospora aestuarii*, ?*Phoma* sp., *Physalospora*

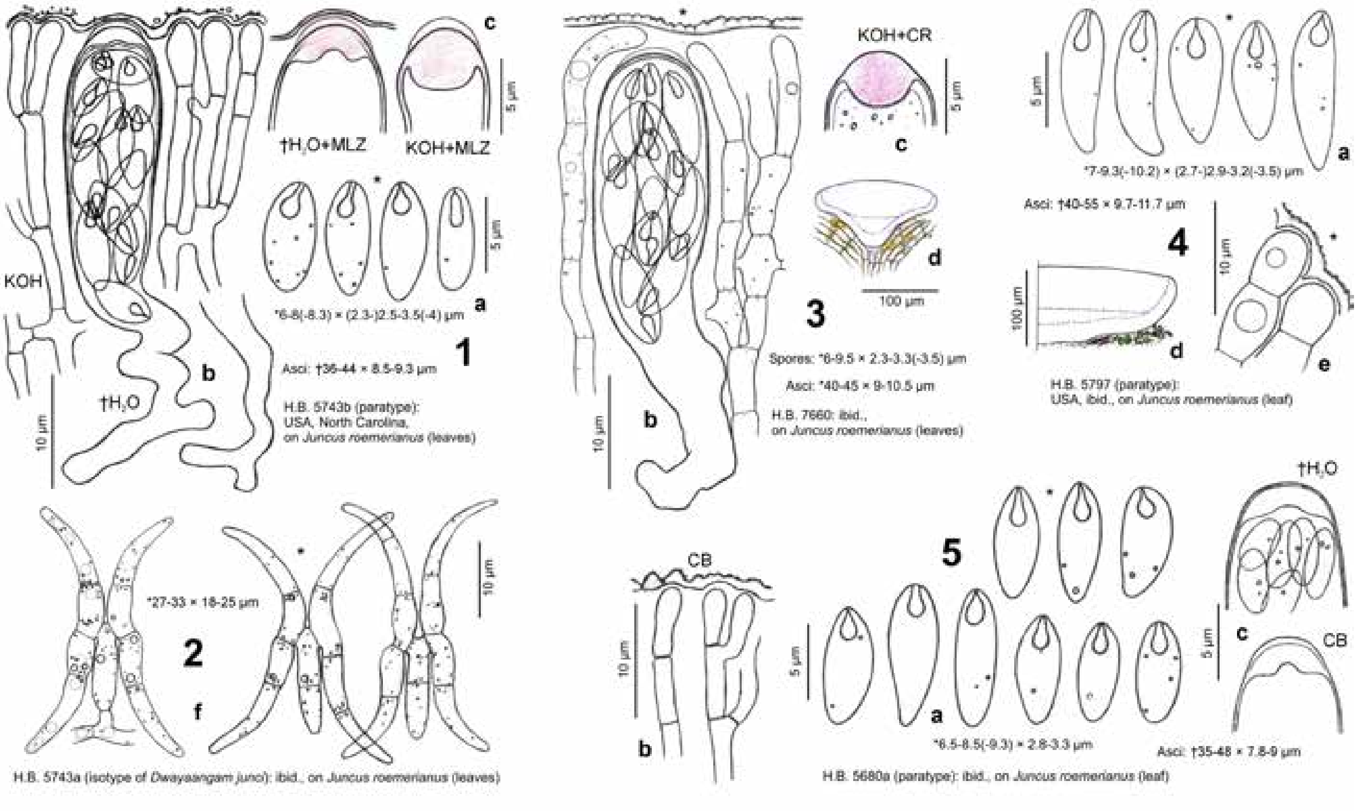


Plate 389. **1–5**: *Orbilia junci*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal cortical cells; **f**. conidia from culture.

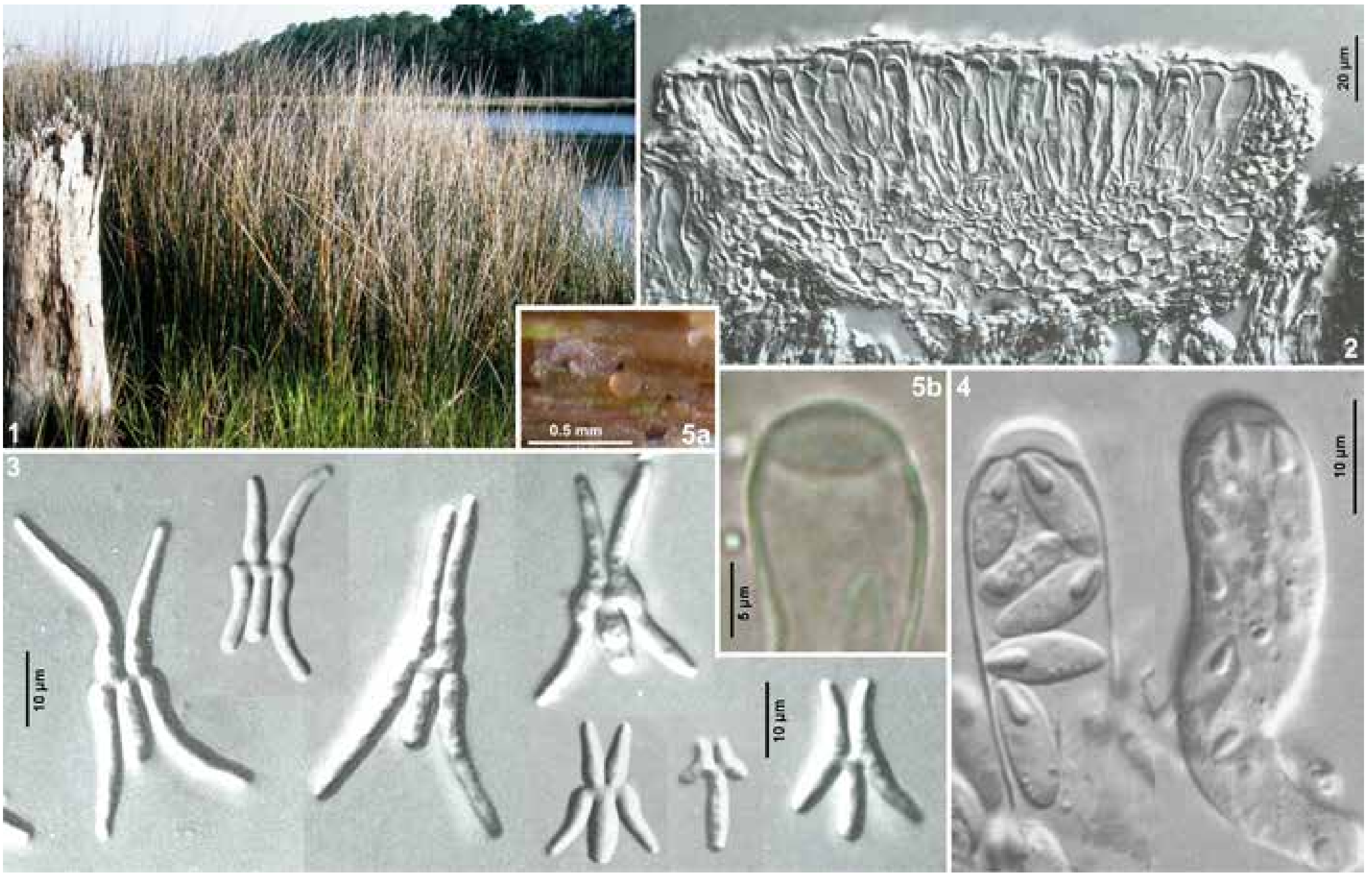


Plate 390. **1–5**: *Orbilia junci*. – **1**. type location, *Juncus roemerianus* stand, with *Spartina alterniflora* below (green); **5a**. rehydrated apothecia; **2**. apothecium in median section; **4**. asci with mature ascospores; **5b**. ascus apex; **3**. conidia from culture. – Living state, except for **2** (cryostat microtome, in ?H_2O), **5b** (in H_2O), asci in **4**. – **1–4**: phot. Kohlmeyer et al. 1998 (DIC). —**1**. USA, North Carolina, Broad Creek, VI.1999; **2**. J.K. 5568 (holotype): ibid.; **3**. J.K. 5604: ibid.; **4**. J.K. 5574: ibid.; **5a–b**. H.B. 7660: ibid. (all on *Juncus roemerianus*).

citogerminans, *Scirrhia annulata*. **Desiccation tolerance**: submature asci still viable after 6 days, excipular cells after 3 weeks, ascospores after 8 months, conidia after min. 1 week (but dead after 4 months). The species is probably also halotolerant since the upper halves of the leaves are exposed to occasional spray from the surrounding estuarine water. **Altitude**: 1 m a.s.l. **Geology**: Quaternary sedimentary deposits. **Phenology**: I, III–VI, XI (possibly throughout the year).

Taxonomic remarks. *Orbilia junci* is characterized by ± ellipsoid ascospores with tear-shaped to ampulliform spore bodies, and by 16-spored asci with strong apical thickenings. The species might have a somewhat isolated position within section *Hemiorbilia*. With series *Vibrioides* it shares the thick apical dome. The shape of ascospores and SBs resembles species of series *Hesperideae* (like *O. palmicola* and *O. australiensis*), species in which the apical domes are always much thinner and the apothecia often much larger.

Variation. Hardly any variation was noted among the collections which all originate from the type locality. Often only 8–14 of the 16 spores were viable within the asci, a phenomenon that in earlier studies misled to consider the asci as 8-spored. Dead spores are easily overlooked among the living spores (Pl. 390: 4), whereas when mounted in MLZ or CB_L always 12–16 spores could be seen.

Anamorph. *O. junci* possesses an extraordinary anamorph with staurosporous, dwayaangam-like conidia having 4 outwards curved arms. The conidia resemble, e.g., those of *Dwayaangam cornuta* in shape, but are distinctly smaller and their arms tend to be more curved, moreover, *D. cornuta* tends to higher-branched conidia. Matsushima (1993: 16, fig. 739) reported under the name *D. cornuta* a species from angiosperm leaves (Ecuador) which is quite similar to *D. junci*. The conidia are slightly longer (40–57 × 13–25 µm according to scale) and have more septa, and the proximal part of the 4 arms is more incurved, resulting in strongly protruding hips at the centre of the conidia (see p. 233–234).

Ecology. According to Kohlmeyer et al. (1998) and Kohlmeyer & Volkmann-Kohlmeyer (2001), *O. junci* has so far only been collected at the type locality, a warm-temperate humid coastal salt marsh of eastern North America, and there exclusively on dead xeric leaves of *Juncus roemerianus*. On that host it appears to be ‘the most frequent species among the 10 tiny discomycetes found so far’. *J. roemerianus* is a common halophyte forming monoculture-like stands, though in association with *Spartina alterniflora*, on salt marshes along estuaries of the United States’ east and Gulf coasts. The leaves very slowly die back from the tip and here bear the first settlers, whereas the basal parts of the leaves are flooded during high tides. The leaves may remain standing for several years in the dead state. *O. junci* is among the last species to appear, and its desiccation-tolerant apothecia occur exclusively on the brittle tips of the senesced standing leaves after the cuticle has been shed. Despite the closeness to seawater, mycelia did not grow on seawater medium in pure cultures, therefore, apothecial growth appears to be supported by rain or dew.

Apothecia of *O. junci* have been collected mainly in winter and spring, but were not found during July–September, the hottest summer months. During severe hurricanes which broke off the oldest leaves, apothecia of *O. junci* vanished, but conidia of the anamorph were discovered to occur abundantly on recently senesced leaves, though exclusively in small holes having been eaten by grasshoppers into the living tissue. Here, the species appears to survive as anamorph until enough senescent, well weathered leaf tips occur.

Specimens included. **USA**: **North Carolina**, Carteret, 43 km E of Jacksonville, 11 km SW of New Port, Broad Creek, 1 m, leaves of *Juncus roemerianus*, 19.IV.1996, J. Kohlmeyer & B. Volkmann-Kohlmeyer (J.K. 5584, H.B. 5680a). – ibid., 20.XI.1995 (ex J.K. 5568, anam. cult., IMS, **holotype of teleomorph**; UME, **isotype**; H.B. 5680b, **isotype** [slide]). – ibid., 21.V.1996 (J.K. 5586, anam. cult.). – ibid., 27.IV.1997 (J.K. 5611, H.B. 5797). – 26.I.1997 (ex J.K. 5604, IMS, anam. cult., **holotype of anamorph**; H.B. 5743a, **isotype**). – ibid., 2.III.1997, (J.K. 5606, H.B. 5743b). – ibid., 6. & 13.VI.2000 (ex J.K. 5652, 5653, IMS, anam. substr.). – ibid., 13.I.2005, J. Kohlmeyer (J.K. 5767, H.B. 7660 ø).

Subgenus *Habrostictis*

Orbilia subgenus ***Habrostictis*** (Fuckel) Baral & E. Weber, **comb. & stat. nov.**, MB 815006 – Lectotype species: *Habrostictis rubra* Fuckel [= *O. carpoboloides* (P. & H. Crouan) Baral], designated by Höhnel (1917: 330)

Basionym: *Habrostictis* Fuckel, Jahrb. Nassau. Ver. Naturkd. 23–24: 249 (1870)

Description: — **TELEOMORPH**: **Apothecia** hydrated whitish, yellowish, rose, orange, lilaceous, margin glabrous or dentate to hairy, sessile or short-stipitate, superficial to erumpent. **Ascus apex** (†) slightly to mostly medium to strongly truncate, not or slightly to distinctly indented and laterally inflated, hemispherical in profile view, thin-walled; **base** T-, L-, Y- or h-shaped, only exceptionally H-shaped. **Ascospores** variously shaped; **SBs** apically affixed to spore wall, rarely subapically in some taxa in series *Ellipsospermae*, often filiform to vermiform or subulate, usually flexuous, also tear-shaped to globose, apically narrowed to a small point, filum absent or very short (to short to sometimes long). **— ANAMORPH**: anguillospora-like, dicranidion-like, dwayaangam-like, helicoon-like, pseudotripoconidium-like, trinacrium-like, tridentaria-like, vermispora-like. **Trapping organs**: unknown.

Habitat: on xeric or sometimes hygric to semiaquatic wood and bark of gymno- and angiosperms, also caulicolous, foliicolous, or fungicolous, from boreal to tropical, humid to arid climates.

Recognized sections: *Aurantiorubrae*, *Habrostictis*, *Helicoon*, with 173 recognized species plus 3 with a provisional name, and 31 unnamed species ('affinis').

General remarks. The present circumscription of subgenus *Habrostictis*, which comprises three sections (*Habrostictis*, *Aurantiorubrae*, *Helicoon*), is mainly based on molecular phylogenetic data. A morphological feature common to all its members is the thin-walled, truncate ascus apex which is, however, characteristic also of subgenus *Orbilia* and series *Ovales* of subgenus *Hemiorbilia*. The paraphyses are frequently inflated at the apex, but this feature is likewise also found in the two mentioned and some other groups. The predominant absence of H-shaped ascus bases is in contrast to their frequent presence in subgenus *Orbilia*. Many taxa of the three included sections possess characteristic, vermiform to filiform or subulate, often flexuous SBs in the mature ascospores, but section *Aurantiorubrae* includes also taxa with globose SBs, while some taxa of section *Hemiorbilia* feature similar vermiform SBs.

Section delimitation. Sections *Habrostictis* and *Helicoon* are rather well characterized by comparatively long and narrow, often ± flexuous to helicoid, sometimes uncinate SBs, though a few taxa have rather short and wide SBs. Within section *Aurantiorubrae*, subulate to filiform, ± flexuous SBs occur in some species of series *Abutilones*, *Piliferae*, and *Poitevinicae,* whereas in the other included series SBs are always straight (or follow the curvature of the spores), either rod-shaped or usually narrowly tear-shaped to globose. Further distinguishing features between the sections concern, e. g., length/width ratio of ascospores, spore numbers, length of terminal cell of paraphyses in relation to lower cells, glassy processes, and crystalloid SCBs.

The two large sections *Habrostictis* and *Aurantiorubrae* contain almost exclusively desiccation-tolerant species with yellow-orange to rose-red apothecia. Apothecia of section *Helicoon*, on the contrary, are desiccation-sensitive or at best slightly tolerant, and are often whitish to pale rose-lilaceous but also yellow-orange.

Anamorphs. Members of sections *Habrostictis* and *Aurantiorubrae* form two very different types of conidia: stauroconidia (mainly trinacrium-like, also tridentaria- or dwayaangam-like) or curved phragmoconidia (vermispora-like, rarely anguillospora- or dactylella-like). Also in section *Helicoon* two very different types of conidia occur: phragmoconidia (anguillospora- to vermispora- or dactylella-like), and inversely pyramidal ameroconidia with small protuberances (pseudotripoconidium-like). Taxa with predatory capabilities are unknown within subgenus *Habrostictis*.

Phylogeny. In the phylogenetic analysis of SSU+ITS+LSU rDNA in Baral et al. (2017b), subgenus *Habrostictis* formed an unsupported paraphyletic clade which contains also section *Lentiformes* of subgenus *Hemiorbilia*. Sections *Helicoon* and *Habrostictis* formed two strongly supported independent clades, whereas section *Aurantiorubrae* clustered in no less than six independent, strongly supported clades with more or less distant kinship and unsupported nodes. Paraphyly of section *Aurantiorubrae* is also obvious in Phyl. 7.

The present phylogenetic analyses do not allow to elucidate the evolutionary pathways of the different types of spore bodies within subgenus *Habrostictis*. The phenomenon that SBs of the elongate type change in overmature spores to shorter and wider and finally globose could be interpreted as a regression to a plesiomorphic character, by considering vermiform to filiform SBs as an apomorphy within the genus *Orbilia*, i. e., a higher step in evolution compared to taxa with globose SBs. However, the largest clade within section *Aurantiorubrae*, which includes series *Aurantiorubrae*, *Commatoideae*, *Regales*, and *Rubellae*, comprises globose, tear-shaped, and subulate but never filiform SBs, and it would seem logical that, within this clade, SB shape developed from globose over tear-shaped to subulate. Moreover, the general occurrence of long and narrow SBs in sections *Habrostictis* and *Helicoon* does not seem to trace back to a common ancestor with elongate SBs, since these two sections are placed in our analyses in two rather distant clades. If the hypothesis of SB development holds true, we may conclude that elongation of SBs within *Orbilia* occurred by convergence in different lineages.

Similar as in subgenus *Orbilia*, the frequently observed desiccation-sensitivity in section *Helicoon* is thought to be an apomorphy, which would mean that the common ancestor of this section was a desiccation-tolerant fungus (see also p. 160).

Specific nucleotide positions. No molecular motifs being characteristic of the entire subgenus *Habrostictis* have been discovered in any of the frequently recorded regions of nuclear rDNA. However, some of the included sections or series show a few rather consistent nucleotides by which they can be distinguished (see there).

Section *Aurantiorubrae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** Baral & E. Weber, **sect. nov.**, MB 815007 – Type species: *Orbilia aurantiorubra* Boud.

Latin diagnosis: *Apothecia plerumque tolerantia ad siccitatem, flavida, ochracea, aurantia, rosacea vel rubra, raro hyalina, ad marginem partim pilis septatis vel processis vitreis, vacuolae refringentae plerumque absentes, ascosporae saepe angustae et falcatae vel helicoideae, conidia plerumque elongatae, multiseptatae, falcatae, raro rectae vel ramosae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.3–1.5(–3) mm diam., whitish, pale to bright rose, red, orange or yellow to ochraceous, ± smooth to whitish fimbriate or toothed, sessile or with a short stipe. **Asci** *(23–)30–70(–82) × (3–)3.5–6(–7.5) µm, 8-, rarely 16(–32-)spored, lower (rarely upper) (0–)3–5(–7) spores inverted (if 8-spored); **apex** (†) slightly to strongly truncate, not or partly distinctly indented and laterally inflated; **base** T-, L-, Y-, or h-, exceptionally H-shaped. **Ascospores** *(4–)5–15(–19) × 0.6–2.8(–3) µm, broadly to usually narrowly subcylindric- to ellipsoid- or fusiform-clavate, apex rounded to acuminate, base attenuated or not, partly tail-like or sometimes with a distinct tail or a subbasal constriction, straight or slightly to strongly curved or geniculate near base or as a whole (falcate or helicoid); **SBs** attached to spore apex, globose, tear-shaped, ampulliform, subulate or filiform, apically narrowed to a small, more rarely to a wide point, mostly with a very short filum. **Paraphyses** not or slightly to strongly clavate-capitate or spathulate to mammiform at the apex, rarely lageniform or lanceolate, terminal cells (0.8–)1–3(–5)× longer than lower cells, usually unbranched at upper septum. **Ectal excipulum** at flanks of textura (globulosa-) angularis(-prismatica), cells isodiametric or vertically to irregularly elongated, (†) thin-walled to medium gelatinized (common walls †0.2–1.7 µm thick), cells near base *(6–)9–25(–38) × (5–)7–18(–25) µm (on ± xeric substrate), */†(9–)15–50(–70) × (7–)12–45(–60) µm (on hygric substrate); **glassy processes** absent or 1–10 µm up to 20–80(–200) µm long, **hairs** absent or (10–)20–65(–93) µm long, thin- or thick-walled, septate. **SCBs** globose and/or crystalloid, or absent; **VBs** rarely present, medium refractive; **carotenoids** in **LBs** observed in many species. — **ANAMORPH**: anguillospora-like, dactylella-like, dicranidion-like, dwayaangam-like, trinacrium-like, vermispora-like. **Conidiophores** unbranched or branched, short to long, 2–200 µm long. **Conidiogenous cells** monoblastic or sympodial. **Conidia** mainly unbranched (phragmo- to scolecosporous), straight or often ± curved, more rarely branched (staurosporous), with 2–4 straight or curved arms, with or without stipe; conidial dimorphism not observed. **Trapping organs**: none observed.

Habitat: mainly desiccation-tolerant, also desiccation-sensitive.

Recognized series: *Abutilones*, *Albovinosae*, *Aurantiorubrae*, *Commatoideae*, *Hyalinia*, *Piliferae*, *Poitevinicae*, *Regales*, *Rubellae*, and *Xanthoguttulatae*, with 67 recognized species plus 1 with a provisional name and 10 unnamed species ('affinis').

Taxonomic remarks. Section *Aurantiorubrae* includes taxa with predominantly narrow ascospores which are frequently curved, either at the base (geniculate), or entirely (falcate or helicoid). The spore apices vary from rounded to acuminate, and the bases from slightly to strongly tapered, sometimes with a prominent tail or basal constriction. Spore body shape varies from globose to tear-shaped or filiform. Spathulate to mammiform paraphysis apices are frequent, but capitate ones also often occur. Short to very long, septate marginal hairs and/or glassy processes are typical of a majority of the species.

Most of the included species are desiccation-tolerant and lack VBs in the paraphyses. VBs were exceptionally observed in *O. caulicola*, *O. neocomma*, *O. milinana*, *O. nemaspora*, and *O. pilifera*, though never in the often studied desiccation-sensitive *O. crenatomarginata*. The asci are always 8-spored, except for some species of series *Albovinosae* which are 16–32-spored.

Series delimitation. Ten series are tentatively recognized within section *Aurantiorubrae*: series *Regales*, *Commatoideae*, *Rubellae*, *Aurantiorubrae*, *Xanthoguttulatae*, *Hyalinia*, *Abutilones*, *Poitevinicae*, *Piliferae*, *Albovinosae*. Some series (*Xanthoguttulatae*, *Abutilones*) were mainly based on molecular data. Series *Commatoideae* and *Rubellae* are difficult to maintain against series *Aurantiorubrae* and *Regales*. Questionable is also the relationship between *O. caulicola* (*Commatoideae*) and the unsequenced *O. rosella* which we tentatively placed in series *Abutilones*.

Anamorph. The predominant anamorph of section *Aurantiorubrae* is represented by rather uniform phragmosporous, vermispora-like conidia, which occur throughout the first four here recognized series, as far as the anamorph is known, but also in series *Poitevinicae*. The conidial ends are usually slightly to strongly curved (C-like, or resembling a square bracket). Many of these conidial states resemble *Lecophagus navicularis*, from which they differ in the lack of ampulliform conidiogenous cells, as far as conidiophores were studied, in consistently much narrower conidia, and especially in the lack of cubical SCBs in the centre of the conidial cells. '*Chionomyces*' *ponapensis* has quite similar conidia, and this species also fits section *Aurantiorubrae* in conidial size. *O. caulicola* of series *Commatoideae* possesses the longest conidia, which can be classified as anguillospora-like and which are partly ± straight as a whole.

Three series of section *Aurantiorubrae* include species with stauroconidia. Dicranidion-like conidia with parallel arms without a stipe are verified for *O. xanthoguttulata*, and strongly resemble those of the rather unrelated *O. eucalypti* and *O. tremulae* (series *Orbilia*). Likewise, the 2–4-armed, stipitate dicranidion-like conidia of *O. siculispora* resemble those of *O. fissilis* of series *Orbilia*. Trinacrium-like conidia are found in two series, and have always curved-down arms: in series *Piliferae* they resemble *Trinacrium incurvum* and serve as a key character of the group, whilst in series *Albovinosae* they are much more slender and are only known in two species (*O. albovinosa*, *O. pseudoaristata*). Series *Albovinosae* comprises also dwayaangam-like conidia (*O. albidorosea*, exceptionally also in *O. albovinosa*) with either straight or curved arms. Series *Hyalinia* and series *Xanthoguttulatae* p.p. are extraordinary in forming straight, dactylella-like conidia. The conidiophores in section *Aurantiorubrae* are short to medium long, but in series *Hyalinia* and *Xanthoguttulatae* partly very long.

Phylogeny. As already stated under subgenus *Habrostictis*, in the analysis in Baral et al. (2017b) section *Aurantiorubrae* formed six independent but strongly supported clades with unclear relationship to each other. Two unsupported main clades were formed which each comprises three of these six clades but also one or two clades of other sections by making section *Aurantiorubrae* paraphyletic: (1) series *Piliferae*, *Abutilones*, and *Hyalinia* loosely group with section *Helicoon*; (2) series *Xanthoguttulatae* and *Albovinosae* loosely group with the large and strongly supported core clade of section *Aurantiorubrae*, which includes series *Aurantiorubrae*, *Commatoideae*, *Regales*, and *Rubellae*, but also with sections *Habrostictis* and *Lentiformes.* However, all nodes outside the six supported clades remained unsupported.

The most unexpected results within this group include the high molecular distance between *O. aurantiorubra* and *O. xanthoguttulata*, and between *O. crenatomarginata* and *O.*

Table 68. Characteristic motifs in the nuclear 5.8S, ITS2, and LSU rDNA within the 3 sections of subgenus *Habrostictis*. Position numbers starting with AAAACTTT (5.8S), after GAGCGTC (ITS2), and with TGACCT (LSU, herr by omitting predominant gaps in alignment of all groups of *Orbiliomycetes*). The number of species within each group for each gene region is given in brackets. Species which deviate from their group are listed separately.

Series/Section	5.8S (129–134)	ITS2 (1–4)	LSU (239–245)	LSU (497–503)
Aurantiorubrae *Aurantiorubrae* (2 ITS/2 LSU), *Rubellae* (2 ITS/1 LSU), *Commatoideae* (4 ITS/3 LSU)	TCCTTT	ATTT	TTACTTC	ATCAGTT
- *O. caulicola* (*Commatoideae*)	TCCGAA	ATTT	TTACTTC	ATCAGTT
- *Orbilia* sp. B.L. 4099	TCCTTT	ATTA	TTACTTC	ATCAGTT
Xanthoguttulatae (4 ITS/3 LSU)	TCCGAT	ATTA	TTACTTC	ATCGGTT
- *O. vermiformis*	TCCGTT	ATTA	?	ATCGGTT
- *O. nemaspora*	TCCGAT	ATTA	TTTTGGC	ATCGGTT
Regales (4 ITS/4 LSU)	TCCGAT	ATTT	TTTCAAT	ATCGGTT
- *O. aradi, O. mali*	TCCGAT	ATTA	TTTCAAT	ATCGGTT
- *O. denticulata*	TCCGAT	ATTT	TTTCAAC	ATCGGTT
Poitevinicae (1 ITS/1 LSU)	TCCGAA	ATTT	TTACTTC	ATCAGTT
Abutilones (4 ITS/3 LSU)	TCCGAA	ATTT	TTACTTC	ATCGGTT
- *O. amarilla*	TCCGAA	ATTT	TTACTTC	ATCAGTT
- *O. milinana* TFC Mic. 23222	TCCGAA	ATTT	?	?
- *O. milinana* B.L. X098	TCCGAA	ATAT	TTGCTTC	ATCGGTT
- *O. aethiopica*	TCCGAA	ATAT	TTACTTC	?
- *O. paravitalbae*	TCCGAT	ATAT	CTACTTC	ATCAGTT
Piliferae (5 ITS/5 LSU)	TCCGAA	ATTT	TTACTTC	ATCAGTT
- *O.* aff. *farnesianae*	TCCGAA	ATTT	TTGCTTC	ATCAGTT
Albovinosae (5 ITS/5 LSU)	TCCGAT	ATTA	TTACTTC	ATCAGTT
- *O. gemma*	TCCGAT	ATTA	TTTCAAC	ATCGGTT
Hyalinia - *O. crenatomarginata*	TCCGGA	ATGT	CTGCAAC	ATCGGTT
- *O. laevimarginata*	TCCGGA	ATGT	?	?
- *O. crenatofalcata*	TCCGGA	ATCT	CTGCGCT	ATCGGTT
- *O. scolecospora* B.L. 243	TCCGGA	ATGT	TTGCTTC	ATCGGTT
- *O. scolecospora* H.B. 9154	TCCGGA	ATGT	CTGCTTC	ATCGGTT
Helicoon (7 ITS/7 LSU)	TCCGAA	ATTT	TTACTTC	ATCAGTT
- *O. rosea* s.l.	TCCGAA	ATTT	CTACTTC	ATCAGTT
- *O.* aff. *sarraziniana* B.L. 730	TCCGAA	ATTT	CTACTTC	ATCAGTT
- *O sinensis* YMF 1.01843	TCCGAA	ATTT	CTACTTC	ATCGGTT
- *O. tianmushanensis*	TCCGAA	ATTA	TTGCTTC	ATCAGTT
Habrostictis p.p.maj. (~27 ITS/24 LSU)	TCCGAA	ATTA	TTACTTC	ATCGGTT
- *O. multimaeandrina*	TCCGAA	ATTA	TTACTTC	ATCAGTC
- *O. ungulata*	TCCGTA	ATTA	TTACTTC	ATCGGTT
- *O. cylindrosoma*	TCCGAA	ATTA	CTACTTC	ATCGGTT
- *O. carpoboloides*	TCCGAA	ATTT	TTACTTC	ATCGGTT

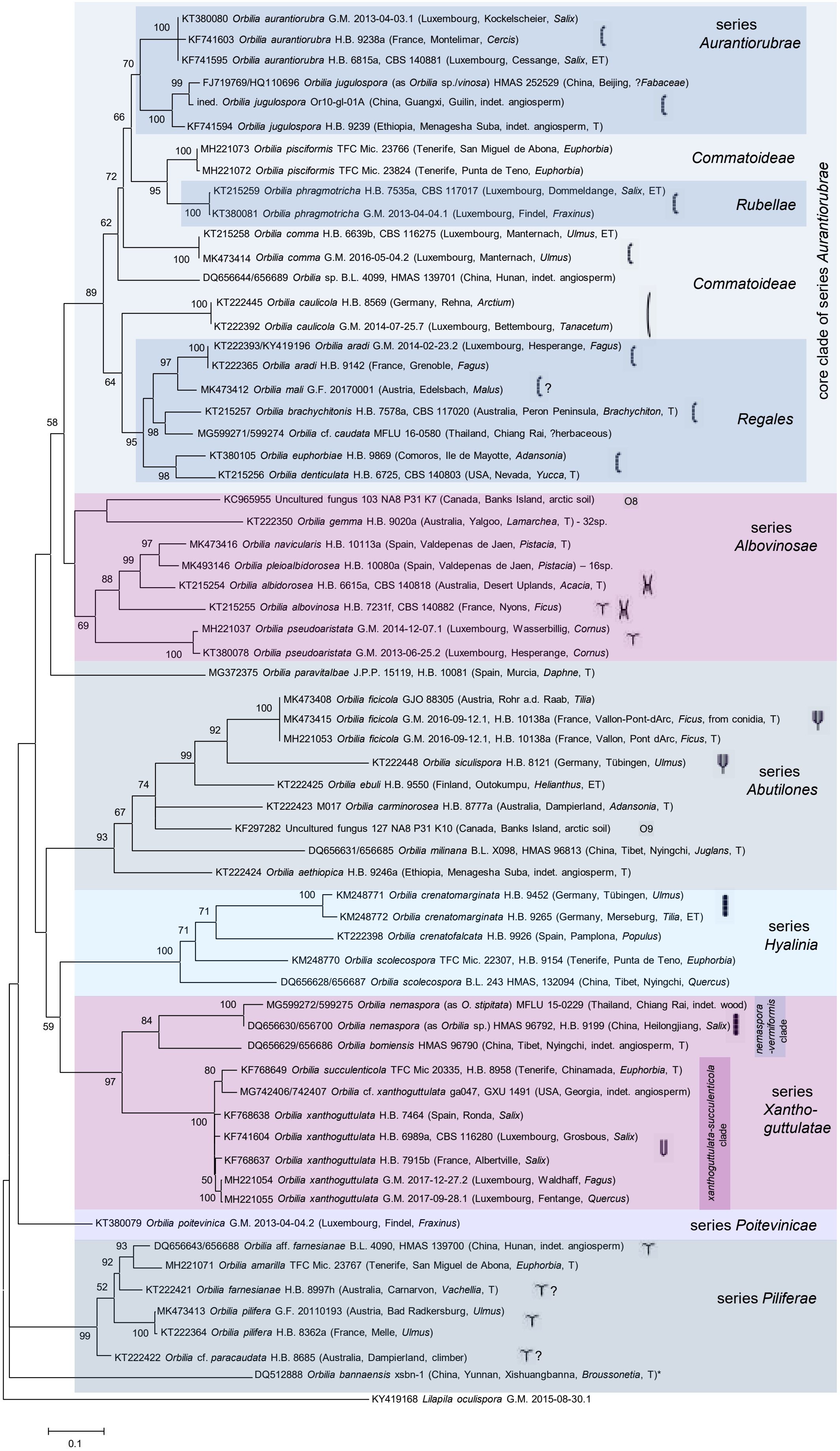
vermiformis, and the low distance between *O. xanthoguttulata* and *O. vermiformis* (Phyls 13, S15–S16). Within the core clade of section *Aurantiorubrae*, series *Regales* formed with medium or high support a sister clade of the three remaining core series *Commatoideae*, *Rubellae*, and *Aurantiorubrae*, whereby *O. caulicola* clustered with low or medium support with series *Regales* (Phyls 13, S15). Separation between the three remaining core series is not supported by our molecular data but we maintained these series because of striking morphological differences.

Specific nucleotide positions. No molecular motifs being characteristic of section *Aurantiorubrae* have been discovered. Three motifs in the rDNA are informative regarding relationships within section *Aurantiorubrae* (Tab. 68). At pos. 129–134 of the 5.8S region the motif TCC**TTT** is characteristic of series *Aurantiorubrae*, *Rubellae*, and *Commatoideae*, whereas other members of subgenus *Habrostictis* have TCC**GAA**, TCC**GAT**, TCC**GGA**, or rarely TCC**GTA** or TCC**GTT** (Tab. 68). *O. caulicola* has TCC**GAA**, which would suggest that it does not belong in either of the three series mentioned. Another motif is found at the 5'-end of ITS2 (pos. 1–4 after GAGCGTC): a majority of section *Aurantiorubrae* has AT**TT**, which is also characteristic of section *Helicoon*, whereas a minority have AT**TA** (series *Xanthoguttulatae*, *Regales* p.p., *Albovinosae*), and series *Hyalinia* AT**GT** or AT**CT** (see also Tab. 20). The motif AT**TA** occurs in combination with TCC**GAT** (rarely TCC**GTT**), and both are exclusive for the three groups within section *Aurantiorubrae*.

Another motif is located at pos. 239–245 in the D1 domain of LSU (Tab. 68). This is characteristic of series *Regales* (TT**T**C**AAT** or TT**T**C**AAC**) and to some extent of series *Hyalinia* (YT**G**CDHY), whereas the current motif within section *Aurantiorubrae* is TT**A**C**TTC** (but some deviations from this occur). Also pos. 500 of LSU D2 is informative, being consistently ATC**A**GTT in series *Aurantiorubrae*, *Rubellae*, *Commatoideae*, *Poitevinicae*, *Piliferae*, and *Albovinosae*, but G in series *Regales*, *Xanthoguttulatae*, and *Hyalinia*. Yet, it is G in the disputable *O. gemma*, and it varies between A and G in series *Abutilones*. In section *Helicoon* it is mostly A and in section *Habrostictis* mostly G.

In the SSU (V8–V9) little variation is observed, and the different series cannot be recognized because some taxa of different groups share exactly the same sequence.

Ecology. Members of section *Aurantiorubrae* have been recorded worldwide. A majority of species are desiccation-tolerant and grow on exposed (xeric), woody or herbaceous substrates. In contrast, members of series *Hyalinia* and some of series *Xanthoguttulatae* occur on permanently moist (hygric) substrate. Various species are found in temperate to montane or (sub)alpine-boreal, more or less humid areas, whereas others appear to be adapted to (sub)tropical (sub)



Phylogenetic analysis 13. Phylogram of section *Aurantiorubrae* (and *Helicoon*) inferred from combined ML analysis of ITS1-5.8S-ITS2+LSU (D1–D2) rDNA dataset (64 sequences, 1456 positions, aligned with MUSCLE) using the GTR+G+I model in MEGA6 (500 replicates). Two environmental strains from GenBank are included representing unidentified species (O8, O9). The tree is rooted with *Lilapila oculispora*. Asci 8-spored except when otherwise stated; T = type, ET = epitype, * = only ITS available.

Key to series and species of section *Aurantiorubrae*

1. Spore apex rounded to obtuse or subacute, spores never strongly helicoid; SBs globose to ellipsoid or broadly tear- to pear- or rod-shaped, sometimes with a vermiform to subulate upper part, (0.7–)1–3(–4.7) µm long (if spore apex acute then SBs globose) 2
1. Spore apex subacute to acuminate, if rounded to subacute then spores strongly helicoid; SBs broadly to narrowly tear-shaped or subulate to filiform, (1.7–)2–4.5(–5.5) µm long 14

2. SBs 1.5–4.7 µm long, rod-shaped or divided into an ellipsoid to tear-shaped lower and a vermiform to subulate upper part.............3
2. SBs (0.7–)1–2.3(–2.7) µm long, globose to broadly tear- or pear-shaped 5

3. SBs ± rod-shaped, ascospores often with tails or tail-like bases; paraphyses often spathulate to mammiform............. **series *Piliferae*** (p.p.), p. 915
3. SBs divided into an ellipsoid to tear-shaped lower and a vermiform to subulate upper part, ascospores without a tail.............4

4. Spores with rounded apex, subcylindric- to fusoid-clavate, *(6–)7–8(–9) × 2.2–2.8 µm; paraphyses uninflated or capitate-clavate .... **series *Poitevinicae*** (*O. poitevinica*, p. 913)
4. Spores with broadly subacute apex (forming a > 90° angle), cylindric-clavate, *4.8–6.3 × (1.8–)2–2.3(–2.5) µm; paraphyses often sublanceolate to lanceolate .... **series *Abutilones*** (*O. aethiopica*, p. 912)

5. Spores ± cylindrical, base not or only slightly tapered, ± straight, *5.5–8.7 × 1.7–2.3 µm, SBs 1.3–1.9 × 0.4–0.7 µm............. **series *Regales*** (*O. pseudocylindrospora*, p. 798)
5. Spores medium to strongly tapered at base and/or ± curved (especially at base) 6

6. Apothecial margin ± smooth, without distinct hairs or glassy processes 7
6. Apothecial margin usually ± distinctly crenulate, dentate or hairy, at least with short glassy processes and/or septate projecting hairs ...10
A sample on *Urtica* with ± smooth apothecia and spores similar to *O. phragmotricha* is mentioned under that species (p. 830).

7. Paraphyses apically capitate-clavate, rarely uninflated .... **series *Commatoideae***, p. 802
If spores ± straight and *1–1.2 µm wide see **series *Piliferae*** (*O. bannaensis*, p. 930).
7. Paraphyses apically ellipsoid-clavate, spathulate to lageniform, or uninflated 8

8. Paraphyses covered by 1–3 µm thick glassy caps; apothecia rose-lilaceous or yellowish; SBs globose to tear-shaped, with short filum .... **series *Regales*** (*O. kingsiana*, p. 793, *O. aradi*, p. 777)
8. Paraphyses without glassy caps; apothecia rose-orange or orange 9

9. Spores with rounded to obtuse apex; SBs ± ampulliform .... **section *Hemiorbilia*** (*O. concoloris*, p. 672)
9. Spores with subacute apex; SBs ?broadly tear-shaped............. **series *Piliferae*** (*O.* aff. *farnesianae*, p. 925)

10. Marginal hairs consisting of short to long glassy processes which emerge directly from thin-walled marginal cortical cells of the compact excipular texture, free septate hairs absent .... **series *Regales*** (p.p.), p. 773
If paraphyses capitate and spore apex subacute compare *O. neocomma* (series *Commatoideae*, p. 817).
10. Marginal hairs septate, thin- or thick-walled, with or without terminal glassy processes 11

11. Paraphyses clavate-capitate; spores fusoid, †(7–)7.5–9(–9.8) × (1.5–)1.6–1.8(–2) µm; SBs ?tear-shaped; apothecial margin finely crenulate; caulicolous (*Atropa*)............. series ***Abutilones*** (*O. rosella*, p. 908)
11. Paraphyses spathulate to lageniform or mammiform.............12

12. Marginal hairs with †(0.3–)0.5–1.5(–2.7) µm thick walls, (10–)30–60(–93) µm long, 1–3- up to 3–10-septate, with or without terminal glassy processes; spores *1–1.9 µm wide .... series ***Rubellae***, p. 820
12. Marginal hairs with †0.2–0.5(–0.8) µm thick walls, usually without terminal glassy processes 13

13. Spores *5–9.2 × 2–2.7 µm, ellipsoid-clavate; SBs broadly tear-shaped to subglobose, 1–1.3 µm wide; marginal hairs 35–55 µm long, 2–6-septate; apothecia ochre-orange, 0.3–1.8 mm diam.; bark of *Ulmus* .... **series *Piliferae*** (*O. pilifera*, p. 918)
13. Spores *(6.5–)8–11(–11.5) × (1.5–)1.6–1.8(–2) µm cylindric(-clavate); SBs ± ampulliform, 0.7–1 µm wide; marginal hairs 7–20 µm long, 0–1-septate; apothecia rose-orange, 0.2–0.7 mm diam.; wood of *Abies*, *Lonicera*........ **section *Hemiorbilia*** (*O. concoloris*, p. 672)

14. Margin ± crenulate by coherent, indistinct, < 20 µm long hair-like projections, glassy processes absent or < 5 µm long; spores ± straight, *(8–)9–11(–12) × 1.3–1.7 µm, narrowly fusoid; SBs with a tear-shaped lower and a filiform upper part; apothecia pale rose-cream, caulicolous .... **series *Abutilones*** (*O. ebuli*, p. 900)
14. Margin with glassy processes or long hairs, if smooth then spores distinctly curved 15

15. Spores min. *(1.3–)1.5 µm wide, straight to slightly curved; apothecial margin with 1–7 up to 10–120 µm long glassy processes .... **series *Albovinosae***, p. 932
15. Spores max. *1.4–1.7 µm wide, usually medium to strongly curved, or with a basal constriction 16

16. Apothecia whitish (but yellow-orange in *O. bomiensis*), often desiccation-sensitive; margin smooth or often with small to large triangular teeth of agglutinated glassy processes; spores generally distinctly helicoid, rarely falcate .... **series *Hyalinia*** (including link to ***nemaspora-vermiformis*** **clade** of **series *Xanthoguttulatae***), p. 868
16. Apothecia orange to yellow, rarely whitish, always desiccation-tolerant; margin smooth or with long, septate hairs or short (up to 18 µm) glassy processes; spores straight to falcate, also helicoid or basally bent.............17

17. Paraphyses mainly ellipsoid-spathulate or lageniform; apothecial margin smooth or crenulate to hairy.............18
17. Paraphyses uninflated or clavate-capitate; apothecial margin smooth.............20

18. Margin with 15–65 µm long, septate, thin-walled hairs without glassy processes; spores *6.5–10.5 µm long, slightly to strongly curved (sickle-shaped) but usually not distinctly helicoid, base partly constricted or strongly geniculate; SBs filiform to subulate or narrowly tear-shaped, (1.7–)2–4(–4.5) × 0.2–0.7(–0.9) µm .... **series *Abutilones***, p. 885
18. Margin hairless or with short glassy processes (9–18 µm) or hair-like projections; SBs subulate to tear-shaped, 1.7–3 × 0.6–1.3 µm 19

19. Spores *(9–)10–14(–16) × (1–)1.2–1.5(–1.7) µm, falcate to helicoid, with often strongly curved base; apothecia yellow(-ochraceous), sometimes turning orange-red with age, rarely whitish.. series ***Xanthoguttulatae*** (*O. xanthoguttulata*, p. 848, *O. succulenticola*, p. 853)
19. Spores †6.5–7.5(–8) × (0.9–)1–1.3(–1.4) µm, fusiform, with a thin, curved, tail-like base; apothecia cream red to bright pink .... series ***Abutilones*** (*O. carminorosea*, p. 906 & *O. rehmii*, p. 904)

20. Spores *(9–)10–14(–17.2) × 1–1.6 µm, ± helicoid (S-shaped in profile view), with strongly curved base .ser**ies *Aurantiorubrae***, p. 833
20. Spores *7–10 µm long, slightly to strongly falcate but usually not distinctly helicoid, spore base partly constricted, strongly geniculate to reflexed .... **series *Abutilones*** (*O. milinana*, p. 897 & *O. lobeliae*, p. 899)

humid regions. In semihumid to arid areas the observed species diversity is not significantly higher as it was observed within section *Habrostictis*.

Core clade of section *Aurantiorubrae*
(series *Regales*, *Commatoideae*, *Rubellae*, *Aurantiorubrae*)

Series *Regales*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Regales*** Baral & E. Weber, **ser. nov.**, MB 815010 – Type species: *Orbilia regalis* (Cooke & Ellis) Baral

Etymology: named after the type species, *O. regalis*.

Latin diagnosis: *Seriei* Rubellae *similis sed pili solum ex processis vitreis compositi sunt, absque hyphis septatis, cellulae excipuli corpusculis crystalloides carentes.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–1.8(–3) mm diam., pale to bright cream-rose, yellow-ochraceous to orange-red, rarely rose-lilaceous, margin smooth or usually finely rough to fimbriate, crenulate, or with prominent whitish teeth, sessile or with a short stipe **Asci** *40–66(–74) × 4–5.5 µm, 8-spored, (1–)2–5(–7) lower spores inverted; **apex** (†) slightly to strongly truncate, not or slightly, rarely strongly indented and/or laterally inflated; **base** T-, L-, Y- or h-, rarely H-shaped. **Ascospores** *(5.8–)6.5–12(–14.5) × (1.1–)1.3–2.3(–2.6) µm, cylindric-ellipsoid or mostly cylindric- to fusoid-clavate, apex rounded to obtuse (exceptionally subacute), base partly tail-like, straight or usually slightly to strongly curved or geniculate near base (sometimes slightly helicoid), **SBs** (0.8–)1–2(–2.3) × 0.3–1(–1.2) µm, globose to tear-shaped or ampulliform, also plug-shaped, apically narrowed to a small to wide point, very short filum often present. **Paraphyses** very slightly to strongly inflated at the apex, often spathulate(-mammiform) but also clavate-capitate, terminal cells (1–)1.5–3(–5)× longer than lower cells. **Ectal excipulum** cells near base *(7–)10–20(–25)((–38)) × (5–)7–15(–20)((–25)) µm, near margin of textura prismatica-angularis-globulosa to textura prismatica-porrecta oriented at a medium to high angle (rarely under a low angle: *O. peudocylindrospora*); **glassy processes** absent or (1–)5–20(–60)((–100)) µm long, **hairs** absent. **SCBs** absent or globose; **VBs** consistently absent. **Exudate** (0.2–)0.5–2(–4) µm thick, cloddy-granular or cap-like, firmly attached over protruding part of paraphyses, hyaline to pale yellowish. — **ANAMORPH**: vermispora-like. **Conidiophores** short (9–25 µm). **Conidiogenous cells** monoblastic or sympodial. **Conidia** phragmosporous, *20–62 × 3–7.5 µm (in situ), 3–12(–15)-septate, slightly to strongly curved at both ends, rarely straight.

Habitat: wood and bark of angiosperms (rarely gymnosperms), also on branches of *Cactaceae* or caulicolous on small to large monocots, exceptionally on liverworts (*Radula*, *O. mali*), all species desiccation-tolerant, temperate to subtropical or ?boreal, humid to arid, always desiccation-tolerant.

Recognized species: 11, plus 1 unnamed species (‘affinis’).

Taxonomic remarks. Series *Regales* in the present circumscription is characterized by more or less narrow, somewhat comma-shaped ascospores with rounded to obtuse apices, rather short, usually globose to broadly tear-shaped SBs, and the frequent presence of glassy processes. *O. kingsiana*, *O. pseudocylindrospora*, and partly *O. mali* deviate from the more typical members of the group in lacking glassy processes, *O. pseudocylindrospora* also in mainly straight, basally only slightly attenuated spores. *O. denticulata* has the broadest spores of the series.

Typical members of series *Regales* resemble those of series *Microsomates* (section *Orbilia*, e.g., *O. microsoma*, *O. microlentiformis*). The latter mainly differ in more broadly attached, plug-shaped SBs, although similar SBs occur in *O. denticulata*. Moreover, a species placed in series *Microsomates* of section *Orbilia* (*O. myriopseudoregalis*) shows SBs very similar to typical members of series *Regales*. However, the very different anamorphs, the frequency of polysporous asci in series *Microsomates*, and the available DNA-data indicate that the two series are not closely related. For the similar series *Rubellae* see p. 821. Series *Aurantiorubrae* differs from series *Regales* in acute spore apices containing narrowly tear-shaped to subulate SBs.

Species delimitation. The included species are partly very similar and only tentatively separated by morphological markers. Six of them were repeatedly collected and found to be morphologically either quite constant (*O. aradi*, *O. euphorbiae*, *O. kingsiana*) or showed some variation between the collections, perhaps because different species were included (*O. brachychitonis*, *O. denticulata*, *O. mali*).

Anamorph. Very similar vermispora-like anamorphs were obtained in pure culture in four species of series *Regales*, while in three further species they were only seen on the natural substrate.

Phylogeny. Sequences of the ITS region were available for five species (*O. aradi*, *O. brachychitonis*, *O. denticulata*, *O. euphorbiae*, *O. mali*), LSU for three of them (*O. aradi*, *O. brachychitonis*, *O. denticulata*), and SSU for the latter three. The S1506 intron exists in *O. euphorbiae* (from Comoros) and *O. brachychitonis* but is absent in *O. euphorbiae* from Australia and the other three species. In our analyses of ITS+LSU and ITS series *Regales* forms a strongly (Phyl. 13), or medium (S15) supported clade, to which *O. caulicola* is associated as a sister clade. In the combined analyses (Baral et al. 2017b, Phyl. 13), series *Regales* clustered highly or medium supported in the core clade of section *Aurantiorubrae*. When analysing the S1506 intron, *O. euphorbiae* and *O. brachychitonis* clustered in a highly supported clade with unresolved position (S14).

Specific nucleotide positions. Series *Regales* shows a highly conserved motif near the 5’-end of the ITS2 region (CTGYACCAGTTAATTTTGGT), by which it distinctly deviates from all other series of section *Aurantiorubrae* which are much more variable here. In the LSU D1 domain, series *Regales* deviates at position 242–245 (CAAT or CAAC) from most other groups of subgenus *Habrostictis* which have CTTC, except for *O. gemma* and *O. crenatomarginata* which concur with *O. denticulata* (CAAC, see Tab. 68). The SSU V8–V9 region does not show any unique motifs but includes at pos. 248–271 combinations of nucleotides that are shared with other series.

Ecology. All included species are desiccation-tolerant. They occur on wood and bark, mainly of angiosperms, but also on herbaceous stems. Records derive from various climatic regions: the majority of species grew in semihumid to arid area and are known from Northern and Middle America, southern Europe, Africa, and Australia. Collections are also known from alpine subhumid South America (*O. puyae*) and tropical humid Australia (*O.* cf. *puyae*). Only two species are known from cold-temperate humid Europe (*O. aradi*, *O. mali*), one from orotemperate southern Europe (*O. pseudocylindrospora*), and one from warm-temperate humid eastern North America (*O. regalis*).

Key to species of series *Regales*

1. Glassy processes at margin absent 2
1. Glassy processes at margin present (sometimes only 1–5 µm long) 4

2. Spores *(6.5–)8–11.5(–12.3) × (1.5–)1.6–2 µm; SBs 1.5–2.7 × 0.7–1 µm, ± ampulliform; paraphyses spathulate to lageniform, not covered by glassy caps; apothecia rose-orange, margin with 7–19 µm long hair-like, ± freely protruding cortical cells; wood of *Abies*, *Lonicera*, montane-subalpine humid western North America, central Asia .... ***O. concoloris*** (section *Hemiorbilia*), p. 672
If apothecia yellow and SBs ± globose, on bark of *Fagus*: see under 17 (*O. aradi*)
2. Spores *5.5–8.8 µm long; SBs 1.3–1.9 µm long; paraphyses partly or consistently capitate-clavate; apothecia pinkish-rose to lilaceous, exceptionally orange 3

3. Paraphyses covered by 1–3 µm thick glassy caps, terminal cells 1–5× longer than lower cells; spores *(1.4–)1.5–1.7(–1.8) µm wide, slightly to medium curved at the mostly strongly tapered base; SBs 0.8–1.1 µm wide; apothecial margin 0–10 µm protruding; herbaceous stems or bark of *Fabaceae* & *Myrtaceae*, subtropical semihumid to semiarid western Australia .... ***O. kingsiana***, p. 793
3. Paraphyses covered by 0.2–0.5 µm thick exudate, terminal cells 1–3× longer than lower cells; spores *1.7–2.3 µm wide, ± straight, never strongly tapered below; SBs 0.4–0.7 µm wide; apothecial margin 10–25 µm protruding; bark of *Salix*, orotemperate humid Europe .... ***O. pseudocylindrospora***, p. 798
If exudate 0.2–2 µm, spores strongly tapering, SBs 0,7–1.2 µm wide, temperate to submediterranean Europe: see *O. mali* (p. 781)

4. Asci 16–64-spored; in semihumid to arid regions .... see **series *Microsomates*** (section *Orbilia*), p. 1295
4. Asci 8-spored 5

5. Spores *1.2–1.6(–1.7) µm wide 6
5. Spores predominantly > *1.6 µm wide; paraphyses often covered by thick glassy caps 14

6. Spores *(8–)9–12(–14.5) × 1.3–1.5 µm; SBs 0.4–0.7 µm wide; paraphyses ± spathulate to lageniform; branches of *Carnegiea gigantea*, subtropical semiarid western North America .... ***O. carnegieae***, p. 792
6. Spores max. *9.5(–10.5) µm long 7

7. Paraphyses consistently slightly to strongly spathulate or lageniform 8
7. Paraphyses uninflated, capitate or only sometimes slightly spathulate, often covered by glassy caps 10

8. Spores *(6–)7–9(–10.5) × 1.3–1.6 µm, slightly to medium tapered and curved below; SBs 0.8–1.3 × 0.3–0.5(–0.6) µm; apothecia yellowish-orange, with denticulate margin; branches of *Acacia*, *Adansonia*, *Euphorbia*, *Ipomoea*, stems of *Solanecio*, warm-temperate to tropical, humid to arid Macaronesia, Africa, Australia .... ***O. euphorbiae***, p. 787
If apothecia cream-ochre-brownish, SBs *1.2–1.8 × 0.5–1 µm, see ***O. pseudeuphorbiae*** (section *Arthrobotrys*, p. 1476).
8. Spores *5.5–7.3 × 1.4-1.7 µm, ± strongly tapered 9

9. Spore bases strongly tapered, partly tail-like, geniculate; glassy processes ± straight; apothecial margin rough; bark of *Malus*, warm-temperate humid eastern North America .... ***O. regalis***, p. 775
9. Spore bases medium to strongly tapered, spores partly entirely curved (C-shaped); glassy processes curved downwards; apothecial margin crenulate-dentate; bark of *Acacia*, *Eucalyptus*, subtropical semihumid western Australia .... ***O. austroregalis***, p. 776

10. Glassy processes 1–4 µm long; apothecia rose-lilaceous .... see under 3 (*O. kingsiana*)
10. Glassy processes min. 5–14 µm long; apothecia ± orange 11

11. Spores *5.7–8 µm long; glassy processes 5–14 µm long 12
11. Spores *8–9.5(–10) µm long; glassy processes 5–60 µm long; paraphyses ± capitate 13

12. Spores *5.7–8 × (1.3–)1.4–1.5(–1.7) µm; paraphyses ± uninflated; tropical Middle America .... ***O. cocois*** (section *Arthrobotrys*), p. 1474
12. Spores *6–7 × 1.2–1.4 µm; paraphyses ellipsoid-capitate; culms of *Phragmites*, tropical humid northeastern Australia .... ***O.* cf. *puyae***, p. 796

13. Spores ± strongly tapered below; SBs 0.8–1 µm wide; inflorescence stem of *Puya*, high-montane subtropical subhumid South America .... ***O. puyae***, p. 796
If paraphyses ± uninflated, compare *O. pseudeuphorbiae* (section *Arthrobotrys*, p. 1476).
13. Spores not or only slightly tapered below; SBs ~0.3–0.6 µm wide; branch of *Cylindropuntia*, subtropical semiarid western North America .... ***O.* cf. *carnegieae***, p. 793

14. Apothecia orange-rose without distinct yellow component 15

14. Apothecia yellow-orange, rarely with rose component (cells often with abundant yellow LBs, especially in paraphyses and marginal ectal excipulum) 16

15. Spores *(6–)7–12(–13.5) × 1.6–2.2 µm; SBs tear-shaped to globose; bark & wood of *Brachychiton*, *Nuytsia*, *Adansonia*, (sub)tropical subhumid to semiarid Australia .... ***O*. *brachychitonis***, p. 784

15. Spores *(6–)7–9(–10) × 1.8–2.2 µm; SBs tear- to pear-shaped; bark of angiosperms, temperate humid to mediterranean (semi)humid Europe..***O*. *mali***, p. 781

16. Apothecial margin usually with distinct prominent teeth; anchoring hyphae 2.5–5 µm wide; SBs tear- to plug-shaped; spores *6–10(–12) × 1.8–2.6 µm; paraphyses apically medium to strongly capitate-clavate or spathulate; branches of *Myrtillocactus* and *Yucca*, warm-temperate to subtropical (semi)arid Northern and Middle America .... ***O*. *denticulata***, p. 798

16. Apothecial margin crenulate but without distinct teeth; anchoring hyphae 1.8–3.5 µm wide; SBs ± globose..17

17. Spores *(6–)7–9.5(–11) × (1.6–)1.7–2 µm; SBs ± globose; paraphyses uninflated to slightly clavate, rarely subspathulate; ascus base never H-shaped; bark of *Fagus*, cold- to orotemperate humid western & central Europe .... ***O*. *aradi***, p. 777

17. Spores †8–11.8 × 1.6–2 µm; SBs unknown; paraphyses consistently spathulate; ascus base partly H-shaped; wood of *Cistus*, mesomediterranean semihumid southern Europe..***O*. aff. *aradi***, p. 781

Orbilia regalis (Cooke & Ellis) Baral, **comb. nov.**, MB 814377 — Pl. 391

Basionym: *Peziza regalis* Cooke & Ellis, Grevillea 6: 91 (1878)
≡ *Pezizella regalis* (Cooke & Ellis) Sacc., Syll. Fung. 8: 284 (1889)
≡ *Hymenoscyphus regalis* (Cooke & Ellis) Kuntze, Revis. Gen. Pl. 3: 486 (1898)

Etymology: apparently because the apothecia had a crenulate margin similar as a crown.

Typification: USA, New Jersey, Newfield, unlocalized, branch of *Malus domestica*, undated, J.B. Ellis (M.C. Cooke 2778, K(M) 35323, apothecia on inner surface of bark, lectotype, designated here, MBT202653).

Misapplied name: Nannfeldt (1932: 252), as ?*Hyalinia rubella*.

Misinterpretation of *O*. *regalis*: J.B. Ellis (N. Amer. F. 438), = *Orbilia occulta*.

Description: — **TELEOMORPH**: **Apothecia** superficial, ± gregarious, rehydrated 0.35–0.8 mm diam., in total 0.11 mm high, light cream-ochraceous throughout, turning orange-brownish (Cooke & Ellis: 'miniate' = saturn-red), round, somewhat lobate when large, disc flat or slightly concave, margin rough, scarcely protruding; broadly sessile. **Asci** †40–49 × 3.3–3.6 µm, cylindrical, 8-spored, spores biseriate in upper part, ~4 lower spores inversely oriented, pars sporifera †20–31 µm; **apex** (†) slightly to medium truncate; **base** with long, thin, flexuous stalk, L- to h-shaped. **Ascospores** frequently seen within asci (especially in CB_L), †6–7.3 × 1.4(–1.5) µm, cylindric- to fusoid-clavate, apex (rounded to) obtuse, base strongly attenuated to form a tail-like end, here distinctly geniculate (slightly helicoid), **SBs** not seen. **Paraphyses** apically medium to strongly spathulate to lageniform-mammiform, rarely lanceolate, terminal cells †14–25 × 2.3–3.5 µm, exceeding the asci by 3–6 µm, lower cells †7–10 × 1–1.5(–1.8) µm, branched only near base. **Medullary excipulum** 40 µm thick, of ± dense, horizontally oriented textura intricata with rather numerous inflated cells, sharply delimited. **Ectal excipulum** of thin-walled, vertically oriented t. angularis from base to flanks, 40 µm thick at lower flanks, cells †8–14 × 6–10 µm, margin not clearly seen, probably of t. angularis, cortical cells with **glassy processes** 8–15 × 3.5–5 µm, ± straight, strongly stratified, abundantly present from lower flanks to margin. **Anchoring hyphae** abundant at base, hyphae †1.5–2.7(–3.5) µm wide, walls 0.2–0.4(–0.7) µm thick, forming as a loose t. intricata up to 50 µm thick. **Exudate** over paraphyses strongly refractive, pale yellowish, 0.3–1.4(–1.8) µm thick, firmly attached, cap-like. **— ANAMORPH**: unknown.

Habitat: on slightly rotten bark (bast) of a branch of *Malus domestica*, on inner surface, no algae. **Associated**: *Orbilia occulta*, brown hyphae of *Sporidesmium* sp. among anchoring hyphae, crustose and fruticose lichen. **Desiccation tolerance**: certainly tolerant, according to the associated lichens and *O. occulta*. **Altitude**: ~35 m a.s.l. **Geology**: Miocene sedimentary rock. **Phenology**: unknown.

Taxonomic remarks. *Orbilia regalis* is characterized by rather small, cylindric-fusoid ascospores with strongly attenuated, short, geniculate tail-like bases, distinctly spathulate to mammiform paraphysis apices, and short, not clearly curved glassy processes at the margin. The species is very close to the European *O. aradi*, which is confined to bark of *Fagus* and rather sharply delimited by consistently less inflated, never lageniform paraphysis apices, slightly larger spores, and usually more yellow apothecia. For the very similar *O. austroregalis* see below.

O. euphorbiae and *O. puyae* are distinguished by longer spores with a less tapered base, the latter also by never lageniform or mammiform paraphyses. In spore shape *O. regalis* also somewhat resembles *O. mali* and *O. comma* (series *Commatoideae*), but these species sharply differ in capitate paraphyses, partly also in the absence of glassy processes.

Type studies. Cooke & Ellis (1878) considered *Peziza regalis* to be close to *P. lasia* (= *O. carpoboloides*). A specimen of *P. regalis* (M.C. Cooke 2778, K), which contains two small pieces of *Malus* bark, was reexamined and found to be a mixture of two very different species of *Orbilia*. One grew on the rather undecayed inner surface of both pieces of bark, with ~30 mature, rehydrated 0.35–0.8 mm large apothecia, and on this the above description is based (Pl. 391). The apothecia of the other species measured rehydrated only 0.15–0.3 mm and grew abundantly on the rather decayed outer surface of one of the two pieces (IVV: H.B. 5344). These have a more distinctly crenulate margin made up of glassy processes (3–)10–30(–35) µm long. The asci measured 37–43 × 4–4.3 µm and were apically hemispherical, but no distinct apical thickening could be seen, and the paraphyses were apically not inflated, but heavily covered by exudate. No spores could be found, even within the asci, but these features suggest that the fungus belongs to section *Hemiorbilia*. Very probably it represents *O. occulta* (see p. 731), mature material of which was collected by J. B. Ellis in Newfield on bark of *Vitis* and *Malus*.

The brief original description by Cooke & Ellis does not allow to decide on which of the two species it was based. Indeed it seems likely that both influenced the protologue. The apothecia were described as 0.1 mm diam., with raised, white-crenulate margin, the paraphyses as globose-clavate, and the spores as linear, straight, 0.007 mm. Obviously the apothecial size stated by Cooke & Ellis is erroneous. The crenulate margin, on which the name *regalis* was undoubtedly based, was probably taken from the population of immature apothecia, but the reported

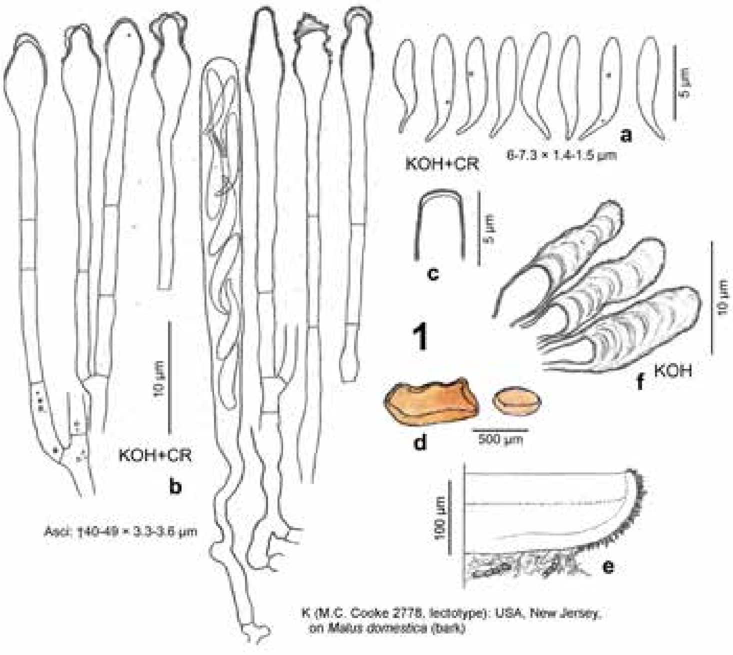


Plate 391. **1**: *Orbilia regalis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., marginal cortical cells with glassy processes.

spores exclude *O. occulta*, while apically inflated paraphyses occur in both species. In order to settle the identity of *O. regalis*, we here designate the mature apothecia growing on the inner surface of bark in M.C. Cooke, Fungi – New Jersey, U.S.A., No. 2778, K(M) 35323 as the **lectotype** of *Peziza regalis* (Pl. 391). This choice results in a clear identity of the name *P. regalis*, but has the disadvantage that the rough apothecial margin does not match the etymology of the name. On the other hand, apothecia of the very similar *O. austroregalis* described below look like a crown, but vary between populations in the length of the glassy processes, the paratype showing partly an almost smooth margin.

Massee (1894b: 100) considered *P. regalis* to be a synonym of *P. cruenta*. Nannfeldt (1932: 252) believed that these two taxa were possible synonyms of *Hyalinia rubella* (s. Nannfeldt, = *Orbilia phragmotricha*). Massee examined another specimen under the name *P. regalis* in K (J.B. Ellis, N. Amer. F. 438, unlocalized, 'on loose hanging bark of old apple trees, summer and autumn', published in 1880) which might be a topo- or even isotype of Cooke 2778). Its reexamination revealed identity with *O. occulta*, which supports that the above immature population also represents this species (see also under *O. occulta*, p. 731, and under *O. cruenta*, p. 1668). Dennis (1964: 61) studied the type at K and stated that he could not find ripe ascospores, but it is unclear which of the two populations he had examined.

Ecology. *O. regalis* grew on rather undecayed bark of a probably xeric branch of *Malus domestica* in the warm-temperate humid lowlands of eastern North America.

Specimens included. **USA**: **New Jersey**, Newfield, unlocalized, ~35 m, branch of *Malus domestica*, on bark, undated, J.B. Ellis (M.C. Cooke, 2778, K(M) 35323, **lectotype**, H.B. 5343 ø).

Orbilia austroregalis Baral, **sp. nov.**, MB 813750 — Pl. 392–393

Etymology: named after the similarity with *Orbilia regalis*.

Typification: Western Australia, Wannamal, twig of *Eucalyptus*, 3.IX.2006, G. Marson (ex H.B. 8662b, MEL 2389247, holotype).

Latin diagnosis: Orbiliae regali *persimilis sed ascosporae partim arcuatae, margo excipuli processis vitreis partim curvatis praeditus. Habitat ad corticem putridum ramorum siccorum* Acaciae *vel* Eucalypti *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.35–0.55 × 0.2–0.4 mm diam., 0.15–0.2 mm high (receptacle 0.12 → 0.08–0.11 mm), light orange- to brick-red, hardly translucent, ellipsoid, ± scattered; disc slightly to medium concave, margin 5–30 µm protruding (incl. glassy processes), distinctly whitish crenulate-dentate; sessile on a broad base, superficial or immersed in cracks. **Asci** *40–45 × 3.5–3.8 {T} or 55–57 × 4–4.3 µm {1}, 8-spored, spores *biseriate, (2–)3–4(–5) lower spores inverted {2} (not or ± mixed); **apex** (†) strongly truncate (slightly indented, laterally distinctly inflated), hemispherical in side view, thin-walled; **base** not studied. **Ascospores** *(5.3–)5.7–6.5(–7) × 1.4–1.6(–1.7) µm {2} (~7–8 µm actual length), †5–6 × 1.4–1.5 µm {T}, cylindric-clavate, apex rounded to obtuse, gradually tapered towards partly tail-like base, medium to strongly curved; **SBs** *1.3–1.6 × (0.7–)0.8–0.9 µm {2}, globose to broadly tear-shaped, apically abruptly narrowed to a very short filum. **Paraphyses** apically slightly or strongly lageniform to mammiform, terminal cells †21–23 × (3–)3.5–4.2 µm {T}, *2.5–3.5 µm wide {1} (†2.3–2.7 µm), beak 2–4(–5) × 1.5–2 µm {T}, exceeding the dead asci by 5–7 µm, lower cells *9–11 × 1.8–2 µm {T}; unbranched at upper septum, hymenium pale orange. **Medullary excipulum** hyaline, 30–40 µm thick, of dense textura intricata with many inflated cells, indistinctly or sharply delimited by a t. porrecta at flanks. **Ectal excipulum** hyaline, of (†) thin-walled, indistinctly vertically oriented textura globulosa-angularis from base to mid flanks, 60–100 µm thick near base, cells *10–15(–19) × 8–10(–14) µm {2}; 15–25 µm thick at flanks, of vertically oriented t. angularis(-prismatica), cells at mid flanks *8–9 × 3–3.5 µm, oriented at a 70–80° angle to the surface, 15–20 µm thick at margin, of t. prismatica-porrecta oriented at 30–70°, marginal cortical cells *9–11 × 2–2.5 {1} or *8–10 × 4–5 µm {T}; **glassy processes** 10–25 {1} or 30–70 {T} × 2.5–4 µm {2}, high-refractive, not stratified, hyaline to light orange-yellow, outwards curved, coherent to form teeth. **Anchoring hyphae** rather sparse and only at base, †2–3(–4) µm wide, walls 0.2 µm thick {1}. **SCBs** in paraphyses and ectal excipulum apparently absent {2}; **LBs** in lower ectal excipulum 1–2.7 µm diam., very pale orange (carotenoids). **Exudate** over paraphyses and margin 0.1–0.8 µm thick, finely rough to granular, firmly attached. **— ANAMORPH**: unknown.

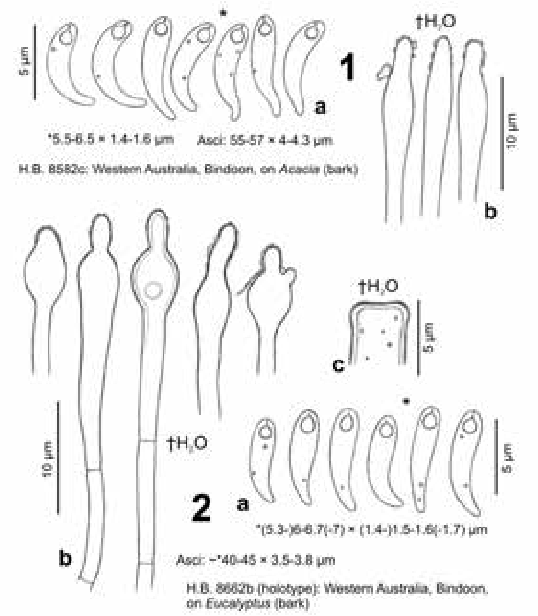


Plate 392. **1–2**: *Orbilia austroregalis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex.

Plate 393. **1–2**: *Orbilia austroregalis*. – **2a**. semihumid Eucalypt open forest with *Macrozamia*; **1a–b**, **d–f**. rehydrated apothecia; **1c**. dry apothecium; **2b**. apothecium in median section; **1g**, **2f**. id., marginal region with glassy processes; **2c–e**. asci and paraphyses. – Living state, except for ascus in **2d**. — **1a–g**. H.B. 8662b (holotype): Western Australia, Bindoon, on *Eucalyptus*; **2a–f**. H.B. 8582c: ibid., on *Acacia*.

Habitat: collected 0.5–1.5 m above the ground, corticated, 6–11 mm thick branches of *Acacia* sp. {1}, *Eucalyptus* sp. {T}, on strongly decayed bark {2} (bast), partly on inner surface of detached bark, partly blackened, no algae. **Associated**: *Orbilia albidorosea* {1}, *O. austroocculta* {1}, *O. pleiocrescens* {1}, *Tryblidaria* sp. {1}. **Desiccation tolerance**: ectal excipulum and a few mature asci still viable after 14 months. **Altitude**: 272 m a.s.l. **Geology**: Archean granulite with granitic gneiss (red-brown soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia austroregalis* is very similar to *O. regalis*. It is tentatively separated here by thicker apothecia, slightly shorter spores with a partly more curved (sickle-shaped) upper part and less attenuated base (but these differences could be due to the living vs. dead state), and in downwards curved, longer glassy processes in the holotype. Together with a different climate (subtropical semihumid vs. warm-temperate humid), we suspect that the Australian specimens belong to a different species.

Variation. In the sparse paratype the asci are much larger, the paraphyses narrower and less mammiform, the marginal cortical cells much narrower, and the glassy processes much shorter compared to the holotype.

Ecology. *O. austroregalis* is only known from two sparse collections made at a single site, where it grew on rotten bark of xeric twigs and branches of *Acacia* and *Eucalyptus* in a subtropical semihumid eucalypt woodland with *Macrozamia* located in the Jarrah Forest ecoregion of southwestern Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 272 m, branch of *Acacia*, on bark, 4.IX.2006, G. Marson (ex H.B. 8582c, mixture in MEL 2389242 [type of *O. pleiocrescens*]). – ibid., twig of *Eucalyptus*, on bark, 3.IX.2006, G. Marson (ex H.B. 8662b, MEL 2389247, **holotype**).

Orbilia aradi Baral & G. Marson, **sp**. **nov**., MB 813751 — Pls 394–395, Map 66

Etymology: named after *Aradus conspicuus*, a mycophagous flatbug repeatedly encountered under *Fagus* bark together with the *Orbilia*.

Typification: Luxembourg, Senningerberg, trunk of *Fagus sylvatica*, 27.XI.2004, G. Marson (ex H.B. 7628c, M-0276433, holotype).

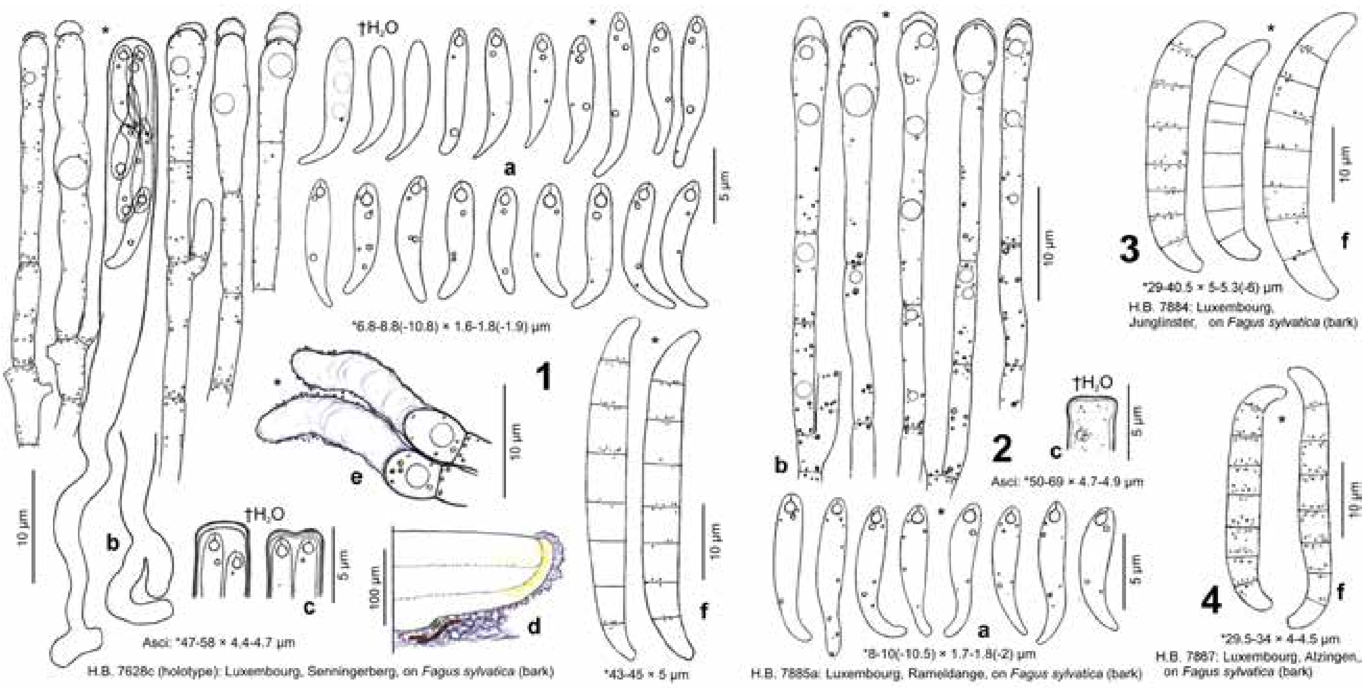


Plate 394. **1–4**: *Orbilia aradi*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal cortical cells with glassy processes; **f**. conidia (**1**: grown from apothecium inside Petri dish, **3–4**: from substrate).

Latin diagnosis: *Apothecia rehydratata 0.2–0.1 mm diam.*, *lutea*, *(sub)sessilia*, *margine subtiliter crenulato. Ascosporae *6–11 × 1.6–2 µm*, *cylindrico- vel fusoideo-clavatae*, *apice rotundatae ad obtusae*, *basi leniter vel valde attenuatae et curvatae*, *in statu vivo corpusculum refringens globosum*, *filo brevi affixum continentes. Paraphyses ad apicem non vel leniter inflatae*, *subcapitatae vel subspathulatae. Cellulae excipuli marginalis et paraphysium guttulas minutas luteas oleosas continentes. Margo excipuli processis vitreis brevibus praeditus. Habitat ad paginam inferiorem corticis sicci*, *haud putridi*, *leniter separati*, *in truncis* Fagi sylvaticae *erectis*, *etiam in ramis projectis in zona supra- ad orotemperata humida Europae centralis et meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–0.8(–1.2)((–1.8)) mm diam., 0.12–0.3 mm high [receptacle 0.09–0.15(–0.2) mm], pale to light (to bright) (chlorinaceous-)yellow(-ochraceous), also yellow-orange, exceptionally greyish-white, ± translucent, round to slightly undulating, scattered to subgregarious; disc slightly concave to flat, margin 5–25 µm protruding (incl. glassy processes, 0–15 µm without), finely crenulate to pubescent; broadly sessile or often with a hidden, obconical to abrupt stipe 0.02–0.05(–0.2) × 0.07–0.25 mm, superficial; dry light to bright yellowish-ochraceous to yellow-orange-amber or orange-red, margin only slightly inrolled. **Asci** *45–58(–69) × 4.4–5.3 µm {6}, †40–55(–70) × 3.8–4.4 µm {2}, 8-spored, spores *2–3-seriate, (2–)3–5(–6) lower spores inverted {7} (sometimes mixed), pars sporifera *(17–)19–27 µm long; **apex** (†) medium to strongly truncate (not or rarely strongly indented, slightly laterally inflated or not); **base** with short to very long, thin or thick, flexuous stalk, T-, L- or Y-shaped. **Ascospores** *(6–)7–9.5(–11) × (1.6–)1.7–2((–2.2)) µm {8}, †7–9.7 × 1.5–1.7 µm {2}, cylindric- to fusoid-clavate to clavate, apex rounded to obtuse, base mostly medium to strongly attenuated, often with a tail-like end, slightly to strongly curved or geniculate near base; **SBs** *(1–)1.2–1.6(–1.8) × (0.6–)0.7–0.9(–1) µm {5}, divided into a globose (to tear-shaped) lower part and a fine, slightly shorter, apically attached filum. **Paraphyses** apically not or often slightly inflated, subcapitate-clavate to subspathulate, very exceptionally sublageniform or slightly moniliform, terminal cells *(9–)14–22(–27) × (2–)2.5–3.5(–4.2) µm {5}, exceeding the dead asci by 4–6 µm whereas living asci projecting 0–5 µm beyond paraphyses, lower cells *(5–)8–12(–14) × 1.6–2.3(–2.8) µm {3}, very rarely branched at upper septum, lower part of hymenium usually pale to light yellow(-orange). **Medullary excipulum** hyaline, 30–120 µm thick, of medium loose to dense textura intricata with many inflated cells, indistinctly to very sharply delimited, especially towards margin. **Ectal excipulum** subhyaline at base, pale to bright yellow-orange at flanks and margin, of thin-walled to slightly gelatinized, indistinctly vertically oriented t. globulosa(-prismatica) from base to margin, 25–100(–140) µm thick near base, cells *8–18(–23) × (6–)8–12(–17) µm {2}; at flanks 15–20 µm thick, 15–30 µm thick, of t. (globulosa-)prismatica(-porrecta) oriented at a 40–80° angle to the surface, marginal cortical cells */†5–10 × 4–5(–6) µm {3}, at uppermost margin *13–15 × 3 µm; **glassy processes** 0–2 {2} or mostly (2–)4–12(–15) {5} × (2.5–)3–4(–5) µm {6}, low- to medium refractive, indistinctly stratified, straight or more or less outwards curved, coherent in fascicles by partly forming indistinct teeth. **Anchoring hyphae** sparse to abundant, */†1.8–3.5(–4) µm wide, walls 0.2–0.5(–1) µm thick {4}, forming a loose hyaline t. intricata ~20–80 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.5–2.5 µm diam. **LBs** pale to bright golden yellow(-orange) due to carotenoids, more or less abundant in lower part of paraphyses, here 0.2–0.3 µm diam., especially near septa, at flanks and margin up to 0.8(–1.5) µm diam., abundant towards margin, staining very indistinctly dirty bluish-greenish in IKI. **Exudate** over paraphyses (0.2–)0.4–1.5(–2.5) µm thick {5}, strongly refractive, hyaline, sometimes stratified, firmly attached, always as single glassy caps, surface CR pale to bright rose; over marginal glassy processes absent or 0.2 µm thick, granular. — **ANAMORPH**: vermispora-like (from ascocarp in Petri dish {1} and natural substrate {3}). **Conidiophores** simple, short. **Conidia** phragmosporous, slightly to strongly curved at both ends, ± straight in middle part, sometimes slightly contorted, *(29–)32–41(–45) × (4–)4.3–5.2(–6) µm (in situ), 6–7-septate {4}.

Habitat: collected 0.2–4 m above the ground, corticated or partially decorticated, ~15–70 cm thick, standing, living or recently dead trunks (southeast-, south-, west- to northwest-exposed side), rarely lying on ground, also 4–8 cm thick, still-attached branches, of *Fagus sylvatica* {18}, on detaching, firmly to loosely adhering bark {18} (on bast), trunk bark split into large rectangular parts, branches often decorticated at their underside, on inner surface of bark, often also near or on edges of bark, not or very slightly, sometimes medium decayed, partly in beetle galleries or on boring dust of bark beetles, sometimes associated with wounds, ungreyed, green algae absent but near edges of bark

Plate 395. **1–8**: *Orbilia aradi* (all on *Fagus*). – **4a**. recently dead tree with splitted bark; **6b**. dead attached branch with detaching bark; **1b**. inner surface of undecayed *Fagus* bark; **1a**, **c–e**, **3c**, **4b**, **4c–d**, **7**. rehydrated apothecia (**5c** rare whitish form); **3a–b**, **4c**, **5e**. dry apothecia; **2**, **4a**. apothecia in median section; **8a**. id., marginal region; **8b**. id., at flanks; **1f**, **4d**, **6a**. apices of asci and paraphyses; **5b**. ascospores; **3d**. conidia from substrate. – Living state, except for **4d** (in KOH+CR). — **1a–g**. H.B. 8179a: Germany, Tübingen; **2**. H.B. 7995a: Luxembourg, Bettembourg; **3a–d**. H.B. 7884: ibid., Junglinster; **4a–d**. H.B. 7628c (holotype): ibid., Senningerberg; **5a–e**. H.B. 7867: ibid., Alzingen; **6a–b**. H.B. 9142: France, Grenoble; **7**. 5.III.2007: Luxembourg, Mensdorf; **8a–b**. H.B. 7760a: ibid., Esch-sur-Alzette.

medium abundant. **Associated**: *Coniochaeta subcorticalis* {1}, *Fomes fomentarius* {1}, *Hyalorbilia juliae* {1}, *Lasiosphaeria* aff. *sorbina* {1}, *Orbilia aristata* {5}, *O. xanthoguttulata* {2}, *Orthotrichum* sp. {1}, *Parmelia sulcata* {1}, *Pyrenopeziza* sp. {1}, *P.* ?*caespiticia* {1}, ?*Teichospora* sp. {2}. **Desiccation tolerance**: fully viable for at least 8 weeks, about 50% of spores still viable after 10 months. **Altitude**: 270–460 m a.s.l. (central Europe), 1240 m (southern Europe). **Geology**: Keuper (marl & sandstone), Lower Jurassic sand- & limestone, Minette, Cretaceous siliceous shale, Pleistocene loess. **Phenology**: II–III, V, VII–XII (throughout the year).

Taxonomic remarks. *Orbilia aradi* is characterized by yellow(-orange) apothecia and fusoid-clavate, basally geniculate ascospores. The short glassy processes evoke a finely crenulate margin, and the paraphyses are apically only slightly inflated and tipped by glassy caps of exudate, but do not show any trace of beaks. The very similar North American *O. regalis* (p. 775) and Australian *O. austroregalis* (p. 776) differ particularly in paraphysis shape but also in apothecial colour. An Australian collection mentioned under *O. puyae* (on *Phragmites*, Pl. 408: 2) has paraphyses very similar to *O. aradi* but differs in smaller spores and a tropical origin. For the mediterranean *O.* aff. *aradi* on *Cistus* see below.

Variation. Although the typical colour of *O. aradi* is light (ochraceous-)yellow, populations with yellow-orange or almost hyaline apothecia were occasionally seen. In their microscopical features the 17 samples studied showed only very little variation.

Anamorph. The observed vermispora-like conidia are very similar as in other species of series *Regales* and also of, e. g., *O. comma* (series *Commatoideae*) or *O. phragmotricha* (series *Rubellae*). The conidia obtained in culture (at the lid of a Petri dish) were distinctly longer (*43–45 µm, Pl. 394: 1f) than those on the natural substrate (*29–40.5 µm, Pls 394: 3–4; 395: 3d), but were also less curved at the ends, so that their actual length is less divergent. The number of septa did not vary noticeably.

Phylogeny. Sequences of *O. aradi* were taken from apothecia of a sample from French Alps and from pure culture of a sample from Luxembourg, comprising ITS and partial LSU. From the culture also complete SSU and almost complete LSU were gained. All three sequences lack the large S1506 intron and completely concur in their overlapping parts. *O. aradi* shows a minimum ITS distance of 7.5% to *O. mali* and 8% to *O. brachychitonis*, and 2.5% in the LSU D1–D2 to *O. brachychitonis*. *O. aradi* formed with *O. mali* a supported clade (see under *O. mali*, p. 784).

Ecology. *O. aradi* grows very hidden on the inner surface and edges of detaching, ± undecayed xeric bark of large, mostly standing, damaged living or recently dead *Fagus* trees. As an exception (26.X.2010, Graulinster) the tree was lying on the ground, thrown by a storm about 3 years earlier. At three sites the species was instead collected on attached branches. *O. aradi* appears to be restricted to *Fagus* and was so far only collected in subcontinental central cold-temperate and a single time in orotemperate humid southern Europe. Very probably the species has a much wider distribution within the area of European beech, being overlooked due to its unusual habitat.

When occurring on the main trunk, the trees are either in the process of dying or recently dead: the bark detaches by splitting into large, ± rectangular pieces (Pl.395: 5a). Apothecia are formed during the initial stage of bark decay; at later stages the *Orbilia* becomes more sparse and soon vanishes. A bark beetle (*Taphrorhychus bicolor*) often has its galleries in the bast close to the apothecia and is possibly involved in the death of the trees, but in those collections on very undecayed bark the beetle was not present yet. Apothecia have never been found on bark being internally strongly destroyed by the bark beetle, and are usually absent on trunks or branches fallen to the ground.

Map 66. Known distribution of *O. aradi* in Europe.

Some associated ascomycetes, particularly *O. aristata* and an unidentified *Pyrenopeziza*, inhabit the same or closely adjacent pieces of bark, which are usually smaller and more strongly detached from the trunk by curling outwards. The inhabited trees were either half-shaded or fully sun-exposed, standing near edges of forests or in clearings caused by storms or wood-logging. Due to sunburn effects, bark damage and occurrence of *O. aradi* are usually limited to the sun-exposed side of the trunk. The inhabited trees might have died due to water stress caused by a rapid increase of sun exposition when the trees around were removed. Local wounds with detaching small bark pieces might also be induced mechanically during cutting of adjacent trees, perhaps also by deer, accompanied by *Fomes fomentarius* fruitbody formation. The associated flatbug *Aradus conspicuus* was repeatedly observed under the bark, partly in association with the *Orbilia*.

Specimens included (all on bark of *Fagus sylvatica*). **LUXEMBOURG**: **Gutland**, **Diekirch**, 3.5 km W of Beaufort, 1.3 km SSW of Eppeldorf, Süddig, 400 m, trunk, 15.III.2006, G. Marson (ø). – **Capellen**, 11.5 km NW of Luxembourg, 0.8 km SW of Dondelange, S of Telpeschholz, Uesbach 305 m, trunk, 12.III.2007, G. Marson (ø) – **Echternach**, 18.5 km NE of Luxembourg, NW of Graulinster, Marscherwald, 400 m, trunk, 26.VII.2009, G. Marson (H.B. 9586). – ibid., N of Graulinster, 390 m, trunk, 26.IX.2010, G. Marson (ø). – **Grevenmacher**, 13.5 km NE of Luxembourg, 1.7 km WNW of Junglinster, Bierger, 350 m, trunks, 21.VIII.2005, G. Marson (H.B. 7884a ø, anam. substr.). – 15 km ENE of Luxembourg, 1.5 km NE of Mensdorf, Widdebierg, 380 m, trunk, 5.III.2007, G. Marson (ø). – 13 km ENE of Luxembourg, 2.3 km WNW of Beyren, Kazeboesch, 320 m, branch, 18.VII.2009, G. Marson (ø). – **Luxembourg**, 12 km NE of Luxembourg, 1.8 km ESE of Ernster, E of Engelshaff, Engelsbësch, 297 m, branch, 29.VIII.2007, G. Marson (ø). – 9 km NE of Luxembourg, 0.8 km W of Rameldange, Rammeldangerhéicht, 400 m, trunk, 30.VIII.2005, G. Marson (H.B. 7885a). – 7 km NE of Luxembourg, 1.5 km WSW of Senningerberg, Gréngewald, Kuelebierg, 395 m, trunk, 27.XI.2004, G. Marson (ex H.B. 7628c, M-0276433, **holotype**, anam. apoth.). – 6 km NNE of Luxembourg, 1.2 km WNW of Waldhaff, Gréngewald, Stafelter, 419 m, trunks, 27.XII.2017, G. Marson (G.M. 2017-12-27.1). – 5.3 km S of Luxembourg, 1.8 km WSW of Hesperange, Fennerholz, 307 m, trunk, 23.II.2014, G. Marson (G.M. 2014-02-23.2; sq.: KT222393, KY419196). – 7.5 km SE of Luxembourg, 2.5 km SE of Alzingen, Kircheboesch, 330 m, trunk, 28.VII.2005, G. Marson (H.B. 7867, anam. substr.). – **Esch-sur-Alzette**, 5.5 km E of Bettembourg, 1 km NW of Frisange, Ieweschteboesch, 270 m, trunk, 1.X.2005, G. Marson (H.B. 7995a). – 5 km WNW of Esch-sur-Alzette, 0.5 km NW of Belvaux, Galgebierg, 400 m, trunk, 24.V.2005, G. Marson (H.B. 7760a, anam. substr.). — **GERMANY**: **Baden-Württemberg**, Schönbuch, 6.5 km NE of Tübingen, 1.5 km NNE of Pfrondorf, Brand, 460 m, trunk, 21.V.2006, H.O. Baral (H.B. 8179a). — **FRANCE**: **Rhône-Alpes**, **Isère**, Vercors, 19 km SW of Grenoble, 2 km SE of Villard-de-Lans, N of Les Glovettes, 1240 m, branch, 11.VIII.2009, H.O. Baral, G. Marson & B. Liu (H.B. 9142; sq.: KT222365).

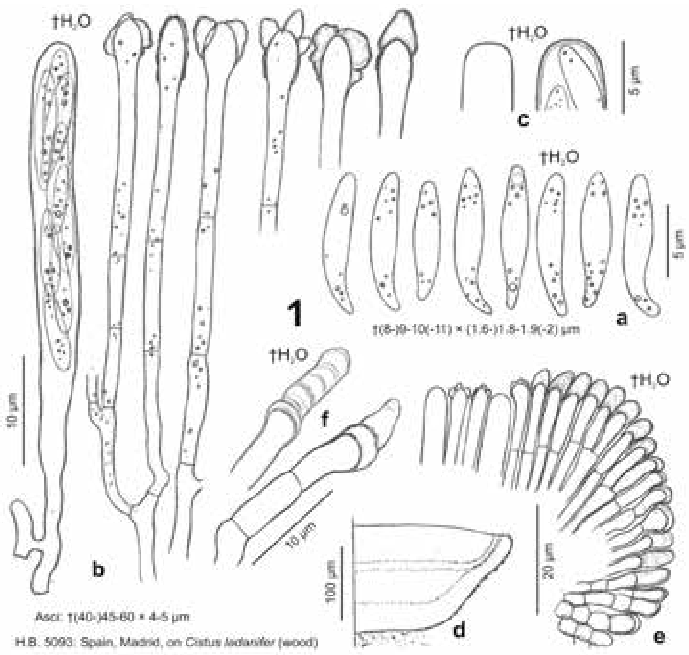


Plate 396. **1**: *Orbilia* aff. *aradi*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum; **f**. cortical cells with glassy processes.

Orbilia aff. *aradi* — Pl. 396

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.7 × 0.25–0.5 mm diam., 0.14 mm high, pale orange-ochre (light yellow-amber with a rose tint when fresh), round to often elliptical, ± scattered; disc flat, margin thick, 5 µm protruding, finely rough; broadly sessile, partly ± immersed in clefts; dry orange-yellow. **Asci** †(40–)45–60 × 4–5 µm, 8-spored, spores †2–3-seriate, lower spores inverted, pars sporifera †30 µm long; **apex** (†) slightly to medium truncate (not indented, laterally not inflated), hemispherical in side view, thin-walled; **base** with medium long stalk, partly H-shaped. **Ascospores** †(8–)9–10(–11.8) × (1.6–)1.8–1.9(–2) µm, narrowly fusoid(-clavate), apex obtuse (rarely subacute), base medium tu rather strongly attenuated, sometimes tail-like, slightly to medium curved; **SBs** not observed (?globose), with several minute LBs in each half. **Paraphyses** apically slightly to medium inflated, consistently spathulate, terminal cells †16–22 × 2.4–3.2(–3.7) µm, lower cells †6.5–12.5 × 1.2–1.7 µm; unbranched at upper septum. **Medullary excipulum** 55 µm thick, of t. intricata. **Ectal excipulum** of vertically oriented textura angularis from base to mid flanks, 40–50 µm thick near base, cells †10–20 × 8–14 µm; 15–20 µm thick at flanks, cells †4–9 × 4–6 µm, 30 µm thick at margin, of t. porrecta oriented at a 30–60° angle to the surface, marginal cortical cells †6–13 × 2.5–3.2 µm; **glassy processes** 2–10 × 3–5 µm, high-refractive, yellowish, stratified. **Anchoring hyphae** sparse at base, †1.7–2.7 µm wide, walls 0.2–0.7 µm thick. **SCBs** and **VBs** unknown; **LBs** in paraphyses minute, scattered. **Exudate** over paraphyses (0.3–)1–2.5 µm thick, forming conical caps, pale yellowish, firmly attached, 1 or often several on each apex, over glassy processes absent. **— ANAMORPH**: unknown.

Habitat: decorticated, xeric, ?15 mm thick branch of *Cistus ladanifer*, on slightly decayed wood, greyed, with a few green algae. **Associated**: '*Helotium*' aff. *uvidulum*, *Orbilia vinosa*. **Desiccation tolerance**: unknown (certainly desiccation-tolerant). **Altitude**: ~650 m a.s.l. **Geology**: Quaternary clay and sand. **Phenology**: XII (but probably long-lived).

Taxonomic remarks. This taxon was only studied in the dead state from a single collection 10 years after it was collected. It differs from *O. aradi* in the paraphyses being more distinctly inflated (spathulate) at the apex and covered by often more than one glassy cap on each tip. The ascospores are slightly longer and more fusoid, and a H-shaped ascus base was drawn which has never been seen in *O. aradi*. The other characters are quite similar, but in combination with a different ecology this collection appears to represent a separate species. From *O. denticulata* it differs especially in shorter glassy processes and consequently absent marginal teeth, and in narrower anchoring hyphae. *O. regalis* differs in distinctly smaller spores.

The presence of a H-shaped ascus base might point to a relationship with section *Orbilia* or *Arthrobotrys*. Series *Microsomates* could be the right place for the taxon. Particularly *O. microlentiformis* looks similar but has more subcylindric-ellipsoid spores, and the indistinctly observed globose SB remote from the spore apex seen in a single spore (see Pl. 396: 1a) questions identity with this species.

Ecology. *O.* aff. *aradi* grew on slightly rotten wood of a xeric branch of *Cistus ladanifer* in the mesomediterranean semihumid subcontinental Meseta of Castile of the Iberian Peninsula in southeastern Europe.

Specimens included. **SPAIN**: **Madrid**, 14 km NNW of Madrid, El Pardo, ~650 m, branch of *Cistus ladanifer*, on wood, 5.XII.1984, G. Moreno, R. Galán & J.T. Palmer (AH 6402-1, as *O. ?luteorubella*, H.B. 5093 ø).

Orbilia mali Baral, **sp. nov.**, MB 813745 — Pls 397–398, Map 67

Etymology: named after the substrate in the type, bark of *Malus*.

Typification: France, Ariège, Rimont, branch of *Malus sylvestris*, 23.V.2007, J. Fournier (ex H.B. 8502a, M-0276508, holotype; sq.: KT222353).

Latin diagnosis: *Similis* Orbiliae commae *sed ascosporae multo minus curvatae, cellulae excipuli in statu vivo absque corpusculis crystalloideis, cellulae marginales partim processis vitreis praeditae. Habitat ad corticem leniter putridum ramorum vel truncorum siccorum angiospermarum in zona supratemperata humida ad submediterranea Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.6 {4} or 0.6–1.2 {2} mm diam., (0.1–)0.12–0.14(–0.16) mm high (receptacle 0.1–0.14 → 0.08 mm), light (to bright) orange-rose, ± translucent, ± round, scattered to subgregarious; disc flat, margin thin, 0–15 µm protruding, smooth to very finely crenulate; broadly sessile or with a short hidden stipe ~0.05 × 0.12 mm, superficial; dry bright orange(-rose). **Asci** *47–58(–63) × 4–5 µm {3}, †35–50(–56) × 3.5–4.5(–5) µm {4}, 8-spored, spores *2–3-seriate, (2–)3–5(–6) lower spores inverted {5} (sometimes mixed), pars sporifera *(21–)23–28(–35) µm long; **apex** (†) strongly truncate (not or slightly indented, laterally sometimes slightly inflated); **base** with medium to very long, slender, flexuous stalk, T-, L- or h-shaped. **Ascospores** *(6–)7–9(–10) × 1.8–2.2((–2.5)) µm {6}, †(5–)6–8(–9) × 1.8–2(–2.4) µm {2}, ellipsoid- to fusoid-clavate, apex obtuse (rarely rounded or subacute), base medium to strongly attenuated in an often tail-like base or sometimes short tail, mostly slightly (to medium) curved especially near base; **SBs** *(1.5–)1.7–2(–2.3) × (0.7–)0.8–1(–1.2) µm {5}, tear- to pear-shaped or ampulliform, with a very short filum. **Paraphyses** apically (slightly to) medium to (very) strongly capitate(-clavate), terminal cells *(12–)17–23(–29) × (2.2–)2.8–4.2(–4.8) µm {4}, lower cells *(5–)7–11(–15) × 1.5–2.5(–3) µm {4}; never branched at upper septum. **Medullary excipulum** hyaline to very pale rose, 30–50(–70) µm thick, of medium dense textura intricata with many inflated cells, indistinctly to sharply delimited from ectal excipulum by a t. porrecta at flanks. **Ectal excipulum** subhyaline to very pale rose-orange, of (†) thin-walled (externally slightly gelatinized), (indistinctly) vertically oriented t. globulosa-angularis-prismatica from base to mid flanks or margin, (20–)30–50 µm thick near base, cells *(7–)9–20(–25) × (5–)7–12(–16) µm {4}; 20–40 µm thick at lower flanks, 15–25 µm near margin, of t. prismatica(-globulosa) oriented at 70–

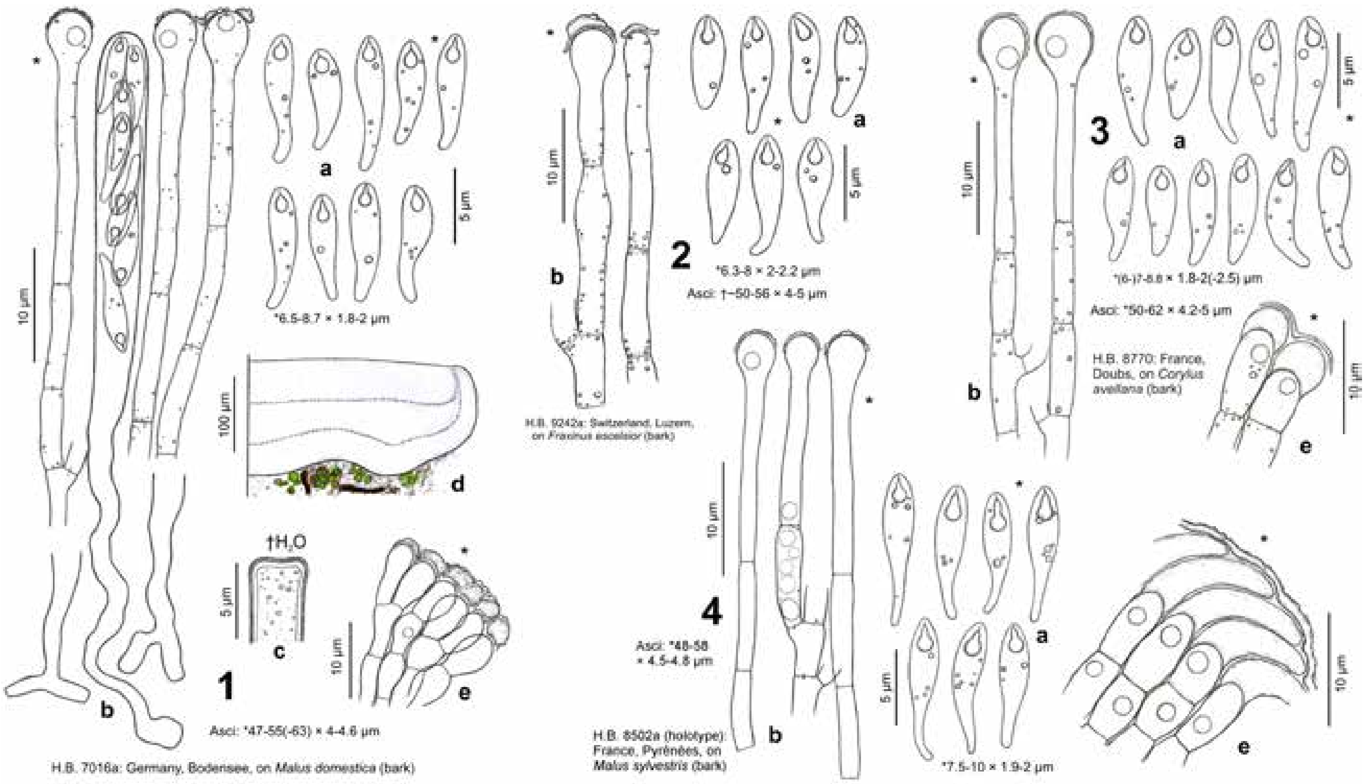


Plate 397. **1–4**: *Orbilia mali*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. apothecium in median section; **e**. id., marginal ectal excipulum with or without glassy processes.

90°, marginal cortical cells *5–10 × 3–5 µm {4}, **glassy processes** absent {3} or present, 2–6 × 3–4(–5) {4} or 8–14 × 2.5–3.3 µm {T}, medium to high-refractive, not or indistinctly stratified, outwards curved {T}. **Anchoring hyphae** sparse to abundant, *1.7–3.5(–4.5) µm wide, walls 0.2 µm thick {3}, or *3–6(–7) µm wide, walls 0.2–0.5 µm thick {*Radula*}, with a gel sheath, forming a loose t. intricata. **LBs** in lower part of hymenium and in excipulum towards margin with yellow-orange carotenoids {2}. **SCBs** globose, in paraphysis apices 1–1.8 µm diam., in marginal cells of ectal excipulum 1.3–2 µm diam., crystalloid SCBs absent {4}. **Exudate** over paraphyses 0.2–1(–2) µm thick, granular to cloddy, firmly attached; over margin and flanks 0.3–1 or 2–5 µm thick, cloddy to continuous, hyaline. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {2}). **Conidiophores** not seen. **Conidia** unbranched, slightly (to medium) curved, *50–69 × 3–3.5 µm, †41 × 3.5 µm, 7–8-septate {2}.

Habitat: collected 0.5–1.5 m above the ground, corticated, ~20 cm thick living trunks or 5–20 mm thick, still-attached, dead branches of *Corylus avellana* {1}, *Fraxinus excelsior* {1}, *Malus domestica* {3}, *M. sylvestris* {1}, *Punica granatum* {1}, *Salix* sp. {1}, on outer surface of bark {7}, on periderm {3} or bast {6} (either in cracks of periderm or on inner surface of detaching bark), on black mould of *Helicoma muelleri* (anamorph of *Thaxteriella pezizula*) {T}, slightly to medium decayed, slightly to strongly greyed, with a few to many green algae; on partly bleached leaves of *Radula* {1}. **Associated**: *Arthonia cinnabarina* {1}, *Cosmospora* sp. {1}, *Graphis scripta* {1}, *Hyalorbilia orbiliicola* (parasitic on *O. mali*) {1}, *Karstenia idaei* {1}, *Metzgeria* sp. {1}, *Mollisia ligni* {1}, *Orbilia aristata* {2}, *O. aurantiorubra* {1}, *O. clavuliformis* {1}, *O. eucalypti* {1}, *O. ?flagellispora* {1}, *O. gambelii* {1}, *O. subaristata* {1}, *O. xanthoguttulata* {1}, *Orthotrichum* sp. {1}, *Radula complanata* {1}, *Thaxteriella pezizula* {1}, *Tympanis alnea* {1}, *Unguiculariopsis* sp. {1}, indet. lichen and pleurocarpous moss. **Desiccation tolerance**: some mature asci and paraphyses still viable after 8 days, a single spore after almost 6 months. **Altitude**: 210–540 m a.s.l. **Geology**: Middle & Upper Jurassic limestone, Cretaceous marl-, sand- & limestone, Tertiary molasse & flysch, Pleistocene till & sand. **Phenology**: I–II, V, IX–X (probably throughout the year, long-lived).

Taxonomic remarks. *Orbilia mali* shows a certain similarity to *O. brachychitonis* and *O. aradi*, from which it differs in more fusoid-clavate ascospores and never spathulate paraphyses, *O. aradi* also differs in the yellow apothecial colour and occurrence on *Fagus* bark, also in shorter, more globose SBs and much less inflated paraphyses. In gross morphology *O. mali* also resembles members of series *Commatoideae*, e. g., *O. comma*, from which it differs in much less curved, scarcely helicoid spores, also in the living excipular cells lacking crystalloid SCBs, and in the predominant presence of glassy processes. *O. caulicola* and *O. cookei* differ in more straight spores without a tail, shorter SBs due to a shorter and less distinct attachment, and in the consistent absence of glassy processes, *O. caulicola* also in less inflated paraphyses. For the similar *O. pisciformis* see p. 808. *O. caudata* (series *Piliferae*) differs from *O. mali* in wider spores with much more broadly attached SBs.

Variation. Although four of the included collections grew on the same host genus (bark of *Malus*), they differ from each other in several respects. In the holotype (Pl. 398: 1) and the sample from Austria (IVV: 18.II.2017) the apothecia are larger than in the other collections. The holotype has medium long glassy processes at the margin (Pl. 397: 4e), which are absent or very short in the other collections studied, or the margin is covered by exudate or a hyphal layer (Pl. 397: 1, IVV: H.B. 8770, 9242a, 1.V.2016 etc.). The spores in the holotype are slightly longer, with more distinct tails and somewhat longer, more pear-shaped SBs compared to all the remaining samples. Nevertheless, the collections on *Fraxinus*, *Salix*, and *Radula* (on *Corylus*) fit well some of those on *Malus*.

Anamorph. Only a few conidia of the presumed vermispora-like anamorph were seen in the two *Malus* collections (Pl. 398: 1j, IVV: H.B. 7016a) resembling those of *O. comma*. In both collections a few similar but larger conidia with many more

Plate 398. **1–6**: *Orbilia mali*. – **1a**. clearing in mixed *Acer-Fraxinus* forest with *Malus sylvestris*; **1d–e**. fresh apothecia; **1b–c**, **2a–d**, **3a–d**, **5a–b**, **6a**. rehydrated apothecia; **1f**. apothecium in median section; **1h**, **2e**, **5c**. id., marginal region; **1g**. id., basal excipulum; **1i**, **6b**. ascospores, in **1i** attached to air bubble; **1j**, **4**, **5d**. 3 types of conidia from substrate. – Living state, except for **4** (in H_2O). – **1a**: phot. J. Fournier, **3d**: phot. G. Moyne, **5** & **6**: phot. B. Perić. — **1a–k**. H.B. 8502a (holotype): France, Pyrénées, on *Malus*; **2a–e**. H.B. 9242a: Switzerland, Luzern, on *Fraxinus*; **3a–d**. H.B. 8770: France, Doubs, on *Radula* (on *Corylus*); **4**. H.B. 7016a: Germany, Bodensee, on *Malus*; **5a–d**. B.P. Dgf/C7D-01-05-16b: Montenegro, Podgorica, on *Punica*; **6a–b**. ibid.

septa were found (*/†62–92 × 6–7 µm, with 13–17 septa, Pl. 398: 4, IVV: H.B. 8502a), which might as well represent the anamorph of *O. mali*. In the sample on *Punica* similar but much shorter 3-septate conidia occurred on the natural substrate (*20–27 × 3 µm, Pl. 398: 5d).

Phylogeny. Sequences were gained from apothecia of the holotype (ITS) and the sample from Austria (ITS+LSU D1–D2) (both on *Malus* and without S1506 intron). The ITS distance is 1.1 % (6 nt and 1 gap) between them, and 7 % to *O. aradi*, 10 % to *O. brachychitonis*, 13.5–14 % to *O. caulicola* and 14.5–15 % to *O. comma*. The lowest LSU distance is 1.8 % (11 nt) to *O. aradi*. In our analyses of ITS+LSU or LSU (Phyls 13, S16) *O. mali* clustered with *O. aradi* in a strongly supported clade.

Ecology. *O. mali* was collected on ± decaying bark of living or dead xeric trunks or branches of different angiosperm trees, also on ± living leaves of a liverwort (*Radula*). Although four times recorded on *Malus*, the other collections disprove a strict host specificity. Most of the apothecia of the *Radula* collection (on *Corylus*) grew on the liverwort and only a few on bark. The eight known collections are from cold-temperate, subatlantic to subcontinental central Europe (Bodensee, Bayerischer Wald, Luzern, Côte d'Or, Doubs), also from atlantic (Pyrénées) and submediterranean southern Europe (Dinaric Alps). The vegetation includes a cold-temperate humid orchards with apple trees (Germany), a warm-temperate humid deciduous forest with *Fraxinus*, *Corylus*, *Acer campestre*, *Prunus avium*, *Malus sylvestris* etc. (Pyrénées), and a mesosubmediterranean (semi)humid orchard with *Punica granatum* and *Vitis vinifera* (Dinaric Alps).

Specimens included. **GERMANY**: **Baden-Württemberg**, Bodensee, 6.5 km NW of Überlingen, NW of Sipplingen, 430 m, trunk of *Malus domestica*, on bark, 1.IX.2001, H.O. Baral (H.B. 7016a, anam. substr.). – **Bayern**, **Oberbayern**, 17 km NE of Traunstein, 2 km NNW of Tittmoning, Schlichten, 407 m, branch of *M. domestica*, on bark, 23.II.2020, P. Karasch (T.R.L., doc. vid.). — **SWITZERLAND**: **Luzern**, 24 km NNW of Luzern, 1.2 km E of Aesch, Gitzitobel, 540 m, branch of *Fraxinus excelsior*, on bark, 9.I.2010, U. Graf (H.B. 9242a). — **AUSTRIA**: **Steiermark**, 5.5 km NW of Feldbach, SW of Edelsbach, 315 m, twig of *Malus domestica*, on bark, 18.II.2017, A. Gallé, vid. G. Friebes (G.F. 20170001, doc. vid.; sq.: MK473412). — **FRANCE**: **Bourgogne**, **Côte-d'Or**, 2.3 km NW of Selongey, 1 km SE of Foncegrive, Ruisseau de la Venelle, 310 m, branch of *Salix*, on bark, 30.X.2009, J.P. Priou (J.P.P 29209, H.B. 9267 ø). – **Franche-Comté**, **Doubs**, 24 km SE of Besançon, 1.2 km SW of Châteauvieux-les-Fossés, Vallon de Vergetolle, 430 m, on trunk of *Corylus avellana*, on bark and mainly on leaves and stems of *Radula complanata*, 12.II.2008, G. Moyne (J.P.P 28027 ø, H.B. 8770). – **Midi-Pyrénées**, **Ariège**, 12 km ENE of St.-Girons, 2 km NE of Rimont, Ruisseau de Peyrau, 430 m, branch of *Malus sylvestris*, on bark, 23.V.2007, J. Fournier (ex H.B. 8502a, M-0276508, **holotype**, anam. substr.; sq.: KT222353). — **MONTENEGRO**: 15 km NNW of Podgorica, 1.9 km NE of Donje Selo, Glizica, 210 m, twig of *Punica granatum*, on bark, 1. & 8.V.2016, B. Perić (B.P. Dgf/C7D-01-05-16b, doc. vid.).

Map 67. Known distribution of *O. mali* in Europe.

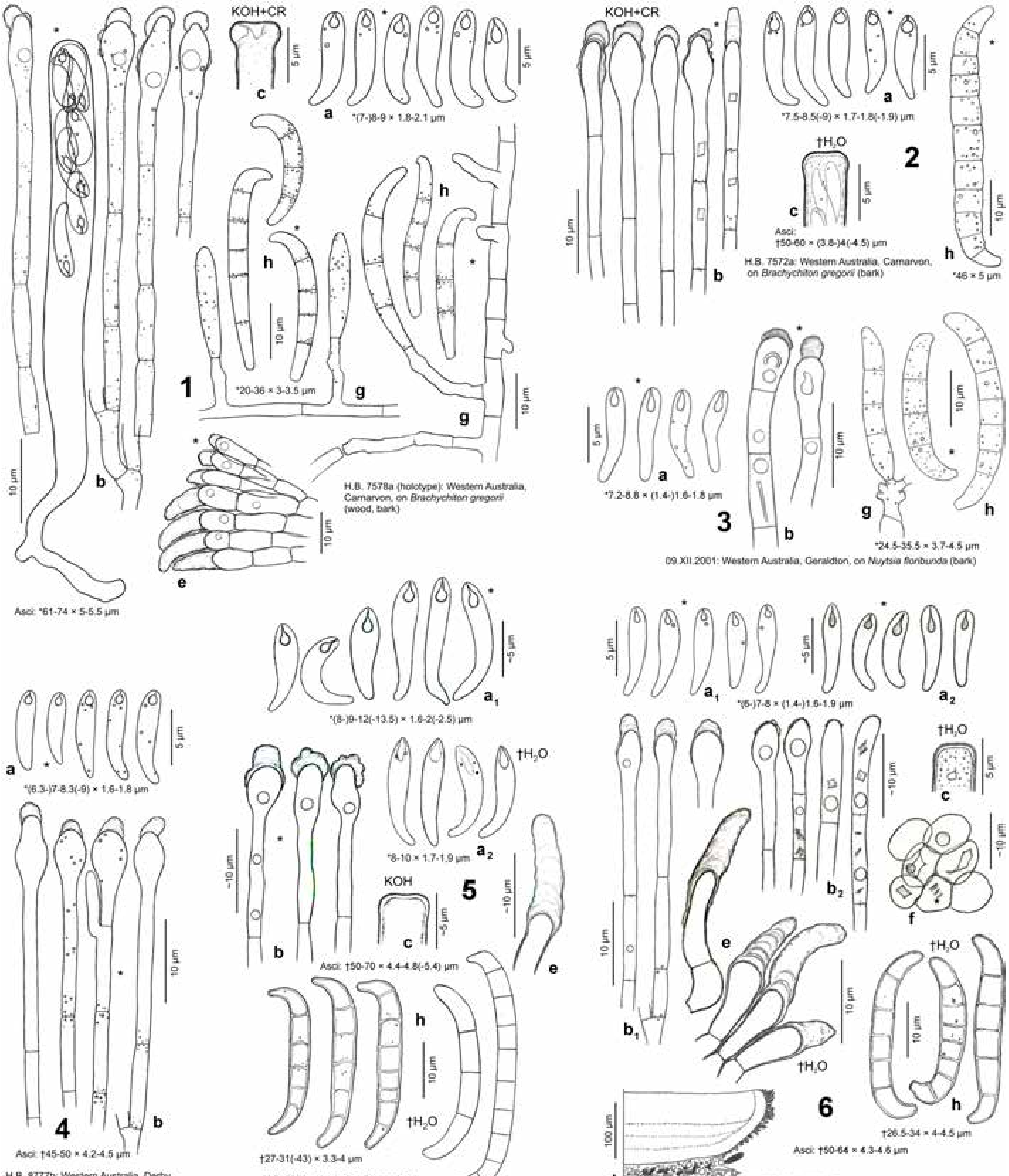
Orbilia brachychitonis Baral & G. Marson, **sp. nov.**, MB 813752 — Pls 399–400, Map 68

Etymology: after the host genus, *Brachychiton*.

Typification: Western Australia, Peron Peninsula, branches of *Brachychiton gregorii*, 8.XII.2001, G. Marson (ex H.B. 7578a, MEL 2389237, holotype, ex-type culture: CBS 117020; sq.: KT215257).

Latin diagnosis: *Similis* Orbiliae regali *sed ascosporae latiores, basi minus attenuatae. Habitat ad lignum vel corticem putridum ramorum siccorum* Adansoniae, Brachychitonis *et* Nuytsiae *in zona (sub)tropica semiarida vel subhumida Australiae occidentalis et orientalis et Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.4–1.2(–1.6) × 0.3–1 mm, 0.12–0.2(–0.35) mm high (receptacle 0.09–0.13 mm), pale to bright cream-isabelline to orange-red or orange-rose, slightly translucent, round to elliptical, sometimes irregularly lobate, scattered to subgregarious; disc slightly concave to flat, margin (0–)5–10 µm protruding (10–25 µm incl. hairs), whitish fimbriate or crenulate by forming short teeth; broadly sessile, sometimes with obconical or small abrupt peg-like stipe 0.05–0.06 × 0.04–0.08 mm, superficial to slightly erumpent, partly completely immersed in cracks; dry light to deep orange-ochraceous or brick-red, somewhat closed, often strongly lobate. **Asci** *61–74 × 5–5.5 µm {1}, †45–65(–70) × (3.5–)4–4.7(–5.4) µm {5}, 8-spored, spores *2–3-seriate, (2–)3–6(–7) lower spores inverted {4} (sometimes mixed), pars sporifera *19–35 µm long; **apex** (†) strongly truncate (slightly indented, laterally slightly to strongly inflated); **base** with short to long, thin, flexuous stalk, T- to L-, rarely h-shaped. **Ascospores** *(6–)7–8.5(–9) {5} or (8–)9–12(–13.5) {1} × ((1.4–))(1.6–)1.7–2(–2.2)((–2.5)) µm {6}, †7–9(–10) × 1.6–1.9 µm {4}, cylindric- (to fusoid-)clavate, apex rounded to obtuse, rarely subacute, base usually slightly to ± strongly attenuated (rarely with a tail-like end), here medium to strongly geniculate; **SBs** *(1.2–)1.4–2(–2.3) × (0.5–)0.7–1 µm {4}, broadly tear-shaped to globose, apically abruptly narrowed to a (very) short filum. **Paraphyses** apically narrowly to broadly spathulate to sublageniform, also ellipsoid, rarely clavate-capitate or uninflated, terminal cells *13–33 × (2–)2.5–3.5(–4.2) µm {3}, †(11–)14–28 {2} × (1.7–)2.5–4(–5) µm {4}, exceeding the dead asci by 5–8 µm, lower cells *6–14(–20) × 1.5–2.4 µm {2}, †6–14 × 1.4–2 µm {3}; rarely branched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline or pale orange above, 30–120 µm thick, of dense or loose textura globulosa-intricata, sometimes 2-layered: upper part ~20–30 µm thick, of dense t. intricata, (medium) sharply delimited mainly towards margin. **Ectal excipulum** hyaline to light rose, of thin-walled († slightly gelatinized), (irregularly) vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 30–180 µm thick near base, cells *(7–)9–20(–25) × 7–15(–20) µm {4}; 20–50 µm thick near margin, of light yellow-orange t. prismatica(-porrecta) oriented at a 30–80° angle to the surface, marginal cortical cells */†(4.5–)6–13 × (2.7–)3–4(–5) µm {3}; **glassy processes** (2–)5–20 × (2–)3–4(–5) µm {6}, stratified, refractive, hyaline to pale yellowish, straight or often ± outwards curved, somewhat coherent to form small, ± distinct teeth. **Anchoring hyphae** abundant, */†2–3(–3.5) µm wide, walls 0.2–0.3(–1) µm thick {4}, forming a loose, slightly gelatinized t. intricata ~30–40 µm thick. **SCBs** in paraphyses and ectal excipulum globose, 0.8–2.3 µm diam. {4}, partly also crystalloid SCBs in paraphyses and/or ectal excipulum {3}. **LBs** in paraphyses small, sparse, hyaline, in marginal ectal excipulum sometimes present {1}, minute, light orange (carotenoids). **Exudate** over paraphyses (0.3–)0.7–2.3(–3)((–4)) µm thick, forming glassy, hyaline to pale yellowish, firmly attached caps, CR–, CRB turquoise then deep violet; over margin and flanks replaced by glassy processes (CRB–). — **ANAMORPH**: vermispora-like (from ascospore isolate {1} and natural substrate {4}). **Conidiophores** *9–25 × 2–2.5 µm, simple. **Conidiogenous cells** sympodial. **Conidia** phragmosporous, C- to canoe-shaped; from culture: *20–36 × 3–3.5 µm, 3–5-septate {1}, straight to slightly curved, at the upper end mostly strongly so; from substrate:



H.B. 7578a (holotype): Western Australia, Carnarvon, on *Brachychiton gregorii* (wood, bark)

H.B. 7572a: Western Australia, Carnarvon, on *Brachychiton gregorii* (bark)

09.XII.2001: Western Australia, Geraldton, on *Nuytsia floribunda* (bark)

H.B. 8777b: Western Australia. Derby, on *Adansonia gregorii* (wood)

H.B. 7276e: Australia, Queensland, on indet. climber (bark)

H.B. 5681b: USA, Texas, on *Baccharis salicifolia* (bark)

Plate 399. **1–6**: *Orbilia brachychitonis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum, cortical cells with glassy processes; **f**. crystalloid SCBs in cells of ectal excipulum; **g**. conidiophores; **h**. conidia (**1g–h** in culture, **2h**, **3h**, **5h**, **6h** from substrate).

*/†(24.5–)27–43(–46) × (3.3–)3.5–4.5(–5) µm, (3–)5–8(–10)-septate {4}, ± straight, with usually both ends medium to very strongly curved, with some small, rarely also large LBs in each cell.

Habitat: collected 2–3 m above the ground, corticated or decorticated, 7–20 mm thick branches of *Adansonia gregorii* {1}, *Baccharis salicifolia* {1}, *Brachychiton gregorii* {2}, *Nuytsia floribunda* {1}, indet. climber {1}, on 0.1–0.3 mm deep medium to strongly decayed bark {5} (periderm and bast) and wood {3}, sometimes in cross-clefts, slightly to strongly greyed, algae absent or sometimes present.

Associated: *Dacrymyces* sp. {1}, *Haematomma* sp. {1}, *Hyalorbilia ?erythrostigma* {1}, *Hysterobrevium smilacis* {1}, *Hysterographium fraxini* {1}, *Hysteropatella* sp. {1}, *H. ?prostii* {1}, *Orbilia acaciae*

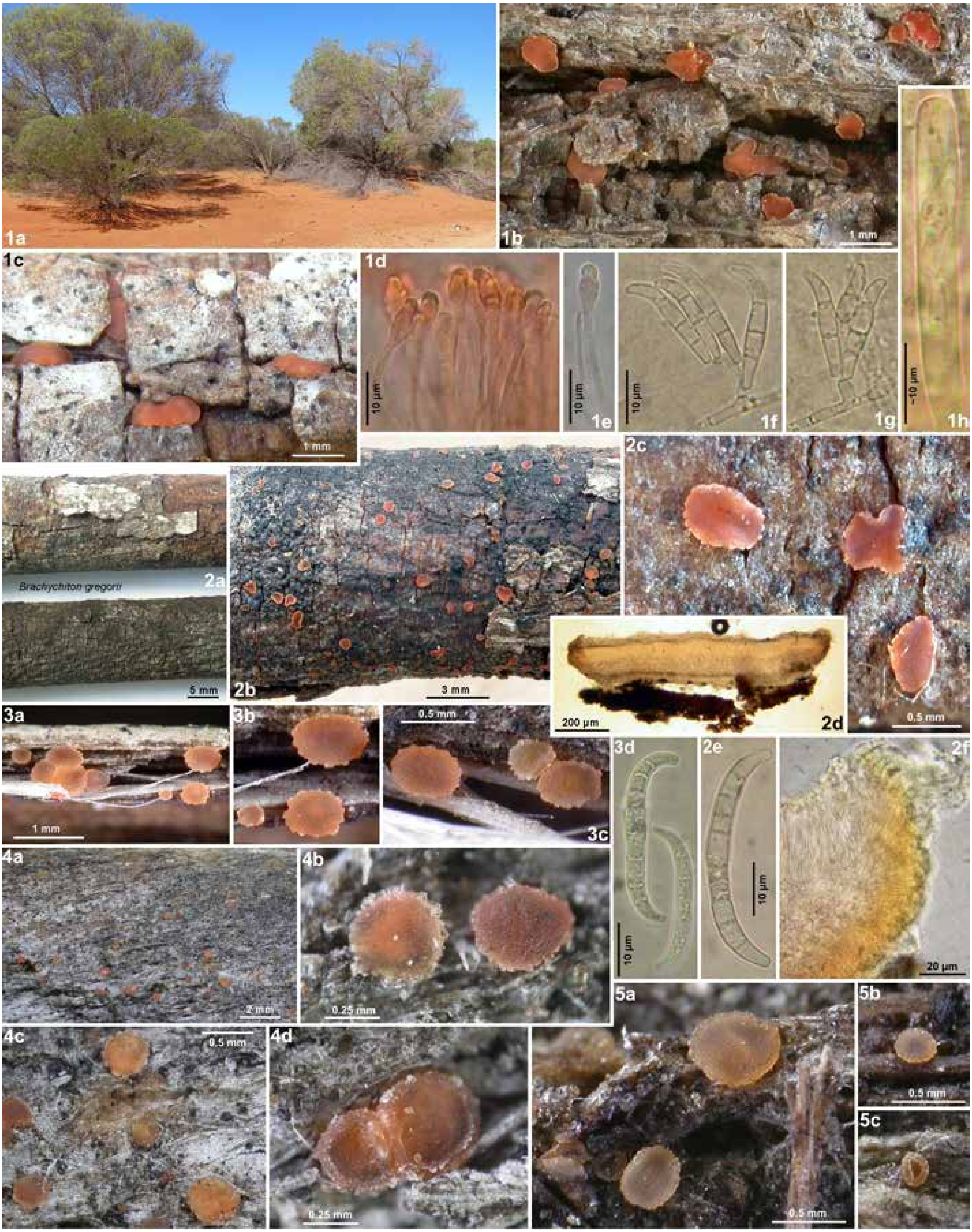


Plate 400. **1–5**: *Orbilia brachychitonis*. – **1a**. semiarid acacia shrubland; **2a**. corticated xeric branches; **1b–c**, **2b–c**, **3a–c**, **4a–d**, **5a–c**. rehydrated apothecia (**2b** with *Dacrymyces*); **2d**. apothecium in median section; **2f**. id., marginal region; **1d–e**. paraphyses; **1h** mature ascus; **1f–g**, **2e**, **3d**. conidiophores and conidia (**1f–g** from culture, **2e** and **3d** from substrate). – Living state: **1f–h**, **2e**; dead state: **1d–e** (KOH+CR), **2f** (in KOH), **3d** (in H_2O). — **1a–h**. H.B. 7578a (holotype): Western Australia, Carnarvon, on *Brachychiton*; **2a–f**. H.B. 7572a: ibid., on *Brachychiton*; **3a–d**. H.B. 7276e: Australia, Queensland, on indet. climber; **4a–d** H.B. 8777b: Western Australia, Derby, on *Adansonia*; **5a–c**. H.B. 5681b: USA, Texas, on *Baccharis*.

{1}, *O. carminorosea* {1}, *O. ?eucalypti* {1}, *O. euphorbiae* {1}, *O. gregorii* {1}, *O. mammifera* {1}, *O. ?multigambelii* {1}, *O. neocomma* {1}, *O. ?pleiogambelii* {1}, *O. scandens* {1}, *O. subcryptogena* {1}, *Patellaria ?andina* {1}, various crustose & foliose lichens. **Desiccation tolerance**: fully viable for 34 months, conidia still alive after 4 years. **Altitude**: 12–278 m a.s.l. **Geology**: Australia: Cenozoic regolith (red-brown gravel), granite, granitic gneiss; USA: Tertiary-Quaternary clay & mud. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia brachychitonis* resembles European *O. aradi* and American *O. regalis*, from which it differs in slightly wider ascospores being usually less attenuated at the base, from *O. aradi* also in apically inflated paraphyses, larger SBs, and in an orange-rose apothecial colour. *O. kingsiana* resembles *O. brachychitonis* in the spores and mainly deviates in the more clavate paraphyses, absence of glassy processes, narrower spores, and mostly pinkish apothecia. *O. euphorbiae* mainly differs in narrower spores and SBs.

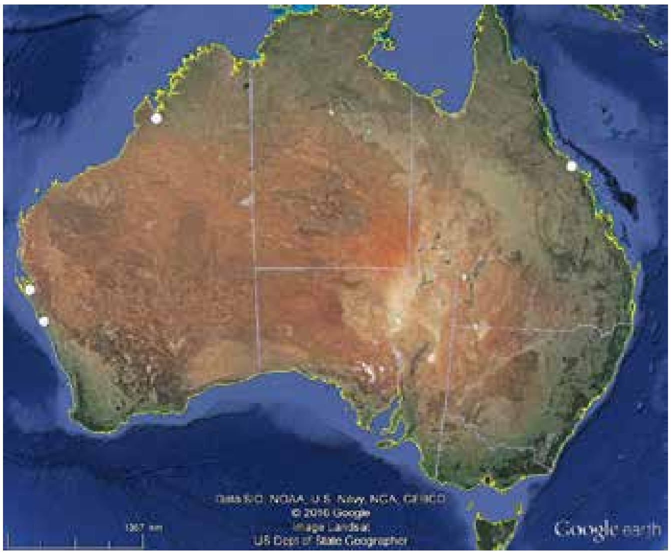
Variation. The holotype (on *Brachychiton*) and the specimen from Queensland (on indet. climber) differ from the remaining paratypes (including another sample on *Brachychiton* close to the type locality) in slightly wider spores, the latter also in longer, sometimes strongly curved (sickle-shaped), apically more subacute spores (especially in the dead state). Inconspicuous crystalloid SCBs were observed in the few living paraphyses in the other sample on *Brachychiton* and more distinct ones in those on *Nuytsia* and *Baccharis*, but none were seen in the holotype and in the samples on *Adansonia* and indet. climber. The North American collection on *Baccharis* differs in comparatively small SBs (*1.2–1.5 × 0.5 µm), but that on *Adansonia* has also smaller SBs than the remaining specimens. Yet, a sketch from a different apothecium without exact scale (Pl. 399: $6a_2$) questions this difference. Only in this apothecium crystalloid SCBs were seen in paraphyses as well as excipulum. The presence of exudate caps on the paraphyses was inconsistent especially in this sample.

Anamorph. The conidia obtained in pure culture of the holotype (Pls 399: 1; 400: 1f–g) are slightly smaller, especially narrower and with fewer septa compared to those found on the natural substrate in four further collections (Pls 399: 2h, 3h, 5h, 6h; 400: 2e, 3d).

Phylogeny. A sequence was gained from a culture of *O. brachychitonis* (H.B. 7578a, western Australia) which comprises SSU (with S1506 intron), ITS, and LSU. The species shows a minimum ITS distance of 8 % to *O. aradi* and 10 % to *O. mali*. In the LSU D1–D2 the minimum distance is 2.5 % to *O. aradi* and 2.8 % to *O. denticulata*, and in the intron 18 % to *O. euphorbiae* (H.B. 9869). *O. brachychitonis* clustered strongly supported with *O.* cf. *caudata* (Phyls 13, S16).

Ecology. *O. brachychitonis* was collected on ± rotten bark and wood of xeric branches of *Nuytsia* and *Brachychiton* in subtropical semiarid acacia shrublands in (south)western Australia, and of *Adansonia* and unidentified climber in tropical wet and dry eucalypt woodlands (savannah) in subhumid northwestern (edge of Kimberley Mts.) and tropical northeastern Australia (east of Great Dividing Range). The North-American collection was on bark of *Baccharis* in a subtropical subhumid woodland at a dry rivulet in the Coastal Prairies at the southern end of the Great Plains.

Specimens included. **AUSTRALIA**: **Western Australia**, Dampierland, SW-border of Leopold Ranges (Kimberleys), 47 km SSW of Derby, 12 km WNW of Willare Bridge over Fitzroy River, 20 m, branch of *Adansonia gregorii*, on wood, 1.XI.2007, G. Marson (H.B. 8777b). – Carnarvon, 165 km SSE of Carnarvon, Peron Peninsula, 24 km SE of Shell Beach, 41 m, branches of *Brachychiton gregorii*, on bark & wood, 8.XII.2001, G. Marson (ex H.B. 7578a, MEL 2389237, **holotype**, CBS 117020, anam. cult.; sq.: KT215257). – 18 km SE of Shell Beach, 48 m, branches of *B. gregorii*, on bark, 8.XII.2001, G. Marson (H.B. 7572a, anam. substr.). – Geraldton Sandplains, 60 km N of Geraldton, 12 km N of Northampton, 278 m, branch of *Nuytsia floribunda*, on bark, 9.XII.2001, G. Marson (ø, anam. substr.). – **Queensland**, Brigalow Belt North, 49 km SE of Ayr, 4 km ESE of Gumlu, 12 m, branches of indet. climber, on bark & wood, 19.X.1998, G. Marson (H.B. 7276e, anam. substr.). — **USA**: **Texas**, Coastal Prairies, 100 km WNW of Houston, 13 km WNW of Hempstead, W of bridge over Brazos river, 70 m, branch of *Baccharis salicifolia*, on bark, 19.VI.1996, G. Marson (H.B. 5681b, anam. substr.).



Map 68. Known distribution of *O. brachychitonis* in Australia.

Orbilia euphorbiae (Henn.) Svrček, Česká Mykol. 28: 134 (1974) — Pls 401–403, Map 69

≡ *Humaria euphorbiae* Henn., Bot. Jahrb. Syst., Pflanzengesch. Pflanzengeogr. 14: 369 (1891)

Etymology: named after the substrate of the type, *Euphorbia polyacantha*.
Typification: Eritrea, Keren, branch of *Euphorbia polyacantha* (as *E. thii*), 4.IV.1891, G. Schweinfurth (herb. Sydow, S-F41427, lectotype, designated here, MBT202374).
Misapplied name: Korf (1992, 510 p.p.: CUP MM 2694), as *O. occulta*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1.5 {4} or 1–3 {2} mm diam., 0.13–0.45 mm high (receptacle 0.16–0.2 → 0.1 mm), light to bright yellow-orange-ochraceous (Hennings: orange to miniate [saturn-red]), not or slightly translucent, ± round to elliptical, scattered to gregarious in smaller or larger groups; disc young slightly to strongly concave, finally flat, margin often rather thick, 0–30 µm protruding (incl. glassy processes), finely warted to often crenulate-denticulate, at flanks partly forming up to 30–50 × 50–70 µm large teeth or squamules; broadly sessile or with a broad stipe-like base, superficial or slightly immersed; dry bright orange-ochre or orange-red, strongly lobate or often completely closed (hysterioid). **Asci** *(44–)47–60(–66) × 3.9–4.7(–5) µm {4}, †(36–)40–55(–60) × (3–)3.4–4.2(–4.5) {4}, 8-spored, spores *2–4-seriate, (2–)3–5 lower spores inverted {3} (often mixed), pars sporifera *(13–)18–22(–34) µm long; **apex** (†) slightly to strongly truncate (not or hardly indented or laterally widened); **base** with a short to very long, ± thin, flexuous stalk, T-, L-, or Y-shaped, exceptionally H-shaped. **Ascospores** *(6–)7–9(–10.5) × (1.2–)1.3–1.5(–1.6) µm {6}, †(5.5–)7–9(–10.5) × 1.2–1.5(–1.8) µm {3}, narrowly cylindric- to fusoid-clavate, apex rounded to obtuse, base slightly to mostly medium attenuated (sometimes tail-like), slightly to usually medium curved or geniculate (often only in lower third of spore); **SBs** *0.8–1.3 × 0.3–0.5(–0.6) µm {4}, subglobose to tear-shaped, apically abruptly narrowed to a very short filum. **Paraphyses** slightly to strongly spathulate or lageniform-mammiform, terminal cells *17–33 × (2.5–)3–

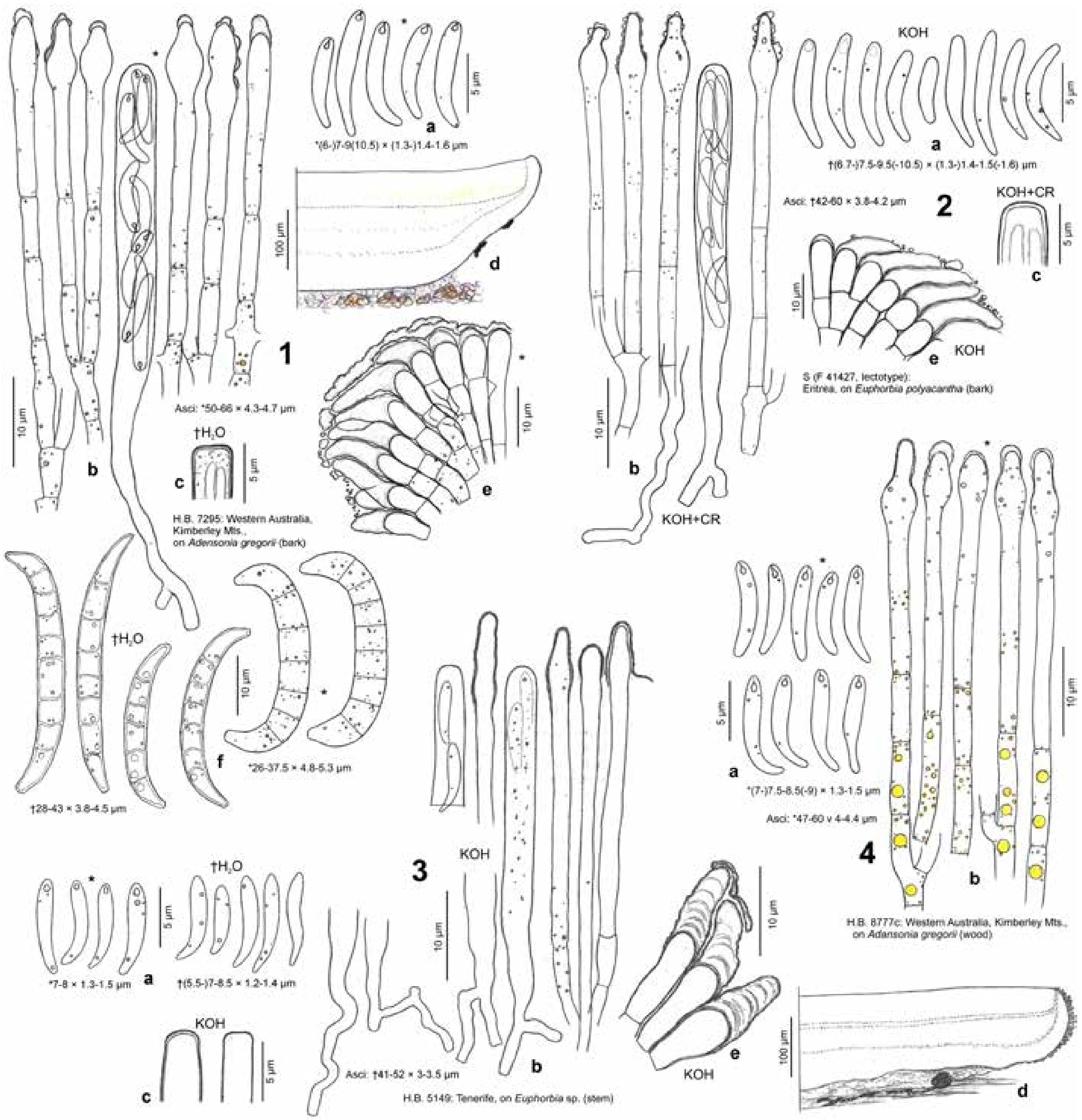


Plate 401. **1–4**: *Orbilia euphorbiae*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum, cortical cells with glassy processes; **f**. conidia from substrate.

4.2 µm {3}, †(15–)20–29(–35) × (1.8–)2.3–3.8 µm {2}, exceeding the dead asci by 4–8 µm, lower cells *7–12(–14) × 1.8–2.3 µm {2}, †6–12 × 1.5–2.2 µm {2}; never branched at upper septum. **Medullary excipulum** 35–250 µm thick in centre, of dense textura intricata with many inflated cells, sometimes with a lower part of medium loose t. intricata of wide hyphae, indistinctly or at flanks sometimes sharply delimited by a 10–20 µm thick layer of t. porrecta. **Ectal excipulum** hyaline at base, very pale to light yellow-orange at flanks and margin, of thin-walled († slightly gelatinized), vertically oriented t. globulosa-angularis-prismatica, 40–100(–150) µm thick near base, cells *(7–)10–18(–20) × 6–12(–15) µm {3}, †5–13 × 5–10 {2} or 10–24 × 8–14 µm {1}; 20–40 µm thick at flanks, of t. globulosa-angularis; 20–30(–40) µm thick near margin, of t. (globulosa-)prismatica(-porrecta) oriented at a (50–)70–90° angle to the surface, marginal cortical cells *6–8(–10) × (3–)3.5–4.5(–5.2) µm {1}, †6–12 × 4–6(–7) µm {T}; **glassy processes** 4–13(–18) × (2–)3–5(–6) µm {6}, at flanks partly up to 30–55 µm {T} but also very short, medium to high-refractive, slightly stratified or not, usually coherent to form teeth, curved downwards at margin (at flanks also upwards). **Anchoring hyphae** abundant, */†(1.7–)2–3.5(–4) µm wide {5}, walls 0.2–0.4 {2} or (0.2–)0.4–1(–1.3) µm thick {4}, forming a medium dense, slightly gelatinized, hyaline to yellowish t. intricata 20–40 µm thick. **SCBs** absent {3}; light to bright yellow-orange **LBs** (carotenoids) in lower half of paraphyses (here up to 1–1.5 µm diam.), also in medullary excipulum (partly only in upper half) and in marginal excipulum. **Exudate** over paraphyses 0.2–1(–2) µm thick, finely rough to granular-cloddy or cap-like, hyaline, firmly attached, covering the beaked tips in the upper 3–11 µm; over margin and flanks 0.2–1.5 µm thick, rough-cloddy, (very) pale yellowish. — **ANAMORPH**: vermispora-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** *3–20 × 1.7–2.8 µm {2}, ± moniliform,

Plate 402. **1–5**: *Orbilia euphorbiae*. – **4a**. semihumid Eucalypt open woodland (savannah) with large baobab (*Adansonia*); **1a**. bark surface of dead *Euphorbia*; **3f**. greyed wood of *Adansonia*, **4b**. xeric whitish bast of *Adansonia*; **1b–c**, **2a–b**, **3a**, **c–e**, **4b**, **5a–b**. rehydrated apothecia; **3d**, **e**. dry apothecia; **3g–h**. apothecia in median section; **3i**. id., marginal ectal excipulum with glassy processes; **3k**. id., basal ectal excipulum; **1d**. glassy processes in external view; **2c**, **3j**. paraphyses (**3j**: LBs containing yellow carotenoids); **2d**, **3i**, **5c**. ascospores. – Living state, except for **1d** (in KOH). — **1a–d**. S (F 41427, lectotype): Eritrea, on *Euphorbia*; **2a–d**. H.B. 9309: Ethiopia, on *Solanecio*; **3a–i**. H.B. 8777c: Western Australia, Kimberley Mts., Willare, on *Adansonia*; **4a–b**. H.B. 7295: ibid.; **5a–c**. G.M. 2007-11-01: ibid., Meda.

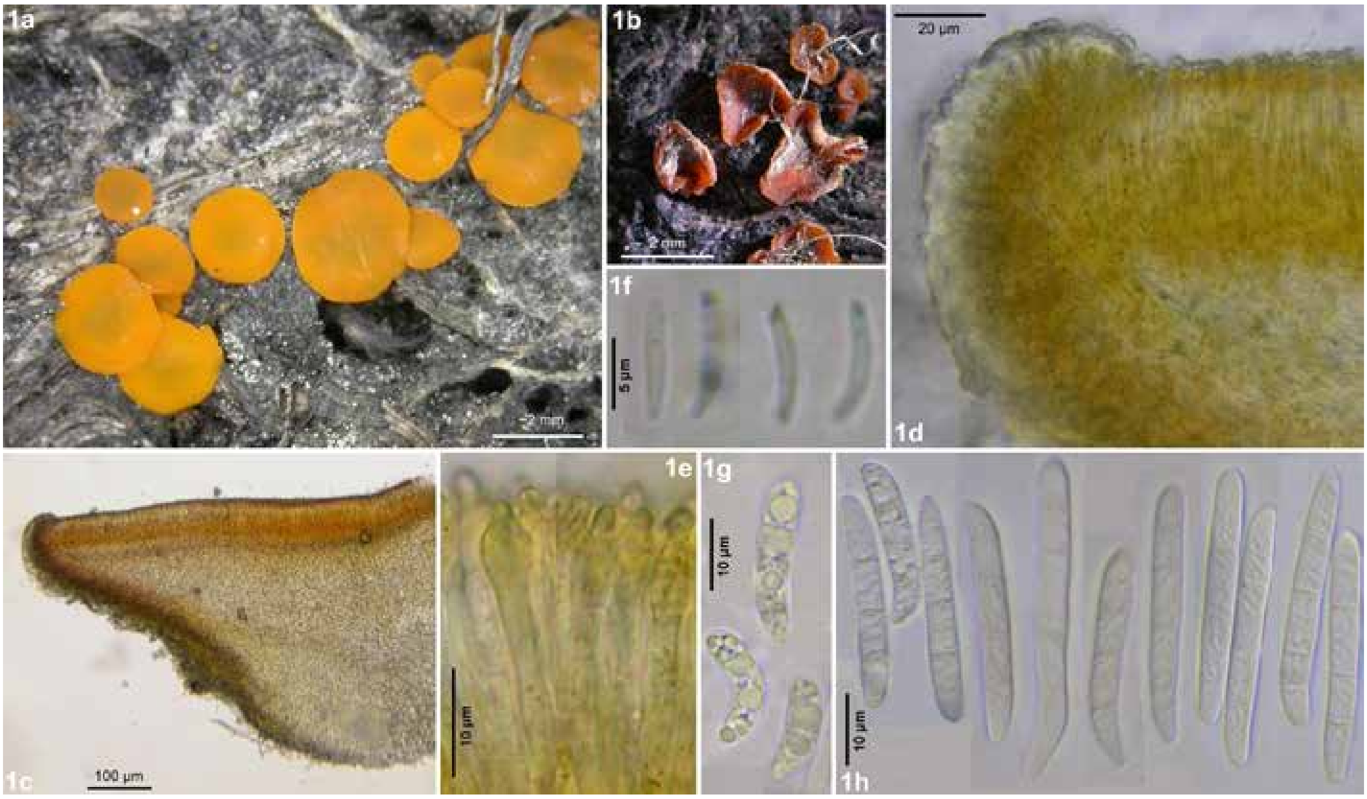


Plate 403. **1**: *Orbilia euphorbiae*. – **1a**. fresh apothecia; **1b**. dry apothecia; **1c**. apothecium in median section; **1d**. id., marginal ectal excipulum **1e**. paraphyses; 1f. ascospores; **1g–h**. conidia from culture (**1g**. on CMA:4, **1h**. on CMA). – **1a**: phot. M. Pélissier. – Living state. – **1a–h**. H.B. 9869: Comoros, on *Adansonia*.

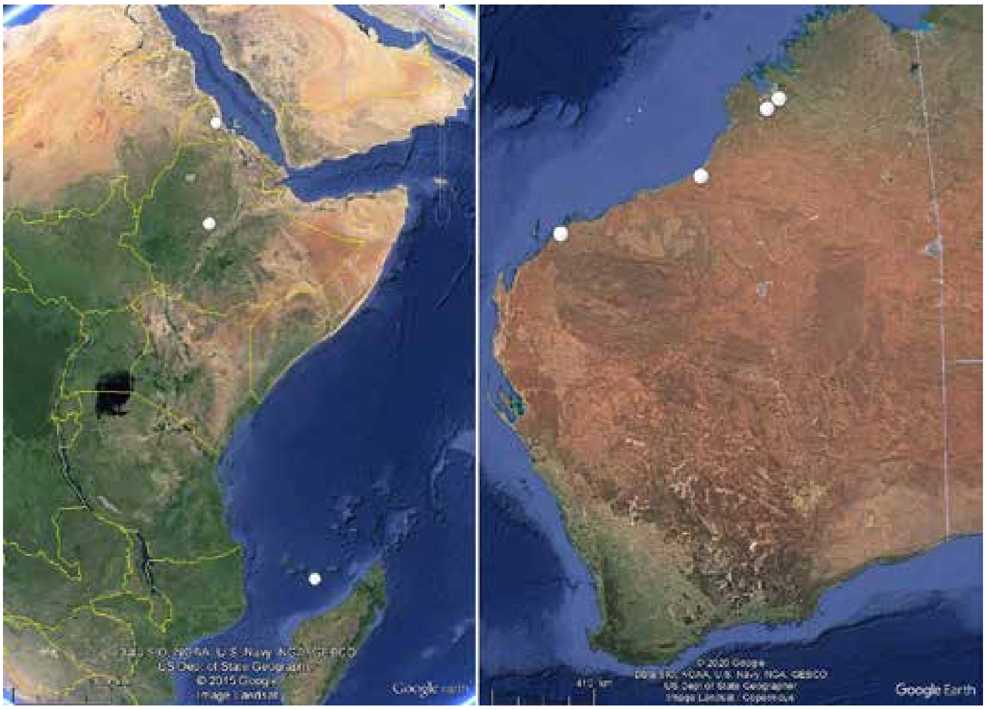
conidia formed terminally or on sparse lateral nodules. **Conidia** unbranched; on natural substrate C-shaped, slightly to often strongly curved at both ends, *26–37.5 × 4.8–5.3 µm, †28–43 × 3.8–4.5 µm, 5–8-septate {1}, with minute LBs at the septa; in pure culture on CMA:4 C-shaped, slightly to strongly curved, *13–23 × 4.2–5 µm, 1–3-septate, containing large LBs when 1-septate; after transfer to CMA:1 *(23–)31–36(–45) × (3.8–)4–4.6 µm, 3–4-septate, straight or slightly to medium curved at the ends only, containing a few minute LBs {1}.

Habitat: collected ± close to the ground or in 0.2–3 m above the ground, corticated, 8–37 mm thick branches of *Acacia aneura* {1}, *Adansonia digitata* {1}, *A. gregorii* {3}, *Euphorbia* sp. {1}, *E. polyacantha* {1}, *Ipomoea costata* {1}, on medium rotten bark (bast) {5} or wood {2}, on outer surface of bark along clefts and on periderm-free areas, or on inner surface of detached bark, 0.3–0.5 mm deep very decayed; herbaceous stem of *Solanecio gigas* {1}, on strongly decayed epidermis or epidermis-free areas; ± greyed, algae absent or very sparse. **Associated**: *Orbilia brachychitonis* {1}, *O. carminorosea* {1}, *O. commarosa* {1}, *O. ?livistonae* {1}, *O. ?menageshae* {1}, *O. ?multiserpens* {1}, *Patellaria ?andina* {1}. **Desiccation tolerance**: fully viable for at least 15 months, some ascospores still alive after more than 4.5 years, conidia after 15 months. **Altitude**: 12–46 m a.s.l. (Australia, Macaronesia, Comoros), 900–2520 m (northeastern Africa). **Geology**: mafic-basaltic volcanic rock and mainly Cenozoic regolith (red-brown gravel). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia euphorbiae* is characterized by spathulate to lageniform paraphyses, narrowly subcylindrical, comma-like ascospores with a small tear-shaped spore body, and comparatively large, ± bright yellow-orange apothecia with a typically denticulate margin due to glassy processes. The very similar *O. carnegieae* differs in longer ascospores and conidia, also in the terminal cells of paraphyses that are partly not longer than the lower cells, apically only sometimes lageniform, containing globose SCBs. Also *O. regalis* is very similar to *O. euphorbiae*. It is tentatively separated by slightly shorter spores with a consistently strongly attenuated and geniculate base, in combination with the occurrence in a temperate humid region. *O. brachychitonis* mainly differs in wider spores and SBs. *O. denticulata* closely matches *O. euphorbiae*, e. g., in macroscopy and in the wide, thick-walled anchoring hyphae, but differs in much wider spores with partly more broadly attached SBs. Species such as *O. puyae* and *O. aradi* differ in the predominant absence of lageniform paraphyses. A North American collection on *Cylindropuntia* mentioned under *O. carnegieae* resembles *O. euphorbiae*, but differs in basally not or only slightly tapered spores and in capitate or only slightly spathulate paraphyses that contain globose SCBs. *O. pseudeuphorbiae* (see Pls 919–920) strikingly resembles *O. euphorbiae* but differs in a number of more or less stable characteristics, including its presumed anamorph (see p. 1476). *O. succulenticola* (series *Aurantiorubrae*) occurs in the same habitat as *O. euphorbiae* but is sufficiently distinct (see Pls 445–446).

Variation. Three of the eight collections of *O. euphorbiae* examined in the present study were studied in the dead state only (Pl. 401: 2–3; IVV: H.B. 8726b), except that a few spores were still alive in one of them (Pl. 401: 3a left), and their conspecificity is somewhat uncertain. Based on a remarkable genetical distance between the two sequenced strains on *Adansonia* (see below), we must conclude that *O. euphorbiae* in the present circumscription is a collective species. However, the morphological differences between these two strains are comparatively low, and similar morphological variation was noted by us in many other species of *Orbilia*.

O. euphorbiae varies considerably in diameter and thickness of the apothecia, which are in the lectotype from Eritrea (on *Euphorbia*, Pls 401: 2; 402: 2) and in the sample from the Comoros (on *Adansonia*, Pl. 403) distinctly larger than in the other collections. Also the paraphyses vary in apical width and



Map 69. Known distribution of *O. euphorbiae* in eastern Africa and western Australia.

in length of the apical beak, partly even within a population. The exudate on the beaks varies from a continuous thin layer (Pl. 401: 3) to thick cloddy caps (Pl. 401: 1, 4). The glassy processes show some variability in length, resulting in a different strength of marginal crenulation. In the lectotype they are partly up to 30–55 µm long, though on the drawing and microphoto only 13–20 µm (Pls 401: 2e; 402: 1d). In the remaining records the processes attain a length of only ~(6–)9–13(–18) µm, and in some apothecia of a population they are even shorter (1–2 or 3–6 µm), resulting in an almost smooth margin (Pl. 402: 5b).

In the lectotype the paraphyses are distinctly lageniform and the SBs could sometimes be seen as a faint, rather large region in the ascospore apex, though their original size remains unclear. In another sample from northeastern Africa (Ethiopia, on *Solanecio*, Pl. 402: 2) the spores are smaller (*7–8.5 × 1.3–1.4 µm), and the SBs (*0.8–1 × 0.4–0.6 µm) and the mammiform paraphyses fit quite well, e. g., those populations from Australia. A collection on wood of *Ipomoea costata* (IVV: H.B. 8726b) deviates from the more typical collections in slightly wider asci (†4–4.5 µm) and spores (†1.5–1.8 µm). Since no vital characters (especially SBs) are known here, the identity of this specimen is uncertain, as it fits also the closely related *O. brachychitonis*.

Only in the specimen from Tenerife an H-shaped ascus base was sometimes seen (Pl. 401: 3b). This collection is thought to belong here rather than to *O. pseudeuphorbiae* (section *Arthrobotrys*) because of its narrow SBs and rehydrated light orange-ochre apothecia. However, the paraphyses are not distinctly lageniform or mammiform in this collection, and *O. pseudeuphorbiae*, which was recorded from various places of Tenerife, occurred also quite close (1 km or less) to the site of this sample at Montaña Roja.

Type studies. The examined syntype specimen in S (Pl. 401: 2, Pl. 402: 1) corresponds quite well to the protologue, except for the spores which Hennings (1891) described as subellipsoid, 3–5 × 2–2.5 µm. The apothecia, reported as 2–9 mm diam. by Hennings, were smaller in the present study (rehydrated 1.5–3 mm) as well as in Svrček's (1974) revision of another syntype (from G, 1–2 mm). Svrček found the asci 40–70 × 3.5–4.5 µm, the spores 9–11 × 1.5–1.8 µm, the paraphysis apices 2.5–4.5 µm wide (present study 1.8–2.6 µm, –3.3 µm incl. exudate), and the excipular cells up to 18 µm diam. (present study 7–13 × 5–9 µm near base). The pruinose exterior and the glassy processes are not mentioned by him. Since the syntype in B, which might have been the basis of Hennings' description, was destroyed during the Second World War, the examined specimen in S (S-F 41427, herb. Sydow) is designated here as **lectotype** of *O. euphorbiae* (Art. 9.11, Turland et al. 2018).

The collection data of the type of *O. euphorbiae* bear some uncertainties. In the region of Gheleb the altitude is around 1700 m, therefore, the statement 'ca. 900 m' in the protologue would point to a valley ENE of Gheleb. However, it could also be a lapsus for 1900 m, since Hennings (1891: 369) mentions another fungus (*Ustilago penniseti*) from near Gheleb at 1900m. The indicated substrate *Euphorbia thii* was newly described from eastern Sudan by the finder G. Schweinfurth, and is today regarded as a synonym of *E. polyacantha*. The collection date of *O. euphorbiae* is noted on the label as 4.V.1891, but in the protologue as 4.IV.1891. The latter must be correct: according to personal plant drawings, Schweinfurth was on the eastern slopes of this mountain range also on the 5th of April (http://www.bgbm.org/de/node/131), and Hennings (1891) stated in his preface that Schweinfurth was in Eritrea from January until April 1891.

Anamorph. In one of the Australian collections on *Adansonia* we observed curved phragmoconidia of the *Vermispora*-type on the substrate near apothecia (Pl. 401: 1f), characteristic of series *Regales*. In that from the Comoros (also on *Adansonia*) conidia developed in pure culture (Pl. 403: 1g–h). These eventually attained a similar size but were much less curved and with fewer septa (1h). The small 1-septate conidia with large LBs observed on CMA:4 are assumed to represent young, untypical conidia which are frequently formed in a young culture (1g).

Misapplication. A Macaronesian collection reported by Korf (1992) under the name *O. occulta* turned out to belong to *O. euphorbiae* (Pl. 401: 3).

Phylogeny. An ITS sequence was gained from apothecia of one of the specimens from Australia (H.B. 8777c, on *Adansonia*), and ITS+LSU from the pure culture from the Comoros (H.B. 9869, on *Adansonia*). In the ITS region a distance of 5% was noted between the two strains. In H.B. 8777c the S1506 intron is absent, whereas in H.B. 9869 it is present. For the time being, we have considered both samples as conspecific (see above).

O. euphorbiae clustered in our phylogenetic analyses of ITS+LSU or ITS with *O. denticulata* in a strongly (Phyls 13–14, S15), with a distance of 8.5–9.5/2.7% in the ITS/LSU D1–D2 (in comparison 13/3.3% to *O. aradi*). In the intron a distance of 18% to *O. brachychitonis* is observed. The morphologically similar *O. pseudeuphorbiae* falls in series *Neodactylella* of section *Arthrobotrys*, with a ~22% ITS distance to *O. euphorbiae*.

Ecology. Collections of *O. euphorbiae* on rotten branches of succulent *Euphorbia* species derive from a inframediterranean hyperarid xerophytic scrub (tabaibal dulce) in Tenerife (Macaronesia) and a subtropical arid steppe of a high plateau in Eritrea. The sample on herbaceous stems of *Solanecio* was from a warm-temperate humid (somewhat winter-dry), evergreen afromontane forest in the central plateau of the Ethiopian highlands. Collections on rotten bark and wood of xeric branches of *Acacia* and *Adansonia* were from a tropical humid (wet & dry) rainforest in the oceanic Comoros and from tropical (to subtropical), arid to semihumid acacia open shrublands (mulga), tussock grasslands, or eucalypt open woodlands (savannah, wet and dry) more or less close to the coastline in northwestern and western Australia south of the Kimberley Mountains adjacent to the Pilbara desert.

Specimens included. **AUSTRALIA**: **Western Australia**, Dampierland, 235 km SW of Broome, 6 km E of Sandfire Roadhouse, 12 m, branch of *Acacia aneura*, on bark, 3.XII.2001, G. Marson (H.B. 7302c). – SW-border of Leopold Ranges (Kimberleys), 47 km SSW of Derby, 12 km WNW of Willare Bridge over Fitzroy river, 20 m, branches of *Adansonia gregorii*, on bark, 30.XI.2001, G. Marson (H.B. 7295, anam. substr.). – ibid., branches of *A. gregorii*, on wood, 1.XI.2007, G. Marson (H.B. 8777c; sq.: KT222351). – S of Kimberley Mts., 35 km ESE of Derby, 5 km W of Meda, 38 m, branches of *A. gregorii*, on bark, 1.XI.2007, G. Marson (G.M. 2007-11-01). – Pilbara, 58 km WSW of Karratha, 37 km NE of Fortescue River Roadhouse, 46 m, branch of *Ipomoea costata*, on wood, 4.XII.2001, G. Marson (H.B. 8726b). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Granadilla de Abona, ~2 km SW of El Médano, Montaña Roja, ~30 m, branch of *Euphorbia*, 15.I.1990, R.P. Korf & J.T. Palmer (CUP-MM-000269, as *O. occulta*, H.B. 5149 ø). — **ERITREA**: **Anseba**, Great Rift Valley, 43 km ENE of Keren, ~8 km ENE of Gheleb, high plateau of Haigett, ~900 m, branch of *Euphorbia polyacantha* (as *E. thii*), on bark, 4.IV.1891, G. Schweinfurth (herb. Sydow, S-F41427, **lectotype**, H.B. 7688 ø). — **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, southern part of Menagesha Suba State Forest, ~2520 m, stem of *Solanecio gigas*, 26.III.2010, U. Lindemann (H.B. 9309a, U.L. 0310-23). — **COMOROS**: **Mayotte**, 1.5 km SW of Bandrele, North Bambo Bay, 14 m, on bark of *Adansonia digitata*, 2.II.2014, M. Pélissier (J.P.P. 14030, H.B. 9869, anam. cult., sq.: KT380105).

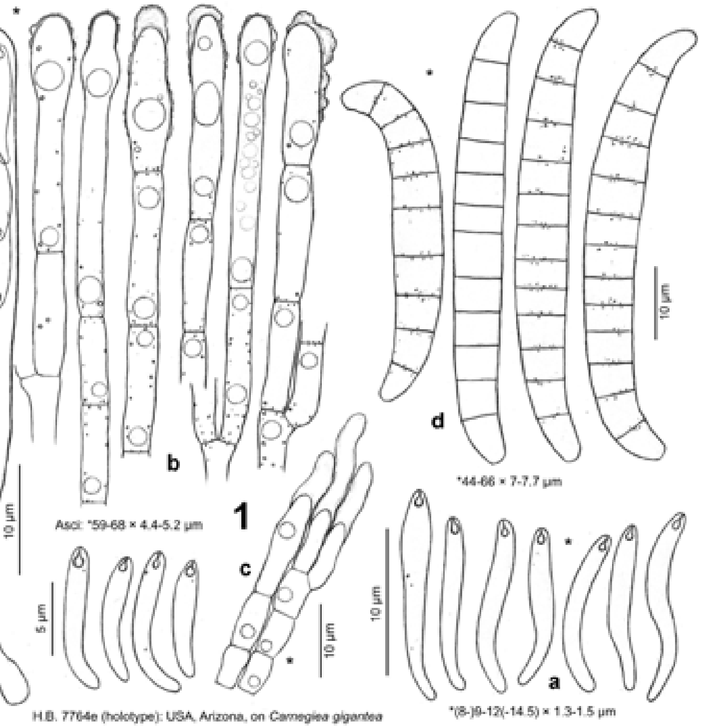


Plate 404. **1**: *Orbilia carnegieae*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. marginal ectal excipulum in median section, with glassy processes; **d**. conidia from substrate.

Orbilia carnegieae Baral & G. Marson, **sp. nov.**, MB 813753 — Pls 404–405

Etymology: named after the substrate of the type, *Carnegiea gigantea* (saguaro cactus).

Typification: USA, Arizona, Lukeville, skeleton of *Carnegiea gigantea*, 28.V.2003, G. Marson (ex H.B. 7764e, M-0276449, holotype).

Latin diagnosis: *Similis* Orbiliae euphorbiae *sed ascosporae longiores*, *basi minus attenuatae*, *paraphyses ad apicem plerumque non lageniformes. Habitat ad residuos trunci putridi sicci* Carnegieae giganteae *in zona subtropica semiarida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1.8 mm diam., 0.25–0.3 mm high (receptacle 0.1–0.12 mm), light orange, scarcely translucent, round, subgregarious in small groups; disc slightly concave to flat, margin with distinct whitish teeth 50–70 × 40 µm which project beyond disc; sessile on a very broad obconical stipe, ± superficial. **Asci** *59–68 × 4.4–5.2 µm, 8-spored (mostly only 5–7 spores developed), spores *2–3-seriate, 3–5 lower spores inverted (often mixed), pars sporifera *21–30 µm long; **apex** (†) strongly truncate (not indented, laterally not widened); **base** with medium long, thick, ± flexuous stalk, L-shaped. **Ascospores** *(8–)9–12(–14.5) × 1.3–1.5((–2)) µm, narrowly subcylindric(-clavate) to sometimes fusoid-clavate, apex rounded to obtuse, base not or usually slightly (to medium) attenuated, slightly to mostly medium (to strongly) curved, especially near base, often ± distinctly helicoid; **SBs** *1.1–1.6 × 0.4–0.7 µm, tear-shaped, apically abruptly narrowed to a very short filum. **Paraphyses** apically uninflated or mostly slightly to medium spathulate, sometimes lageniform, also obtusely lanceolate, terminal cells *13–28 × (2.5–)3–4(–4.5) µm, lower cells *7.5–15 × 2–3.2 µm; frequently unbranched at upper septum. **Medullary excipulum** hyaline, 40–70 µm thick, of medium dense textura intricata-globulosa, sharply delimited. **Ectal excipulum** pale rose, of thin-walled, vertically oriented t. globulosa(-prismatica) from base to mid flanks, 100–160 µm thick near base, cells *14–25(–38) × 10–18(–25) µm; 15–30 µm thick at flanks, 30 µm near margin, of t. prismatica-porrecta oriented at an 80° angle to the surface, marginal cortical cells *7.5–15 × 2.5–4(–5.5) µm; **glassy processes** 5–60 × 2.5–3.5 µm, high-refractive, not stratified, coherent to form distinct teeth, curved outwards at margin but upwards at flanks. **Anchoring hyphae** very abundant, †2.7–3.8 µm wide, walls 0.3–0.7 µm thick, forming a loose t. intricata up to 100 µm thick, also covering flanks. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1.3–3.3 µm diam; **LBs** pale yellow-orange (carotenoids), peripheral and near septa at base of paraphyses and in marginal excipulum. **Exudate** over paraphyses 0.2–2 µm thick, cloddy, hyaline, firmly attached, cap-like; over margin and flanks sparse. — **ANAMORPH**: vermispora-like (presumed, from natural substrate). **Conidiophores** not seen. **Conidia** phragmosporous, slightly to strongly curved at the ends, ± straight in middle part, *44–62 × 7–7.5 µm, 9–12-septate.

Habitat: lying on ground, 15–20 mm thick branches of *Carnegiea gigantea*, on wood in excavation, strongly decayed, greyed, without algae. **Associated**: *Orbilia cactacearum*, *O. saguarina*, *Teichosporella dura*, ?*Trichopeziza* sp. **Desiccation tolerance**: fully viable for at least 27 months, conidia after 30 months. **Altitude**: 750 m a.s.l. **Geology**: lava tuff with basalt, andesite, dacite, rhyolite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia carnegieae* is tentatively segregated from the Afro-Australian *O. euphorbiae* based mainly on longer spores (for further details see p. 790). The South American *O. puyae* differs in shorter, basally more attenuated

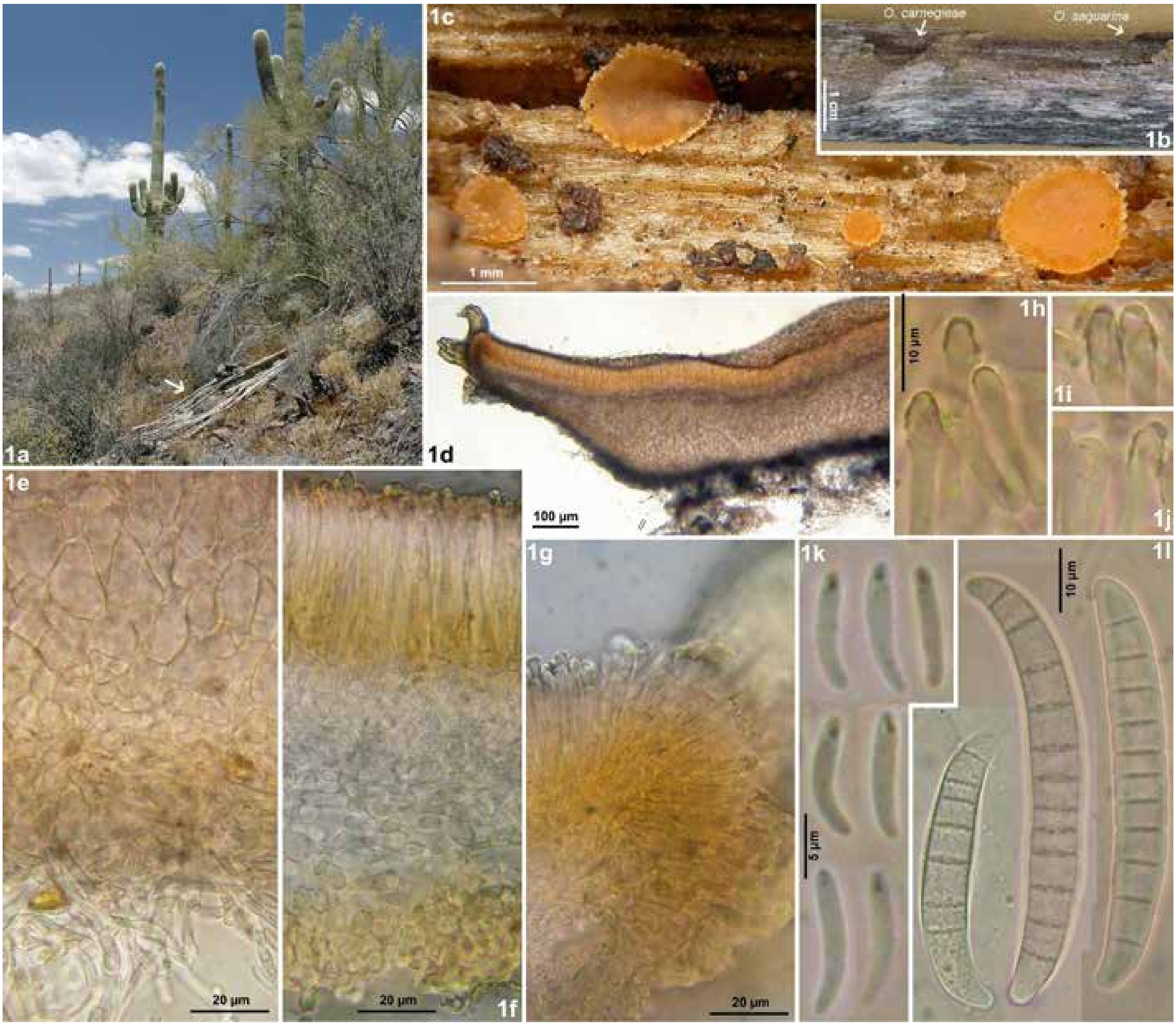


Plate 405. **1**: *Orbilia carnegieae*. – **1a**. semiarid mixed cacti desert scrub with saguaro (*Carnegiea gigantea*), *Parkinsonia microphylla* in foreground, skeleton fragments of *Carnegiea* lying on ground (arrow); **1b**. decayed greyed skeleton fragment; **1c**. rehydrated apothecia; **1d**. apothecium in median section; **1e**. id., basal ectal excipulum and anchoring hyphae; **1f**. id., lower flanks of apothecium; **1g**. id., marginal ectal excipulum; **1h–j**. paraphysis apices; **1k**. ascospores; **1l**. conidia from substrate. – Living state. — **1a–l**. H.B. 7764e (holotype): USA, Arizona, on *Carnegiea*.

spores with distinctly larger SBs, and in capitate paraphyses.

Not included collection. A sparse sample on *Cylindropuntia bigelovii* (Cholla cactus, IVV: H.B. 8355a,) from almost the same collection site as the holotype might be conspecific, but differs in shorter spores (*8–9.2 × 1.2–1.6 µm) and in the paraphyses being never lageniform.

Anamorph. Although *O. carnegieae* is very similar to *O. euphorbiae*, the larger conidia with more septa (Pls 404: 1d; 405: 1l) clearly differ from the more C-shaped conidia on the natural substrate of *O. euphorbiae* (Pl. 401: 1f) or the almost straight, also shorter conidia obtained in culture of *O. euphorbiae* (Pl. 403: 1h).

Ecology. *O. carnegieae* was collected in the Sonoran Desert on rotten, xeric fragments of the vascular skeleton of fallen branches of the saguaro cactus in a subtropical semiarid (almost arid) Sonoran mixed cacti desert scrub in the southwest of Northern America.

Specimens included. **USA**: **Arizona**, Sonoran Desert, 17 km NNE of Lukeville, Ajo Mountain Trail, Organ Pipe, 750 m, branches of *Carnegiea gigantea*, 28.V.2003, G. Marson (ex H.B. 7764e, M-0276449, **holotype**, anam. substr.).

Not included. **USA**: **Arizona**, Sonoran Desert, 17.5 km NNE of Lukeville, Ajo Mountain Trail, Organ Pipe, 710 m, branch of *Cylindropuntia bigelovii*, 5.V.1995, G. Marson (H.B. 8355a).

Orbilia kingsiana Baral & G. Marson, **sp. nov.**,

MB 813754 — Pls 406–407, Map 70

Etymology: named after the type locality, Kings Park (Perth).

Typification: Western Australia, Perth, on stem of an indet. herbaceous dicot, 7.IX.2006, G. Marson (ex H.B. 8459, MEL 2389240, holotype).

Latin diagnosis: *Apothecia rehydratata 0.25–0.65 mm diam., vivide roseo-lilacea, (sub)sessilia, margine glabro. Ascosporae *5.8–8.8 × 1.4–1.8 µm, cylindrico- vel fusoideo-clavatae, apice rotundatae, basi leniter vel valde attenuatae, saepe leniter vel modice curvatae, in statu vivo corpusculum refringens globosum continentes. Paraphyses ad apicem leniter vel valde inflatae, capitatae ad spathulatae, exsudato calyptriforme tectae. Margo excipuli absque processis vitreis distinctis. Habitat ad corticem putridum ramulorum vel ramorum siccorum arborum (*Fabales *et* Myrtales) et *culmos siccos* Anigozanthi *in zona subtropica, semiarida ad semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.65 mm diam., 0.13–0.2 mm high (receptacle 0.11 mm), light to bright pure salmon-rose-lilaceous, exceptionally orange, ± translucent,

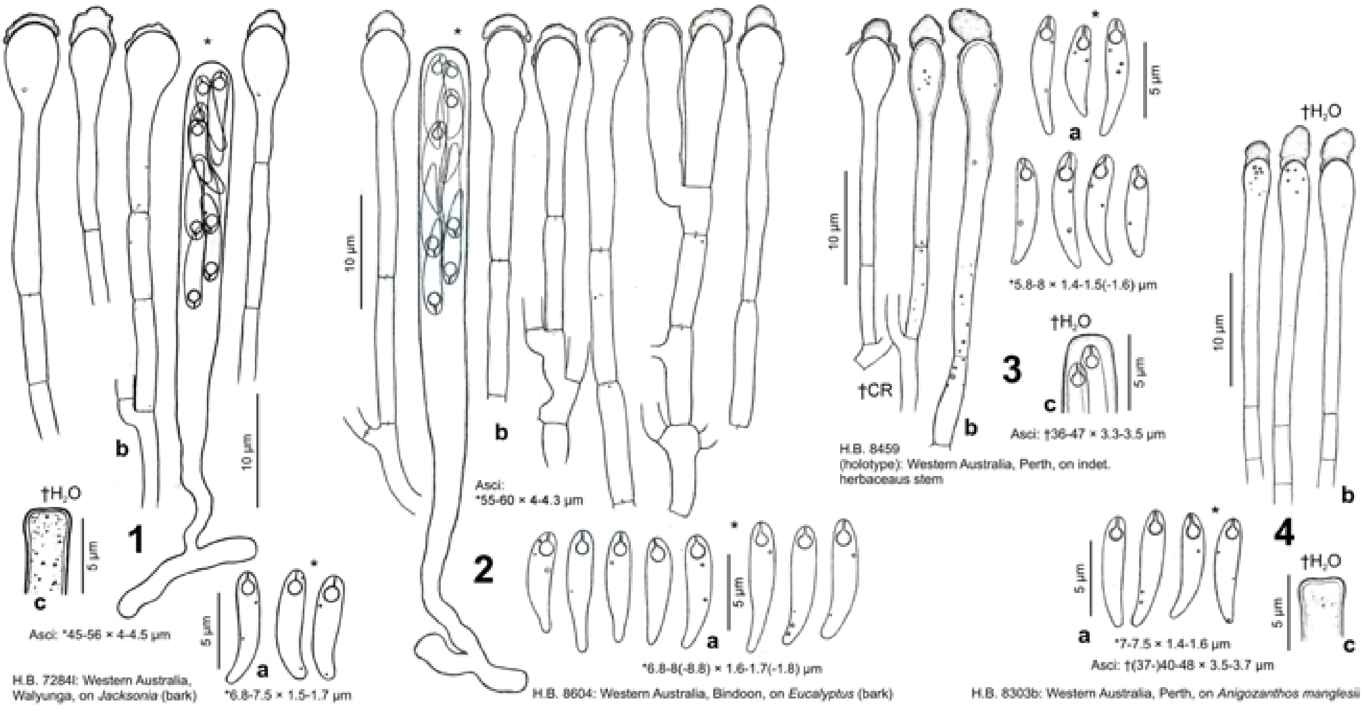


Plate 406. **1–4**: *Orbilia kingsiana*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices.

round, scattered or in small groups; disc flat, margin distinct, thin, 0–10 µm protruding, ± smooth; sessile on an obconical base or ill-defined broad stipe, superficial or slightly immersed in detritus, also erumpent from small cracks; dry bright to deep rose-pink. **Asci** *44–60 {2} × 4–4.5 µm {3}, †(36–)40–53 × 3.2–3.7 µm {3}, 8-spored, spores *2(–3)-seriate, (2–)3–5 lower spores inverted {3} (sometimes mixed), pars sporifera *22–26(–29) µm long; **apex** (†) (medium to) strongly truncate (not or slightly indented, laterally sometimes ± inflated); **base** with medium to long, thin, flexuous stalk, T- to L-shaped. **Ascospores** *(5.8–)6.3–8(–8.8) × (1.4–)1.5–1.7(–1.8) µm {5}, narrowly cylindric- to fusoid-clavate, apex rounded, base slightly to strongly attenuated, ± inequilateral to often slightly to medium curved near base; **SBs** *1.5–1.8 × 0.8–1.1 µm {5}, globose to tear-shaped, apically abruptly narrowed to a very short filum. **Paraphyses** apically slightly to rather strongly clavate(-capitate) to often spathulate, rarely moniliform, terminal cells *(12–)15–25(–33) {2} × (2.7–)3.3–4.3(–4.7) µm {4}, †15–28 × (1.8–)2.2–3.8 µm {2}, lower cells *8–13 × 1.3–2.2 µm {2}, †4–8 × 1.2–2 µm {1}; unbranched at upper septum, hymenium pale rose. **Medullary excipulum** very pale rose, 30–70 µm thick, of medium dense textura intricata-angularis with many inflated cells (especially in lower part), distinctly delimited from ectal excipulum only at flanks by a thin t. porrecta. **Ectal excipulum** hyaline, pale rose towards margin, of (†) thin-walled to slightly gelatinized, indistinctly or vertically oriented t. globulosa-angularis from base to submargin, 40–90 µm thick near base, cells *(8–)10–20(–26) × (6–)8–16(–20) µm {3}; 20–25 µm thick at flanks, 15 µm at submargin, of t. prismatica-angularis oriented at a 70–90° angle to the surface, 10 µm thick at upper margin, of t. prismatica(-angularis) to t. porrecta oriented at 10–50°, marginal cortical cells *6–13(–16) × 3–4(–5) µm {4}, †7–13 × 2.5–3.5 µm {1}; **glassy processes** absent {3} or (0.5–)1–3(–4) × 2.5–3 µm {2}, refractive, not stratified. **Anchoring hyphae** sparse to abundant, */†2–3.5(–4.3) µm wide, walls 0.2–0.5(–1) µm thick {5}, forming a loose, slightly gelatinized t. intricata. **SCBs** in paraphyses sometimes present, globose, ~1–1.3 µm diam. **Exudate** over paraphyses forming 0.5–3(–4) µm tall {5}, hyaline to very pale yellowish, firmly attached, strongly refractive glassy caps, over margin and flanks (0.5–)1–2(–3) µm thick, rough-cloddy, pale to light yellow(-chlorinaceous). — **ANAMORPH**: unknown.

Habitat: collected 1–2 m above the ground, on 3–35 mm thick corticated twigs and 10–18 cm thick trunk of *Eucalyptus* sp. {1}, *Jacksonia* sp. {1}, *Lamarchea hakeifolia* {1}, on very rotten bark {3} (bast), bark sometimes strongly detached, on upper- and underside of bark, also at edges, medium to strongly greyed, without algae; on 4–6 mm thick medium to strongly decayed herbaceous stems of *Anigozanthos manglesii* {1}, indet. angiosperm {1} lying ± close to sandy soil. **Associated**: *Capronia* sp. {2}, *Claussenomyces* spp. {2}, *Durella* sp. {1}, *D.* aff. *connivens* {1}, *Gloniopsis praelonga* {1}, *Hyalorbilia pleioerythrostigma* {1}, *Orbilia albidorosea* {1}, *O. anigozanthi* {1}, *O. australiensis* {1}, *O. austroobtusispora* {1}, *O. curvativitalbae* {1}, *O. eucalypti* {1}, *O. gemma* {1}, *O. lamarcheae* {1}, *O. macrotrapeziformis* {1}, *O. microserpens* {1}, *O. myriofusiclava* {1}, *O. myriolilacina* {1}, *O. myrioobliqua* {1}, *O. ?nothoaprilis* {1}, *O. nothovinosa* {1}, *O. pseudoflagellispora* {1}, *O. ?pubescens* {1}, *Ostropales* {1}, *Symbiotaphrina desertorum* {1}, ?*Xerotrema* sp. {1}. **Desiccation tolerance**: fully viable for at least 11 months, many paraphyses and submature asci after 17 months. **Altitude**: 37–271 m a.s.l. **Geology**: Cretaceous sedimentary rock, Cenozoic regolith, granulite with granitic gneiss. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia kingsiana* is characterized by pure rose-lilaceous apothecia with a smooth margin, rather small, slightly curved, cylindric-fusoid-clavate ascospores, and glassy caps on the paraphyses, though glassy processes on the margin are absent or very short. Several species with similar spores and glassy caps on the paraphyses, such as *O. aradi*, *O. brachychitonis*, or *O. puyae*, differ from *O. kingsiana* in the presence of distinct glassy processes at the margin, and in longer and/or wider spores, also in differently coloured apothecia.

Map 70. Known distribution of *O. kingsiana* in southwestern Australia.

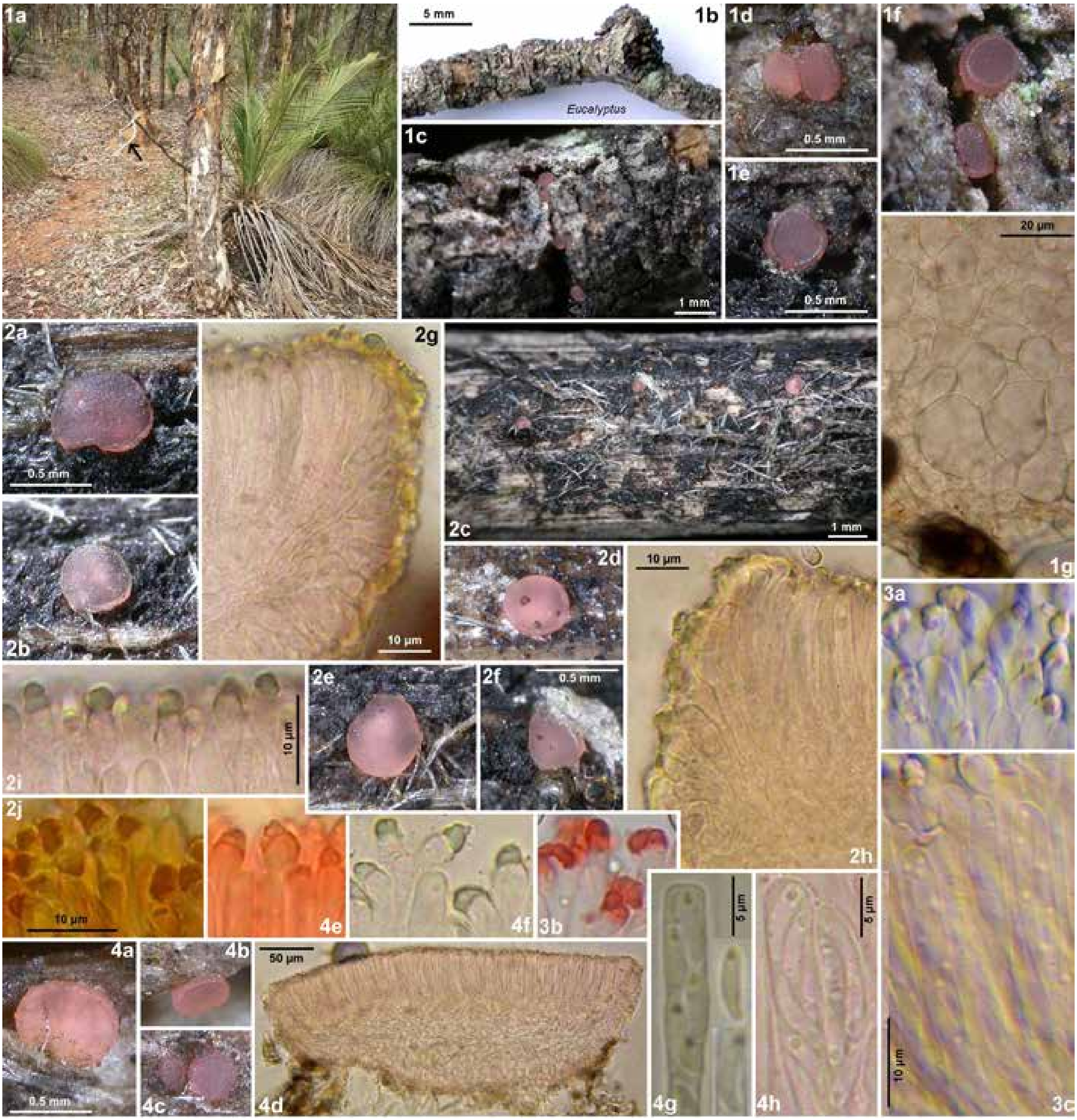


Plate 407. **1–4**: *Orbilia kingsiana*. – **1a**. semihumid Eucalypt open forest with *Macrozamia*, **1b**. dead corticated twig; **2c**. xeric herbaceous stem; **1c–f**, **2a–f**, **4a–c**. rehydrated apothecia; **4d**. apothecium in median section; **2g–h**. id., marginal ectal excipulum; **1g**. id., basal excipular cells; **3c**, **4g–h**. asci with ascospores; **2i–j**, **3a–b**, **4e–f**. paraphysis apices. – Living state, except for **2g–i**, **4f** (in H_2O), **2j** (in IKI), **4e** (in CR), **3b** (in KOH+CR), asci in **4g–h**. — **1a–g**. H.B. 8604: Western Australia, Bindoon, on *Eucalyptus*; **2a–i**. H.B. 8459 (holotype): Perth, on indet. herbaceous dicot; **3a–b**. H.B. 8303b: ibid., on *Anigozanthos*; **4a–i**. H.B. 9020d: Geraldton, on *Lamarchea*.

Variation. The collections on woody substrates deviate from those on herbaceous substrate solely in very slightly wider spores and SBs, and in slightly wider paraphysis apices, with the terminal cells only 1–3 × as long as the lower cells compared to 2–5 ×. In two collections (on *Anigozanthos* and *Lamarchea*) very short (0.5–4 µm) glassy processes could be observed on the marginal cells. These and partly also the caps on the paraphyses did not distinctly stain in IKI and CR (Pl. 407: 4e), therefore, they are assumed to consist of cell wall material covered by a thin layer of exudate. However, in other collections of *O. kingsiana* the caps on the paraphyses stained more distinctly in IKI and CR (Pl. 407: 2j, 3b).

Ecology. *O. kingsiana* was collected on dead, xeric herbaceous stems of *Anigozanthos* (*Commelinales*) and on rotten bark of xeric twigs and branches of *Fabales* and *Myrtales* in subtropical semihumid banksia-eucalypt-acacia open forests and woodlands (partly with *Macrozamia*) in the northern part of the Swan Coastal Plain and adjacent Darling Range of southwestern Australia, and in a semiarid acacia shrubland in the Yalgoo ecoregion of western Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, twig and trunk of *Lamarchea hakeifolia*, on bark, 8.XI.2007, G. Marson (H.B. 9020d). – Swan Coastal Plain, 30 km NE of Perth, 4 km N of Upper Swan, W of Walyunga, 37 m, branches of

Jacksonia, on bark, 23.XI.2001, G. Marson (H.B. 7284l). – 3 km SW of Perth, NE of Matilda Bay, Kings Park, 50 m, stem (or leaf sheath?) of *Anigozanthos manglesii*, 7.IX.2006, G. Marson (H.B. 8303b ø). – ibid., stem of indet. angiosperm, 7.IX.2006, G. Marson (ex H.B. 8459, MEL 2389240, **holotype**). – Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 271 m, twigs of *Eucalyptus*, on bark, 3.IX.2006, G. Marson (H.B. 8604).

Orbilia puyae Baral & Priou, **sp. nov.**, MB 813757 — Pls 408–409

Etymology: named after the host plant, *Puya raimondii*.

Typification: Peru, Catac, inflorescence stem of *Puya raimondii*, 23.X.2005, J.P. Priou (ex H.B. 8043a, M-0276574, holotype).

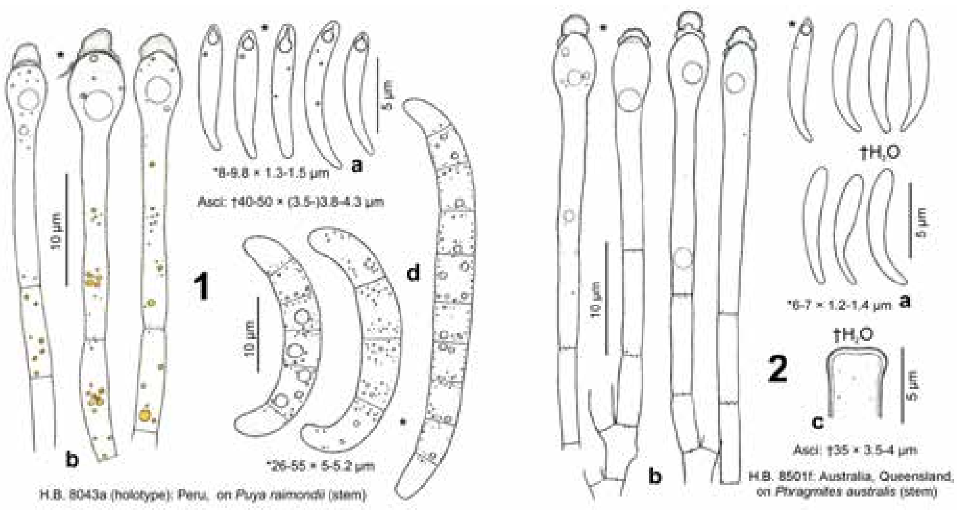


Plate 408. **1**: *Orbilia puyae*; **2**: *O.* cf. *puyae*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex; **d**. conidia from substrate.

Latin diagnosis: *Similis* Orbiliae carnegieae *sed ascosporae breviores, paraphyses ad apicem capitatae, semper pileis vitreis tectae. Habitat ad caulem inflorescentiae putridum semisiccum* Puyae raimondii *in zona alpina subhumida Americae australis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–0.8 mm diam., 0.11–0.25 mm high (receptacle 0.09–0.15 → 0.07–0.1 mm), light rose-orange(-cream), medium translucent, round, (scattered to) gregarious; disc young cupulate then slightly concave to flat, margin distinct, not protruding, very finely crenulate to sometimes distinctly toothed; sessile on a broad, stipe-like base, superficial; dry bright orange-red. **Asci** †40–50 × (3.5–)3.8–4.3 µm, 8-spored, spores (*) biseriate, (1–)3 lower spores inverted (sometimes mixed); **apex** (†) medium to strongly truncate (not indented, laterally not widened); **base** with medium to long, thin, flexuous stalk, T- to L-shaped. **Ascospores** *8–9.5(–10) × 1.3–1.5 µm, †7.3–9.5 × 1.2–1.4 µm, narrowly cylindric- to fusoid-clavate, apex rounded to obtuse, base slightly to medium (rarely strongly) attenuated, slightly to medium curved (entirely or only near base); **SBs** *1.4–1.6(–2) × 0.8–1 µm in situ, globose to broadly tear-shaped, apically abruptly narrowed to a very short filum. **Paraphyses** apically medium to strongly capitate(-clavate) or ellipsoid, terminal cells *19–25 × 3–4(–5) µm, lower cells *5–11 × 2–2.4 µm; unbranched near apex, with or without yellow-orange **LBs** (carotenoids) in lower part, hymenium pale to light orange. **Medullary excipulum** pale orange, 20–35 µm thick, of dense textura intricata-angularis, sharply delimited from ectal excipulum only at flanks by a ± distinct t. porrecta, hyphae with pale orange LBs. **Ectal excipulum** subhyaline, of thin-walled, irregularly oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 25–170 µm thick near base, cells *8–18 × 6–12 µm; 20–30 µm thick at flanks and margin, at margin of t. porrecta oriented at a 70–80° angle to the surface, marginal cortical cells †7–12 × 3–5 µm; **glassy processes** 10–30 × 3.5–4(–5) µm, sometimes only 2–3 µm long, refractive, not stratified, straight to ± outwards curved, sometimes coherent to form distinct teeth. **Anchoring hyphae** abundant, †2–4 µm wide, walls 0.2–0.5 µm thick. **SCBs** in apex of paraphyses globose, 2–2.5 µm diam. **Exudate** over paraphyses forming 1–2 µm thick, hyaline, firmly attached glassy caps. **— ANAMORPH**: vermispora-like (presumed, from natural substrate). **Conidiophores** not seen. **Conidia** phragmosporous, strongly curved (C-shaped), *(25–)29–31 × (5–)5.2–5.5 µm, 4–7-septate.

Habitat: inner surface of 10 cm broad broken piece of hollow inflorescence stem of *Puya raimondii*, lying on ground inside down, very decayed, partly blackened, no algae. **Associated**: *Cistella* sp., *Coniochaeta* sp. **Desiccation tolerance**: cells of ectal excipulum and some paraphyses still viable after 3 months. **Altitude**: 4223 m a.s.l. **Phenology**: rather long-lived.

Taxonomic remarks. *Orbilia puyae* appears to be closely related to European *O. aradi* and North American *O. denticulata*, from which it differs in distinctly narrower ascospores. With *O. denticulata* it shares the apically inflated paraphyses with glassy caps, and with *O. aradi* the more globose spore bodies. *O. euphorbiae* differs from *O. puyae* in narrowly spathulate-lageniform paraphyses. A North American collection mentioned under *O. carnegieae* (on branches of *Cylindropuntia bigelovii*) resembles *O. puyae* in the spores and paraphyses, but the spores are not so much attenuated towards the base, also the SBs are narrower, and the (rehydrated) yellowish-ochraceous, rather small apothecia are distinctly cupulate. *O. kingsiana* differs from *O. puyae* in pinkish apothecia lacking glassy processes, and wider spores.

Not included collection. A sample on *Phragmites* from subtropical Australia (Pl. 409: 2) is not included in the description because of the deviating ecology, although it could well be conspecific with *O. puyae*. The apothecia differ in 10–20 µm protruding margins which are dotted by black-brown conidia of the associated *Arthrinium* that occurs in abundance on the culms. When studied 11 months after it was collected, the paraphyses and excipular cells were still viable in this specimen, but hardly any spores.

Anamorph. In the holotype material we found some typical C-shaped phragmoconidia near the apothecia on the natural substrate (Pls 408: 1d; 409: 1h).

Ecology. *O. puyae* was detected on decayed, mesic parts of an inflorescence stem of *Puya raimondii* (*Bromeliaceae*), a giant rosette plant with the largest spike in the world, growing in the subtropical (orotemperate) subhumid puna ('Puna subhúmeda'), a rather dry grassland vegetation in the highlands of the Peruvian Andes of South America. The not included Australian specimen, in contrast, was found in a floodplain in the tropical (sub)humid lowland of northeastern Australia between savannah and rainforest, on standing, dead, xeric culms of *Phragmites* which are covered over large areas by a black conidial layer of *Arthrinium arundinis*.

Specimens included. **PERU**: **Ancash**, Cordillera Blanca, 47 km SE of Huaraz, 18.5 km ESE of Catac, 4223 m, inflorescence stem of *Puya raimondii*, 23.X.2005, J.P. Priou (ex H.B. 8043a, M-0276574, **holotype**, anam. substr.; J.P.P. 25140, **isotype**).

Not included. **AUSTRALIA**: **Queensland**, Einasleigh Uplands, 22 km SSW of Mossman, 2 km N of Mount Molloy, Mossman Mt. Molloy Rd, 390 m, leaf sheath of *Phragmites australis*, 28.VIII.2006, G. Marson (H.B. 8501f).

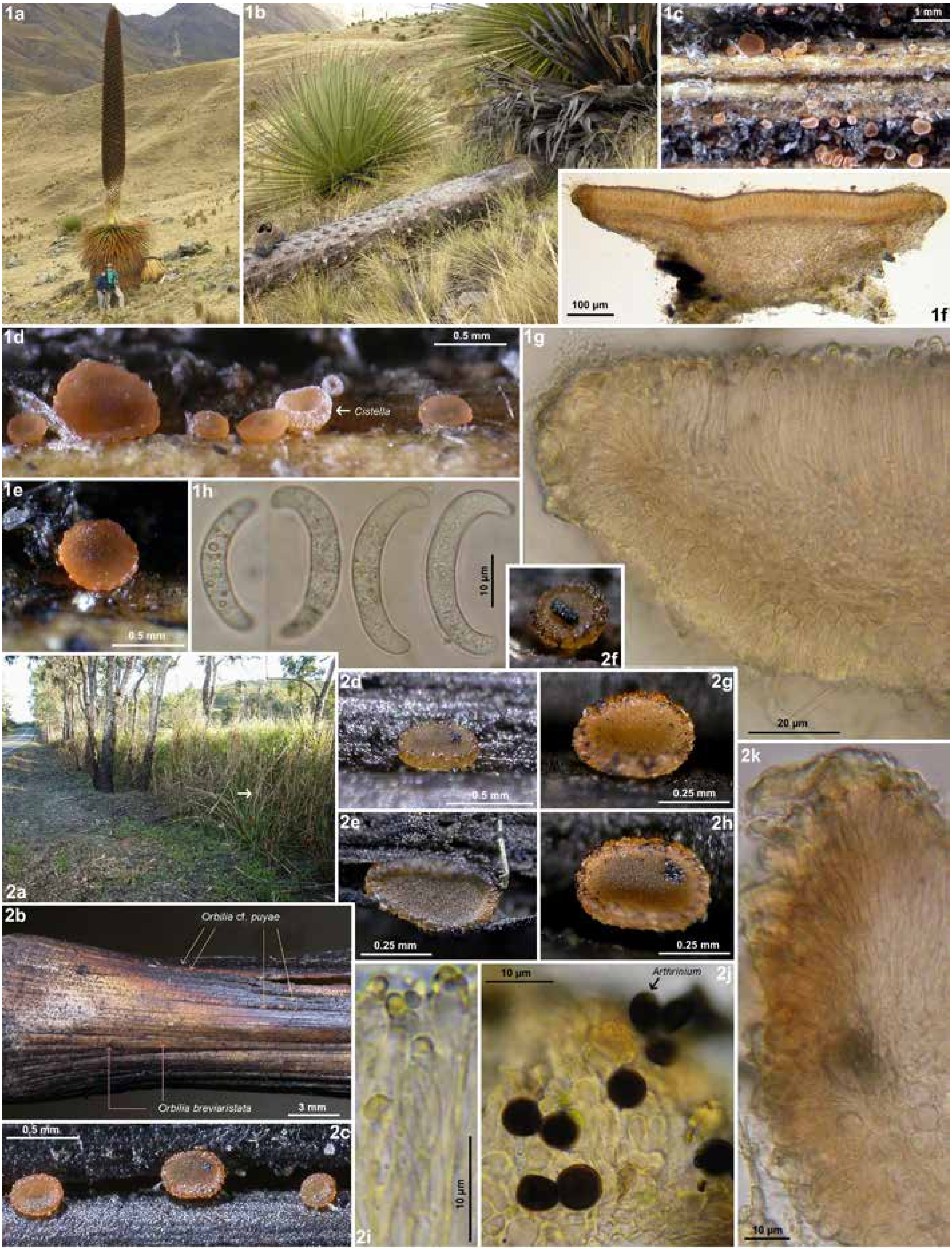


Plate 409. **1**: *Orbilia puyae*; **2**. *O.* cf. *puyae*. – **1a**. alpine subhumid puna grassland with *Puya raimondii* and O. & J.P. Priou; **1b**. young *Puya* and dead fallen stem; **2a**. tropical humid *Phragmitetum*; **2b**. dead culm of *Phragmites* blackened by *Arthrinium arundinis*; **1c–e**, **2c–h**. rehydrated apothecia (**1c–d** associated with *Cistella* sp.); **1f**. apothecium in median section; **1g**, **2k**. id., margin and flanks; **2j**. marginal ectal excipulum in external view, with conidia of *Arthrinium*; **2i**. paraphyses with glassy caps, asci with spores; **1h**. conidia from substrate. – Living state, except for **1f–g** (in H_2O), **2k** (p.p.maj.), asci in **2i**. – **1a–b**: phot. J.P. Priou. — **1a–h**. H.B. 8043a (holotype): Peru, Ancash, on *Puya*; **2a–k**. H.B. 8501f: Australia, Queensland, on *Phragmites*.

Orbilia pseudocylindrospora Baral & G. Marson, **sp. nov.**, MB 813759 — Pls 410–411

Etymology: named after the resemblance to *O. cylindrospora*.

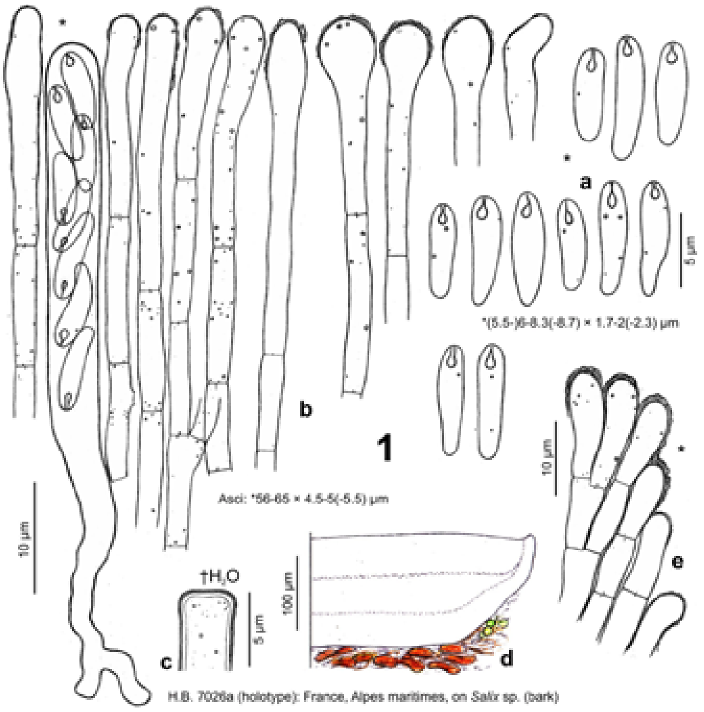
Typification: France, Var, Colmars-les-Alpes, branch of *Salix*, 15.VIII.2001, G. Marson (ex H.B. 7026a, M-0276571, holotype).

Latin diagnosis: Orbiliae concolori s*imilis sed ascosporae breviores*, *minus curvatae*, *corpuscula refringentia minora*, *paraphyses clavato-capitatae vel subspathulatae, apothecia pure rosacea. Habitat ad corticem putridum rami sicci* Salicis *in zona orotemperata Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–0.8 mm diam., 0.15–0.17 mm high, light rose, semitranslucent, ± round, subgregarious in small groups; disc medium concave to flat, margin distinct, 10–25 µm protruding, white, smooth to finely crenulate; broadly sessile, somewhat erumpent from cracks in bast; dry bright apricot-rose. **Asci** *56–65 × 4.5–5(–5.5) µm, †52–67 × 4–4.5 µm, 8-spored, spores *(1–)2(–3)-seriate, 2–6 lower spores inverted (sometimes strongly mixed), pars sporifera *(19–)28–32(–35) µm long; **apex** (†) strongly truncate (sometimes distinctly indented, laterally rarely slightly inflated); **base** with medium to long, thin, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *(5.5–)6–8.3(–8.7) × 1.7–2(–2.3) µm, subcylindrical, sometimes slightly fusoid to clavate, apex rounded, base not or slightly (to medium) attenuated, straight to (very) slightly curved near base; **SBs** *1.3–1.9 × 0.4–0.7 µm, tear-shaped to ellipsoid or subglobose, also ampulliform, apically narrowed to a very short, partly thickened filum. **Paraphyses** apically (uninflated to) slightly or medium (rarely strongly) capitate-clavate, also spathulate to sublageniform, terminal cells *13–30 × (2–)2.5–4.5(–5.3) µm, lower cells *8–16 × 1.8–2.3 µm; unbranched at upper septum, hymenium hyaline. **Medullary excipulum** hyaline, 40–55 µm thick, of ± dense, ± horizontally oriented textura intricata with many inflated cells, very sharply delimited. **Ectal excipulum** hyaline, very pale rose only near margin, of (†) distinctly gelatinized, vertically oriented t. angularis from base to mid flanks, 45–55 µm thick near base, cells *10–22(–31) × 8–17 µm; 25–40 µm thick at lower flanks, 15–20 µm near margin, of t. prismatica-porrecta oriented at a 10–30° angle to the surface, marginal cortical cells *10–15 × (3–)3.5–4.5(–6) µm, (†) thin-walled; **glassy processes** absent. **Anchoring hyphae** sparse, 2–3 µm wide, walls 0.2–0.4 µm thick. **SCBs** in paraphyses and ectal excipulum absent. **Exudate** over paraphyses 0.2–0.5 µm thick; over margin and flanks 0.3–1 µm, rough, firmly attached, forming thin caps. — **ANAMORPH**: unknown.

Habitat: collected 2–3 m above the ground, corticated, 10 mm thick branch of *Salix* sp., on periderm-free area (bast) of strongly decayed bark, greyed, with a few green algae. **Associated**: *Orbilia aristata*, *Physcia* sp., crustose lichen. **Desiccation tolerance**: fully viable for at least 1 month. **Altitude**: 1455 m a.s.l. **Geology**: glacial deposits from Upper Jurassic marl (terres noires) and syenite. **Phenology**: VIII (but probably long-lived).

Taxonomic remarks. *Orbilia pseudocylindrospora* is characterized by subcylindrical, more or less straight ascospores with small tear-shaped SBs which are apically narrowed to a small to wide point, also by a thin, rough, firmly attached exudate, and by rose apothecia with a whitish protruding margin. The paraphysis apices are rather variable in shape: cylindric-sublageniform to spathulate in some apothecia but clavate-capitate in others. The spores of *O. subcylindrospora* (section *Ovoideae*) are similar in size and shape but are usually curved, the SBs are closer to the spore apex, and their connection is mostly invisible. The exudate in *O. subcylindrospora* is more detached and cloddy.



H.B. 7026a (holotype): France, Alpes maritimes, on *Salix* sp. (bark)

Plate 410. **1**: *Orbilia pseudocylindrospora*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. apothecium in median section; **e**. id., marginal ectal excipulum.

The position of *O. pseudocylindrospora* is quite unclear. The species resembles *O. concoloris* of section *Hemiorbilia* in the spores and in the exudate being firmly attached to the paraphyses. *O. concoloris* differs in longer, more curved spores with larger, more ampulliform SBs, and in more distinctly spathulate-lageniform paraphyses. In spore characters *O. pseudocylindrospora* is also similar to the Chinese *O. yuanensis* (section *Helicoon*) and the European *O. cardui* (section *Arthrobotrys*) which both differ in narrower spores and whitish to yellowish, desiccation-sensitive apothecia. Also *O.* aff. *dixiensis* (on *Arctostaphylos*, Pl. 699: 4) resembles *O. pseudocylindrospora* in the spores. It differs in more consistently capitate paraphyses, presence of globose SCBs, smaller apothecia, and especially in a tendency to elongate SBs. For the latter feature we assume that it belongs to section *Habrostictis*.

Ecology. *O. pseudocylindrospora* was collected on rotten bark of a xeric branch of *Salix* at a south-exposed border of a broad-leaved altimontane forest near a rivulet in the orotemperate humid Southern French Alps of southern Europe.

Specimens included. **FRANCE**: **Provence-Alpes-Côte d'Azur**, **Var**, 10 km ENE of Colmars-les-Alpes, 1.3 km N of Entraunes, 6,7 km S of Col de la Cayolle, 1455 m, branch of *Salix*, on bark, 15.VIII.2001, G. Marson (ex H.B. 7026a, M-0276571, **holotype**).

Orbilia denticulata Baral, R. Galán & G. Marson, **sp. nov.**, MB 813760 — Pls 412–413

Etymology: after the denticulate apothecial margin.

Typification: USA, Nevada, Blue Diamond, leaves of *Yucca schidigera*, 22.VI.2000, G. Marson (ex H.B. 6725; M-0276473, holotype; ex-type culture: CBS 140803; sq.: KT215256, MH878178).

Latin diagnosis: *Apothecia rehydratata 0.3–1.8 mm diam., vivide luteo-aurantiaca, sessilia vel subsessilia, margine crenulato vel conspicue albido-dentato. Ascosporae *6–12 × 1.8–2.6 µm, ellipsoideo- ad fusoideo-clavatae, apice rotundatae vel obtusae, basi saepe modice vel valde attenuatae et leniter vel modice curvatae, in statu vivo corpusculum refringens lacrimi- ad obturamentiformem continentes. Paraphyses ad apicem distincte inflatae, capitatae vel spathulatae, calyptra vitrea tectae. Margo excipuli processis vitreis agglutinatis praeditus. Habitat ad ramos putridos siccos* Myrtillocacti *vel folios et caules* Yuccae *in zona mesotemperata ad subtropica semiarida ad arida Americae septentrionalis.*

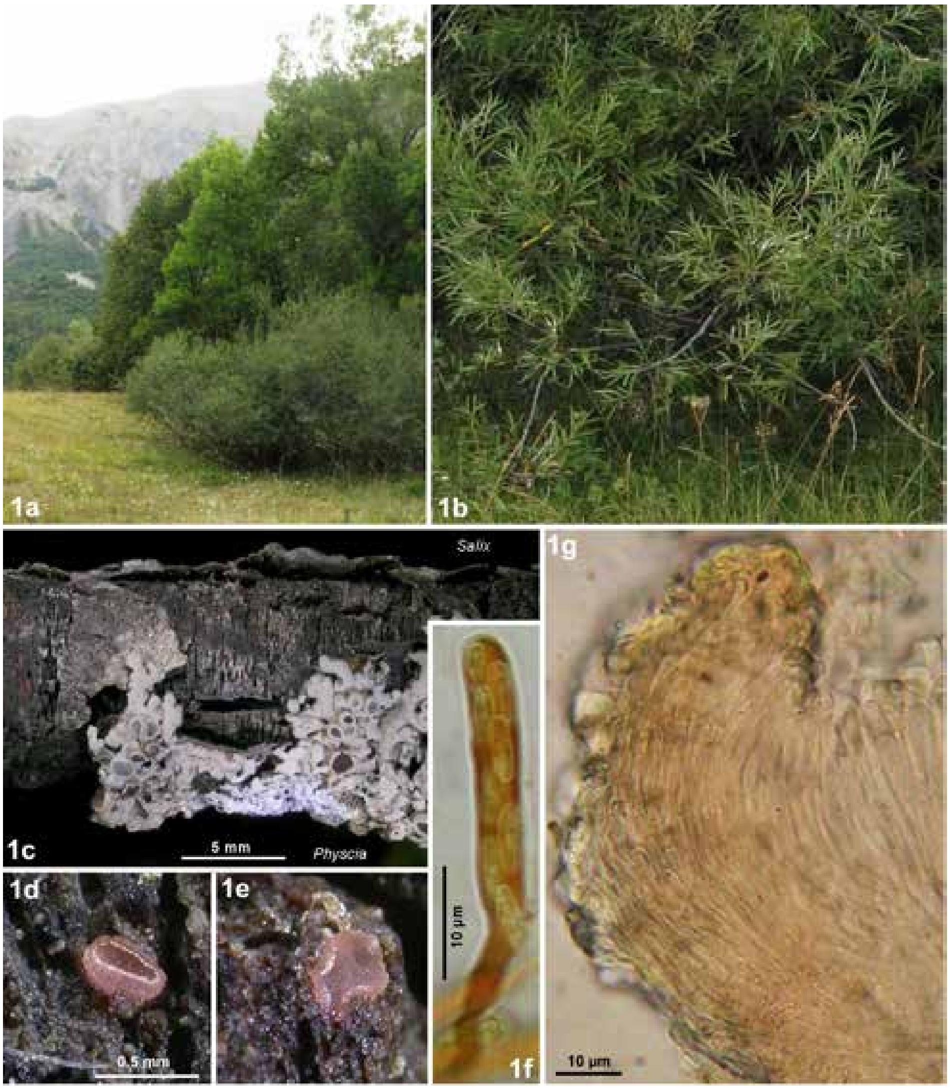


Plate 411. **1**: *Orbilia pseudocylindrospora*. – **1a**. altimontane broad-leaved forest, pasture with group of *Salix* bushes; **1b**. closeup of *Salix* bush; **1c**. dead corticated xeric branch, with *Physcia* sp.; **1d–e**. rehydrated apothecia; **1g**. marginal ectal excipulum in median section; **1f**. ascus with spores. – Dead state: **1f** in KOH+IKI, **1g** in KOH. — **1a–g**. H.B. 7026a (holotype): France, Colmars-les-Alpes, on *Salix*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1.1(–1.8) mm diam., 0.14–0.22(–0.4) mm high (receptacle 0.12–0.17 mm), light to bright yellow-orange (to rose-orange), round, scattered to subgregarious; disc slightly concave to flat, margin crenulate {1} or typically with prominent whitish teeth 25–100 × 50–200 µm {2}; broadly or narrowly sessile or with a stalk ~0.2 × 0.3 mm, ± superficial; dry deep orange-red. **Asci** *47–65(–72) × 4.4–5.3 µm {2}, †(40–)48–60 × 3.7–4.8 µm {3}, 8-spored, spores *2(–3)-seriate, 2–5(–7) lower spores inverted {2} (often mixed), pars sporifera *23–39 µm long; **apex** (†) (medium to) strongly truncate (not or very slightly indented, laterally not widened); **base** with long, thin, flexuous stalk, T- to L-shaped (exceptionally ± H-shaped). **Ascospores** *6–10(–12) × (1.8–)2–2.4(–2.6) µm {3}, †6–9.5 × 1.8–1.9 µm {1}, ellipsoid- to fusoid-clavate, sometimes narrowly ellipsoid, apex rounded to obtuse, rarely subacute, base often medium to strongly attenuated (partly tail-like), straight or basally often slightly to medium curved; **SBs** *1–1.6 × 0.4–0.8 µm {3}, tear- to pear-, also plug-shaped, apically narrowed to a small to often wide point. **Paraphyses** apically slightly to strongly (clavate-)capitate {2}, also spathulate to sublageniform {T}, terminal cells *(14–)17–27 × (3–)4–5(–5.5) µm {2}, †11–23 × 2.6–3.7 µm {1}, lower cells *6–12.5 × 1.8–3 µm {2}; unbranched at upper septum, hymenium light orange. **Medullary excipulum** hyaline or pale yellow-orange, 40–80(–150) µm thick, of loose to dense textura intricata with sparse to abundant inflated cells, sharply delimited. **Ectal excipulum** hyaline to very pale orange (bright orange near margin), of thin-walled († slightly to medium gelatinized), vertically (or indistinctly) oriented t. globulosa-angularis(-prismatica) from base to submargin, 25–50 µm thick near base, cells *10–18(–25) × 7–12(–20) µm {2}, †7–12 × 5–10 µm {1}, cortical cells thick-walled; 20–30 µm thick at lower flanks, cells *7–12 × 5–8 µm; 20–30 µm near margin, of t. prismatica(-porrecta) oriented at a 70–90° angle, marginal cortical cells *7–10 × 2.5–4 µm {1}, †8–15 × 2–4 µm {2}; **glassy processes** at margin 3–10 {1} or 20–50(–100) {2} × (2.5–)3–4(–6) µm {3}, refractive, stratified, coherent to form distinct teeth, on lower and mid flanks much shorter. **Anchoring hyphae** abundant, */†(1.7–)2.5–5(–6) µm wide {3}, walls *(0.3–)0.4–0.8(–1.2) µm {2}, †(0.2–)0.5–1(–2) µm {3}. **SCBs** in paraphyses globose, (1–)2–3 µm diam. {2}; in excipular cells not seen; **LBs** rather abundant in paraphyses and excipular cells, pale to light yellow-orange (carotenoids), 0.5–1.3 µm diam. {2}. **Exudate** on paraphyses forming glassy caps 0.5–1.5(–3.3) µm thick {3}, hyaline, firmly attached; at margin sparse, granular. **— ANAMORPH**: vermispora-like (from ascospore isolate {1} and natural substrate {2}). **Conidiophores** not seen. **Conidia** phragmosporous, slightly curved, *27–38.5 × 5.3–6 µm, 4–6-septate, †41 × 4.5 µm, 10-septate, with low lipid content {T}; †58–60 × 5–6 µm, ~15-septate, with high lipid content {H.B. 5430}.

Habitat: collected 0.2–1.5 m above the ground, branches of *Myrtillocactus cochal* {1}, base of still-attached, hanging leaves of *Yucca schidigera* {1}, 3 cm thick inflorescence stem of *Yucca elata* {1}, on epidermis or on epidermis-free parts, greyed, green algae sparse or absent. **Associated**: *Dothideales* {1}, *Orbilia bicknellensis* {1}, *O. lentiformis* {1}, *O. paradoxoides* {1}, *O. pleiolentiformis* {1}, *Pragmopora* sp. {1}. **Desiccation tolerance**: fully viable for at least 2 months, excipular cells and spores still viable after 26 months. **Altitude**: 500–1510 m a.s.l. **Geology**: Mississippian-Permian sedimentary rock; volcanic rock (basalt, andesite, rhyolite). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia denticulata* is characterized by bright yellow-orange apothecia with a whitish denticulate margin composed of usually long glassy processes, and by capitate to spathulate paraphyses tipped by glassy caps. The European *O. aradi* differs in more globose SBs and much less inflated paraphysis apices. *O. brachychitonis* and *O. concoloris* (the latter in section *Hemiorbilia*) differ in the absence of yellow LBs in the paraphyses and marginal excipulum, *O. brachychitonis* also in wider SBs and *O. concoloris* in lacking glassy processes. *O. euphorbiae* differs in distinctly narrower ascospores and more lageniform paraphyses. A North American collection included in *O. brachychitonis* (on *Baccharis*, Pl. 399: 6) is very similar to *O. denticulata*. However, it lacks, yellow-orange LBs, instead, the cells of paraphyses and ectal excipulum contain globose and crystalloid SCBs. The Australian *O. farnesianae* on branches of

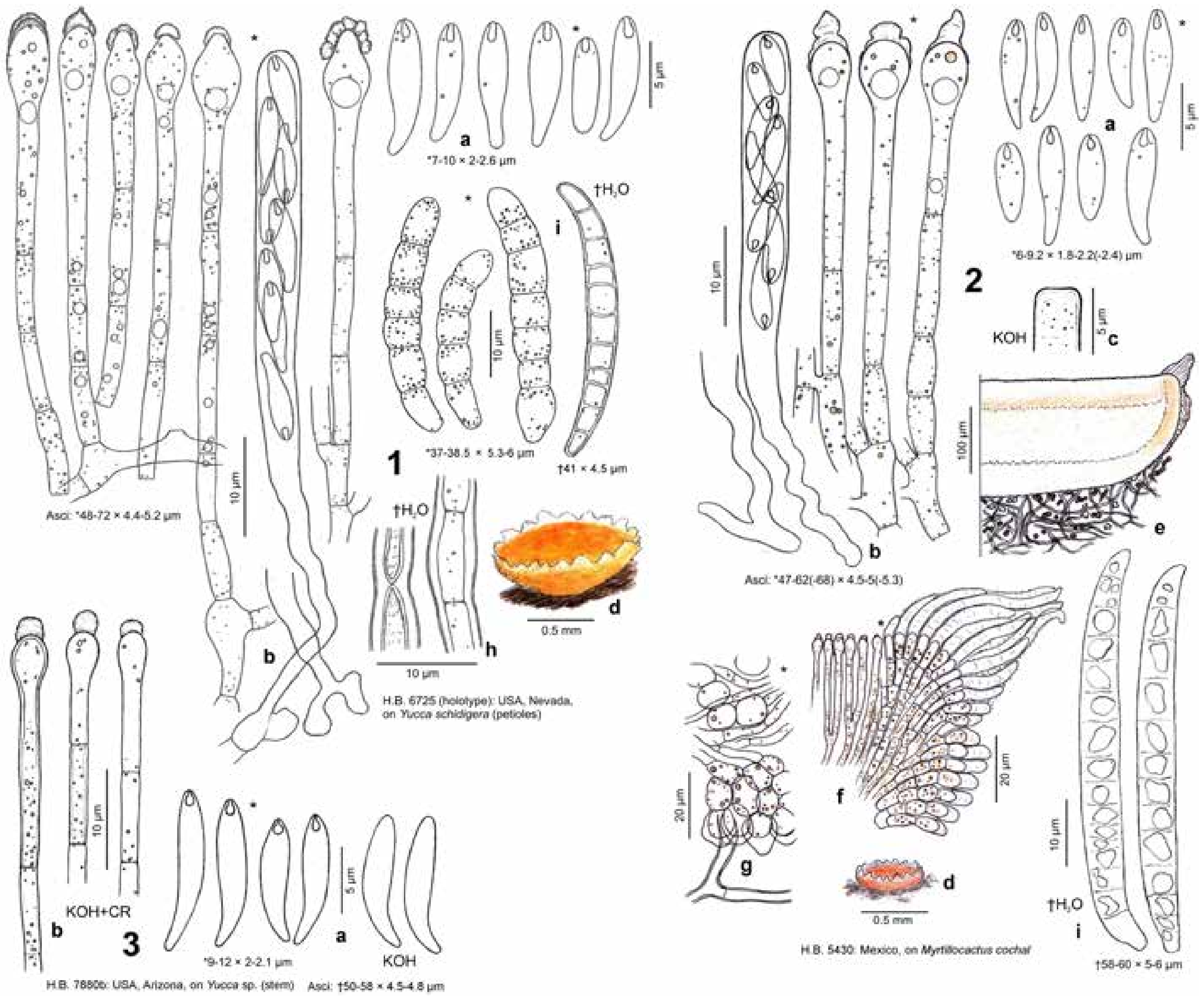


Plate 412. **1–3**: *Orbilia denticulata*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apex; **d**. rehydrated apothecia with dentate margin; **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. id., ectal and medullary excipulum and anchoring hypha at lower flanks; **h**. anchoring hyphae; **i**. conidia from culture (**1**) and substrate (**1** right, **2**).

Vachellia differs in more orange-ochraceous apothecia without yellow LBs, with an only finely rough margin, longer SBs, and thin-walled anchoring hyphae.

Variation. The three collections included in *O. denticulata* are somewhat heterogeneous. The type (on *Yucca schidigera*) differs from the other two in slightly wider spores with more broadly attached SBs, also in spathulate to sublageniform paraphysis apices, and in broader and more thick-walled anchoring hyphae. Only one apothecium was detected on *Yucca elata* (Pl. 413: 2a), which differs from the other two samples in lacking distinct marginal teeth due to very short glassy processes, also in a very thick medullary excipulum.

Anamorph. A few conidia were obtained in pure culture of the holotype, but only after flooding with water (Pl. 412: 1i, three living conidia). Conidia found on the natural substrate in the *Myrtillocactus* sample were much longer and with many more septa, also with a higher lipid content (3i). However, a single conidium on the natural substrate in the holotype (1i right) had distinctly more septa than those in culture.

Phylogeny. A sequence taken from the holotype culture of *O. denticulata* comprises SSU (S1506 intron absent), ITS, and LSU. In our analyses (Phyls 13–14, S15) it clustered in a strongly supported clade with *O. euphorbiae* with an ITS distance of 8.5% (Comoros) or 9.5% (Australia). In the LSU D1–D2 the distance is 2.7–3.5% to other members of series *Regales*, the closest being to *O. euphorbiae*.

Ecology. *O. denticulata* was found on rotten xeric inflorescence stems and leaves of *Yucca* spp. in warm-temperate arid to semiarid desert scrubs (creosotebush and mixed grass-scrubland) of Mojave and Chihuahua in western North America, and on branches of *Myrtillocactus* in subtropical semiarid Baja California.

Specimens included. **USA**: **Nevada**, Mojave Desert, 25.5 km WSW of Las Vegas, 4.5 km SW of Blue Diamond, 1218 m, leaves of *Yucca schidigera*, 22.VI.2000, G. Marson (ex H.B. 6725, M-0276473, **holotype**, anam. substr., anam. cult., CBS 140803; sq.: KT215256, MH878178). – Chihuahuan Desert, 31 km ENE of Safford, 20 km SSE of Clifton, 1510 m, inflorescence stem of *Yucca elata*, on epidermis and wood, 1.VI.2003, G. Marson (ex H.B. 7880b, M-0276551 [in holotype of *O. paradoxoides*]). — **MEXICO**: **Baja California Sur**, ?N of San Ignacio, Sierra de San Francisco, ?500 m, branches of *Myrtillocactus cochal*, 26.I.1996, R. Galán, G. Moreno & M. Lizárraga (H.B. 5430, anam. substr.; AH 6984).

Plate 413. **1–3**: *Orbilia denticulata*. – **1a**. mountainous arid desert scrub with *Yucca schidigera*; **1b–c**. dead hanging leaves with apothecia near their attachment; **1d–f**, **h**, **2a**, **3a–b**. rehydrated apothecia (**2a** with pale rose *O. paradoxoides*); **1g**, **i**. dry apothecia; **1j**, **2c**. marginal ectal excipulum in median section; **1k**. thick-walled anchoring hyphae; **1l**. hymenium with yellow carotenoids in LBs of paraphyses; **1m–n**, **2b**. paraphysis apices with glassy caps; **3c**. conidium from substrate. – Dead state: **1j–n**, **2c**, **3c** (in KOH); **2b** (in KOH+CR). — **1a–l**. H.B. 6725 (holotype): USA, Nevada, on *Yucca*; **2a–c**. H.B. 7880b: USA, Arizona, on *Yucca*; **3a–c**. H.B. 5430: Mexico, on *Myrtillocactus*.

Series *Commatoideae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Commatoideae*** Baral & E. Weber, **ser. nov.**, MB 815008 – Type species: *Orbilia comma* Graddon

Etymology: named after the type species, *O. comma*.

Latin diagnosis: *Seriei* Aurantiorubrae *similis sed ascosporis plus minusve brevioribus et latioribus, apice plerumque obtuso ad subacuto, corpusculum refringens globosum vel late lacrimiformem continentibus differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–1(–1.6) mm diam., whitish to usually pale to bright orange to rose, rarely yellow, margin smooth or sometimes very finely crenulate, sessile or with a short and broad stipe. **Asci** *(25–)30–68(–76) × 3.5–5(–5.8) µm, 8-spored, lower (1–)3–5(–6) spores inverted; **apex** (†) slightly to strongly truncate, not or slightly to strongly indented and/or laterally inflated; **base** T-, L-, Y- or h-, but never H-shaped. **Ascospores** *(5–)6–10(–11.5) × 1.3–2.3(–2.5) µm, cylindric-, ellipsoid- or fusiform-clavate, apex obtuse to subacute (rarely rounded or acute), base often tail-like or with a short to rather long tail, tail sometimes with a bulbous basal inflation, straight or slightly to strongly curved near base (partly distinctly helicoid), **SBs** 0.9–2.3 × 0.7–1.3(–1.5) µm, globose to broadly tear-shaped, rarely ampulliform, apically narrowed to a small point, mostly with a very short filum. **Paraphyses** slightly to strongly clavate-capitate at the apex (rarely not inflated), terminal cells 0.8–3(–4)× longer than lower cells. **Ectal excipulum** cells near base *(8–)10–25(–35) × (5–)8–16(–22) µm; **glassy processes** absent or 1–4(–14) µm long, **hairs** absent. **SCBs** absent or usually globose, also mixed with crystalloid ones; **VBs** absent, rarely low-refractive. **Exudate** 0.2–2(–5) µm thick, continuous to cloddy-granular, loosely to mostly firmly attached, sometimes forming prominent caps, hyaline to light yellow. **— ANAMORPH**: anguillospora-like, vermispora-like. **Conidiophores** 16–25 × 2–4 µm. **Conidiogenous cells** *7–9 × 1.8–2 µm, monoblastic. **Conidia** either phragmosporous (vermispora-like), *22–60 × 2.7–4.8 µm (in situ), 3–8-septate, straight to medium curved, or scolecosporous (anguillospora-like), *90–170 × 3–5 µm (actual length), 7–32-septate, slightly (to medium) curved.

Habitat: on bark and wood of angiosperms, caulicolous on both mono- and dicots, humid, temperate to tropical, always desiccation-tolerant (unclear for *O. disseminata*).

Recognized species: 7.

Taxonomic remarks. Series *Commatoideae* is characterized by comparatively short and wide, ± fusoid-clavate ascospores with obtuse to subacute apices and tapered, partly tailed bases, short and broad, ± globose SBs, and capitate-clavate paraphyses. Delimitation from series *Regales*, based mainly on a different morphology of the paraphysis apices (capitate vs. often spathulate), is not sharp. A close similarity is seen between *O. comma* and *O. aurantiorubra*: both species possess the same type of crystalloid SCBs and similar conidia, and are macroscopically indistinguishable.

Key to the species of series *Commatoideae*

1. Spore tail very thin (†0.1–0.25 µm wide), 1/3–1/2 of total spore length; leaves of large monocots 2
1. Spore tail min. */†0.3–0.4 µm thick, about 1/5–1/3 of total spore length, or absent 3

2. Spores †8–9.3 × 1.2–1.3 µm, sickle-shaped; tropical humid Australasia .... ***O. neglecta*** (section *Arthrobotrys*), p. 1568
2. Spores †9–10 × 1.4–1.6 µm, helicoid; subtropical humid South America .... ***O. disseminata***, p. 818

3. Spores ± strongly curved (helicoid), fusiform-clavate, *(5–)6–8(–9) µm long, with a short, straight or bent, abrupt basal tail; mainly on bark of *Ulmaceae* and *Moraceae* 4
3. Spores straight or only basally distinctly curved, with or without a tail 5

4. Spores * (1.5–)1.7–2.1(–2.4) µm wide, twisted with one turn, tail straight; exudate over paraphyses usually as a continuous to cloddy layer; apothecial margin smooth; bark of *Ulmus* (rarely *Broussonetia* or *Faboideae*), thermoboreal to mesomediterranean Europe .... ***O. comma***, p. 812
4. Spores *(1.3–)1.4–1.5(–1.6) µm wide, twisted with 1–2 turns, tail straight or curved; exudate partly forming individual glassy caps on paraphyses; apothecial margin sometimes very finely crenulate; bark of *Ficus* etc., (sub)tropical (sub)humid Middle and South America, northeastern Australia, southeastern Asia .... ***O. neocomma***, p. 817

5. Asci *6–6.4(–6.7) µm wide (†5.2–5.7 µm); spores *7.3–9.5 × 2–2.3(–2.4) µm, medium to strongly curved at tail-like base, tail base never swollen; bark of *Lonicera*, cold-continental subhumid central Asia .... ***O. basiflexa*** (section *Ovoideae*), p. 1279
5. Asci *3.5–5 µm wide (†3–4.5 µm) 6

6. Spores *(6–)7–9.5(–11) × 1.8–2.3 µm, SBs (1.5–)1.7–2.3 µm long; glassy processes often present, 1–9 µm long 7
6. Spores *(4–)5–8(–9) × 1.3–2 µm, SBs 1–1.8 µm long; glassy processes absent or < 2 µm long 8

7. Crystalloid SCBs present; spores consistently with a short tail with an often slight to distinct basal inflation, spore base straight or only slightly curved; SBs 0.9–1.2(–1.5) µm wide; branches of *Euphorbia*, inframediterranean (semi)arid Macaronesia ..... ***O. pisciformis***, p. 808
7. Crystalloid SCBs absent; spore base attenuated or tail-like, also with a short tail, never inflated at the base, often slightly to medium curved; SBs (0.7–)0.8–1(–1.2) µm wide; bark of angiosperms, also bryicolous, cold-temperate humid to submediterranean (semi)humid Europe .... ***O. mali*** (series *Regales*), p. 781

8. Spores *5.8–7.5(–8.5) × 1.3–1.6 µm, with a 1.3–1.5 µm long tail with a strong globular basal inflation, upper part subcylindrical; culms of *Phragmites*, tropical (sub)humid northeastern Australia .... ***O. stilbospora***, p. 807
A sample on angiosperm bark from southern China merely differs in the predominant absence of a basal inflation of the spore tails (p. 808).
8. Spore base partly tail-like but never or only exceptionally basally inflated 9

9. Paraphyses uninflated to medium capitate, terminal cells mainly 12–18 µm long, often 2 × as long as lower cells; spores *(4–)5–8(–9) × 1.3–1.8 µm; herbaceous stems, rarely wood or bark, cold-temperate to submediterranean (semi)humid Europe .... ***O. caulicola***, p. 803
9. Paraphyses strongly capitate, terminal cells mainly 8–11 µm long, hardly longer than lower cells; spores †5–7 × 1.3–1.9 µm; herbaceous stems of *Conyza*, warm-temperate humid eastern North America .... ***O. cookei***, p. 807

O. cookei seems to be extraordinary in its terminal cells of paraphyses which are hardly longer or partly even shorter than the lower cells, but such short terminal cells are also sometimes seen in *O. stilbospora* and *O. comma*. *O. pisciformis* has the longest SBs of this group, which are broadly tear-shaped to pyriform or ampulliform instead of globose, and the longest glassy processes which, however, vary in length among the collections. *O. disseminata* is exceptional in having yellow apothecia and rather long and thin spore tails.

Anamorph. Merely phragmosporous anamorphs are known, which are ascertained in pure culture only in the former two species: *O. caulicola* is characterized by long anguillospora-like conidia, while *O. comma* and *O. stilbospora* have shorter, vermispora-like conidia.

Phylogeny. Sequences were available for four species of series *Commatoideae* (*O. caulicola*, *O. comma*, *O. pisciformis*, *Orbilia* sp. B.L. 4099). In our analyses of ITS+LSU (Phyl. 13), they clustered in the medium supported core clade of section *Aurantiorubrae*, but did not form a clade of their own. Instead, *O. caulicola*, *O. comma*, and *Orbilia* sp. clustered unresolved, only in the LSU analysis the latter two formed a weakly supported clade (Phyl. S16). *O. caulicola* clustered weakly or medium supported sister to series *Regales* (Phyls 13, S15), whereas *O. pisciformis* clustered strongly (ITS+LSU, ITS) or medium (ITS, Phyl. 14) supported sister to series *Rubellae* (Phyls 13–14, S15). In the phylogenetic analysis in Baral et al. (2017b), the clade containing series *Aurantiorubrae* and *Rubella* and *O. comma* received high support, and here also *O. caulicola* clustered with low support sister to it by rendering series *Commatoideae* paraphyletic. In any case, the two main clades, into which the core clade of section *Aurantiorubrae* is divided, both comprise species with globose and elongate SBs. Which of the two SB types would be the plesiomorphic state cannot be deduced from these analyses. The easier explanation would be that elongate SBs developed from globose ones, so that series *Commatoideae* and *Regales* with predominantly globose SBs would represent the more plesiomorphic groups.

Specific nucleotide positions. No molecular motifs have been found to characterize series *Commatoideae*.

Ecology. Series *Commatoideae* includes only more or less desiccation-tolerant species (no information is available for *O. disseminata*), which occur on wood and predominantly bark of angiosperms but also on herbaceous stems. Records derive from subtropical to tropical humid America and Australia (*O. neocomma*, *O. ?caulicola*, *O. disseminata*, *O. stilbospora*), subtropical semihumid (*O. pisciformis*) or humid (*O. caulicola*) Macaronesia, and temperate humid America (*O. cookei*) and subtropical semihumid to temperate to mountainous humid Europe (*O. comma*, *O. caulicola*, *O. mali*).

Orbilia caulicola Baral & G. Marson, **sp. nov**., MB 813742 — Pls 414–415, Map 71

Etymology: referring to the preference for herbaceous stems.

Typification: France, Vosges, Gérardmer, stem of *Angelica sylvestris*, 2.IX.1996, H.O. Baral (ex H.B. 5561a, M-0276451, holotype).

Latin diagnosis: *Apothecia rehydratata 0.1–0.7 mm diam., aurantiaca, sessilia, margine laevi. Ascosporae *5–9 × 1.3–1.8 μm, fusoideae vel fusiformes, rectae vel basi leniter curvatae, apice obtusae ad acutae, ad basim plerumque valde attenuatae, in statu vivo corpusculum refringens globosum, ad apicem filo brevissime affixum continentes. Paraphyses ad apicem vix vel modice capitato-clavatae. Habitat ad caules putridos siccos herbarum, etiam ad lignum vel corticem putridum ramulorum vel ramorum siccorum fruticum et arborum angiospermarum in zona supratemperata humida et submediterranea semihumida Europae et subtropica humida Macaronesiae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.1–)0.2–0.5(–0.7) mm diam., 0.06–0.12 mm high, whitish, greyish-cream or mostly very pale to light rose, also (rose-)orange, ± translucent, round, very scattered or medium to strongly gregarious; disc flat to ± convex, immarginate, smooth; broadly sessile, superficial; dry light to bright cream, ochraceous, rose or orange(-red). **Asci** *(25–)28–40(–43) × 3.8–4.7 μm {9}, †(22–)26–36(–42) × 3.3–4 μm {6}, 8-spored, spores *2–4-seriate, (1–)3–5(–6) lower spores inverted {17} (not or slightly mixed), pars sporifera *15–21 μm long; **apex** (†) medium to strongly truncate (not or slightly indented, laterally not widened); **base** with short to long, flexuous stalk, L-, T- or h-shaped. **Ascospores** *(4–)5–8(–9) × (1.3–)1.4–1.7(–1.8)((–2)) μm {28}, †5–8.5 × 1.2–1.5 μm {3}, fusoid(-clavate) to fusiform(-clavate), apex obtuse to acute, base slightly to mostly strongly attenuated, with or without a tail-like end (exceptionally inflated at base), straight to sometimes slightly curved near base; **SBs** *(1–)1.2–1.6(–1.8) × 0.7–1.3 μm {18}, globose (to broadly tear-shaped), with a very short filum. **Paraphyses** apically uninflated to medium (rarely strongly) clavate-capitate, terminal cells *(7.5–)12–18(–20) × (2.2–)2.5–4.5(–5.2) μm {9}, lower cells *3–8 × 1.8–2.5(–3.2) μm {3}; sometimes branched at upper septum. **Medullary excipulum** very pale rose, 10–30 μm thick, of textura intricata-angularis, not sharply delimited. **Ectal excipulum** of very pale rose, thin-walled, irregularly vertically oriented t. globulosa-angularis from base to margin, 30–40 μm thick near base, cells *8–18 × 5–18 μm {3}; 25 μm thick at lower flanks, cells *8–12 × 7–9.5 μm, 10–20 μm thick near margin, oriented at a 45–80° angle to the surface, marginal cortical cells *(3–)5–8 × 3.5–7 μm at lower margin, 9–12(–14) × 3–6 μm at upper margin {5}, sometimes hyphoid, hair-like, conglutinate to form radial rows; **glassy processes** absent. **SCBs** absent {6}; **VBs** in paraphyses usually absent {7}, rarely present, elongate, sparse, very low-refractive {1}. **Exudate** over paraphyses 0.2–1(–1.5) μm thick, continuous to cloddy, hyaline to light yellowish-amber, loosely to firmly attached; over margin and mid flanks 0.2–2 μm thick, granular(-cloddy). **Anchoring hyphae** sparse, *2–3(–4.8) μm wide, walls 0.2–0.3 μm thick {2}. — **ANAMORPH**: anguillospora-like (from ascospore isolate {1} and natural substrate {3}). **Conidiophores** not seen. **Conidia** filiform, slightly (to medium) curved, gradually tapered towards both ends, *(90–)110–150(–170) × (3–)3.5–5 μm (actual length), (7–)15–26(–32)-septate {4}, with a few to many small LBs in each cell, especially at the septa, sometimes with 1–2 μm large, globose, medium refractive VBs inside roundish vacuoles in many of the central cells, 1 per cell (Pl. 415: 7, not tested with CRB), VBs disappearing and vacuoles getting larger and elongate when overmature.

Habitat: collected 0.1–1.6 m above the ground, also lying ± moist among moss or grass, on 1–2 years old herbaceous, mostly ± standing stems, rarely leaves or culms, of *Angelica sylvestris* {1}, *Anthriscus sylvestris* {1}, indet. *Apiaceae* {1/1}, *Arctium lappa* {1}, *Conyza canadensis* {1}, *Dactylis glomerata* {1}, *Echinops sphaerocephalus* {2}, ?*Echium vulgare* {1}, *Heracleum sphondylium* {2/2}, *Melilotus* sp. {2}, *M. albus* {1}, *Pastinaca sativa* {1/1}, *Phyllostachys* sp. {1}, *Reynoutria japonica* {1}, *R. sachalinensis* {1}, *Sambucus ebulus* {3}, *Saponaria officinalis* {1}, *Scirpoides holoschoenus* {1}, *Tanacetum vulgare* {1}, *Typha latifolia* (1), *Yucca* sp. {2}; inner parts of very old stems of *Rubus fruticosus* {1}, *R. grandifolius* {1}; 3–35 mm thick, corticated to ± decorticated twigs and branches of *Ficus carica* {1}, *Ononis spinosa* {1}, *Salix* (?)*caprea* {1}, *Ulex europaeus* {1}, on medium to strongly decayed wood {3} and bark (bast) {1}, slightly to strongly greyed, with a few to many green algae; also on excrements of an invertebrate. **Associated**: *Arnium apiculatum* {1}, ?*Bacidia* sp. {1}, **?***Calloriopsis* sp. {1}, *Capronia* sp. {1}, *Cistella grevillei* {4}, *Cyathicula cacaliae* {1}, *C. cyathoidea* {3}, ‘*Dasyscyphus*’ *castaneus* {1}, *Diaporthe arctii* {2}, *D. eres* {1}, *Heterosphaeria patella* {1}, *Hydropisphaera arenula* {1}, *Karstenia rhopaloides* {1}, *Lachnella alboviolascens* {2}, *L. villosa* {2}, ?*Laetinaevia* sp. {1}, *Leptospora rubella* {2}, *Lophiostoma* sp. {1}, *Mollisia* sp. {1}, *M. ?coerulans* {1}, *M. revincta* {1}, *Merismodes* sp. {1}, ?*Nectria* sp. {1}, *Olla*

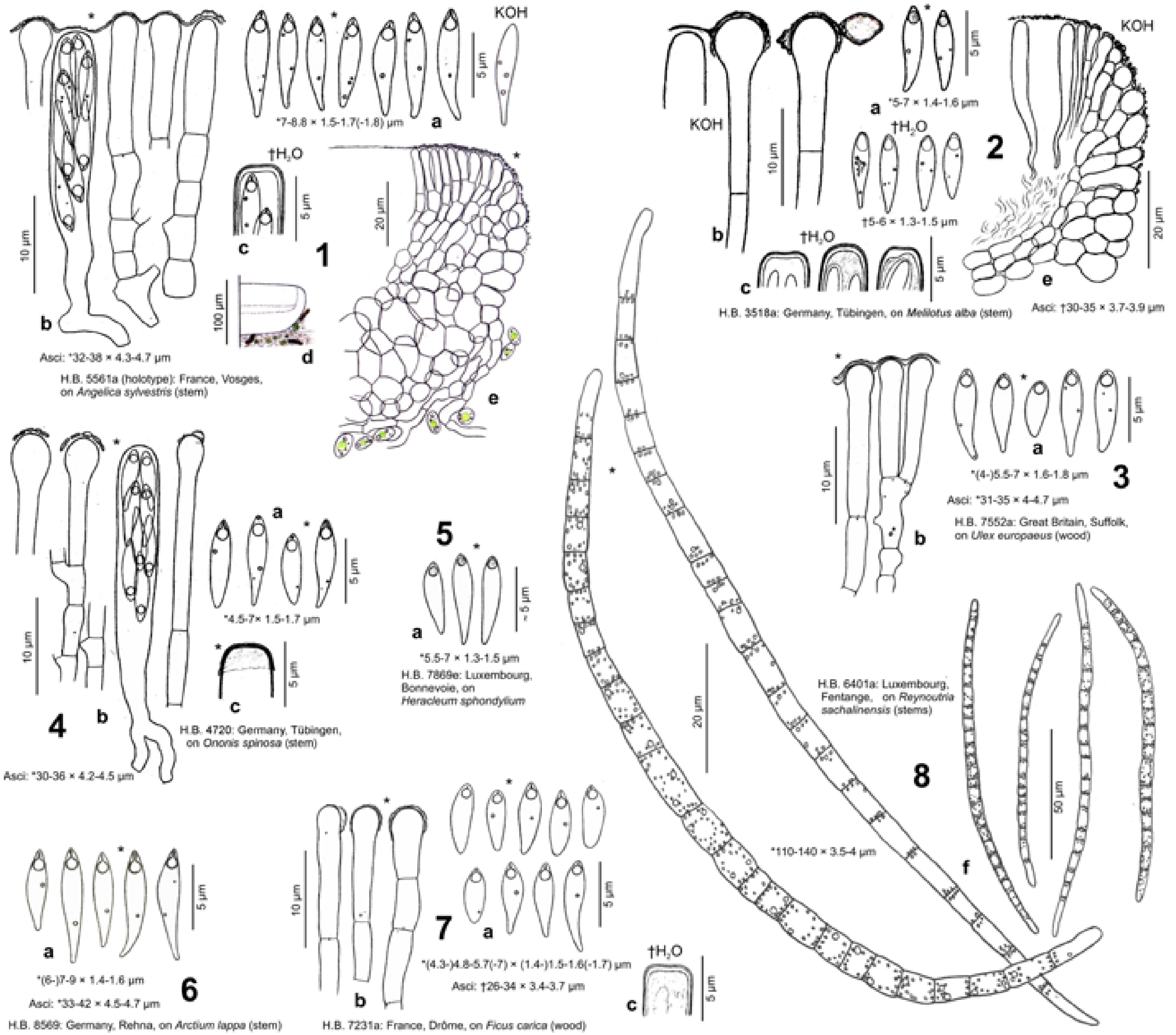


Plate 414. **1–8**: *Orbilia caulicola*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., ectal excipulum (margin and mid flanks); **f**. conidia from substrate.

millepunctata {4}, *Ophioceras leptosporum* {1}, *Orbilia albovinosa* {1}, *O. auricolor* {1}, *O. carpoboloides* {1}, *O. cylindrosoma* {4}, *O. flavida* {8}, *O. flavidorosella* {2}, *O. ocellata* {1}, *O. pleiolentiformis* {1}, *O. quaestiformis* {8}, *O. ungulata* {4}, *O. vitalbae* {3/1}, *Patellaria atrata* {2}, *Peroneutypa* ?*scoparia* {1}, *Phragmocephala atra* {1}, *Pirottaea* ?*imbricata* {2}, *Pyrenopeziza* sp. {2}, *P. atrata* {1}, *P.* ?*rubi* {1}, *Ramichloridium* ?*schulzeri* {1}, *Stictis* ?*stellata* {1}, *Trichopeziza* ?*perrotioides* (immature) {1}, *T. lizonii* {1}, *T. mollissima* {1/2}, *Unguiculariopsis ilicincola* {1}, *Urceolella crispula* {2}, *U.* ?*pani* {1}. **Desiccation tolerance**: fully viable for at least 4.5 weeks, after 2 months only excipular cells alive. **Altitude**: 7–643 m a.s.l. **Geology**: Cambrian silt & wacke, Devonian slate, Carboniferous sand-, mud- & siltstone with coal, Keuper (gypsum, marl & sandstone), Lower Jurassic & Miocene sand, sandstone & shale, Quaternary loess & sand; granite, gneiss, rhyolite, gabbro. **Phenology**: II, IV–XI (apparently throughout the year).

Taxonomic remarks. *Orbilia caulicola* is characterized by small, straight, fusoid to fusiform ascospores being often strongly attenuated and partly slightly curved at the base, with a ± globose apical spore body. The North American *O. cookei* is tentatively segregated by strongly capitate paraphyses with rather equally distibuted septa, whereas the apices in *O. caulicola* are usually less inflated and the terminal cells tend to be distinctly longer than the lower cells. The type of *O. rosella* (tentatively placed in series *Abutilones*) differs from these two taxa in a crenulate apothecial margin due to very short hairs with small glassy caps, also in slightly larger asci and spores. *O. ebuli* differs from *O. caulicola* in distinctly longer spores with elongate spore bodies with an inflated ellipsoid to tear-shaped lower part.

Variation. *O. caulicola* varies strongly in spore length among the collections (from *5–6 µm to 7.5–9 µm), also in thickness of paraphysis apices (from uninflated to medium capitate). Variation in shape of spore apices (from obtuse to acute) and bases (partly tail-like) was noted among but also within populations. Collections on woody substrates did not markedly differ from those on herbs. Very low-refractive VBs were seen in the paraphyses of only one collection consisting of one apothecium (Schwäbisch Hall, 31.VII.1992).

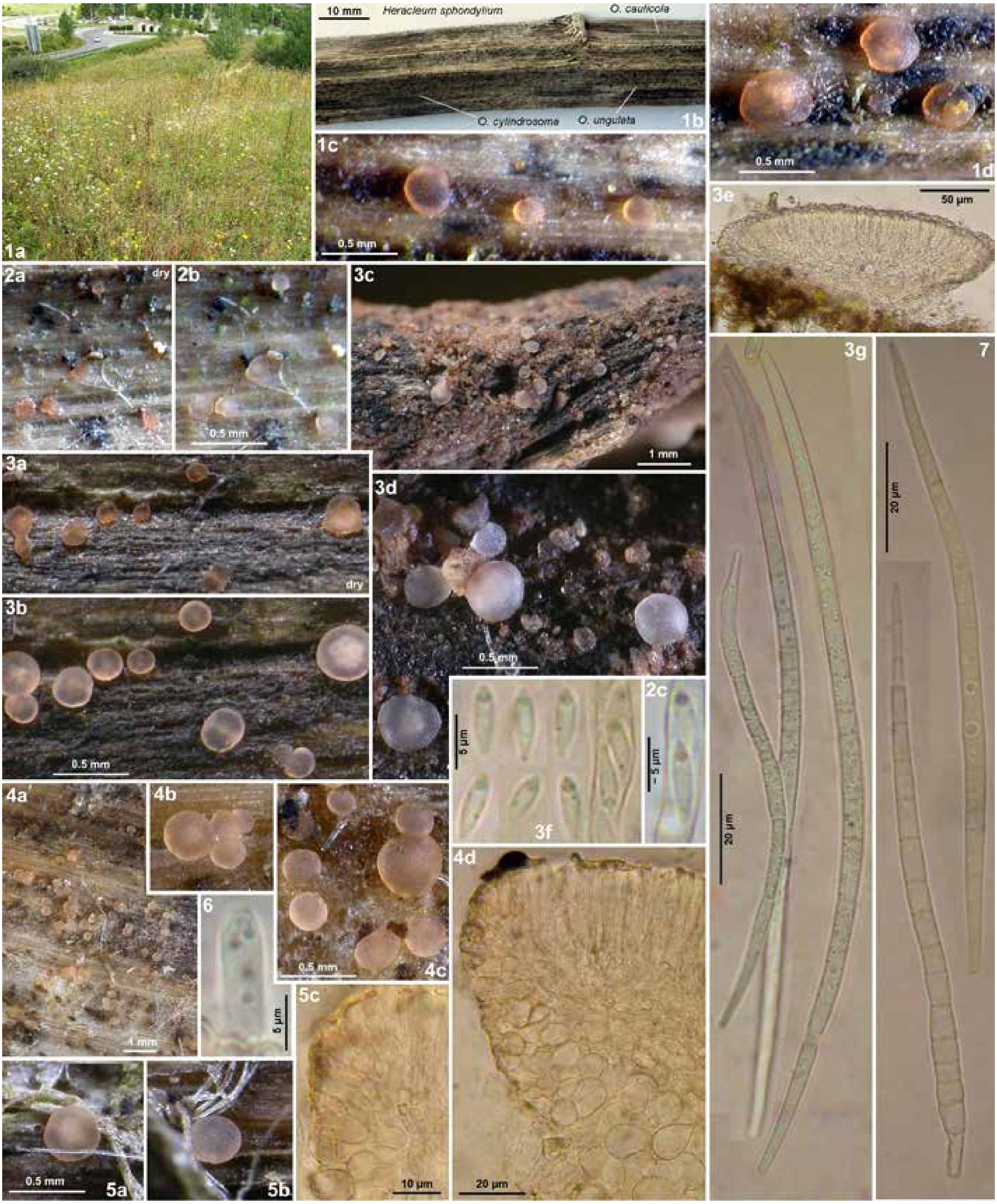


Plate 415. **1–7**: *Orbilia caulicola*. – **1a**. ruderal meadow between railway and road; **1b**. dead xeric stem of *Heracleum sphondylium*; **4a–c**. fresh apothecia; **1c–d**, **2b**, **3b–d**, **5a–b**. rehydrated apothecia; **2a**, **3a**. dry apothecia; **3e**. apothecium in median section; **4d**, **5c**. id., marginal ectal excipulum; **6**. apex of mature ascus; **2c**, **3f**. ascospores; **3g**. conidia from substrate; **7**. conidia from pure culture. – Living state, except for asci in **2c**, **6**. — **1a–d**. H.B. 7869a: Luxembourg, Bonnevoie, on *Heracleum*; **2a–c**. H.B. 7559: ibid., Ettelbruck, on *Heracleum*; **3a–g**. H.B. 8346a: Germany, Tübingen, on indet. ?*Apiaceae*; **4a–d**. H.B. 8569: Germany, Rehna, on *Arctium*; **5a–c**. H.B. 8539c: Luxembourg, Dudelange, on *Melilotus*; **6**. H.B. 7564d: Luxembourg, Junglinster, on *Sambucus ebulus*; **7**. G.M. 2013-07-30.3: Luxembourg, Bettembourg, on *Melilotus*.

Not included collection. A very sparse unillustrated sample from South America differs from *O. caulicola* by thin, filiform to circular crystalloid SCBs in the excipular cells. The fusiform spores (*5.5–7 × 1.7–1.9 µm) with acute ends and broadly tear-shaped SBs of 1.4–1.7 × 0.7–1.1 µm, and the paraphyses with 3 µm wide, slightly to medium clavate apices closely resemble *O. caulicola.*

Anamorph. The anguillospora-like conidia of *O. caulicola* (Pls 414: 8; 415: 3g, 7) resemble those of '*Brachyphoris*' *stenomeces* as described by Drechsler (1963), which has slightly narrower conidia with their widest part more in the lower half (see Pl. 1: b). The anamorph of *O. rosea* (section *Helicoon*), *Anguillospora rosea*, is similar but has much longer conidia and occurs, in contrast, in semiaquatic habitats.

Phylogeny. Sequences were obtained from three collections: on *Arctium* from Mecklenburg (from apothecia), on *Melilotus* and *Tanacetum* from the same site in Luxembourg (from pure culture and apothecia, respectively). They comprise ITS and LSU, the latter two also the S1506 intron, which is not covered by the former. The ITS region is only complete in the *Tanacetum* strain while the *Melilotus* strain lacks IT2 and the *Arctium* strain a part of ITS1. Deviations among the strains concern 4 nt and some gaps in the ITS1, and 2 nt and 2 gaps in the ITS2, resulting in a variation of 0.7–1.3 % (2 nt in the ITS1 differ only between the two strains from Luxembourg). In the LSU D1–D3 domain, 1 nt deviates in the D2 and 1 nt in the D3. In the intron a distance of 1.5 % is observed in the overlapping part.

The closest species in the ITS region was *O. mali* with a distance of 13.5 %, while *O. comma* differs by 16.5 %, and other members of the clade by 15–16 %. In the LSU the distance to other taxa ranges at 4–10 %, whereas in the intron it is generally very high. A close relationship to *O. comma* or *O. pisciformis* is not supported, but for the time being we decided to keep *O. caulicola* for morphological reasons in series *Commatoideae*.

Ecology. *O. caulicola* was collected on both hygric and xeric substrate, predominantly herbaceous stems of various mono- and dicotyledonous biannual or perennial plants, but also on ± rotten wood and bark of twigs and branches of angiosperm trees and shrubs. The vegetation includes thermophilous ruderal places with *Artemisia*, *Conyza*, *Echium*, *Melilotus*, *Pastinaca*, *Reynoutria*, *Sambucus ebulus*, *Solidago* etc., shrublands with *Ulex* and *Yucca*, and wetlands with *Angelica* or *Scirpoides*. The climatic zones comprise planar to submontane, atlantic to subcontinental, cold- to warm-temperate humid, but also suprasub- to mesosub- and supramediterranean semihumid Europe. A single sample was from a suprasubmediterranean humid laurel forest in Madeira (Macaronesia). The not included record from South America was in a subtropical humid forest with planted tropical fruit trees.

Map 71. Known distribution of *O. caulicola* in Europe and Macaronesia.

Specimens included. **GREAT BRITAIN**: **Yorkshire**, **South Yorkshire**, 7.5 km NNW of Sheffield, 1 km NW of Grenoside, Greno Wood, 280 m, stem of *Anthriscus sylvestris*, 18.V.2011, J.H. Petersen & T. Læssøe (J.H.P. 11.161, H.B. 9524a ø). – **East England**, **Suffolk**, 9.5 km SW of Southwold, 5.5 km NNE of Leiston, Minsmere Haven, 12 m, branch of *Ulex europaeus*, on wood, 3.VII.2004, E. Batten (H.B. 7552a ø). — **GERMANY**: **Mecklenburg-Vorpommern**, 5 km N of Rehna, 0.8 km NNE of Törber, Ackersoll, 18 m, stem of *Arctium lappa*, 7.VII.2007, T. Richter (H.B. 8569; sq.: KT222445). – **Baden-Württemberg**, 10 km SW of Schwäbisch Hall, SW of Wielandsweiler, Rotaue, 380 m, stem of (?)*Heracleum sphondylium*, 31.VII.1992, K. Siepe (ø). – 3 km W of Tübingen, 2 km SSE of Hagelloch, Schweigbrühl, 335 m, stem of *Saponaria officinalis*, 29.VI.1992, H.O. Baral (ø). – 3.5 km NE of Tübingen, 1.3 km SW of Pfrondorf, Bitzle, 420 m, stem of *Melilotus albus*, 10.VIII.1988, H.O. Baral (H.B. 3518a). – 0.8 km S of Pfrondorf, Mähder, 375 m, twig of *Ononis spinosa*, 13.VII.1992, H.O. Baral (H.B. 4720 ø). – 0.6 km S of Pfrondorf, 395 m, stem of indet. *Apiaceae*, 21.IX.1998, H.O. Baral (H.B. 6235). – 1 km SSE of Pfrondorf, between Neckar river and canal, 313 m, stem of indet. ?*Apiaceae*, 22.X.2006, H.O. Baral (H.B. 8346a, anam. substr.). – 15 km NW of Freiburg, 3.3 km W of Eichstetten, Kaiserstuhl, N of Eichelspitze, 500 m, stem of *Sambucus ebulus*, 8.VIII.2013, K. Müller (H.B. 9835b ø). — **LUXEMBOURG**: **L'Oesling**, **Diekirch**, 9 km NNW of Ettelbruck, 1.5 km NNW of Bourscheid, Goebelsmühle, railway station, 250 m, stem of *Heracleum* (?)*sphondylium*, 19.VII.2004, G. Marson (H.B. 7559). – 4.5 km SW of Diekirch, W of Ettelbruck, railway station, 197 m, stem of *Pastinaca sativa*, 6.VII.2002, G. Marson (H.B. 7203). – **Gutland**, **Grevenmacher**, 17 km NE of Luxembourg, 3 km NNE of Junglinster, Appelescht, 307 m, stem of *Sambucus ebulus*, 27.VIII.2004, G. Marson (H.B. 7564d ø). – **Luxembourg**, 2 km SSW of Luxembourg, 0.5 km S of Hollerich, railway station, 280 m, stem of *Heracleum sphondylium*, 28.VI.1999, G. Marson (ø). –SW of Bonnevoie, railway depot, 282 m, stem of *H. sphondylium*, 4.VIII.2005, G. Marson (H.B. 7869e). – 5 km S of Luxembourg, 1.5 km W of Hesperange, Biersak/Géisselbierg, 290 m, stem of *Rubus fruticosus*, 20.XI.1994, G. Marson (H.B. 5190a). – 1.2 km SSW of Hesperange, Wéineguecht, 272 m, stem of *Reynoutria sachalinensis*, 31.V.1999, G. Marson (H.B. 6401a, anam. substr.). – ibid., stem of *R. japonica*, 17.VI.1999, G. Marson (H.B. 6402a). – **Esch-sur-Alzette**, 2.5 km W of Esch-sur-Alzette, Belval Usines, 303 m, stem of *Sambucus ebulus*, 10.VI.1999, G. Marson (H.B. 6406c). – 6.5 km S of Luxembourg, 1 km NNE of Bivange, Lëschebann, 265 m, stems of *Echinops sphaerocephalus*, 15.VI.1994, G. Marson (H.B. 5105b). – ibid., stems of *E. sphaerocephalus*, 17.II.1994, G. Marson (H.B. 5113a, G.M. 5196). – 2 km NNE of Dudelange, 1.5 km S of Bettembourg, railway station, 275 m, branch of *Salix* (?)*caprea*, on wood & bark, 15.VI.1994, G. Marson (H.B. 5119d, G.M. 5197). – ibid., stem of ?*Pastinaca sativa*, 9.VII.2002 (H.B. 7176, anam. substr.). – ibid., stem of ?*Echium vulgare*, 9.VII.2002 (H.B. 7167a). – ibid., stem of *Melilotus*, 5.VI.2007 (H.B. 8539c). – ibid., stem of *Melilotus*, 30.VII.2013 (G.M. 2013-07-30.3, anam. cult.; sq.: KT380063, KT380067). – ibid., stem of *Tanacetum vulgare*, 25.VII.2014 (G.M. 2014-07-25.7; sq.: KT222392). — **FRANCE**: **Bretagne**, **Morbihan**, 0.9 km W of La Gacilly, S of La Glouzie, Naveterie, 25 m, culm of *Dactylis glomerata*, 30.V.2006, J.P. Priou (J.P.P. 26150, non vid.). – 1 km N of La Gacilly, Yves Rocher, botanical garden, 27 m, leaf sheath of *Phyllostachys*, 3.VII.2012, J.P. Priou (J.P.P. 12144, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 4 km SE of Pornichet, E of St.-Marguerite, Camp de la Courtine, stem of *Conyza canadensis*, 12.XI.2015, J.P. Priou (J.P.P. 15237, doc. vid.). – **Poitou-Charentes**, **Charente-Maritime**, Île de Ré, 2.5 km NNE of St.-Clément-des-Baleines, Forêt de St.-Clément, 7 m, stem of *Yucca*, 26.IV.2006, J.P. Priou (J.P.P. 26103, non vid.). – **Aquitaine**, **Gironde**, 8 km SSW of Royan, 2.5 km NW of Le Verdon-sur-Mer, 8 m, leaves of *Yucca*, 20.XI.2011, J.P. Priou (J.P.P. 11210, doc. vid.). – **Lorraine**, **Vosges**, 4 km W of Gérardmer, Tourbière de la Morte Femme, 643 m, stem of *Angelica sylvestris*, 2.IX.1996, H.O. Baral (ex H.B. 5561a, M-0276451, **holotype**). – **Bourgogne**, **Saône-et-Loire**, 17 km WNW of Autun, 2.2 km NNE of St.-Prix, Gîtes des fleurs, 523 m, stem of *Typha latifolia*, 21.X.2015, A. Gardiennet, vid. J.P. Priou (J.P.P. 15197, doc. vid.). – **Rhône-Alpes**, **Drôme**, 1 km N of Nyons, W of Col du Pontias, 415 m, branch of *Ficus carica*, on wood, 11.X.2002, G. Marson (H.B. 7231a). — **SPAIN**: **Navarra**, 10 km NNW of Tafalla, 3.7 km NE of Artajona, 475 m, culm of *Scirpoides holoschoenus*, 8.II.2014, M. Tapia, vid. E. Rubio (E.R.D. 6127). — **MACARONESIA**: **Madeira**, 4.5 km NNE of Arco da Calheta, SE of Rabaçal, 1305 m, stem of *Rubus grandifolius*, 15.X.2009, J.P. Priou (J.P.P. 29183, doc. vid.).

Not included. **COLOMBIA**: **Cundinamarca**, Cordillera oriental, 100 km N of Bogotá, Pacho, ~1800 m, twig of indet. angiosperm, on bark, 1.I.1994, W. Jaklitsch (H.B. 5117c ø).

Orbilia cookei Baral, **nom. nov.**, MB 813743 — Pl. 416

Replaced synonym: *Peziza exigua* Cooke, Bull. Buffalo Soc. Nat. Sci. 2: 296 (1875) [non *Orbilia exigua* Velen., Monogr. Discomyc. Bohem.: 100, 1934, = *Hyalorbilia berberidis*]

≡ *Pezizella exigua* (Cooke) Sacc., Syll. Fung. 8: 283 (1889)

≡ *Mollisia exigua* (Cooke) Seaver, North Amer. Cup Fungi (Inop.) p. 207 (1951)

Etymology: *cookei*: named after the author of the basionym, M.C. Cooke; *exigua*: referring to the minute apothecia.

Typification: USA, New Jersey, Newfield, stem of *Conyza canadensis*, VIII.1873, J.B. Ellis (K(M) 36004, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.13–0.32 mm diam., pale cream-reddish-orange (Cooke: miniate = saturn-red, Dennis: pink), round to slightly elliptical, scattered; disc flat (Cooke: concave, eventually flat to convex), margin smooth, scarcely protruding; sessile on a small base, superficial; dry dirty reddish. **Asci** †28–33 × (2.9–)3.4–4(–4.2) µm, 8-spored, spores †2–3-seriate, ?3 lower spores inverted, pars sporifera †20–23 µm long; **apex** (†) strongly truncate (deeply indented, laterally distinctly inflated); **base** with short stalk, Y-shaped. **Ascospores** †5–7 × 1.3–1.9 µm, fusoid to fusoid-clavate, apex obtuse to subacute, base medium to strongly attenuated in a ± acute end, straight or rarely slightly curved at base; **SBs** unknown (perhaps globose). **Paraphyses** apically (very) strongly capitate, terminal cells †(5–)8–11 × 3–4.8 µm, lower cells †(5–)8–10 × 1–1.6 µm; unbranched at upper septum. **Medullary excipulum** not examined. **Ectal excipulum** of (†) thin-walled textura angularis from base to margin, cells near base †9–20 × 7–15 µm; near margin of t. prismatica-angularis oriented at a high angle to the surface, marginal cortical cells †7–12.5 × 3.5–5 µm; **glassy processes** absent. **Anchoring hyphae** not examined. **SCBs** no data available. **Exudate** over paraphyses and marginal cells 0.2–0.3 µm thick, granular, firmly attached. **— ANAMORPH**: unknown.

Habitat: previous year's stems of *Conyza canadense* {1}, on medium decayed epidermis, slightly greyed, no algae. **Associated**: none observed. **Desiccation tolerance**: unknown. **Altitude**: 35 m a.s.l. **Geology**: Miocene sedimentary rock. **Phenology**: VIII.

Taxonomic remarks. Although mature, the type material is not in very good shape, and the ascospores could only be seen inside the asci. No further collections referable to this species came to our notice. *O. cookei* is probably very closely related to *O. caulicola*. The two species have very similar spores and perhaps also spore bodies, which do not appear to permit species recognition. The shape of the SBs in *O. cookei* was indistinctly seen in a single spore (Pl. 416: 1a right). The difference between the two species lies in the paraphyses, which are strongly capitate in *O. cookei* but uninflated to medium capitate in *O. caulicola*. In addition, the terminal cells of *O. caulicola* are often 2(–4)× as long as the lower cells, whereas those of *O. cookei* are rather equal in length, so that the absolute length of the terminal cells in the two taxa hardly overlaps. *O. cardui* (*section Arthrobotrys*) resembles *O. cookei* in spore size and shape, though the spores are distinctly narrower; the species clearly differs in larger apothecia, longer terminal cells of paraphyses with hardly swollen apex, covered by rather thick exudate, and in glassy processes at the margin.

Naevia canadica Rehm was described with characters similar to *O. cookei*, except for the filiform paraphyses (see p. 1663).

Nomenclature and type studies. Cooke's (1875a, b) very brief diagnosis of *Peziza exigua* includes 'lanceolate' asci and linear, scarcely 5 µm long spores. Saccardo (1889) and Seaver (1951) merely repeated Cooke's description, although Seaver examined the type material. Dennis (1964: 46) provided a rather detailed redescription of the holotype, which he found to represent a genuine *Orbilia*, though feeling unable to compare it with any known taxon of that genus. His measurements of asci (35 × 5 µm) and spores (6–8 × 1.5 µm) are slightly larger than in the present study. Apparently without personal examination, Raitviir (1991: 359) referred *P. exigua* to synonymy with *O. cardui*. Due to the existence of *Orbilia exigua* Velen., a new name is proposed here.

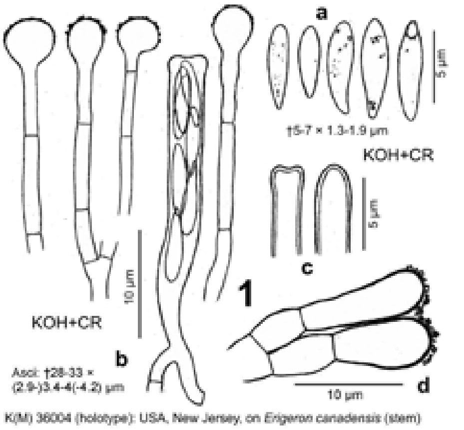


Plate 416. **1**: *Orbilia cookei*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section.

Ecology. *O. cookei* was collected in warm-temperate humid lowlands of New Jersey in eastern North America. According to Seaver (1951), several collections of this species were made by J. B. Ellis (preserved in the New York Botanical Garden), apparently always on stems of *Conyza* (as *Erigeron*).

Specimens included. **USA**: **New Jersey**, ~7 km N of Vineland, Newfield, unlocalized, 35 m, stems of *Conyza canadensis*, VIII.1873, J.B. Ellis (Ellis 1016, K(M) 36004, **holotype**, H.B. 5447 ø)

Orbilia stilbospora Baral, **sp. nov.**, MB 813744 — Pls 417–418

Etymology: named after the stilboid ascospore bases resembling a stalked head.

Typification: Australia, Queensland, Mossman, leaf of *Phragmites australis*, 28.VIII.2006, G. Marson (ex H.B. 8501c, BRI AQ799195, holotype).

Misapplied name: Zhang et al. (2009b: 151), as *O.* aff. *comma* (= *O.* ?*stilbospora*).

Latin diagnosis: *Similis* Orbiliae caulicolae *sed ascosporae basi valde attenuatae et constrictae*, *globulo leniter vel valde inflato terminatae. Habitat ad basim folii sicci*, *leniter putridi* Phragmitis australis *in zona tropica humida Australiae septentrio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.18–0.5 mm diam., 0.09–0.11 mm high, pale orange-rose to cream or light orange, slightly translucent, round, scattered; disc flat, margin distinct, 0–10 µm protruding, ± smooth; broadly sessile, superficial. **Asci** †29–41 × 3.1–3.5 µm, 8-spored, (1–)3–4(–5) lower spores inverted (± mixed or not); **apex** (†) strongly truncate (often distinctly indented, laterally inflated); **base** with medium long, ± thin, flexuous stalk, L-shaped. **Ascospores** *5.8–7.5(–8.5) × 1.3–1.5(–1.6) µm, †6–7.2 × 1.3(–1.4) µm, cylindric(-fusoid), apex (rounded to) obtuse, base abruptly constricted, with a globose to tear-shaped, 0.5–0.9 µm wide appendage-like lower part, straight to slightly inequilateral, tail *1–1.8(–2.2) × 0.6–0.9 µm; **SBs** 1.3–1.5 × 0.8–0.9 µm, globose to broadly tear-shaped, with a very short filum. **Paraphyses** apically (slightly to) medium to strongly (clavate-) capitate, terminal cells *9–20 × 2.8–4.2 µm, †2.8–3.8 µm wide, lower cells *4–8(–11) × 1.8–2.4 µm; unbranched at upper septum. **Medullary excipulum** 20–30 µm thick, of dense textura intricata-globulosa, medium sharply delimited. **Ectal excipulum** pale to light orange, of thin-walled, vertically oriented t. prismatica-globulosa at base, 30–40 µm thick near base, cells *9–16 × 7–12 µm; t. globulosa from flanks to submargin, 15 µm thick near margin, upper margin of t. prismatica-porrecta oriented at a 30–50° angle to the surface, marginal cortical cells

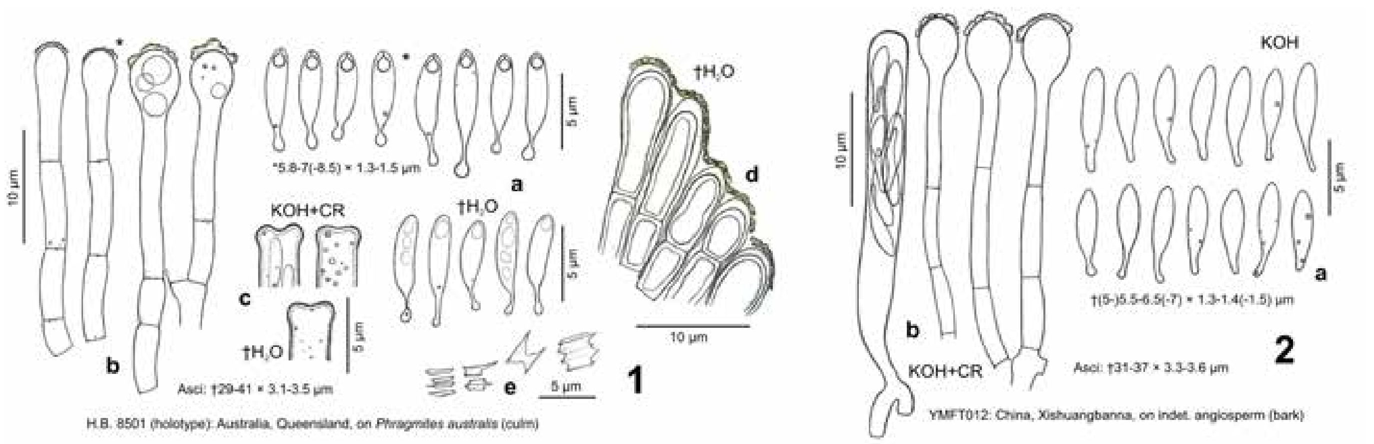


Plate 417. **1**: *Orbilia stilbospora*; **2**. *O.* cf. *stilbospora*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section; **e**. SCBs in ectal excipulum (base and flanks).

†6–10 × 2.7–3.7 µm, covered by indistinct **glassy caps** 1–1.5 × 3–5 µm. **Anchoring hyphae** sparse, †2–3 µm wide, walls 0.2 µm thick. **SCBs** in paraphyses globose, 1.5–2.5 µm diam., in ectal excipulum at base and flanks crystalloid, hyaline to very pale orange. **Exudate** over paraphyses and marginal excipulum 0.2–1.5 µm thick, granular-cloddy, firmly attached, hyaline or yellowish. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {1}). **Conidiophores** not seen. Very few **conidia** seen: †41–47 × 4–4.5 µm (*4.8 µm wide), narrowly fusoid, 5-septate, slightly curved.

Habitat: collected 0.1–0.5 m above the ground, ~10 mm thick standing culms of *Phragmites australis*, at base of leaf sheath on or close to node, slightly rotten, greyed or blackened, no algae. **Associated**: *Arthrinium arundinis*, *Orbilia ?atlantis*, *O. ?breviaristata*, *O. phragmitis*, *O. ?puyae*. **Desiccation tolerance**: many excipular cells and some paraphyses still viable after 11 months. **Altitude**: 390 m a.s.l. **Geology**: Devonian sedimentary rock. **Phenology**: VIII (but long-lived).

Taxonomic remarks. In the ascospores *O. stilbospora* resembles *O. caulicola*, to which it appears to be closely related. The basal globule, which is formed by a constriction of the spore base (similar as in the probably less related *O. abutilonis* and similar species, series *Abutilones*), is easily overlooked inside the asci, especially when these are dead. Like *O. caulicola*, members of series *Regales* differ in the absence of knob-shaped spore bases, partly also in distinctly wider spores, and partly in more spathulate paraphyses with glassy caps and pinkish apothecia.

Not included collection. A specimen on angiosperm bark from China (Pls 417: 2; 418: 2), published as *O.* aff. *comma* by Zhang et al. (2009), resembles *O. stilbospora* in the spore tails which are, however, only sometimes with a small globular inflation (tail size †1–2 × 0.4–0.6 µm). The SBs in this specimen are slightly longer and more tear-shaped than in *O. stilbospora* and more resemble *O. mali* (series *Regales*).

Anamorph. Two slightly curved phragmoconidia (Pl. 418: 1i) were observed near the apothecia. In *O. comma* and many other species of this section, the conidia are more canoe-shaped, i. e. more strongly curved at the ends.

Ecology. *O. stilbospora* was found at the base of the leaf sheath on a standing, dead, xeric culm of *Phragmites* being covered over large areas by the black conidial layer of *Arthrinium arundinis*, in a floodplain at the roadside in a tropical (sub)humid lowland of northeastern Australia between savannah and rainforest. The not included collection was from a tropical humid (winterdry) forest in southern China.

Specimens included. **AUSTRALIA**: **Queensland**, Einasleigh Uplands, 22 km SSW of Mossman, 2 km N of Mount Molloy, Mossman Mt. Molloy Rd, 390 m, leaf sheath of *Phragmites australis*, 28.VIII.2006, G. Marson (ex H.B. 8501c, BRI AQ799195, **holotype**, anam. substr.).

Not included. **CHINA**: **Yunnan**, **Xishuangbanna**, 50 km ESE of Jinghong, 2 km SE of Menglunzhen, Green Stone Forest Park, 600 m, branch of indet. angiosperm, on bark, 3.VIII.2005, M. Qiao (YMFT 012, as *O.* aff. *comma*, H.B. 8731).

Orbilia pisciformis Baral, Quijada & Beltrán-Tej., in Quijada et al., Nova Hedwigia 96: 243 (2012) — Pls 419–420, Map 72

Etymology: named after the ascospores somewhat resembling a fish.
Typification: Macaronesia, Tenerife, Teno Alto, stems of *Euphorbia balsamifera*, 3.V.2009, L. Quijada & R. Castro (TFC Mic. 22122, holotype).
Misapplied name: Korf (1992, p.p. 510: CUP MM 2555), as *O. occulta*.

Latin diagnosis: Orbiliae caudatae *similis sed ascosporae multo longiores, corpuscula refringentia majora, paraphyses apice processis vitreis tectae. Habitat ad lignum siccum* Euphorbiae *in zona subtropica semiarida ad arida Macaronesiae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.35–)0.4–0.8(–0.9) mm diam., (0.13–)0.15–0.23(–0.25) mm high, light to bright orange to rose-orange, not or slightly translucent, ± round, scattered to gregarious; disc flat, margin thin, 0–10 µm protruding, smooth; broadly sessile, superficial to slightly erumpent; dry slightly contracted, bright to deep orange-red. **Asci** *(59–)63–76 × 4.3–5(–5.8) µm {2}, †(45–)52–67 × 3.8–4.8 µm {3}, 8-spored, spores (*) biseriate, 3–5 lower spores inverted {3} (often mixed), pars sporifera *37–43 µm long; **apex** (†) strongly truncate (sometimes slightly indented and laterally inflated); **base** with medium to very long, thin, flexuous stalk, T- to often L-shaped. **Ascospores** *(7–)8–9.5(–11) × 1.9–2.3(–2.5) µm {3}, †(7.5–)8–10(–11.5) × 1.9–2.2(–2.3) µm {2}, fusoid (to fusiform), apex obtuse to subacute, straight, base always provided with a distinct, straight to sometimes slightly, rarely strongly curved, usually basally ± inflated tail *(1.5–)1.8–2.5(–3) × (0.7–)0.9–1.2 µm {1}, †1.5–3(–4) × 0.6–1(–1.2) µm {2}; **SBs** *1.7–2.3 × (0.9–)1–1.2(–1.5) µm in situ {3}, globose to broadly tear-shaped, with a very short filum, usually with 1 large (0.7–1.2 µm) and a few minute LBs. **Paraphyses** apically medium to strongly clavate-capitate, terminal cell *12–22 × (3–)3.5–4.5(–5) µm {1}, †14–23 × 2.2–3.3 µm {1}, lower cells *(7.5–)10–16 × 1.7–2.5 µm {1}, †9–14 × 1.2–2 µm wide {1} (near base *5–9 × 2–3.3 µm); unbranched at upper septum. **Medullary excipulum** hyaline to pale rose-orange, 30–80(–100) µm thick, lower part of ± dense textura intricata-globulosa, sharply delimited from ectal excipulum, sometimes by a distinct parallel 10 µm thick layer of t. porrecta, upper part of dense t. intricata. **Ectal excipulum** hyaline, of (†) slightly to medium gelatinized (common walls †1–1.7 µm thick), vertically oriented t. angularis-prismatica from base to mid flanks, 40–70(–85) µm thick near

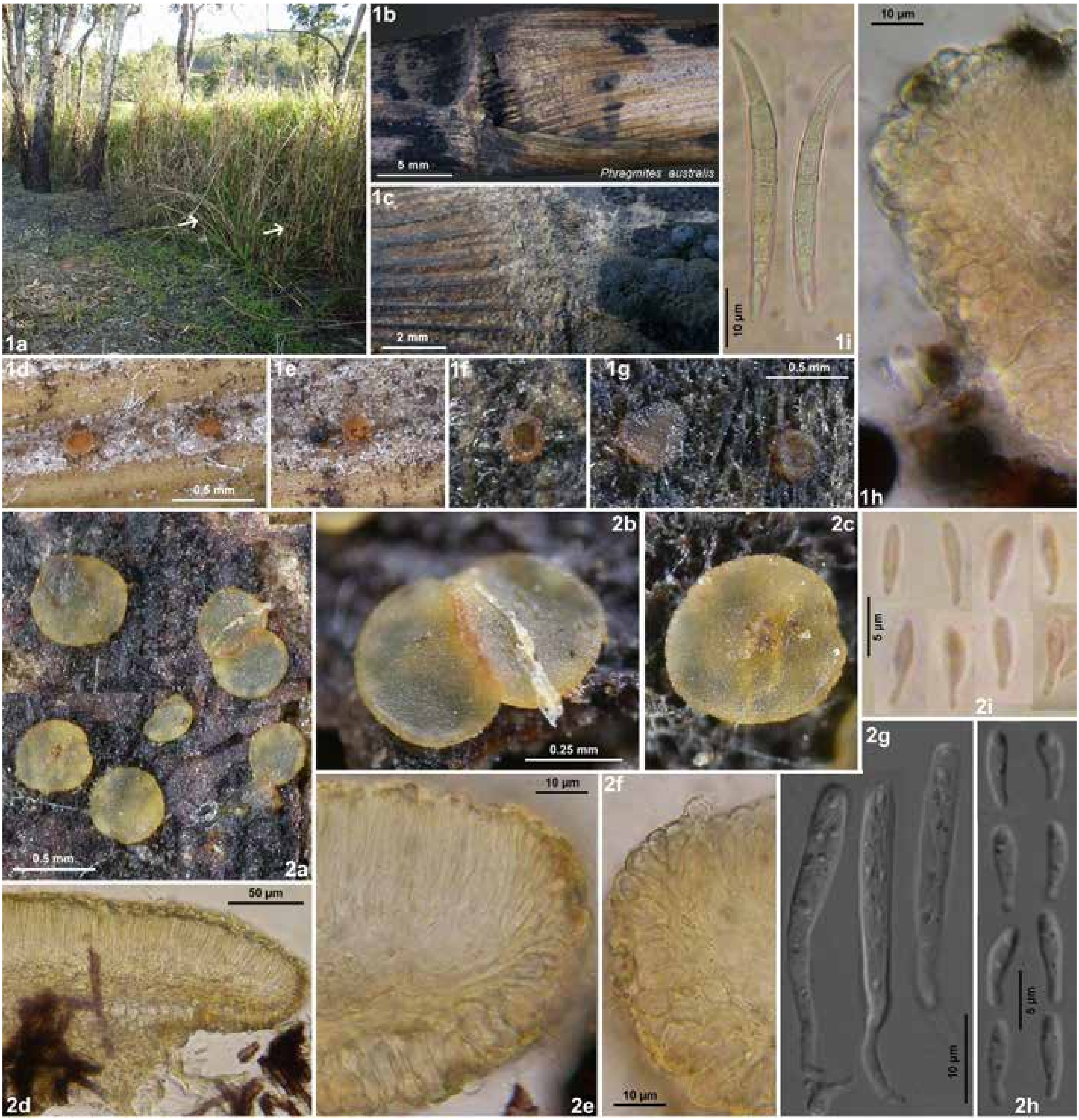


Plate 418. **1**: *Orbilia stilbospora*; **2**: *O.* cf. *stilbospora*. – **1a**. tropical *Phragmitetum* along roadside; **1b–c**. standing culms with black mould (*Arthrinium arundinis*); **1d–g**, **2a–c**. rehydrated apothecia; **2d**. apothecium in median section; **1h**, **2e–f**. id., marginal region; **2g**. asci; **2h–j**. ascospores; **1i**. conidia from substrate. – Dead state (**2d–f** in KOH, **2i–j** in KOH+CR), except for **1h**, spores in **2g–h**, and one conidial cell of **1i**. – **2g–h**: from Zhang et al. (2009b, DIC). — **1a–i**. H.B. 8501c (holotype): Australia, Queensland, on *Phragmites*; **2a–i**. YMFT 012: China, Xishuangbanna, on indet. angiosperm.

base, cells †8–11 × 7–13 µm {1} or */†(12–)15–25(–30) × (8–)9–16(–20) µm {2}; 15–25 µm thick near margin, of t. prismatica oriented at a 40–80° angle to the surface, marginal cortical cells *7–9 × 3.5–6 µm {1}; **glassy processes** 1–9 × 3–4.5 µm {3}, low-refractive, stratified. **Anchoring hyphae** abundant, †2–3(–4) µm wide (at insertion 5–6 µm), walls 0.2–0.5(–0.8) µm thick {3}, slightly gelatinous, forming a very loose t. intricata 40–50 µm thick. **SCBs** in paraphyses and ectal excipulum (near margin) globose, 1–2.3 µm diam.; in lowermost cells of paraphyses and in excipular cells at base and flanks also crystalloid, often delicate, in paraphyses as short lines, in ectal excipulum 5–10 µm large, ring- to irregularly lasso-shaped, also C-shaped or as parallel lines {6}, hyaline; light yellow **LBs** (carotenoids) abundant in cells of lower part of paraphyses, singly or scattered in basal ectal excipulum (here 1–2.5 µm diam.) {1} or absent {2}. **Exudate** over paraphyses and margin 1–4 µm thick, cloddy, loosely attached {1}, or cap-like (then perhaps covering glassy processes) and firmly attached {3}, pale yellowish. **— ANAMORPH**: unknown.

Habitat: lying on ground shaded by shrubs and woody debris, decorticated, 30–80 mm thick branches of *Euphorbia atropurpurea* {1}, *E. balsamifera* {1}, *E. canariensis* {10}, *E. lamarckii* {1}, on medium to strongly decayed outer surface of wood (xylem), sometimes in beetle galleries, not or slightly greyed, no algae. **Associated**: *Orbilia amarilla* {1}, *O. asomatica* {1+}, *O. beltraniae* {1}, *O.* aff. *farnesianae* {1}, overmature pyrenomycete {1}. **Desiccation tolerance**: fully tolerant for at least 3 months, ectal and medullary excipular cells, also

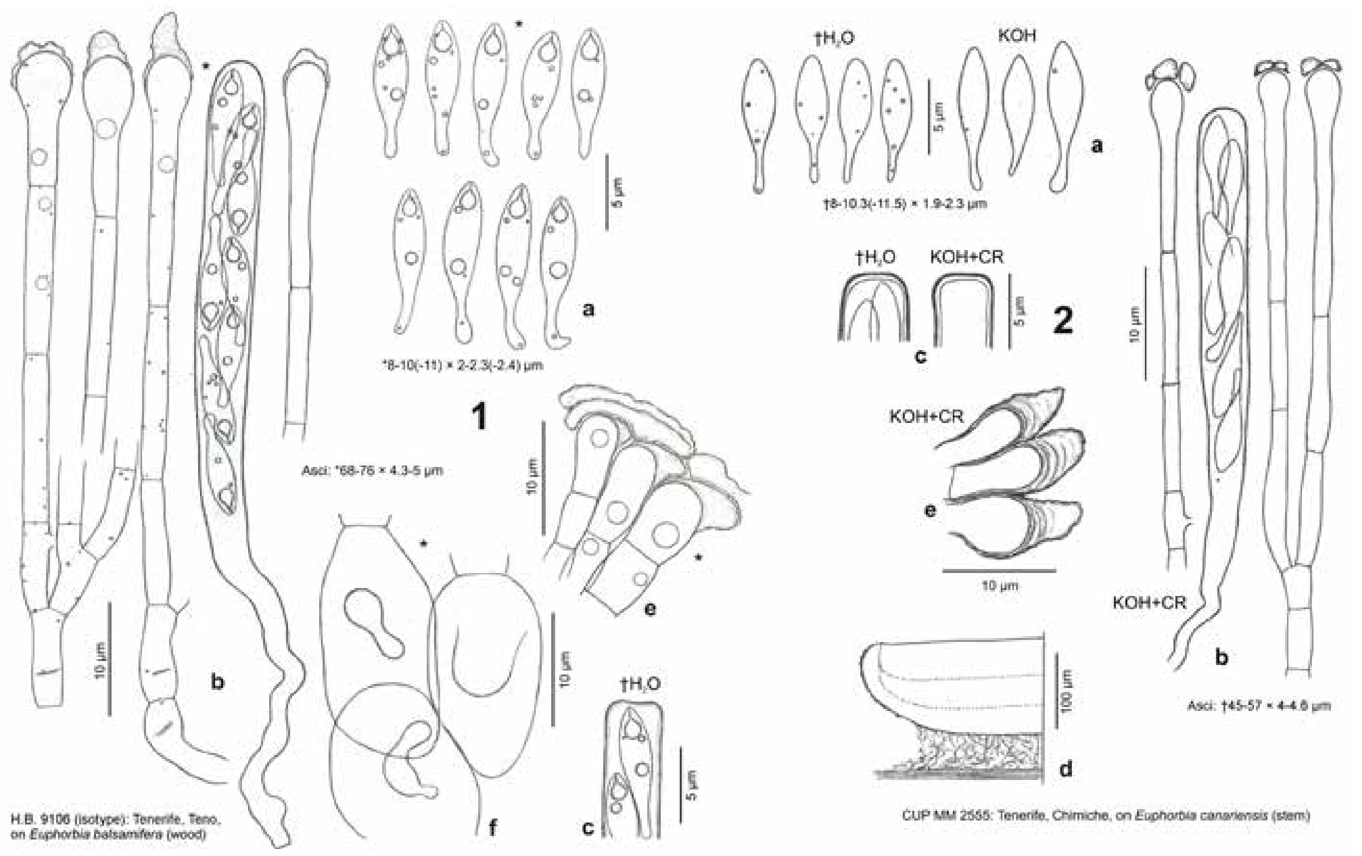


Plate 419. **1–2**: *Orbilia pisciformis*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal cortical cells with glassy processes; **f**. lasso-shaped crystalloid SCBs in cells of ectal excipulum at lower flanks.

ascospores partly alive after 13 months. **Altitude**: 25–345 m a.s.l. **Geology**: basaltic and trachybasaltic flows and pyroclasts, ignimbrite. **Phenology**: IX–VI (probably throughout the year).

Taxonomic remarks. *Orbilia pisciformis* is easily recognized by its fusoid, short-tailed ascospores with broadly tear-shaped SBs. It differs from *O. stilbospora* in distinctly larger spores and SBs, and from the temperate *O. mali* (series *Regales*) in slightly longer spores with a more straight upper part, and in often basally inflated spore tails, also in the presence of ring-shaped crystalloid SCBs in the excipulum. *O. comma* possesses very similar SCBs but sharply differs in helicoid spores with basally uninflated tails. *O. pisciformis* has also strong morphological affinities to *O. caudata* (series *Piliferae*), from which it mainly differs in longer spores, larger SBs, and in the paraphyses having glassy caps and longer lower cells.

Although rDNA data of *O. pisciformis* suggest a close relationship to series *Rubellae*, we prefer not to place it there because it lacks the characteristics of that series, namely septate hairs and spathulate to lageniform paraphyses.

Variation. *O. pisciformis* varied only slightly, mainly in length of the spore tails ranging among the collections between 1.5–2 and 2–3(–4) µm, also in the exudate which usually forms cap-like structures (Pl. 419: 1b), but also loosely adhering clods (2b). In the latter collection, the basal excipular cells were much smaller than in the other specimens whenever these cells were examined.

Misapplication. *O. pisciformis* was reported by Korf (1992) under the name *O. occulta*, a taxon of section *Hemiorbilia* that deviates in much longer and thinner spore tails, wider and shorter spore heads, in rather long marginal teeth, and particularly in hemispherical thick-walled ascus apices. The reexamined specimen (CUP MM 2555) consisted merely of some microtome sections.

Phylogeny. Sequences were taken from apothecia of TFC Mic. 23824 and 23766, comprising SSU (without S1506 intron), ITS, and LSU. Between the two strains only 1 nt differed in the ITS region and 1 nt in the LSU (D1–D3), while in the SSU (V8–V9) they are identical. *O. pisciformis* clustered in our analyses of ITS+LSU or ITS with high or medium support sister to series *Rubellae* (Phyls 13–14, S15). The distance in the ITS region lies at 9.5% to *O. phragmotricha*, 11.5% to *O. rubella*, and 13.5–14% to *O. comma*; in the LSU (D1–D2) the lowest distance is 2.2–2.6% to *O. phragmotricha*, but 3.5% to *O. albidorosea*, *O. comma*, *O. aurantiorubra*, and *O. caulicola*. This means that a close relationship to *O. comma* or *O. caulicola* is not supported, but for the time being we decided to keep *O. pisciformis* for morphological reasons in series *Commatoideae*.

Ecology. *O. pisciformis* is so far only known from Tenerife (Macaronesia), where it was recorded at 10 sites in 1977 and between 2009–2011, on rotten wood of xeric branches of different *Euphorbia* species, mainly *E. canariensis*, in inframediterranean, arid to lower semiarid, also hyperarid xerophytic scrublands along the southern, eastern, and western coastline (Korf 1992, Quijada et al. 2012). The species occurred in various associations, mainly tabaibal dulce (*Ceropegio fuscae-Euphorbietum balsamiferae*), but also cardonal (*Periploco laevigatae-Euphorbietum canariensis*), *Artemisio thusculae-Rumicion lunariae*, and *Launaeo arborescentis-Schizogynetum sericeae* (L. Quijada & E. Beltrán-Tejera pers. comm., most of these were earlier subsumed as *Kleinio-Euphorbietea canariensis*). The branches were always lying on the more or less shaded ground, nevertheless they were dry most time of the year.

Plate 420. **1–8**: *Orbilia pisciformis*. – **1**. subtropical arid tabaibal dulce (*Ceropegio fuscae-Euphorbietum balsamiferae*), dead stems of *Euphorbia canariensis*; **2a–b**, **6f–i**, **7**, **8**. rehydrated apothecia (**6g**, **i** with beetle galleries); **2c**. dry apothecium; **2d–e**. apothecium in median section; **2f**, **6b**. id., marginal ectal excipulum (with or without short glassy processes); **2l**. id., basal ectal and medullary excipulum; **6c**. id., hymenium (lower part with yellow-orange LBs); **2g–k**, **6d–e**. crystalloid, partly lasso-shaped SCBs in cells of ectal excipulum (lower flanks); **2n**, **3a**. mature asci; **2m**. truncate ascus apex; **2o**, **4**. paraphysis apices covered by caps of exudate; **2p–q**, **3b**, **5**, **6a**. ascospores. – Living state (**3a** maximum turgescence), except for **6b–c** (in H_2O), ascus in **2m**, paraphyses in **2o**, ascospore without SB in **2q** (in H_2O). – **1**, **2c**, **2m–o**, **q**, **3a–b**, **4**, **5**, **7**, **8**: phot. L. Quijada (**3b**, **4**, **5**, **7**: from Quijada et al. 2012). — **1**. TFC Mic. 22477: Tenerife, Güímar, on *Euphorbia canariensis*; **2a–b**, **2d–l**, **p**. H.B. 9106 (isotype), **2c**, **m–o**, **q**. TFC Mic. 22122 (holotype): ibid., Teno, on *E. balsamifera*; **3a–b**. TFC Mic. 22676: ibid., Montaña Amarilla, on *E. canariensis*; **4**. TFC Mic. 22870: ibid., Teno, on *E. canariensis*; **5**. TFC Mic. 22778: ibid., Abades, on *E. canariensis*; **6a–i**. H.B. 9670: ibid., Teno, on *E. canariensis*; **7**. 4. TFC Mic. 22151: ibid., Abades, on *E. canariensis*; **8**. 4. TFC Mic. 22294: ibid., Teno, on *E. canariensis*.

Map 72. Known distribution of *O. pisciformis* in Tenerife (Macaronesia).

Specimens included. **MACARONESIA**: **Canary Islands**, **Tenerife**, Buenavista del Norte, 5.2 km WSW of Buenavista del Norte, 3 km NW of Teno Alto, Punta de Teno, 122 m, branches of *Euphorbia balsamifera*, 3.V.2009, L. Quijada & R. Castro (TFC Mic. 22122, **holotype**; H.B. 9106, **isotype**). – ibid., Lomo las Toldas, 190 m, branch of *Euphorbia canariensis*, 27.XII.2012, L. & C. Quijada (TFC Mic. 23824; sq.: MH221072). – 2.8 km NW of Teno Alto, El Tosconito, 240 m, branch of *E. lamarckii*, 8.XI.2009, L. Quijada (TFC Mic. 22491, non vid.). – 2.8 km WNW of Teno Alto, Punta de Teno, 130 m, branch of *E. canariensis*, 18.II.2010, L. Quijada & R. Castro (TFC Mic. 22869–22870, doc. vid.). – 3.5 km WNW of Teno Alto, 100–145 m, branch of *E. canariensis*, 16.VI.2009, L. Quijada (TFC Mic. 22247–51, 22253–57, 22256–73, 22294, 22298–22304 etc., doc. vid.). – Los Silos, 3 km ESE of Buenavista del Norte, 1 km SW of Los Silos, 230 m, branch of *E. canariensis*, 20.III.2011, S. Feusi & E. Zimmermann (H.B. 9670). – Güímar, 4.5 km E of Güímar, 2.5 km S of El Socorro, Malpais de Güímar, 25 m, branch of *E. canariensis*, 5.XI.2009, L. Quijada (TFC Mic. 22473, 22477–80, doc. vid.). – Fasnia, 7.5 km SSW of Güímar, 1.5 km NE of Fasnia, Barranco de Herques, 345 m, branch of *E. atropurpurea*, 5.II.2010, L. Quijada (TFC Mic. 22821, 22835–36, non vid.). – Arico, 1 km WSW of Abades, Barranco la Vera, 50 m, branch of *E. canariensis*, 5.XI.2009, L. Quijada (TFC Mic. 22151–53 etc., doc. vid.). – 2.2 km NW of Abades, Montaña Centinela, 160 m, branch of *E. canariensis*, 23.I.2010, L. Quijada (TFC Mic. 22778). – Granadilla de Abona, 6.5 km ENE of San Isidoro, 5 km SE of Chimiche, Barranco del Rio, near motorway, 70 m, branch of *E. canariensis*, 27.I.1977, N. Lundqvist, vid. R.P. Korf (CUP-MM-002555, slide, as *O. occulta*, H.B. 5148 ø). – San Miguel de Abona, 4 km SSW of Las Chafiras, 1.5 km NE of Costa del Silencio, Montaña Amarilla, 30 m, branch of *E. canariensis*, 27.XII.2009, L. Quijada (TFC Mic. 22676, 22686–87, doc. vid.). – ibid., 35 m, branch of *E. canariensis*, 16.XII.2012, L. Quijada (TFC Mic. 23766; sq.: MH221073).

Orbilia comma Graddon, Trans. Br. Mycol. Soc. 69: 265 (1977) — Pls 421–423, Map 73

Etymology: refers to the spore shape that resembles a comma.

Typification: Great Britain, Warwickshire, Stratford-upon-Avon, branch of *Ulmus*, I.1975, M.C. Clark (K(M) 36048, holotype); Luxembourg, Manternach, branches of *Ulmus*, 4.V.2000, H.O. Baral, G. Marson & L.G. Krieglsteiner (ex H.B. 6639b, M-0291759, epitype, designated here, MBT385117, ex-epitype culture: CBS 116275; sq.: KT215258).

Misapplied names: Breitenbach & Kränzlin [1981, pl. 261 p.p. (colour photo)], as *Habrostictis rubra*; Persoon (1796 p.p.), as *Peziza aurea*.

Misinterpretation of *O. comma*: Baral (1987b: 428), = *O. xanthoguttulata*; Zhang et al. (2009b: 151, as *O.* aff. *comma*), ?= *O. stilbospora* (see p. 808).

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated (0.1–)0.3–1(–1.6) mm diam., 0.13–0.25(–0.3) mm high, light to bright rose-orange(-carneous) to orange, also pale whitish-rose-cream to light amber(-rose), translucent, round, ± strongly undulating when large, medium scattered to mostly (densely) gregarious in often large numbers when on inner surface of bark, fasciculate in small groups when erumpent from holes in periderm; disc young slightly concave, soon flat, rarely slightly convex, margin smooth, at first thick, protruding 0–10 µm, later thin, not protruding; broadly sessile, superficial; dry light to deep (rose-)orange-red to apricot, margin thick, sometimes with sparse white subiculum. **Asci** *(43–)47–65(–68) × (3.7–)4–4.8(–5.3) µm {9}, †38–57(–60) × 3–4.2 µm {5}, 8-spored, spores (*) biseriate, somewhat intertwined, ((1–))(2–)3–5(–6) lower spores inverted {13} (not or slightly mixed), pars sporifera *19–24(–27) µm long (†20–30 µm); **apex** (†) medium to strongly truncate (not indented, laterally sometimes inflated); **base** with medium to very long, slender, flexuous stalk, T-, L- or Y-shaped. **Ascospores** *(5.8–)6.5–7.5(–8) × (1.5–)1.7–2.1(–2.4) µm {21} (~7–9 µm actual length), †(5–)6–8(–8.5) × (1.5–)1.6–1.9(–2) µm {7} (up to 2.3 µm wide if flattened), fusoid- to fusiform-clavate, apex obtuse to subacute (to acute), base strongly attenuated in a tail-like end or distinct tail *1–2.5 × 0.3–0.8 µm, ± strongly helicoid (in profile view appearing 2× geniculate), tail straight; **SBs** *(0.9–)1.1–1.6 × 0.8–1.1(–1.2) µm {7}, (sub)globose to broadly tear-shaped, apically narrowed to a very short filum. **Paraphyses** apically uninflated or slightly (to medium) clavate-capitate, terminal cells *(11–)14–24(–32) × (1.8–)2.5–3.5(–4) µm {6}, †11–20 × (1.5–)2–3.5 µm wide {2}, lower cells *4.5–11 × 1.6–2(–2.5) µm {3}, †6–12.5 × 1.2–1.8 µm {2}; rarely branched at upper septum; hymenium pale to light orange-rose or yellow-orange. **Medullary excipulum** hyaline to very pale rose, 30–90 µm thick in centre, lower or upper part with many inflated cells forming a compact t. globulosa-angularis, otherwise a loose textura intricata, near margin 10–30 µm thick, of a rather loose t. intricata-porrecta, especially here quite sharply delimited. **Ectal excipulum** hyaline to pale orange-rose, of thin-walled or slightly gelatinized, vertically oriented t. globulosa-angularis-prismatica from base to margin, 40–70(–100) µm thick near base, cells *(8–)12–25(–35) × (7–)10–15(–20) µm {6}; 30–50 µm thick at lower flanks, 15–30 µm at mid flanks and margin, oriented at a 70–90° angle to the surface, marginal cortical cells */†(5–)7–15 × (2.5–)4–7(–9) µm {7}, (cylindric-)clavate(-subglobose), **glassy processes** absent. **Anchoring hyphae** abundant, */†1.5–3(–4) µm wide, walls (0.1–)0.2(–0.3) µm thick {7}, forming a dense or loose, hyaline t. intricata(-porrecta) ~10–30 µm thick. **SCBs** in paraphyses absent or globose, 1.5–2 µm diam., sometimes also a few filiform (crystalloid); in ectal excipulum towards margin often globose, 2–4 µm diam., also ring- to C-shaped, also as thin parallel lines, hyaline to pale yellowish-orange, at base and flanks frequently filiform to S- or ring-shaped {15}, 2–5(–8) × 1.5–3.5 µm, sometimes connected to each other; **LBs** in paraphyses sparsely present near septa, small, hyaline, in pigmented apothecia yellow-orange (carotenoids). **Exudate** over paraphyses 0.2–2(–3) µm thick, cloddy, pale to light yellowish-chlorinaceous, often firmly attached, also completely free and continuous; over margin and flanks (1–)2–4(–5) µm thick, rough, continuous or often large-cloddy to granular, subhyaline to light yellowish-chlorinaceous. — **ANAMORPH**: vermispora-like (from ascospore isolate {2} and natural substrate {8}). **Conidiophores** branched, 16–25 × 2–4 µm. **Conidiogenous cells** *7–9 × 1.8–2 µm, conidia formed terminally. **Conidia** unbranched, canoe-shaped, *(22–)30–50(–60) × 2.7–4.2 µm {6}, †21–44 × 2.4–3.2 µm {2} (all in situ), towards ends slightly to strongly curved (by 30–45°, at upper end up to 90°), middle part straight to slightly curved, (3–)7(–8)((–10))-septate; overmature wider [up to 5.5(–7.5) µm], more or less constricted at septa.

Habitat: dead, standing, more rarely fallen, 10–25 cm thick {20} trunks with loosely adhering bark, also on still-attached or fallen corticated twigs and branches, 5–25 mm {20} or 25–100 mm thick {21}, collected 0–4 m above the ground, bark still hanging or fallen in ± large pieces to the ground, of *Broussonetia papyrifera* {1}, *Ficus carica* {2}, *Morus nigra* {1}, *Robinia pseudoacacia* {1}, *Ulmus* sp. {33/8}, *U. glabra* {18/1}, *U. minor* {10/3}, *Wisteria* sp. {1}, on bark {77}, often on inner surface or on edges of bast {> 26}, also on outer surface of bast {15} or periderm {15}, partly over cracks, slightly to medium (to strongly) decayed, sometimes in beetle galleries, ungreyed, usually without but sometimes amidst abundant green algae, especially when on outer surface, then often growing among or on old perithecia or pycnidia {6} in small holes or cracks of periderm provoked by these fungi (*Chaetosphaeria*, *Diaporthe*, *Eutypella*, *Nectria*, *Thyridaria*, ?*Diplodia melaena* and others). **Associated**: *Annulohypoxylon*

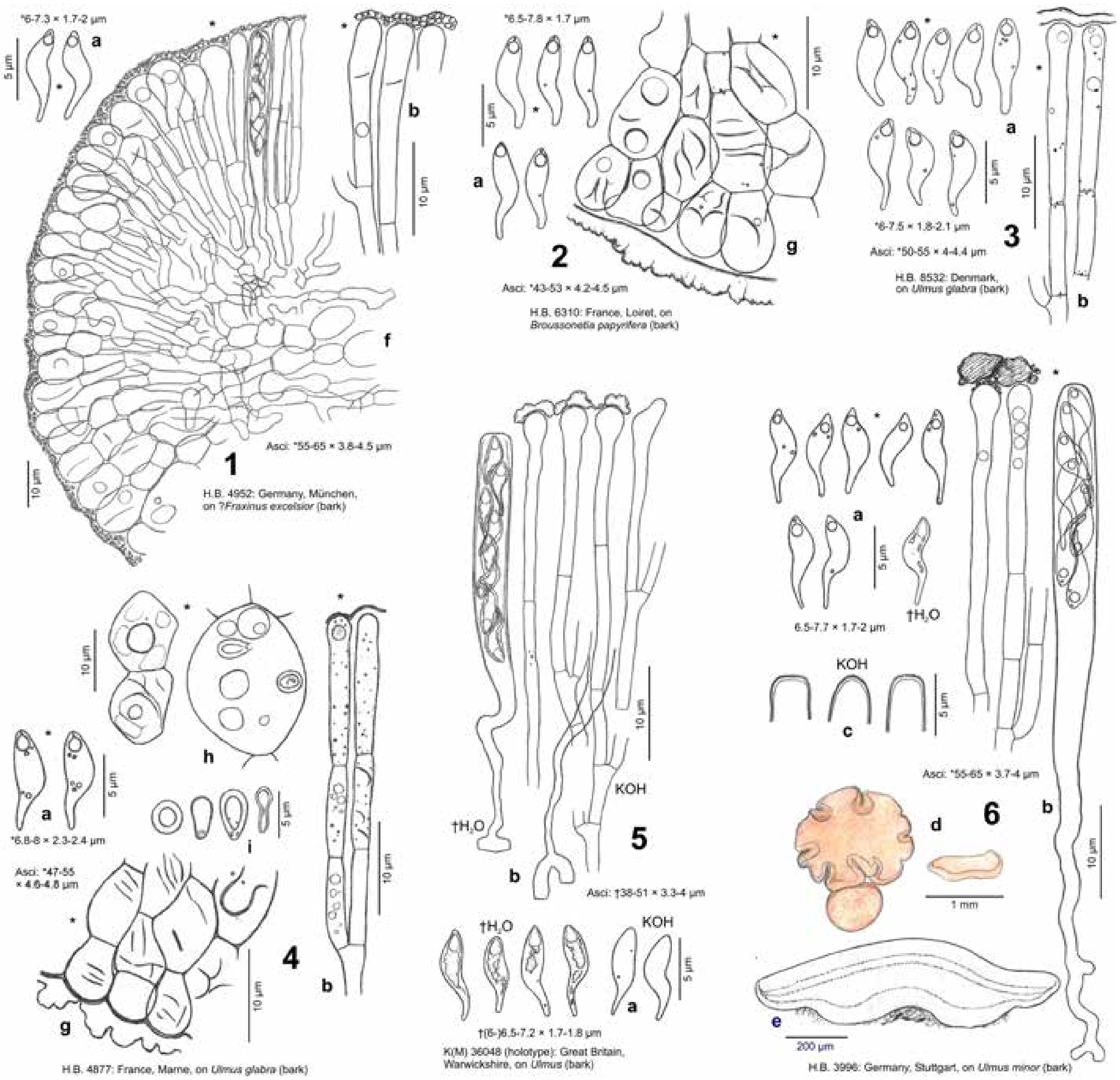


Plate 421. **1–6**: *Orbilia comma*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices (immature); **d**. apothecia (fresh); **e**. apothecium in median section; **f**. id., marginal ectal excipulum; **g**. id., at mid flanks; **g–i**. crystalloid SCBs in cells of ectal excipulum at flanks.

cohaerens {1}, *Auricularia auricula-judae* {1}, *Bionectria ralfsii* {1}, *Chaetosphaeria ovoidea* {1}, *Cistella chlorosticta* {1}, *Crepidotus cesatii* {1}, *Diaporthe* sp. {2}, *D. eres* {1}, *Eutypa* ?*stellulata* {1}, *Helminthosporium velutinum* {2}, *Hyalorbilia erythrostigma* (parasitic on *B. ralfsii*) {1}, *Lachnella alboviolascens* {1}, *Nectria* sp. {2}, *N. pseudopeziza* {2}, *Nitschkia* ?*collapsa* {1}, *Orbilia aurantiorubra* {1}, *O. auricolor* (anamorph) {1}, *O. carpoboloides* {2}, *O. ficicola* {2}, *O. rubella* {2}, *O. subfabacearum* {1}, *O. vitalbae* {1}, *O. xanthoguttulata* {1}, *Parmelia* sp. {1}, *Patellaria atrata* {1}, *Peroneutypa scoparia* {1}, *Pyrenopeziza caespiticia* {1}, *Thyridaria rubronotata* {1}, *Unguiculariopsis rehmii* {1}. **Desiccation tolerance**: Fully viable after 13 months, after 22 months many cells of ectal excipulum alive, after 26.5 months still many spores alive. **Altitude**: 5–900 m a.s.l. **Geology**: Devonian slate, Cambrian greywacke, Permian Zechstein (dolomite), Muschelkalk, Keuper (clay, sandstone), Lower & Upper Jurassic & Cretaceous marl- & limestone, flysch, dolomite, Eocene calcareous marl, Tertiary molasse, Pleistocene loess, sand, silt & till; granite, gneiss, basalt. **Phenology**: throughout the year (long-lived).

Phenology of *O. comma*

Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
4	6	8	8	18	3	3	4	6	6	7	3

Taxonomic remarks. *Orbilia comma* is easily recognized by its curved (helicoid) ascospores consisting of a thick fusoid to fusiform upper part and a ± short tail or tail-like base. Due to the helicoid curvature of about one complete turn, the spores look in profile view ± geniculate near the base and thus provoke a comma-like appearance. In the European *O. mali* (series *Regales*) and the Asian *O. basiflexa* (section *Ovoideae*) the spores are somewhat larger and do not show a helicoid curvature, and no crystalloid SCBs could be observed. The (sub)tropical *O. neocomma* differs from *O. comma* mainly in narrower spores, and the tropical *O. caudata* (series *Piliferae*) in straight spores, elongate SBs, and the partial presence of glassy processes.

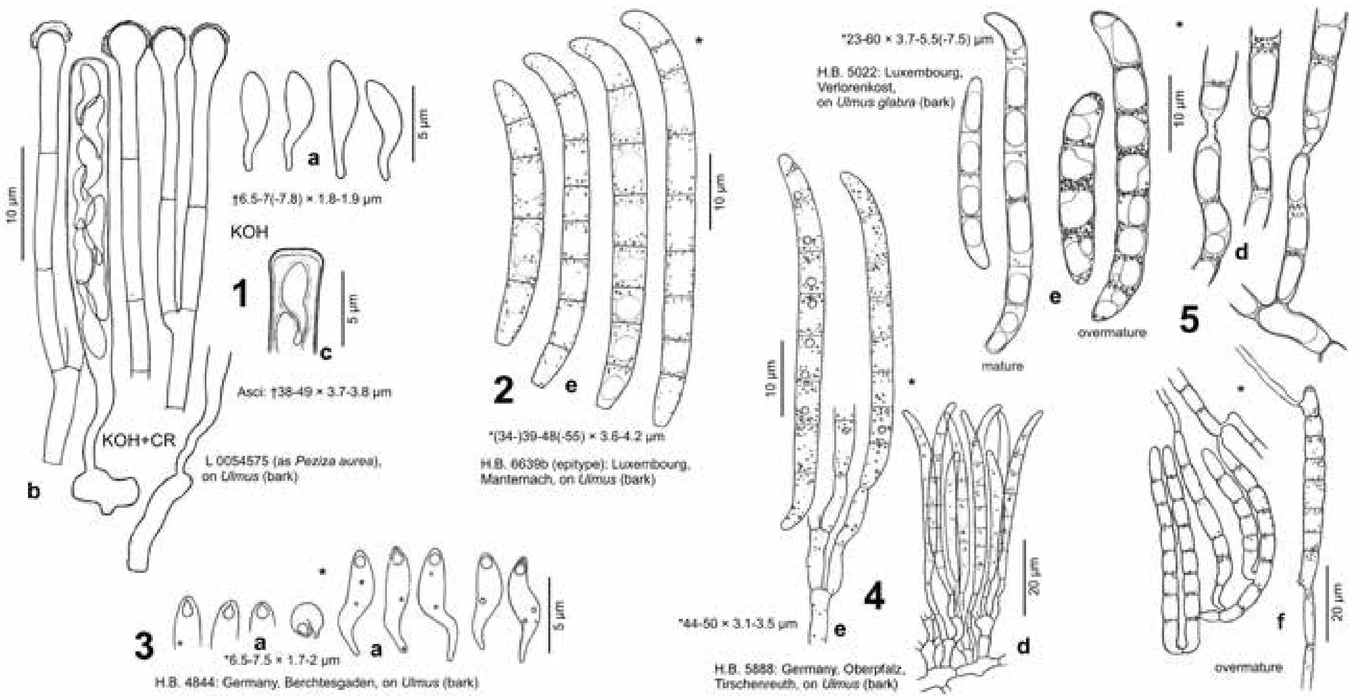


Plate 422. **1–5**: *Orbilia comma*. – **a**. ascospores (one seen from above showing helicoid curvature); **b**. ascus and paraphyses; **c**. ascus apex; **d–f**. conidiophores and conidia (**2** & **5** from culture, 4 from substrate).

Variation. The spores of *O. comma* vary somewhat in the shape of their apex (from obtuse to subacute), also in width (from *1.5–1.8 µm to *1.9–2.4 µm) and in tail length and width, but this variation is partly observed within a collection. The apothecia of *O. comma* are usually light to bright rose-orange but sometimes also much paler. In several collections the pale cream-coloured apothecia grew in populations more or less separate from the bright orange ones, but no microscopical differences were noted. The pale form appears to occur in more shady situations, on bark lying on the ground but also when still-attached. The yellow-orange LBs in the paraphyses and marginal ectal excipulum are only occasionally so abundant that they yield a distinct pale blue-green colour in IKI. Apothecial size may strongly vary among collections. For instance, apothecia in Pl. 423: 7 measured 0.2–0.25 mm diam., in 10b 0.25–0.5 mm, in 10a 0.5–1 mm, and in 2a 0.5–1.5 mm. No differences could be observed in collections on hosts other than *Ulmus*.

Type studies. Several differences between Graddon's (1977) protologue and the data here evaluated from the holotype (Pl. 421: 5) are worth mentioning. The rehydrated apothecia attain a size of 1.1 mm although Graddon gave the size as 'ad 500 µm'. Graddon described and figured the spores as comma-shaped (geniculate), apparently neglecting their helicoid shape (see Fig. 160). His figure shows viable spores which can be concluded from the drawn spore bodies ('guttula unica impleta'); nevertheless, his spore measurements (5–7 × 1.5–1.75 µm) are slightly smaller than evaluated here in the dead state from the type, and the SBs are ellipsoid instead of subglobose and more distant from the spore apex than found in the present reexamination. Graddon described the paraphyses as 'sine epithecio', although they are covered by rather thick exudate (Pl. 421: 5b). The ascus base he described as 'non-furcati', and he figured all 8 spores with their tails pointing downwards, a never seen situation in any of the here studied collections of *O. comma*.

A specimen from Luxembourg (Manternach, on *Ulmus*, ex H.B. 6639b), from which an ascospore isolate (CBS 116275) and a sequence were gained, is designated here as **epitype** of *O. comma*. Only a drawing of the conidia in culture exist for it (Pl. 422: 2), but a photo from an unpreserved topotype shows asci and spores (IVV: 10.II.2007), and from another topotype (G.M. 2016-05-04.2) a further sequence was gained.

Misapplication. The material treated in Breitenbach & Kränzlin (1981) as *Habrostictis rubra* was found to be a mixture: the colour photo shows *O. comma*, whereas the microscopic drawing belongs to *O. carpoboloides* (an older name for *H. rubra*). The report of a distinct blue-green-olive IKI reaction in *O. comma* by Baral (1987b) concerns a misidentification and refers to *O. xanthoguttulata*. Persoon's concept of *Peziza aurea* included a mixture of *O. xanthostigma*, *O. comma*, and *Dacrymyces chrysocomus* (see under *O. xanthostigma*, p. 1405). The *O. xanthostigma* collection is designated here as lectotype of *P. aurea*, because Donk's (1964) designation of the *O. comma* collection is in conflict with the protologue.

Anamorph. The phragmosporous conidia of *O. comma* have repeatedly been observed on the natural substrate close to apothecia (Pl. 422: 4), partly in black fruitbodies of old perithecia or pycnidia of unidentified ascomycetes. In two ascospore isolates the same anamorph developed in pure culture (Pl. 422: 2, 5).

Phylogeny. Sequences were taken from one of our ascospore isolates of *O. comma* (H.B. 6639b, from Luxembourg, *Ulmus*, SSU V8–V9, ITS, LSU D1–D2) and from apothecia from the same site 16 years later (G.M. 2016-05-04.2, ITS, LSU D1–D8). They fully concur in the ITS region with a sequence from apothecia (H.B. 9993, from Germany, Wismar, *Ulmus*, ITS, described and illustrated in Montag & Richter 2017: 62). In all the intron is absent.

O. comma clustered highly supported in the core clade of section *Aurantiorubrae* when analysing (SSU+)ITS+LSU (Baral et al. 2017b, Phyl. 13). The distance in the ITS region is generally high, with 13–14% to *O. aurantiorubra*, 13.5% to *O. phragmotricha*, 14.5% to *O. mali*, 16% to *O. rubella*, and 16–17.5% to *O. jugulospora*. In the LSU region (D1–D2) the minimum distance was 3.7% to *O. phragmotricha* and 4% to *O. aurantiorubra* and *O. jugulospora*. In the SSU (V8–V9) *O. comma* concurs with *O. aurantiorubra* but differs from *O. phragmotricha* by 3 nt. Interestingly, the two strains of *O. comma* deviate at pos. 128 of 5.8S by C instead of T as in all other *Orbiliomycetes*, except for *O. guyanensis* (G), see Tab. 18).

A sequence of a specimen identified by B. Liu as *O. brasiliensis* or *O. decipiens* (B.L. 4099, HMAS 139701), for which no illustration was available, comprises ITS and LSU. It showed a high distance to *O. comma*, with which it formed a weakly supported clade when analysing LSU (Phyl. S16).

Ecology. *O. comma* appears to be rather common in suitable forests at planar to colline but also montane altitude in meso- to orotemperate and hemiboreal humid but also submediterranean semihumid, atlantic to continental Europe. The species was almost exclusively found on slightly or medium decayed bark of *Ulmus* (*Ulmaceae*), on xeric or sometimes recently fallen twigs, branches and trunks, mainly from trees that were killed by the elm disease. Especially those large pieces of bark that detach from the dead main trunk often bear thousands of apothecia of this *Orbilia*. In western and southern Europe a few samples indicate occurrence on *Moraceae* (*Broussonetia*, *Ficus*, *Morus*), Further exceptions concern two collections on *Faboideae*: on *Robinia* in southern France (according to wood anatomy) and on *Wisteria* in Denmark.

The vegetation includes thermophilous but also shady, e.g. riparian, rather undisturbed forests on more or less rich soils, such as *Pruno-Fraxinetum*, *Fraxino-Aceretum pseudoplatani*, and *Querco-Ulmetum*. The collections from southern France on *Ficus* were in small dense mixed angiosperm woodlands with *Fraxinus* etc. in the suprasub- to mesosubmediterranean lower Rhône valley, and that on *Robinia* in a suprasubmediterranean forest in the Massif Central (Cevennes). The sample on *Morus* in Ticino was on branches cut and deposited on a heap a few years ago (F. Delmenico pers. comm.), while that on *Wisteria* was on an attached branch (T. Læssøe pers. comm., see https://svampe.databasen.org/observations/9187203). In eastern Europe, *O. comma* was recorded on *Ulmus* in continental, cold-temperate to thermoboreal Russia (E. Popov pers. comm.) and suprasubmediterranean Ukraine (Yatsiuk 2018).

Previously, *O. comma* has been recorded merely from Great Britain. Clark (1980a, 1980b) discovered the fungus in Warwickshire, but reported also collections from Yorkshire and Scotland (Perth). The database of the British Mycological Society reports 39 records for Great Britain and northeastern Ireland, most of them on *Ulmus*, but also some questionable ones on other hosts (Kirk & Cooper, http://www.fieldmycology.net/Index.htm, accessed III.2015).

Specimens included. **GREAT BRITAIN**: **Yorkshire**, **South Yorkshire**, 18 km ESE of Sheffield, 2 km SE of South Anston, Anston Stones Wood, 80 m, branch of *U. glabra*, on bark, 16.V.2011, P. Thompson & B.M. Spooner (ø). – ibid., 1.3 km SE of South Anston, 90 m, branch of *U. glabra*, on bark, 16.V.2011, H.O. Baral, J.H. Petersen & T. Læssøe (H.B. 9510, J.H.P. 11.108, P.T., K(M) 170582, 1785472). – **East Midlands**, **Nottinghamshire**, 8.5 km SW of Gainsborough, 6 km ENE of Retford, Clarborough, 60 m, branch of ?*Ulmus*, on bark, 3.III.2014, H. Williams (H.W. Box A14, doc. vid.). – **West Midlands**, **Herefordshire**, 10.5 km SW of Ludlow, 8.5 km NNW of Leominster, N of Croft Castle, Fishpool Valley, 197 m, branch of *U. glabra*, on bark, 4.XII.2016, P. Thompson (P.T. 4/12/16-15, anam. substr., doc. vid.). – **Warwickshire**, 6 km WSW of Stratford-upon-Avon, S of Binton, Binton Hill, ~80 m, branch of *Ulmus*, on bark, I.1975, M.C. Clark (W.D. Graddon 2489, K(M) 36048, **holotype**, H.B. 5532 ø). – **East England**, **Suffolk**, 3.7 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 17 m, trunk of *U. minor*, on bark, 19.VII.2004, E. Batten (E.B. 4545, K(M) 158892, doc. vid.). – ibid., branch of *U. minor*, on bark, 22.VIII.2004 (E.B. 4553, K(M) 158893, doc. vid.). – ibid., 12.IX.2004 (E.B. 4560, K(M) 188009, doc. vid.). – ibid., 25.XII.2004 (E.B. 4575, K(M) 158910, doc. vid.). – ibid., 31.X.2004 (E.B. 4570, K(M) 199079, H.B. 7613a, anam. substr.). — **NORWAY**: **Aust-Agder**, 5 km ENE of Arendal, Tromøy, Kvernhuskjerr, 18 m, trunk of *U. glabra*, on bark, 12.IV.2008, T.H. Dahl (H.B. 8962). – ibid., 22.III.2009 (T.H.D. 72/09, doc. vid.). – **Akershus**, 23 km E of Oslo, 3.5 km ESE of Lillestrøm, Fetsund Ravine, 147 m, on bark of *Ulmus*, 5.V.2013, T. Læssøe (T.L. 2013-071b, non vid.). — **SWEDEN**: **Skåne**, Schonen, 8 km SSE of Lyungbyhed, 0.7 km NNW of Röstånga, Nackarp, 85 m, trunk of *U. ?glabra*, on bark, 5.VI.2006, T. Læssøe (T.L., H.B. 8199a, anam. substr.). — **DENMARK**: **Sjælland**, 6.5 km S of Sorø, 4 km S of Frederiksberg, Suserup Skov, 30 m, branch of *U. glabra*, on bark, 25.V.2007, H.O. Baral & B.M. Spooner (H.B. 8505, K(M) 147773). – 10 km WSW of Roskilde, 1.2 km W of Lejre, Ledreborg Skov, 30 m, *U. glabra*, on bark, 5.V.2012, T. Læssøe (ø, non vid.). – 9 km SW of København, 0.9 km WNW of Avedøre, Vestvolden, 8 m, *Ulmus*, on bark, 24.II.2001, T. Læssøe (J.H.P. 01.004, T.L. 6462, non vid.). – 3 km NNE of Virum, E of Holte, Øverød, N of Søllerød Sø, 38 m, branch of *Wisteria*, on bark, 20.II.2017, A. Jørgensen, vid. T. Læssøe (C, doc. vid.). – Møn, 17 km E of Stege, 1.6 km ENE of Busene, Møns Klinteskov, 50 m, branch of *U. glabra*, on bark, 30.V.2007, H.O. Baral (H.B. 8532). – **Syddanmark**, Fyn, 9 km E of Ringe, Lykkesholm, 60 m, *Ulmus*, on bark, 9.X.2001, L.M. Svendsen (J.H.P. 01.352, non vid.). — **GERMANY**: **Mecklenburg-Vorpommern**, 5 km W of Wismar, E of Proseken, Prosekener Grund, 35 m, trunk of *Ulmus*, on bark, 27.IV.2016, T. Richter (H.B. 9993; sq.: MK493130). – **Nordrhein-Westfalen**, 4 km W of Mönchengladbach, 1 km SW of Venn, 70 m, branch of *U. minor*, on bark, 14.XII.2007, H. Bender (doc. vid.). – **Hessen**, Lahntal, 21 km NW of Marburg, Biedenkopf, Schlossberg, 350 m, trunk of *Ulmus*, on bark, 30.IV.2000, L.G. Krieglsteiner & H.O. Baral (H.B. 6626a). – Rhön, 6.3 km NE of Gersfeld, 2.2 km SSW of Ehrenberg, Schwarzwald, 700 m, branch of *Ulmus*, on bark, 24.XI.2003, L.G. Krieglsteiner (ø). – **Baden-Württemberg**, 7.5 km NW of Stuttgart, 1.3 km WSW of Weilimdorf, Fasanenwald, 345 m, trunk of *U. minor*, on bark, 11.II.1990, H.O. Baral & O. Baral (H.B. 3996). – ibid., trunk of *U. minor*, on bark, 2.V.1990, H.O. Baral & O. Baral (ø). – Schönbuch, 3.5 km NE of Tübingen, 1.5 km SW of Pfrondorf, Bitzle, 425 m, trunk of *Ulmus*, on bark, 16.I.1994, H.O. Baral & E. Weber (H.B. 5021). – ibid., branch of *Ulmus*, on bark, 22.V.1994, H.O. Baral (ø). – ibid., branches & trunk of *Ulmus*, on bark, 4.X.1994, H.O. Baral & K. Siepe (H.B. 5157a). – 1.2 km SE of Pfrondorf, 345 m, trunk of *Ulmus*, on bark, 10.III.2002, H.O. Baral & E. Weber (ø). – Schwäbische Alb, 7 km E of Metzingen, 2.2 km S of Neuffen, Winnender Berg, N of Karlslinde, 660 m, trunk of *Ulmus*, on bark, 25.V.2005, H.O. Baral (H.B. 7788 ø). – 6 km SW of Aalen, 3 km WNW of Oberkochen, Hohlgasse, 600 m, branch of *Ulmus*, on bark, 11.VII.1997, K. Neff (H.B. 7589). – 1.3 km N of Oberkochen, Heide, 640 m, branch of *Ulmus*, on bark close to old perithecia, 16.III.1995, K. Neff (K.S., H.B. 5742a, anam. substr.). – ibid., branch of *Ulmus*, on bark and *Thyridaria rubronotata*, 25.III.1996, K. Neff, vid. K. Siepe (K.S. 24/96, H.B. 5770b). – **Bayern**, **Unterfranken**, Maintal, 23 km ENE of Würzburg, 1.7 km SE of Volkach, E of Halbmeile-See, 230 m, trunk of *Ulmus*, on bark, 8.XI.1994, L.G. Krieglsteiner (L.K.). – ibid., branch & trunk of *U. ?minor*, on bark and old *Eutypella stellulata*, 12.XI.1995, H.O. Baral & L.G. Krieglsteiner (L.K., H.B. 5378a). – 4.5 km SSE of Schweinfurt, Senftenhofsee, 212 m, branch of *U. minor*, on bark, 3.IV.1995, L.G. Krieglsteiner (L.K.). – **Oberpfalz**, Oberpfälzer Wald, 12.5 km NE of Tirschenreuth, 1.2 km S of Neualbenreuth, SE of Platzermühle, 550 m, branch of *Ulmus*, on bark and old pyrenomycete, 26.VIII.1997, H.O. Baral (H.B. 5888, anam. substr.). – **Oberbayern**, ~10 km SSE of München, Pullach, unlocalized, ~600 m, branch of *U. minor*, on bark, 5.V.1883, J.N. Schnabl (herb. Allescher, M, as *O. luteorubella*). – 15 km NW of München, 3 km NNE of Ismaning, Isarau W of Fischerhäuser, 485 m, trunk of *Ulmus*, on bark, 18.IX.1993, D. Triebel & G. Rambold (M-0229711, as *Fraxinus*, H.B. 4952). – 5.5 km NNW of Bad Reichenhall, 1.2 km SW of Aufham, Aufhamer Wald, 670 m, branch of ?*Ulmus*, on bark and *Nectria* sp., 21.XI.2014, I. Rößl (doc. vid.). – 1.8 km NW of Berchtesgaden, 1.3 km NE of Stanggaß, S of Aschauerweiher, 660 m, branch of *Ulmus*, on bark, 12.XI.1992, G. Rambold (D. Triebel MFE 82a/b, M-0040064/065, H.B. 4844). — **NETHERLANDS**: **Limburg**, 4 km ESE of Boxmeer, NW of Afferden, Boswachterij Bergen, 12 m, trunk of *Ulmus*, on bark, 19.IV.2010, S. Helleman (S.H. 654, non vid.). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 9 km NW of Redange, 0.7 km W of Holtz, Gebrannte Boesch, 400 m, trunk of *U. glabra*, on bark, 7.V.1999, H.O. Baral & G. Marson (ø). – **Gutland**, **Grevenmacher**, 3.5 km N of Grevenmacher, 1.5 km E of Manternach, W of Fielsmillen, valley of Syre, 190 m, branches of *Ulmus*, on bark, 4.V.2000, H.O. Baral, G. Marson & L.G. Krieglsteiner (ex H.B. 6639b, M-0291759, **epitype**, CBS 116275, anam. cult.; sq.: KT215258). – ibid., branch of *Ulmus*, on bark, 10.II.2007, M.T. Tholl (ø). – ibid., branches of *Ulmus*, on bark, 4.V.2016, G. Marson (G.M. 2016-05-04.2; sq.: MK473414). – **Luxembourg**, 3 km ESE of

Plate 423. **1–10**: *Orbilia comma* (all on *Ulmus*). – **1c**. *Ulmus glabra* mixed forest on cretaceous soil, detached bark pieces hanging from *Ulmus* branch; **4**, **5**, **7**. outer surface of bark; **1–3**, **10b**. inner surface of bark; **10a**. edge of broken bark; **1a–b**, **2a**, **3a–b**, **4**, **5a–b**, **7b**, **10a–b**. fresh or rehydrated apothecia; **2b**. dry apothecia; **2c**. apothecium in median section; **9**. id., marginal ectal excipulum; **2d**. id., basal excipulum containing filiform SCBs; **6**, **8**. ascospores. – Living state, except for asci in **8**. – **3a–b**: phot. K. Homble; **4**: phot. T.H. Dahl; **5a–b**: phot. H. Bender. — **1a–c**. H.B. 8532: Denmark, Møn; **2a–d**. H.B. 8505: ibid., Sjælland; **3a–b**. H.B. 8962: Norway, Arendal; **4**. 15.IV.2009: ibid.; **5a–c**. 14.XII.2007: Germany, Mönchengladbach; **6**. Spain, Gipuzkoa; **7a–b**. H.B. 7613a: Great Britain, Suffolk; **8**. 10.II.2007: Luxembourg, Manternach; **9**. H.B. 8199a: Sweden, Skåne; **10a–b**. H.B. 9510: Great Britain, Sheffield.

Map 73. Known distribution of *O. comma* in Europe.

Luxembourg, Verlorenkost, Durensbësch, 282 m, branch of *U. glabra*, on bark old *Diaporthe*, 23.VIII.1993, G. Marson (H.B. 4935a). – ibid., on bark of *U. glabra*, 28.XII.1993, G. Marson (H.B. 5022, anam. cult.). – 7.5 km ESE of Luxembourg, 1 km NE of Contern, Schlaederbaach, 308 m, trunk of *Ulmus*, on bark, 14.IX.2000, G. Marson (K(M) 80009). – 5 km S of Luxembourg, 1.5 km W of Hesperange, Biersak/Géisselbierg, 290 m, branch of *Ulmus*, on bark, 26.X.1993, G. Marson (H.B. 4970). – **Esch-sur-Alzette**, 8 km E of Bettembourg, 1.5 km E of Frisange, Homet, 240 m, trunk of *U. minor*, on bark, 30.V.2004, G. Marson (ø). – **Capellen**, 17 km N of Esch-sur-Alzette, 1.5 km SSE of Dippach, railway station, 320 m, branch of (?)*Ulmus*, on bark and pyrenomycete, 8. XI.1994, G. Marson (ø). — **FRANCE**: **Bretagne**, **Morbihan**, 2 km NE of La Gacilly, Lieuvy, 10 m, trunk of *U. minor*, on bark, 30.III.2013, J.P. Priou (J.P.P. 13062, doc. vid.). – **Champagne-Ardenne**, **Marne**, Brie, 14 km W of Sézanne, 2.3 km WSW of Esternay, Bois de Nogentel, 185 m, branch of *U. glabra*, on bark, 15.V.1993, H.O. Baral & G. Marson (H.B. 4877). – **Centre**, **Loiret**, 4.5 km N of Montargis, SW of Cepoy, SE of Montenon, 81 m, branch *Broussonetia papyrifera*, on bark and old perithecia, 3.II.1999, L. Gauthier (H.B. 6310, anam. substr.). – **Haute-Normandie**, **Seine-Maritime**, Normandie, 10 km SE of Rouen, 2 km SW of Boos, Bois des Dames, trunk of *Ulmus*, on bark, IV.1997, J.C. Malaval (J.C.M. 97055, H.B. 5802). – **Poitou-Charentes**, **Deux-Sèvres**, Poitou, 15 km NE of Melle, E of Chenay, 135 m, branch of *U.* (?)*minor*, on bark, 28.IV.2011, B. Rivault (ø). – **Vienne**, 6.5 km NW of Adriers, 1 km S of Nérignac, E of Les Aimardières, 160 m, trunk of *Ulmus*, on bark, 19.III.2006, B. Coué (H.B. 8157). – **Languedoc-Roussillon**, **Gard**, 13 km WSW of Alès, 5.5 km SE of St.-Jean-du-Gard, W of Corbès, 163 m, branch of *Robinia pseudoacacia*, on bark, 25.IX.1993, G. Marson (H.B. 4994). – **Rhône-Alpes**, **Drôme**, 13.5 km SSE of Montélimar, 2 km NNE of Roussas, 150 m, branch of *Ficus carica*, on bark, 13.X.2016, G. Marson (G.M. 2016-10-13.3). – **Ardèche**, 1.5 km SSE of Vallon-Pont-d'Arc, S of La Combe St.-Pierre, 90 m, branches of *F. carica*, on bark, 12.IX.2016, G. Marson (G.M. 2016-09-12.2, H.B. 10138b). — **SWITZERLAND**: **Schaffhausen**, 2 km ENE of Schaffhausen, W of Gennersbrunn, Langegerten, 485 m, branch of *Ulmus*, on bark, ~2.I.1987, P. Blank (P.B. 463). – **Obwalden**, 3.3 km WNW of Alpnach, 2.3 km NW of Schoried, Gärteli, 900 m, branch of *Ulmus*, on bark and old *Neonectria* ?*coccinea*, 28.IV.1979, T. Honermann (NMLU 2804-79 Ho3, as *Rhamnus frangula* [= *Frangula alnus*]). – **Graubünden**, 6.3 km ENE of Landquart, NW of Grüsch, SE of Seewis, 860 m, trunk of *U. glabra*, on bark, 20.VIII.2014, E. Weber (ø). – **Ticino**, 4 km ENE of Mendriso, 2.7 km NE of Castel San Pietro, SE of Monte, 645 m, branches of *Morus nigra*, on bark, 5.V.2015, F. Delmenico (anam. substr., doc. vid.). — **AUSTRIA**: **Niederösterreich**, Wienerwald, 17 km SW of Wien, 2 km W of Gießhübl, N of Wassergspreng, 400 m, branch of *U. glabra*, on bark, 15.V.2004, H. Voglmayr (ø). – 21 km SW of Wien, 1.1 km W of Gaaden, Schlößlwald, Dürnbach, 340 m, branch of *U. glabra*, on bark, 1.XII.2015, M. Mann (M.M. 151115-6, doc. vid.). – **Tirol**, Inntal, 11 km ESE of Nassereith, 0.5 km W of Stams, Stamser Eichenwald, 650 m, branch of *U. glabra*, on bark, 1.IX.2003, W. Jaklitsch (W.J. 2348, non vid.). – 10 km WNW of Graz, 2 km E of St. Oswald, Burg Plankenwarth, 600 m, branch of *Ulmus*, on bark, 19.I.2014, I. Wendelin, vid. G. Friebes (G.F. 20140013, doc. vid.). – ibid., 7.XII.2014 (GJO 73847, doc. vid.: Friebes 2017: 23, figs 21, 23o). — **SERBIA**: **Vojvodina**, Fruška Gora, 12.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, W of WWII memorial, 430 m, log of *Ulmus*, on bark, 7.V.2019, D. Savić (FG-1062, doc. vid.). – ibid., WSW of WWII memorial, 460 m, branch of *Ulmus*, on bark, 5.VI.2019, D. Savić (FG-1081, non vid.). — **SPAIN**: **País Vasco**, **Gipuzkoa**, 11 km SSE of Zarautz, 2.8 km WSW of Asteasu, 265 m, branch of *U. glabra*, 8.III.2014, J. Martin (ARAN-F A3042092, doc. vid.). — **POLAND**: **Kuyavia-Pomerania**, 14 km NW of Bydgoszcz, 1 km W of Mochle, 100 m, trunk of *Ulmus*, on bark, 12.II.2019, P. Drzewiecki (anam. substr., doc. vid.). — **RUSSIA (West)**: **Leningrad**, **Kirovsk**, 68 km E of St. Petersburg, 5 km N of Naziya, S of Ladoga Lake, Canyon of Lava River, 42 m, on bark of *Ulmus*, 11.VI.2009, E.S. Popov (LE 247357, doc. vid.). – **Bryansk**, **Suzemka**, Bryanskiy Les, 95 km SSW of Bryansk, 14 km SSE of Trubchevsk, NW of Chukhrai, Nerussa River, 138 m, branch of *Ulmus*, on bark, 23.X.2012, E.S. Popov (LE 247942, doc. vid.). — **UKRAINE**: **Kharkiv**, 41 km S of Kharkiv, 8 km SSW of Zmiiv, 1 km E of Haidary, Homilsha forest, 145 m, branch of ?*Ulmus*, on bark, 21.VII.2000, A.Y. Akulov, vid. I.I. Yatsiuk (CWU Myc AS2014, doc. vid.). — **UNLOCALIZED**: on bark of *Ulmus*, undated, C.H. Persoon (L 910.261-29, L0054575, H.B. 8773 ø). – branch of ?*Ulmus*, on bark, 1839, F.M.J. Welwitsch (herb. Martius, BR, H.B. 8790 ø).

Orbilia neocomma Baral, S.F. Li, J.W. Guo, Z.F. Yu & G. Marson, **sp. nov.**, MB 825632 — Pls 424–425, Map 74

Etymology: named after the close resemblance to *O. comma*.

Typification: Australia, Queensland, Mingela, branch of indet. climber, 17.X.1998, G. Marson (ex H.B. 6280f, BRI AQ799182, holotype).

Latin diagnosis: *Similis* Orbiliae commae *sed ascosporae angustiores, cauda basali distincte curvata. Habitat ad corticem putridum ramulorum vel ramorum siccorum fruticum angiospermarum in zona tropica vel subtropica humida ad subhumida Americae septentrionalis et meridionalis, Asiae et Australiae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.25–)0.3–1(–1.5) mm diam., 0.13–0.2 mm high (receptacle 0.09–0.1 mm), pale to bright orange-rose, ± translucent, round to somewhat undulating, scattered to gregarious; disc slightly concave to slightly convex, margin distinct, 0–10(–30) µm protruding, smooth to very finely crenulate; sessile on a broad or narrow base, superficial, partly, immersed between fibres; dry light to deep orange(-rose). **Asci** *45–52 × 4.2–4.5(–5) {T}, †(25–)35–47(–53) × (3–)3.2–4(–5) µm {4}, 8-spored, spores *2–3-seriate (†1–2-seriate), intertwined, 4–5(–6) lower spores inverted {2} (often mixed); **apex** (†) strongly truncate (not or very slightly indented, laterally sometimes inflated); **base** with short to long, ± thin, flexuous stalk, T- to L-shaped. **Ascospores** *(5–)6–8(–9) × (1.3–)1.4–1.5(–1.6) µm {3} (~6–10 µm actual length), †(6–)6.5–7.5(–8.5) × 1.1–1.4 µm {3}, fusoid-clavate, apex obtuse to subacute, base strongly attenuated in a tail-like end or distinct tail *(1–)1.5–2(–2.5) × 0.3–0.6 µm, strongly helicoid (in profile view appearing 2–3× geniculate), tail straight or often slightly to strongly curved, entire spore strongly helicoid, performing ~1–1.5(–2) turns; **SBs** *0.9–1.5 × 0.7–0.9 µm {2}, (sub)globose to broadly tear-shaped, apically narrowed to a very short filum. **Paraphyses** slightly to medium (rarely strongly) clavate-capitate, terminal cells *14–22 × 3–4.2 µm {T}, †12.5–20.5 × 2.5–3.5 µm {1}, lower cells *9.5–14 × 1.5–2 µm {T}, †6–11 × 1.3–2 µm {1}; unbranched at upper septum. **Medullary excipulum** 50–90 µm thick, of dense textura intricata with many inflated cells, medium to sharply delimited. **Ectal excipulum** of (†) thin-walled to slightly gelatinized, vertically oriented t. globulosa-prismatica from base to margin, 40–100 µm thick near base, cells *10–19(–26) × 9–16(–19) µm {3}; 30–40 µm thick at lower flanks, 15–20 µm near margin, of t. prismatica oriented at a 40–80° angle to the surface, marginal cortical cells */†6–10 × 2.5–4 µm {3}; **glassy processes** absent {4} or 1–3 × 3 µm {1}. **Anchoring hyphae** abundant, */†1.7–3 µm wide, walls 0.2–0.3(–0.5) µm thick {3}, forming a loose t. intricata or dense t. porrecta up to 50 µm thick, partly gelatinized. **SCBs** in paraphyses globose, 1.5–2.5 µm diam., in ectal excipulum ~2.5–3 µm {3}, small ring-shaped or rhomboid crystalloid SCBs sometimes seen {2}, **VBs** absent {2} or present {1}, slightly refractive. **Exudate** over paraphyses (0.3–)0.5–2(–3) µm thick, cloddy to often cap-like, hyaline to pale yellow, firmly attached, over margin and flanks 1–2 µm thick. — **ANAMORPH**: unknown (but see below).

Habitat: collected 0.2–3.5 m above the ground, corticated to partially decorticated, 5–13 mm thick twigs and branches of indet. climbers {3}, *Ficus* ?*benjamini* {1}, indet. angiosperm {1}, on strongly decayed bark {4} (periderm {T} and bast {4}), on textile {1}; partly in clefts, sometimes on old pyrenomycete, ± greyed, no algae. **Associated**: *Hyalorbilia* cf./aff. *orbiliicola* (parasitic on *O. neocomma*) {1/2}, *Hysteropatella* ?*prostii* {2}, *Orbilia brachychitonis* {1}, *O. floridensis*

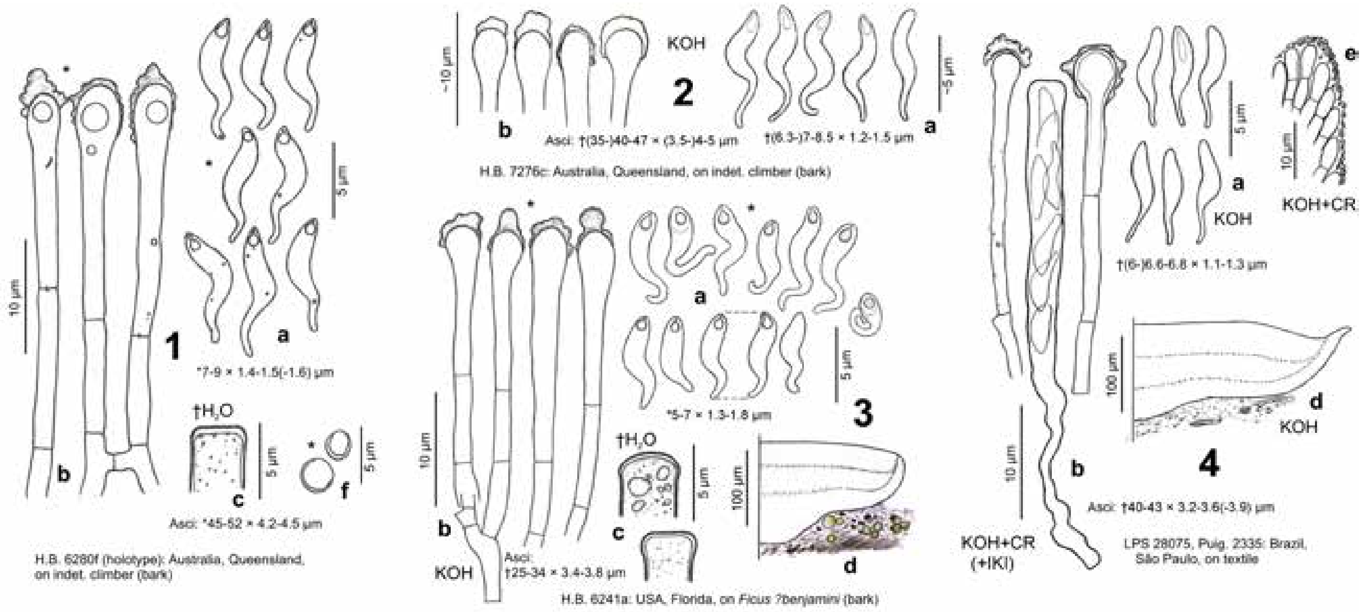


Plate 424. **1–4**: *Orbilia neocomma*. – **a**. ascospores (in 3a two ± in top view); **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia in median section; **e**. id., marginal ectal excipulum; **f**. SCBs in ectal excipulum.

{1}, *O. mammifera* {2}, *O. paracaudata* {1}, *O. scandens* {2}, *O. subfabacearum* {1}, *Rhytidhysteron ?rufulum* {1}. **Desiccation tolerance**: mature asci still viable after 2 months, some spores and many excipular cells still alive after 1 year. **Altitude**: 5–1850 m a.s.l. **Geology**: Devonian & Quaternary sedimentary rock; granite, metamorphic rock. **Phenology**: possibly throughout the year (rather long-lived).

Taxonomic remarks. *Orbilia neocomma* is very similar to European *O. comma*, from which it is separated by distinctly narrower ascospores with a tendency to perform 1.5(–2) turns, the curvature encompassing also the tail. Moreover, the exudate on the paraphysis apices of *O. neocomma* tends to form firmly attached caps. For the somewhat similar Australian *O. flexispora* (series *Orbilia*) see p. 1429.

Variation. Among the three Australian samples, two (Pl. 424: 1–2) have slightly longer spores than that from near Cairns (*/†6.5–7 × 1.2–1.3 µm) and a sample from Brazil (Pl. 424: 4). The shortest spores were found in the specimens from Florida (3) and China (Pl. 425: 3, *5–6 × 1.3–1.4 µm). In the Chinese one the paraphyses contained slightly refractive VBs, which were not seen in the three samples studied in the living state, instead, small crystalloid SCBs were seen in two of them (from Australia: Pl. 424: 1f; from Florida: IVV: H.B. 6241a). In the South American collection on textile (Pl. 424: 4) the margin distinctly protrudes, a feature not observed in the other specimens. Very short glassy processes were only seen in the sample from Cairns.

Map 74. Known distribution of *O. neocomma* in northeastern Australia.

Anamorph. In the holotype we found phragmoconidia (†47–63 × 3.3–4 µm, 9–11-septate, Pl. 425: 4) with curved ends which are similar in size and shape to the conidia of *O. comma*. However, in this collection several further *Orbilia* and one *Hyalorbilia* species were observed in the neighbourhood of *O. neocomma* to which the conidia might also belong.

Ecology. *O. neocomma* was found on rotten bark of xeric twigs and branches of angiosperms, mainly on twines of climbers, also on textile, in tropical to subtropical, humid to subhumid, winter-dry (monsoon-influenced) rainforests and savannahs in the Everglades of Florida (North America), South America, northeastern Australia (east of Great Dividing Range, here partly in eucalypt open woodlands), and southern China (montane evergreen broad-leaved forest).

Specimens included. **AUSTRALIA**: **Queensland**, Wet Tropics, 3 km NW of Cairns, 0.7 km E of Edge Hill, Cairns Botanical Garden, 5 m, branch of indet. climber, on bark, 26.VIII.2006, G. Marson (H.B. 8608a ø). – Einasleigh Uplands, 75 km SSW of Townsville, 2 km WSW of Mingela, 286 m, branches of indet. climber, on bark, 17.X.1998, G. Marson (ex H.B. 6280f, BRI AQ799182, **holotype**). – Brigalow Belt North, 49 km SE of Ayr, 4 km ESE of Gumlu, 12 m, twigs & branches of indet. climber, on bark, 19.X.1998, G. Marson (H.B. 7276c). — **USA**: **Florida**, 55 km SW of Miami, 12 km SW of Homestead, entrance to Everglades, branch of *Ficus ?benjamini*, on bark, ~12.IX.1998, L. Ferron (H.B. 6241a). — **BRAZIL**: **São Paulo**, 110 km NNE of Curitiba, Apiaí, ~900 m, on textile, X.1888, J. Puiggari (Puig. 2335, LPS 28075, separate convolute in holotype of *O. brasiliensis*, H.B. 6951b ø). — **CHINA**: **Yunnan**, **Yuxi**, Yimen, 54 km NW of Yuxi, NW of Fangtunxiang, Dalongkou, 1850 m, on branch of indet. angiosperm, V.2008, S.F. Li & J.W. Guo (J.W.G. ym2-16, YMFT, doc. vid.).

Orbilia disseminata (Henn.) Baral & E. Weber, **comb**. **nov**., MB 813747 — Pls 426–427

Basionym: *Helotium disseminatum* Henn., Hedwigia 41: 25 (1902)

Etymology: referring to the numerous, densely gregarious apothecia.

Typification: Brazil, Santa Catarina, Blumenau, leaves of *Arecales*, 1892, A. Möller (herb. Sydow, S-F9997, lectotype, designated here, MBT202635).

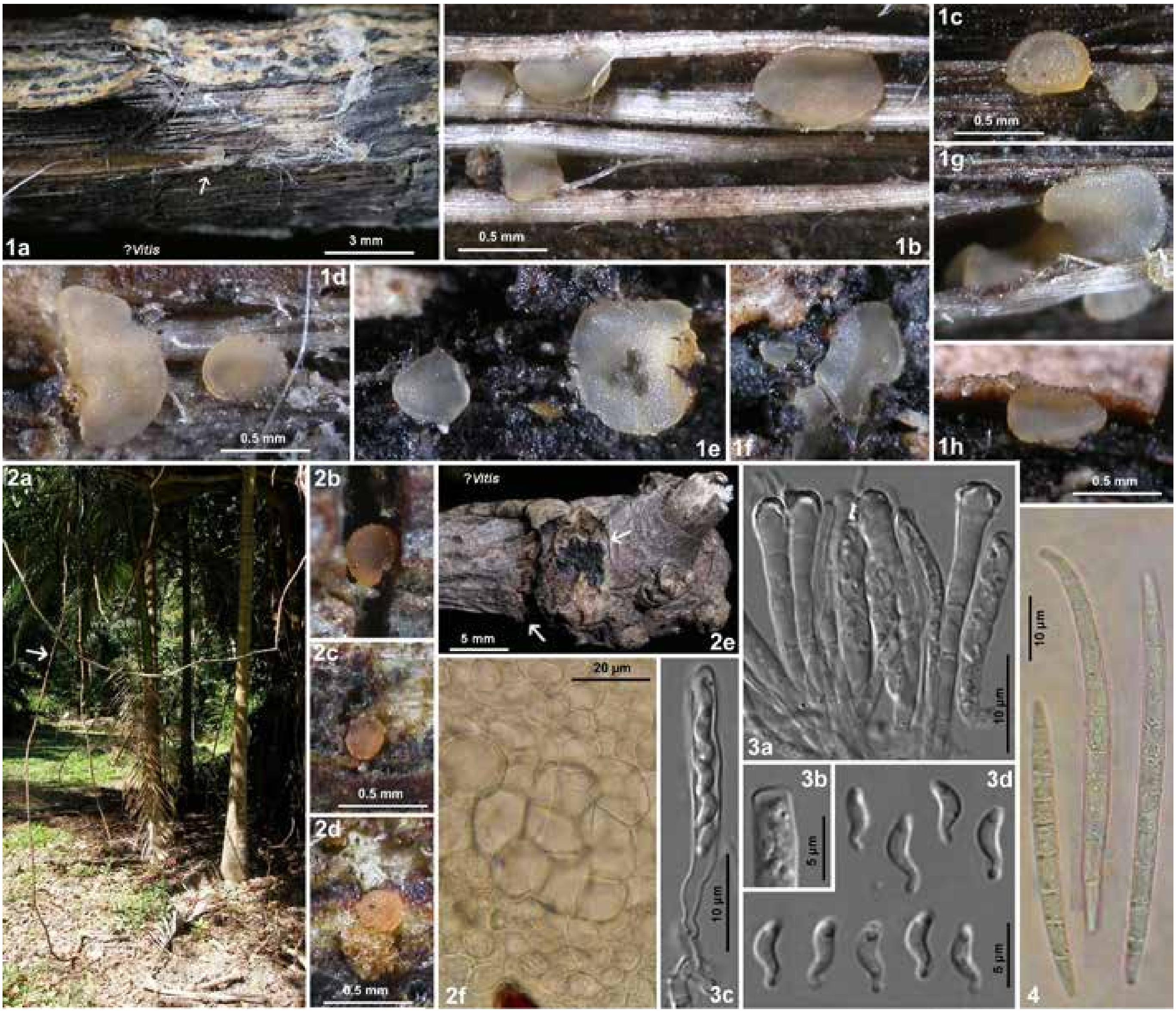


Plate 425. **1–4**: *Orbilia neocomma*. – **2a**. tropical rainforest with *?Cocos* and bamboo, hanging twines of indet. climber; **1a**. dead corticated twine; **1b–h**, **2b–d**. rehydrated apothecia; **2f**. basal excipular cells; **3a–c**. asci and paraphyses, ascus apex; **3d**. ascospores; **4**. conidia from substrate. – Living state, except for asci and conidia. – **3a–c**: phot. Z.F. Yu (DIC). — **1a–h**. H.B. 7276c: Australia, Queensland, Guthalungra, on indet. climber; **2a–f**. H.B. 8608a: ibid., Cairns, on indet. climber; **3a–d**. J.W.G. ym2-16: China, Yunnan, Yuxi, on indet. angiosperm; **4**. H.B. 6280f (holotype): Australia, Queensland, Mingela, on indet. climber.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1.2 mm diam., 0.26–0.3 mm high, light amber-ochraceous-brownish (Hennings: light yellow), slightly translucent, ± round, gregarious over large areas; disc flat, margin thin, not protruding, smooth or finely rough; broadly sessile or with an obconical broad base, superficial; dry bright reddish ochre-brown, without subiculum. **Asci** †35–42 × 3.6–4 µm, 8-spored, spores †2–3-seriate, 2 lower spores inverted; **apex** (†) strongly truncate (scarcely indented, laterally hardly inflated); **base** with short to medium long, ± thin, flexuous stalk, Y- or h-shaped. **Ascospores** †9–10 × 1.4–1.6 µm (~10–11 µm actual length), with narrowly fusoid upper part and sharply differentiated, very thin tail of †2.7–4 × (0.15–)0.25 µm, i. e., about half to nearly the length of the upper part, apex obtuse to subacute, medium to strongly helicoid; **SBs** visible as a very faint tear-shaped area. **Paraphyses** apically (medium to) strongly (to very strongly) capitate(-clavate), terminal cells †15–25 × 3–4.5 µm, lower cells †5–9.5 × 1.4–2.2 µm; unbranched at upper septum. **Medullary excipulum** 15–20 µm thick, of dense small-celled texture, sharply delimited. **Ectal excipulum** of thin-walled to slightly gelatinized, vertically oriented textura angularis-globulosa(-prismatica) from base to margin, 200–220 µm thick near base, cells †14–25 × 10–22 µm, common walls 0.2–1 µm thick; 20 µm thick near margin, oriented at a 70° angle to the surface, uppermost margin of t. prismatica oriented at ~45°, marginal cortical cells †11–19 × 5–10 µm, walls 0.3–1 µm thick; **glassy processes** absent. **Anchoring hyphae** restricted to the base, †2–4 µm wide, walls 0.2–0.4 µm thick, forming a dense, hyaline, 10 µm thick t. intricata-porrecta spreading over the substrate. **SCBs/VBs** no data available. **Exudate** over paraphyses (0.3–)1–2 µm thick, cloddy, hyaline, firmly or partly loosely attached, over margin and flanks 0.3–1 µm thick, sparse. **— ANAMORPH**: unknown.

Habitat: on medium rotten upperside of leaf sheaths of indet. *Arecales*, among the hairs and setae emerging from the host epidermis. **Associated**: none observed. **Desiccation tolerance**: unknown. **Altitude**: ~100 m a.s.l. **Phenology**: unknown.

Taxonomic remarks. *Orbilia disseminata* is easily recognized by its ascospores having abrupt, very thin tails. Herein the species differs from *O. comma* and *O. neocomma* which have spores of an otherwise similar shape and helicoid curvature. The spores of *O. disseminata* resemble in size and shape also those of *O. neglecta* (here assigned to series *Arthrobotrys*), but that species has falcate instead of helicoid spores, smaller and thinner apothecia with a distinct subiculum, almost no exudate at all, and partly H-shaped ascus bases.

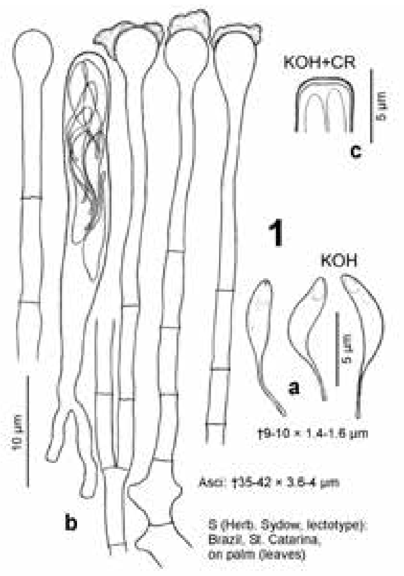


Plate 426. **1**: *Orbilia disseminata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex.

Type studies. Hennings (1902a) described the spores as 'fusoid-acicular, strongly acute at both ends, 2-guttulate, 5–7 × 1–1.5 µm'. Dumont (1981: 334) stated the 'holotype' of *Helotium disseminatum* (in S) to be orbiliaceous, but he could not see any spores. In the present reexamination of this material, which is labelled 'isotype', only a few free spores could be found, and inside the asci they were only very difficult to see. Nevertheless, the apothecia in this rich material appear to be quite mature. The population looks homogeneous, for which reason a mixture would be highly improbable. Undoubtedly, Hennings overlooked the characteristic spore tails.

The convolute examined is obviously a syntype of *H. disseminata* and was sent by Hennings to Sydow, while Hennings' personal specimen in B was destroyed during the Second World War. The here redescribed duplicate in Sydow's herbarium is herewith designated as **lectotype** of *Helotium disseminatum* (Art. 9.11, Turland et al. 2018).

Ecology. *O. disseminata* was collected on dead, slightly rotten leaf sheaths of a palm in subtropical humid South America.

Specimens included. **BRAZIL**: **Santa Catarina**, 90 km NW of Florianopolis, Blumenau, ~100 m, leaf sheaths of *Arecales*, 1892, A. Möller (herb. Sydow, S-F9997, **lectotype**; H.B. 7690 [slide]).

Series *Rubellae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Rubellae*** Baral & E. Weber, **ser. nov.**, MB 815009 –
Type species: *Orbilia rubella* (Pers.) P. Karst.

Etymology: named after the type species, *O. rubella*.

Latin diagnosis: *Apothecia rosea vel aurantia, margine albido-pilosa vel -dentata, pili marginales 1–10-septati, 3.5–6.5 µm lati, plus minusve crassitunicati, paraphyses apice spathulatae vel mammiformes.*

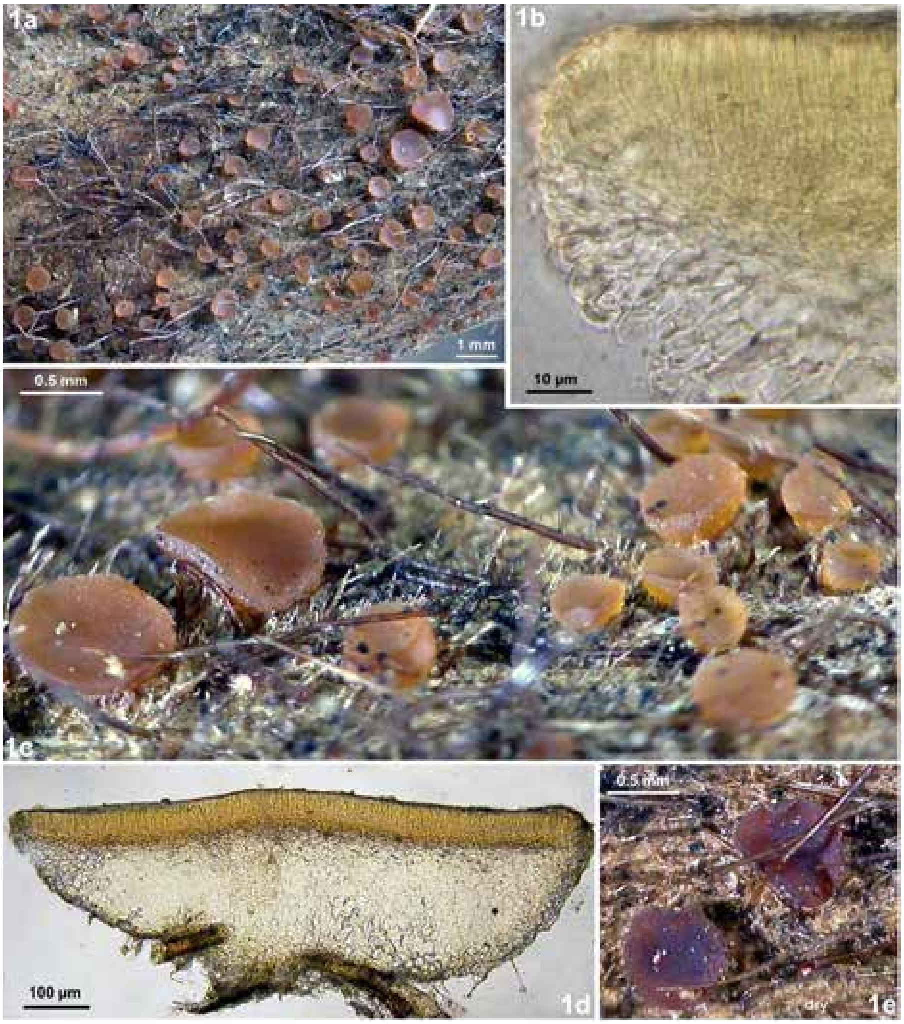


Plate 427. **1**: *Orbilia disseminata*. – **1a**, **c**. rehydrated apothecia; **1e**. dry apothecia; **1d**. apothecium in median section; **1b**. id., marginal ectal excipulum. – Dead state (in KOH). — **1a–e**. S (herb. Sydow, lectotype): Brazil, Santa Catarina, on indet. *Arecales*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.5–1.5(–3) mm diam., pale to bright rose-pink to orange-ochraceous, often somewhat urceolate, margin whitish pubescent-fimbriate or toothed, sessile or with a ± indistinct short stipe. **Asci** *35–60 × 3.3–5 µm, 8-spored, lower (2–)3–5(–7) spores inverted; **apex** (†) slightly to strongly truncate, not or slightly indented and laterally inflated; **base** T-, L- to Y-shaped. **Ascospores** *5.5–9.7 × 1–1.9 µm, subcylindric- to ellipsoid- or fusoid-clavate, apex obtuse to subacute, rarely rounded or acute, base often tail-like or with a distinct tail, straight or usually slightly to ± strongly curved or geniculate near base (often slightly helicoid), **SBs** 0.8–1.8 × 0.4–1 µm, globose to tear-shaped, apically narrowed to a small (sometimes wide) point, with a very short filum or attachment invisible. **Paraphyses** slightly to strongly spathulate to lageniform-mammiform at the apex, terminal cells (1.2–)1.5–3(–4)× longer than lower cells. **Ectal excipulum** cells near base *(7–)10–22(–34) × (5–)7–15(–18) µm, near margin forming thin- or often thick-walled cell rows; **hairs** free, 1–3- up to 3–10-septate, (10–)30–60(–93) × 3.5–6.5 µm, with †(0.3–)0.5–1.5(–2.7) µm thick lateral wall, **glassy processes** absent or present on tip of hairs, 10–60(–130) µm long. **SCBs** globose, often mixed with crystalloid ones; **VBs** consistently absent. **Exudate** 0.2–0.3 µm thick, continuous, indistinctly rough to granular, ± firmly attached over protruding part of paraphyses, rarely absent, over hairs sometimes up to 0.8 µm thick. — **ANAMORPH**: vermispora-like. **Conidiophores** not observed. **Conidia** phragmosporous, *28–78 × 3.5–6.7 µm (in situ), 3–15-septate, slightly to strongly curved (C- to ± canoe-shaped).

Key to the species of series *Rubellae*

1. Cellular part of hairs 30–60(–90) µm long, with 3–8(–10) septa, without or rarely with very short glassy caps of max. 1/10 of hair length 2

1. Cellular part of hairs 10–50 µm long, with (0–)1–3 septa, always tipped by glassy processes that are mostly longer than the cellular part 3

2. Spores *(5.5–)6–8.5(–9.8) × (1–)1.1–1.3(–1.5) µm, with a *0.3–0.6(–0.8) µm wide tail; bark of angiosperms (mainly *Salix*), thermoboreal to (oro)temperate and orosubmediterranean humid Europe, central Asia .... ***O. phragmotricha***, p. 826

2. Spores *(6.5–)7.5–9.3(–9.7) × (1.6–)1.7–1.8(–1.9) µm, base partly tail-like or with a *0.7–1 µm wide tail; inflorescence stems of *Yucca*, warm-temperate semiarid western North America .... ***O. paradoxoides***, p. 831

3. Spores †5.5–6.5 × 1.2–1.4 µm, sharply divided into an ellipsoid head and a filiform, †0.2–0.3 µm wide tail; glassy processes 10–22 µm long; bark of *Liquidambar*, warm-temperate humid eastern North America .... ***O. saccharifera***, p. 821

3. Spores *(7–)7.5–9.5 × 1.1–1.4 µm, with *0.4–0.8 µm wide tail or tail-like base; glassy processes 15–70(–130) µm long; bark of *Salix*, *Tilia* & *Ulmus* in cold-temperate humid central and northern Europe, bark of *Eucalyptus* & *Nerium* in inframediterranean semihumid southern Europe .... ***O. rubella***, p. 822

If cellular part of hairs with thin lateral walls, glassy processes 1–15 µm long, spores with acute apices: see *O. rehmii* (p. 904).

Habitat: on bark (exceptionally wood) of angiosperms, also inflorescence stems of large monocots, temperate to subtropical, humid to semiarid, always desiccation-tolerant.

Recognized species: 4.

Taxonomic remarks. Series *Rubellae* is erected here to include four species which are characterized by prominent, septate, mainly 4–6 µm broad, thick-walled hairs being partly tipped by glassy processes. Further characteristics include spathulate paraphyses and small, narrowly clavate ascospores with obtuse to subacute apices and slightly curved to geniculate tails or tail-like bases. The spore bodies are globose to broadly tear-shaped.

Series *Rubellae* appears to be morphologically close to series *Regales*, the latter differing mainly in the absence of septate marginal hairs and of crystalloid SCBs. Series *Commatoideae* and *Aurantiorubrae* differ from series *Rubellae* in the absence of septate hairs, predominant absence of glassy processes, in consistently capitate paraphyses, and the latter series also in narrowly tear-shaped to subulate SBs.

Species delimitation. The two European species *O. rubella* and *O. phragmotricha* have been confused in the past because of similar ascospores and hairs. However, the presence vs. absence of short to long glassy processes on the hair tips and differences in spore size unequivocally permit distinction between them.

Anamorph. Curved, vermispora-like phragmoconidia are known from pure culture in *O. phragmotricha* and from natural substrate in *O. rubella, O. saccharifera,* and *O. paradoxoides*. *O. phragmotricha* and *O. rubella* differ in longer conidia with more septa in comparison to *O. saccharifera,* and *O. paradoxoides*.

Phylogeny. DNA-data were available for two samples of *O. phragmotricha* (SSU+ITS+LSU) and two of *O. rubella* (ITS). When analysing (SSU+)ITS+LSU, series *Rubellae* clustered in the strongly or medium supported core clade of section *Aurantiorubrae* (Baral et al. 2017b, Phyl. 13) by forming a strongly or medium supported subclade with *O. aurantiorubra*/*O. jugulospora* and *O. comma*. Although *O. pisciformis* clustered highly supported as a sister taxon to series *Rubellae*, we preferred to keep it in series *Commatoideae* for morphological reasons.

Specific nucleotide positions. Molecular motifs to characterize series *Rubellae* have not been found, except for pos. 9 in the ITS2 region, which is ATTTCAAC**C** compared to **A** or **T** in other members of section *Aurantiorubrae* (*O. pisciformis* has ATTTCAAC**T**). Yet, species with **C** also occur in series *Abutilones*, *Albovinosae*, *Hyalinia*, and *Poitevinicae*, but only two share the motif ATTTCAAC**C** (*O. poitevinica*, *O. milinana* TFC Mic. 23222).

Ecology. All four included species are desiccation-tolerant and occur on woody angiosperms, mainly on bark, also on herbaceous stems. Different climatic regions are inhabited: *O. rubella* and *O. phragmotricha* were recorded from temperate to subalpine-boreal, humid to semihumid Europe and central Asia, whereas *O. saccharifera* is from subtropical humid eastern and *O. paradoxoides* from orotemperate semiarid western North America.

Orbilia saccharifera (Berk.) Baral, **comb. nov.**, MB 813748 — Pl. 428

Basionym: *Peziza saccharifera* Berk., Grevillea 3: 157 (1875)

≡ *Hymenoscyphus sacchariferus* (Berk.) Lindau, in Engler & Prantl, Nat. Pflanzenfam.1: 204 (1897)

≡ *Pseudohelotium sacchariferum* (Berk.) Sacc., Syll. Fung. 8: 298 (1889)

Etymology: referring to the marginal hairs of the apothecia resembling sugar-like granules.

Typification: USA, Alabama, unlocalized, branch of *Liquidambar*, undated, T.M. Peters (M.J. Berkeley 5208, K, holotype).

Misapplied name: Nannfeldt (1932: 252), as ?*Hyalinia rubella*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.7 mm diam., 0.12 mm high, light ochraceous throughout (Berkeley: 'pale orange'), round or often irregularly ellipsoid, margin ± undulating, gregarious; disc strongly concave, margin whitish-pubescent by short hairs projecting ~30 µm, exterior pubescent to furfuraceous; broadly sessile, superficial; dry deep ochre, margin ± incurved. **Asci** †(33–)35–47 × 3.2–3.6 µm, 8-spored, spores ± biseriate, ~4 lower spores inversely oriented; **apex** (†) slightly to medium truncate; **base** with long, thin, flexuous stalk, Y- to mostly L-shaped. **Ascospores** †5.5–6.5 × 1.2–1.4 µm, with ellipsoid-fusoid upper part and rather sharply differentiated narrow tail 2–2.8 × 0.2–0.3 µm, apex obtuse, tail often ± geniculate; **SBs** not seen. **Paraphyses** apically slightly clavate or often spathulate to obtusely lanceolate, terminal cells †(11.5–)15–22 × 2.4–3 µm, exceeding the asci by 3–6 µm, lower cells †6.5–9 × 1.3–2 µm, unbranched at upper septum. **Medullary excipulum** hyaline, 30–40 µm thick, of dense textura intricata, horizontally oriented, individual cells not clearly seen. **Ectal excipulum** hyaline, of thin-walled, indistinctly vertically oriented t. angularis from base to flanks, 20–25 µm thick near base, cells †7–12 × 5–9 µm, 15 µm thick at mid flanks, 10 µm at margin, here of t. prismatica oriented at a 30° angle; marginal cortical cells terminated in numerous hairs 30–50 × 4–6.5 µm, with a basal ~ 1–3-septate cellular part with †0.5–1 µm thick lateral walls, terminated by **glassy processes** 10–22 × 3–4.5(–5.5) µm, strongly stratified, medium refractive, curved ± outwards, hairs slightly agglutinated to form indistinct small teeth. **Anchoring hyphae** abundant, †2–3.4 µm wide, walls (0.2–)0.3–0.8 µm thick, forming a ± loose, gelatinized t. intricata 40–60 µm thick, covering lower flanks as a 5–20 µm thick gelatinized layer. **SCBs** no data available. **Exudate** over paraphyses very thin, smooth or finely rough, covering the protruding part, on hairs almost absent. **— ANAMORPH**: vermispora-like (presumed, from natural substrate {1}). **Conidiophores** not seen. **Conidia** unbranched, strongly curved (C-shaped), †28–30.5 × 4.5–4.8 µm, 3–5-septate.

Habitat: on thin, slightly decayed bark of corticated, ?thin branch of *Liquidambar* sp., in and along small cracks in periderm, slightly greyed, nearly no algae, closely associated with old black subperidermal ?pycnidia of unknown fungus. **Desiccation tolerance**: unknown, but certainly a desiccation-tolerant species, judging from orange-coloured, hairy apothecia and the greyed bark surface. **Altitude**: unknown (< 500 m a.s.l.). **Phenology**: unknown.

Taxonomic remarks. *Orbilia saccharifera* is characterized by short marginal hairs consisting of a solid glassy upper part and a basal thick-walled and septate lower part, and by small ascospores with a distinct tail. The species is similar to the European *O. rubella*, especially in hair characters. The spores more resemble those of the European *O. phragmotricha* but have a broader, more ellipsoid upper part and a thinner, more abruptly separated tail. The latter species also differs in the absence of glassy processes. The Australian *O. nanosperma* is comparable in having almost the same spore shape and size. However, this species is assigned to section *Hemiorbilia* here because the asci are provided with an apical dome.

Type studies. Although the protologue is devoid of microscopic features, it clearly concurs with the holotype which contains a single piece of bark with over a hundred apothecia. The sketch on the convolute shows apothecia, an ascus and a paraphysis probably drawn by Berkeley, with the remark 'spores not seen'. Free spores are indeed rare, but spores within asci were sometimes visible in CR mounts. A further remark 'cells on exterior darker brown and larger, forming granules on the surface' does not appear in the protologue. Such cells were not seen in the present reexamination, and probably refer to black yeasts on the apothecial exterior.

Nannfeldt (1932: 252) believed that *Peziza saccharifera*, *P. cruenta* Schwein. and some other taxa represented possible synonyms of *Hyalinia rubella* (s. Nannfeldt, = *Orbilia phragmotricha*), based on Massee's (1894b) redescription who examined the type material of *O. saccharifera* and considered it as a synonym of *P. cruenta*. Obviously, Massee overlooked the distinct spore tails when describing the spores as cylindric-oblong. Perhaps he saw spores only in the type of *P. cruenta* which could not be located in the present study (see p. 1668).

In the paper of Berkeley (1875), the type collection of *O. saccharifera* ('Berk. 5208') is, apparently in error, cited a second time under *Peziza rubella* a few lines before. As is seen on the label, this collection was first identified as *P. rubella* and later changed to *P. saccharifera*. It shares indeed many features with the European *O. rubella*.

Anamorph. The presumed anamorph of *O. saccharifera* with its strongly curved, canoe-shaped conidia is similar to that of *O. aurantiorubra* and many other species of this section (Pl. 428: 1g).

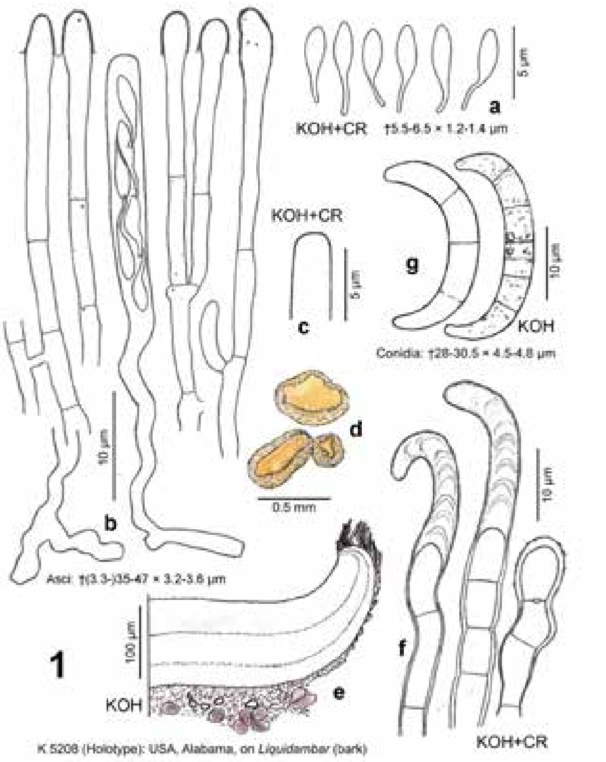


Plate 428. **1**: *Orbilia saccharifera*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. marginal hairs with glassy processes; **g**. conidia from substrate.

Ecology. *O. saccharifera* was collected on slightly decayed bark of a probably thin, obviously xeric branch of *Liquidambar* in warm-temperate humid eastern North America. The unknown type locality might have been in the centre of Alabama in the forests around the university, or in the hilly north where T.M. Peters also used to collect.

Specimens included. **USA**: **Alabama**, unlocalized, branch of *Liquidambar* [*styraciflua*], on bark, undated, T.M. Peters (herb. Berkeley 5208, K, **holotype**, H.B. 5345 ø, anam. substr.).

Orbilia rubella (Pers.) P. Karst., Not. Sällsk. Fauna Fl. Fenn. Förh. 11: 248 (1870) — Pls 429–430, Map 75

≡ *Peziza rubella* Pers., Syn. Meth. Fung.: 635 (1801); Fr., Syst. Mycol. 2(1): 141 (1822), nom. sanct.
≡ *Pezizella rubella* (Pers.) Fuckel, Jahrb. Nassau. Ver. Naturkd. 23–24: 299 (1870)
≡ *Calloria rubella* (Pers.) Rehm, Ber. naturhist. Augsburg 26: 112 (1881) [non *C. rubella* Fuckel 1870: 283, = *Hymenula callorioides* Sacc. fide Saccardo 1886: 669, Rehm 1891: 459]
≡ *Mollisia rubella* (Pers.) Gillet, Champ. Fr., Discomyc.: 124 (1882)
≡ *Ombrophila rubella* (Pers.) Quél., Compt. Rend. Associated Franç. Avancem. Sci. 11: 402 (1883) [1882]
≡ *Craterocolla rubella* (Pers.) Sacc., Syll. Fung. 6: 778 (1888)
≡ *Fungus rubellus* (Pers.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 480 (1898)
≡ *Hyalinia rubella* (Pers.) Nannf., Nova Acta Regiae Soc. Sci. Ups., ser. 4, 8: 252 (1932)

Etymology: referring to the reddish apothecial colour.

Typification: location unknown, ?branch of indet. angiosperm, undated, collector unknown (herb. Persoon, L0054584 = L 910.261-535, holotype); Norway, Arendal, trunk of *Salix caprea*, on bark, 15.IV.2009, T.H. Dahl (ex T.H.D. 116/09 & ex H.B. 9046a, M-0291772, epitype, designated here, MBT385119; sq.: KT222354).

Misinterpretation of *O. rubella*: Beyer (1994: 207, 1998: 191), = *Orbilia* sp. (section *Arthrobotrys*); Feltgen (1899: 54), = *O. sarraziniana*; Karsten (1870: 248, 1871: 102), = *O. phragmotricha* (& *O. xanthoguttulata*); Karsten (1885: 142 p.p.), = *O. rehmii*; Rehm (1891: 458 p.p.), = *O. rehmii*; Schröter (1893: 120), = *O. aurantiorubra*; Nannfeldt (1932: 252, as *Hyalinia*), = *O. phragmotricha*, *O. rehmii*, *O. saccharifera*, *O. fibriseda* (= *O. carpoboloides*), and *O. regalis*.

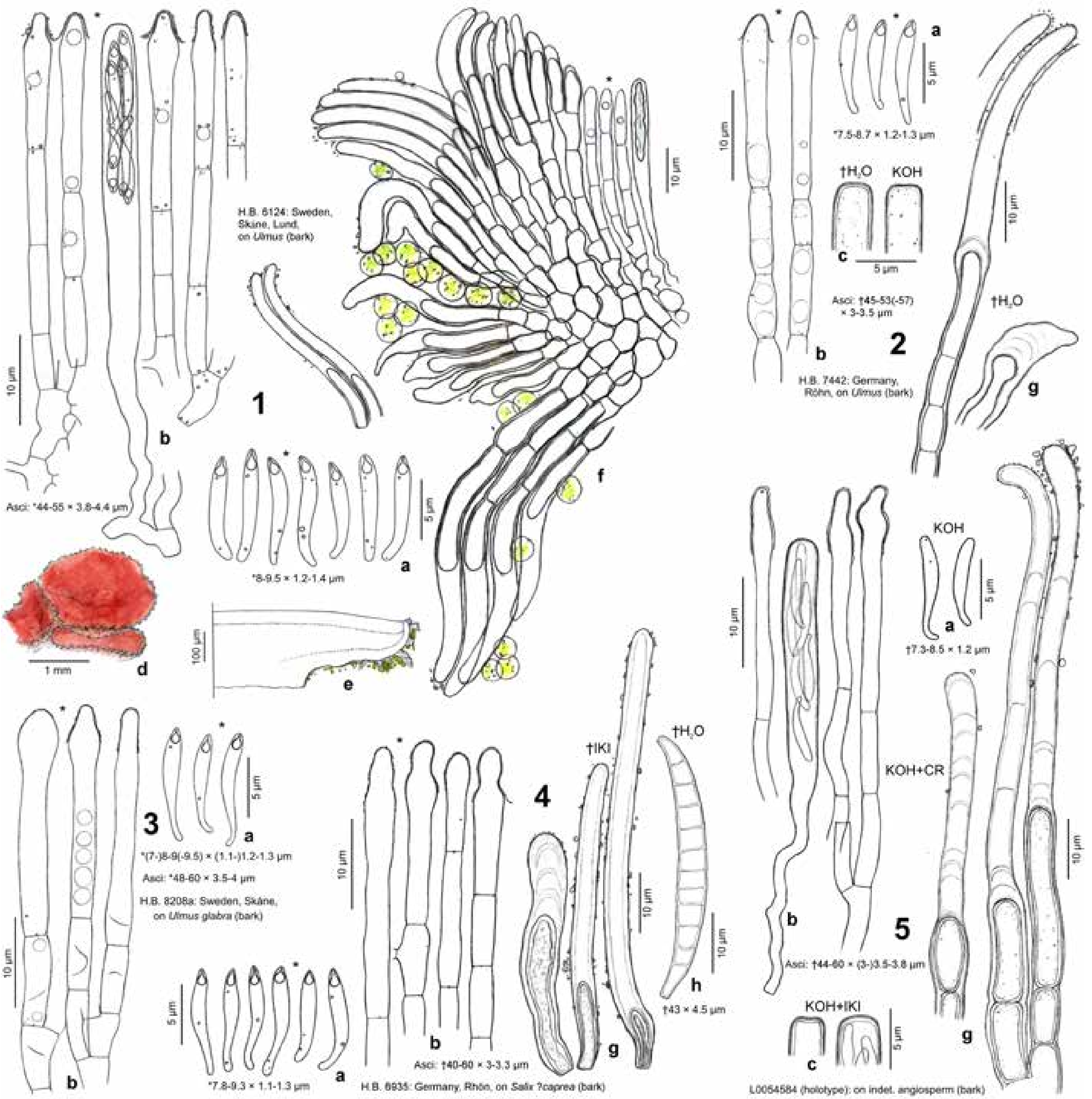


Plate 429. **1–5**: *Orbilia rubella*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia with dentate-hairy margin; **e**. apothecium in median section; **f**. id., ectal excipulum and hairs at margin and mid flanks; **g**. hairs tipped by long glassy processes; **h**. conidium from substrate.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.4–)0.6–2(–3) mm diam., 0.14–0.25 mm high (receptacle 0.1–0.18 mm), light to bright orange-rose to rose-pink, round to elliptical, somewhat compressed or undulating when fasciculate, scattered to loosely or densely gregarious in smaller or larger groups; disc young urceolate with incurved margins, soon ± flat, sometimes slightly convex, margin distinctly whitish(-yellowish) hairy or usually toothed, 10–90(–130) µm protruding (incl. hairs), teeth 50–160 × 50–100 µm; broadly sessile or with a broad, ± distinct stipe-like base 0.06–0.1 × 0.3–0.6 mm, superficial; dry light to bright cream- to orange-rose, margin somewhat inrolled. **Asci** *44–60 × (3.5–)3.7–4.5 µm {4}, †40–60 × 3–3.8 µm {4}, 8-spored, spores *4-seriate, (2–)3–5(–6) lower spores inverted {5} (sometimes mixed), pars sporifera *20–25 → 19 µm long; **apex** (†) medium to strongly truncate (not indented, laterally sometimes very slightly inflated); **base** with medium to very long, thin, flexuous stalk, T- to L-shaped. **Ascospores** *(7–)7.5–9.5 × 1.1–1.4 µm {6}, †7–8.5(–9.5) × 1–1.2 µm {2}, cylindric- to fusoid-clavate, partly subcylindrical, apex obtuse to subacute (to acute), base medium to strongly, rarely hardly attenuated, tail-like or with a distinct tail 1–3 × 0.4–0.8 µm, straight to somewhat curved, near base often slightly to medium geniculate (partly even helicoid); **SBs** *1.3–1.8 × 0.8–1 µm {5} tear-shaped, apically narrowed to a small point or very short filum. **Paraphyses** apically obtusely lanceolate to spathulate or lageniform, exceptionally ± cylindrical, terminal cells *(11–)14–25(–30) × 2.3–3.7(–4.2) µm {4}, †20–25.5 × 2.3–3 µm {1}, exceeding the living submature asci by 0–6 µm, lower cells *(5–)7–15 × 2–3.2(–4) µm {4}, †8–12 × 1.5–2(–2.7) µm {1}; unbranched at upper septum; hymenium pale rose. **Medullary excipulum** hyaline to pale rose, 40–120 µm thick, of medium dense textura intricata with many inflated cells, or of t. globulosa-angularis, indistinctly to sharply delimited from ectal excipulum from base to margin by a 10–40 µm thick layer of t. porrecta. **Ectal excipulum** subhyaline to light rose, of (†) thin-walled, vertically oriented t. globulosa-angularis-prismatica from base to mid flanks, 50–90 µm thick near base, cells *(8–)10–22(–30) × 7–17 µm {4}; 40–50 µm thick at lower flanks, 20–30 µm at mid flanks and margin, at submargin of t. prismatica(-angularis) oriented at a 45–80° angle to the surface, partly slightly gelatinized, at margin of t. prismatica oriented at 10–80°, marginal cortical cells */†(7–)9–18(–27) × 3–5(–6) µm {4}, agglutinated or somewhat free; **hairs** at margin and flanks 30–160 µm long, cellular basal part 10–50 × 3.5–6.5 µm, (0–)1–2(–3)-septate, lateral walls †(0.3–)0.5–1(–1.7) µm thick, terminated by **glassy processes** (3–)15–60(–100) {6} or (20–)100–130 {T} × (2.8–)3.5–5(–7.3) µm {7}, refractive, not or distinctly stratified, free or cohering to form teeth, usually more or less strongly outwards curved (but apices sometimes strongly inwards). **Anchoring hyphae** abundant, */†1.7–3 µm wide (near insertion 3.5–5 µm), walls 0.2 µm thick {3}, without or with up to 1 µm thick gelatinous sheath, forming a loose to medium dense hyaline t. intricata ~20–70 µm thick. **SCBs** usually present, globose, very low-refractive {4}, 1.5–2.5 µm diam., also thin plate-like or filiform, crystalloid SCBs in lower part of paraphyses and in excipular cells near base {3}. **Exudate** over paraphyses and glassy processes 0.1–0.3 µm thick, continuous to finely rough or granular, ± firmly attached. **— ANAMORPH**: vermispora-like (presumed, from natural substrate {4}). **Conidiophores**: not observed. **Conidia**: */†(28–)42–51 × 3.5–4.5 µm, (5–)8(–11)-septate {3}.

Habitat: (0–)1–2 m above the ground, on corticated, 6–60 mm thick (or more), still-attached, dead branches or standing trunks, also broken branches or detached bark lying on the ground (more or less exposed), of *Eucalyptus* sp. {1}, *Nerium oleander* {1}, *Salix caprea* {3/1}, *Tilia* sp. {1}, *Ulmus* sp. {2}, *U. glabra* {7}, on medium to very decayed bark {17} (bast, sometimes periderm), bark ± detaching, on outer but also inner surface, apothecia partly on periderm-free areas, sometimes entirely covered by loose periderm, often over or in holes of periderm, ungreyed, mostly without but sometimes covered by abundant green algae, closely associated with old perithecia of *Nitschkia* {1}, ?*Eutypella* {1}, indet. pyrenomycete {1}. **Associated**: ?*Eutypella* sp. {1}, *Graphis scripta* {1}, *Nitschkia* ?*collapsa* {1}, *Orbilia comma* {2}, *O. phragmotricha* {1}, *O. xanthoguttulata* {3}. **Desiccation tolerance**: a few asci survived for 2 weeks, ectal and medullary excipular cells and some paraphyses still viable after 3 months. **Altitude**: 5–135 m a.s.l. (Scandinavia), 590–800 m (central Europe), 110–530 m (southern Europe). **Geology**: humid Europe: Buntsandstein; granite, granitoid, gneiss, basalt; semihumid Europe: Carboniferous schist and greywacke, Lower Jurassic dolomite & marl. **Phenology**: I–VI, XI (rather long-lived).

Taxonomic remarks. *Orbilia rubella* is a rather constant, easily recognizable species, being characterized by prominent hairs consisting of a long, solid glassy upper part and a thick-walled, often septate, mostly shorter lower part. The closely related *O. phragmotricha* and *O. paradoxoides* differ in multiseptate hairs with or without very short glassy processes, the former also in smaller ascospores with a more distinct, thinner tail-like base and smaller SBs. Hairs similar as in *O. rubella* occur in the North American *O. saccharifera*, which deviates in much smaller spores with an abrupt tail. Species of series *Regales* (e. g., *O. aradi*, *O. euphorbiae*, *O. puyae*) have similar spores but are devoid of septate hairs, instead, their short glassy processes emerge directly from the marginal cells. *O. rehmii* (series *Abutilones*), on bark of *Malus*, resembles *O. rubella* but differs in much shorter glassy processes on thin-walled hairs, partly clavate paraphyses, and spores with acute apices.

Variation. Mainly the length of the glassy processes varies to some extent among the studied populations of *O. rubella*, being longest in the holotype. Yet, this character was generally found to vary considerably within *Orbilia* at the species level. Also the spores vary somewhat between cylindric- and fusoid-clavate, their bases being usually distinctly but sometimes only scarcely attenuated. One of the mediterranean samples from Portugal (on *Nerium*, IVV: H.B. 9980) did not deviate from those from cold-temperate Europe; its spore size of *7.5–9.5 × 1.2–1.4 µm fits perfectly, but the glassy processes were with 13–45 × 3–3.5 µm at the lower end of the range. The other (on *Eucalyptus*) was not studied by us, and only macrophotos of the apothecia and a microphoto of the hairs exist.

Nomenclature and type studies. The diagnoses of earlier authors are not adequate enough to recognize *O. rubella* as circumscribed in the present study. Except for a few of their voucher specimens which were reexamined and identified here as *O. phragmotricha*, *O. xanthoguttulata*, and *O. rehmii*, the identity of these reports remains unclear. This inadequacy was also emphasized by Rehm (1891: 459) who doubted whether the identity of Karsten's concept of *O. rubella* with that of Persoon will ever become clear. Phillips (1887: 334) described *C. rubella* with smooth apothecia and cylindrical spores of 6 × 2 µm, data excluding any of these species. Nannfeldt's (1932: 252) rather broad concept of *Hyalinia rubella* includes various orbiliaceous species (see under *O. phragmotricha*, p. 826, also under *O. cruenta*, p. 1668), whereas Saccardo's (1888: 778) interpretation refers to a basidiomycete (?*Sebacinales*).

Persoon (1801: 635), who collected *Peziza rubella* 'in spring on rotten bark', briefly described the apothecia as: 'fleshy-gelatinous, smooth, flesh-red (incarnato-rubra), subflexuous, margin finely subserrate' and '1.5 lin. (= ~3 mm) wide, at first subglobose'. In the Persoon Herbarium a single specimen under the name *P. rubella* (without collection data, L0054584 = L 910.261-535) can be found (Pl. 429: 5). About 10 apothecia were seen which measured 0.8–1.5 mm diam. when dry, growing on the outer surface of periderm and mainly bast of a min. ~3 cm thick branch of an unidentified, probably broad-leaved tree.

In the absence of any further voucher specimens studied by Persoon, this obviously authentic material is presumed here to be the **holotype** of *Orbilia rubella*, an opinion also shared by R. Arendholz (in sched.). The well-preserved specimen turned out to be conspecific with the below listed recent collections, but it is specifically distinct from those on which Karsten and Nannfeldt based their interpretation of *O. rubella*, and which are assigned to *O. phragmotricha* here. The Norwegian specimen from which a sequence was gained (ex H.B. 9046a, Pl. 430: 4, sq.: KT222354) is herewith designated as **epitype** of *O. rubella*.

Misapplication. A specimen identified by Fuckel (1871: 336, without description) as *Pezizella rubella* (on rotten wood and branches, autumn, near Oestrich, Fungi Rhenani 2382, M), was examined but no apothecia could be found. It was accepted by Rehm (1891: 459) as belonging to '*O. rubella*' (= *O. rehmii*). Fuckel's (1870: 299) brief description of this sample refers to a collection on wood of *Juglans regia*, with cylindrical, slightly curved spores of 6 × 2 µm; no information on the hairs is given, but Fuckel apparently saw no hairs since his generic diagnosis of *Pezizella* describes the apothecia as smooth, hence, the specimen can hardly have belonged in series *Rubellae*.

Beyer (1994: 207, 1998: 191) referred a collection on stems of *Rumex hydrolapathum* to *O. rubella* (in 1998 only tentatively). The purely microscopic description comprises slightly falcate spores *7–11 × 0.8–1 µm with a minute globose subapical

Plate 430. **1–5**: *Orbilia rubella*. – **1a**. moist *Fraxino-Aceretum pseudoplatani* with *Ulmus*; **1b–d**, **2a–c**, **3**, **4a**. fresh or rehydrated apothecia; **1f**, **4b**. marginal ectal excipulum in median section, with hairs tipped by glassy processes; **1g**, **5**. hairs in external view; **1e**. basal ectal excipulum in median section, with filiform SCBs; **4c**. id., with medullary excipulum and anchoring hyphae; **1h**. hymenium with protruding paraphyses; **4d**. mature ascus (SBs stained in CRB); **1i**, **4e**. ascospores. – Living state, except for **5** (KOH+CR), asci in **1h**, **4d**. – **2a–c**: phot. K. Homble. — **1a–i**. H.B. 8208a: Sweden, Skåne, on *Ulmus*; **2a–c**. 22.III.2009: Norway, Arendal, on *Ulmus*; **3**. H.B. 7442: Germany, Rhön, on *Ulmus*; **4a–e**. H.B. 9046a (epitype): Norway, Arendal, on *Salix*; **5**. L0054584 (holotype): unlocalized, on indet. angiosperm.

SB, rather unstalked asci with a partly H-shaped base, and 0–1-septate, flexuous, thin-walled (or solid?) hairs up to 50 × 5 µm. Considering the falcate spores with a gradually tapered base and globose SBs, this collection appears to be a member of section *Arthrobotrys* rather than *Aurantiorubrae*, perhaps related to *O. cardui*.

A few collections reported by R. Galán (in Pando & & Hernández 2001: 125) from southern and eastern Spain (on *Populus* wood and *Rubus* stems) under the name of *O. rubella* require reexamination.

Anamorph. We found four times near apothecia of *O. rubella* a few vermispora-like conidia which resemble those of *O. comma* but tend to be wider and to have more septa (Pl. 429: 4h). However, confusion between their anamorphs cannot be excluded, because *O. comma* was found two times in association with *O. rubella*.

Phylogeny. ITS sequences were taken from apothecia of two samples: on *Salix* from Norway and on *Nerium* from Portugal. They clustered with a 4.3 % distance in a medium supported clade. In both sequences the included short part of SSU shows that, in contrast to *O. phragmotricha*, the S1506 intron is absent. *O. rubella* clustered with a 5.3–5.5 % distance in a strongly supported clade with *O. phragmotricha* (Phyls 14, see also S15). Other members of section *Aurantiorubrae* show much higher distances, the closest being 11–11.5 % to *O. pisciformis* and 11–13 % to *O. jugulospora*. Further sequences are required to clarify whether mediterranean populations form a genetically distinct group.

Ecology. *O. rubella* was found on ± rotten bark of xeric branches, mainly of *Ulmus* and *Salix*, on ± acidic to basic, non-calcareous soil in supra- to orotemperate or hemiboreal (Norway) humid, subcontinental Europe. The scattered sites include the montane Rhön mountain range in central Europe and the lowlands of south Scandinavia. Krieglsteiner (2004: 657 fig. 50, as *Orbilia* spec. aff. *rubella*; pers. comm.) reported *O. rubella* from the Rhön area as not infrequent in ± montane, humid, cold and shady, medium base- and nutrient-rich ravine forests, preferably on *Ulmus glabra*. The vegetation there and in Scandinavia was a *Fraxino-Aceretum pseudoplatani*, in the Rhön sometimes also an *Epilobio-Salicetum capreae*, a transitional stage which develops in basalt quarries. Two samples were from inframediterranean semihumid Algarve of southern Portugal: on branch of *Nerium* in a scrubland (maquis) along a rivulet on calcareous soil, and on branch of *Eucalyptus* from a mixed eucalypt woodland on top of a mountain of acidic soil.

Specimens included. **NORWAY**: **Aust-Agder**, 5 km ENE of Arendal, Tromøy, Kvernhuskjerr, 18 m, branch of *Ulmus glabra*, on bark, 22.III.2009, T.H. Dahl (T.H.D. 73/09, doc. vid.). – ibid., trunk of *Salix caprea*, on bark, 15.IV.2009, T.H. Dahl (T.H.D. 116/09, H.B. 9046a, M-0291772, **epitype**; sq.: KT222354). – ibid., S of Alvekilen, 5 m, of *U. glabra*, on bark, 9.IV.2009, T.H. Dahl (T.H.D. 98B/09, non vid.). — **SWEDEN**: **Skåne**, 9 km ESE of Lund, NW of Dalby, Dalby Söderskog, branch of *Ulmus*, on bark, 3.V.1998, H.G. Unger, vid. T.R. Lohmeyer (T.R.L. 98/10, H.B. 6124, anam. substr.). – 6 km WNW of Röstånga, Söderåsen, Kvärkabäckens ravine, 135 m, branch of *U. glabra*, on bark, 3.VI.2006, T. Læssøe & H.O. Baral (H.B. 8208a, anam. substr.). — **GERMANY**: **Hessen**, Rhön, 18.3 km ESE of Fulda, 4.5 km N of Gersfeld, NE of Guckaisee, below Wasserkuppe, 800 m, branch of *Salix caprea*, on bark, 3.IV.2006, L.G. Krieglsteiner (L.K., non vid.). – 7 km NNE of Gersfeld, 2.5 km WNW of Wüstensachsen, Schafstein, 750 m, branch of ?*S. caprea*, on bark, 12.IV.2001, L.G. Krieglsteiner (H.B. 6935, anam. substr.). – ibid., 720 m, branch of *U. glabra*, on bark, 23.II.2007, L.G. Krieglsteiner (L.K., non vid.). – 6.3 km NE of Gersfeld, 2.2 km SSW of Ehrenberg-Wüstensachsen, Schwarzwald, 700 m, branches of *Ulmus*, on bark, 24.XI.2003, L.G. Krieglsteiner (L.K., H.B. 7442, anam. substr.). – **Bayern**, **Unterfranken**, Rhön, 27 km SE of Fulda, 3.5 km N of Bischofsheim, SSE of Holzberghof, Schwarzbach, Teufelsmühle, 700 m, branch of *U. glabra*, on bark, 3.IV.2006, L.G. Krieglsteiner (L.K., non vid.). – ibid., E of Holzberghof, 750 m, branch of *U. glabra*, on bark, 26.II.2007, L.G. Krieglsteiner (L.K., non vid.). – 5.3 km W of Sondheim, 3.5 km NW of Oberelsbach, Gangolfsberg, Elsbachschlucht, 605 m, branch of *Tilia*, on bark, 11.IV.2001, L.G. Krieglsteiner (L.K., non vid.). – 7.2 km NNW of Oberelsbach, 3 km W of Hausen, Eisgraben, 740 m, branch of *U. glabra*, on bark, 24.II.2007, L.G. Krieglsteiner (L.K., non vid.). – 4 km NNW of Oberelsbach, 3.2 km NW of Urspringen, Lichtenstein, 590 m, branch of *Salix caprea*, on bark, 25.IV.2001, L.G. Krieglsteiner (L.K., non vid.). — **PORTUGAL**: **Faro** (Algarve), 7.7 km ESE of São Bartolomeu de Messines, 2.8 km WSW of Alte, 110 m, branch of *Nerium oleander*, on bark, 14.II.2016, L.G. Krieglsteiner (H.B. 9980; sq.: MK493128). – 1.1 km N of Monchique, SE of Peso, 530 m, branch of *Eucalyptus*, on bark, 1.I.2018, L. Krieglsteiner (L.K., doc. vid.). — **UNLOCALIZED**: indet. angiosperm, ?branch of indet. angiosperm, on bark, undated, collector unknown (herb. Persoon, L0054584, = L 910.261-535, **holotype**, H.B. 7700 ø)

Map 75. Known distribution of *O. rubella* in Europe (samples from Portugal genetically deviating).

Orbilia phragmotricha Baral, E. Weber & L.G. Krieglst., in Krieglsteiner, Regensb. Mykol. Schr. 14: 12 (2007) — Pls 431–432, Map 76

≡ *Orbiliaster paradoxus* Huhtinen, Karstenia 32: 63 (1992, as *paradoxa*) [non *Orbilia paradoxa* Ade, ?= *O. flavida*; nec *Orbilia paradoxa* Velen., = *O. xanthostigma*]

= *O. texticola* Allesch. (nom. nud. in sched.)

Etymology: *phragmotricha*: according to the septate marginal hairs; *paradoxus*: referring to the paradox situation of very remote type localities of the two species included in *Orbiliaster* (S. Huhtinen pers. comm.); *texticola*: growing on textile.

Typification: Finland, Varsinais-Suomi, Parainen (Pargas), ?branch of ?*Populus tremula* or *Salix*, 19.X.1985, S. Huhtinen (TUR 99719, holotype of ***Orbiliaster paradoxus***); Luxembourg, Dommeldange, branch of *Salix caprea*, 12.V.2004, G. Marson (ex H.B. 7535a, M-0291767, epitype, designated here, MBT385118, ex-epitype culture: CBS 117017; sq.: KT215259).

Misapplied names: Karsten (1870: 248, 1871: 102, p.p.maj.), as *Orbilia rubella*; Nannfeldt (1932, 252, p.p.), as *Hyalinia rubella*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.4–)0.5–1.5(–2)((–2.5)) mm diam., 0.1–0.26 mm high (receptacle 0.055–0.11 mm), (very pale to) light to bright (cream-salmon-)rose(-pink) or orange-rose, semitranslucent, round to ± irregularly shaped when large, scattered to densely gregarious; disc medium to strongly concave, partly urceolate, sometimes flat to slightly convex when old, margin distinctly whitish fimbriate to ± crenulate, 15–60 µm protruding (including hairs); broadly sessile, sometimes on a stipe-like base 0.07–0.13 × 0.1–0.45 mm, superficial, also distinctly erumpent from beneath periderm or cracks in bast; dry light to deep ochre-orange to orange-red, white-haired,

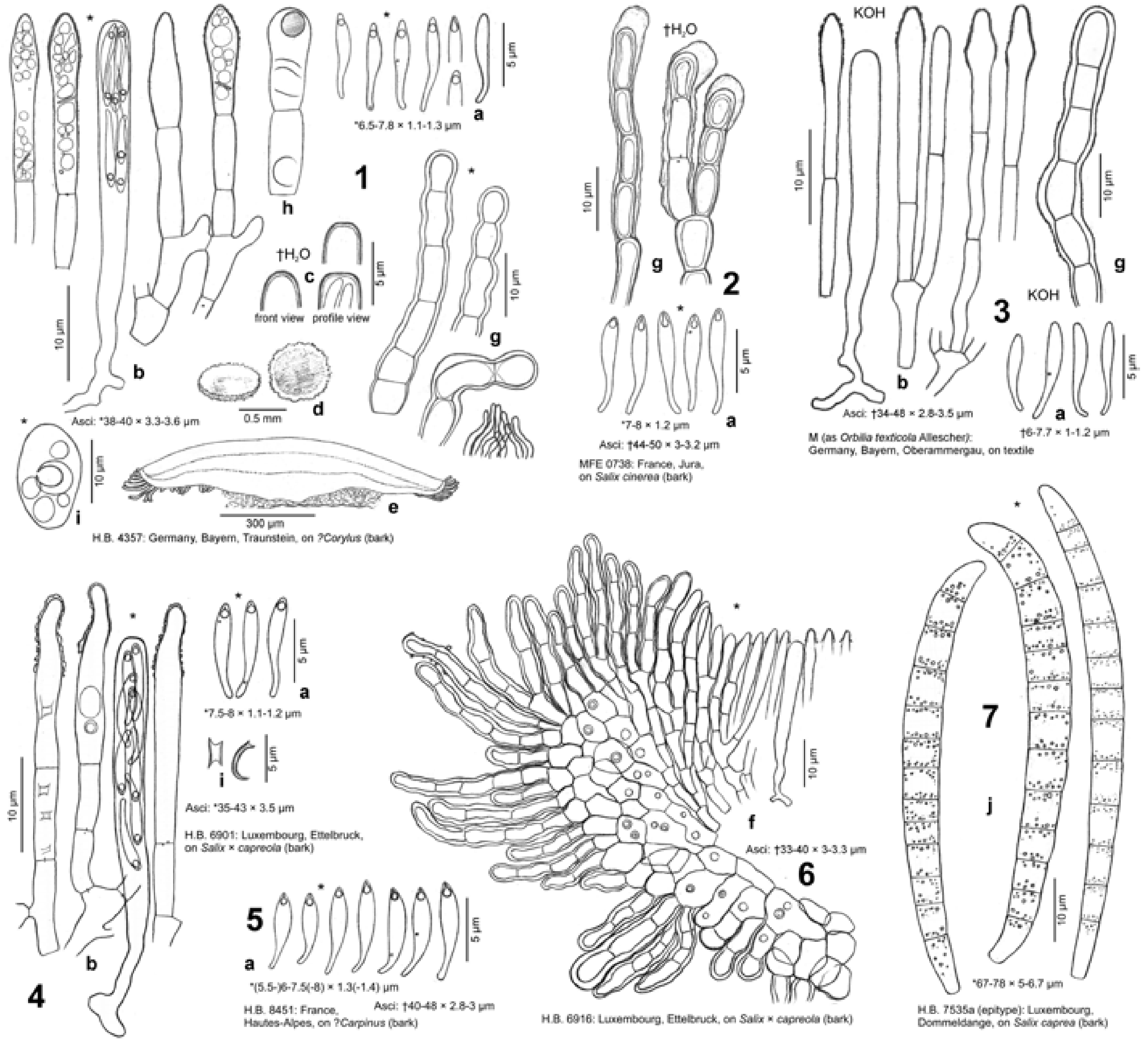


Plate 431. **1–7**: *Orbilia phragmotricha*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia (fresh); **e**. apothecium in median section; **f**. id., margin and mid flanks; **g**. hairs; **h**. marginal element between paraphyses and hairs; **i**. SCBs in cells of ectal excipulum at base and flanks; **j**. conidia from culture.

partly hysterioid. **Asci** *35–50(–54) × 3.3–4.2 µm {5}, †30–50 × 2.8–3.5(–3.7) µm {6}, 8-spored, spores *2(–4)-seriate, (2–)3–6(–7) lower spores inverted {9} (sometimes ± mixed), pars sporifera *(12.5–)19–25 µm long; **apex** (†) medium to strongly truncate (rarely slightly indented, without lateral inflation); **base** with medium long, thin, flexuous stalk, T- or Y-shaped. **Ascospores** *(5.5–)6–8.5(–9.8) × (1–)1.1–1.3(–1.5) µm {15}, †6–8(–8.8) × 1–1.2 µm {10}, narrowly fusoid- to fusiform-clavate, apex obtuse to subacute, rarely acute, base attenuated in a tail-like end or short tail *1–3 × 0.3–0.6(–0.8) µm, upper part straight or somewhat inequilateral, tail ± geniculate (partly slightly helicoid); **SBs** *(0.8–)1–1.3(–1.6) × (0.4–)0.5–0.8(–0.9) µm {9}, tear-shaped or globose, attachment ± invisible. **Paraphyses** apically slightly to medium (obtusely) lanceolate to spathulate, sometimes sublageniform, terminal cells *(12–)15–24(–27) × (2.5–)2.8–3.8(–4) µm {6}, †12–21 × 2.5–3.5(–4) µm {1}, exceeding the dead asci by (2–)3–7(–9) µm (the living by 2–7 µm), lower cells *5–13.5 × 2–3(–3.5) µm {4}, †8–14 × 1.5–1.8 µm {1}; never branched at upper septum. **Medullary excipulum** hyaline, 10–80 µm thick, of medium loose or dense textura intricata or t. globulosa, sharply delimited from ectal excipulum, partly only at flanks, by an indistinct, 7–30 µm thick, hyaline to pale rose t. porrecta. **Ectal excipulum** pale to light rose to orange, of ± thin-walled († slightly gelatinized), vertically oriented t. (globulosa-)angularis(-prismatica) from base to mid flanks or margin, 35–130 µm thick near base, cells *7–23(–28) × (5–)7–12(–18) µm {8}, 20–40 µm thick at lower flanks, 15–25 µm thick at mid flanks and margin, here of t. angularis or t. prismatica-porrecta oriented at a 10–45° angle to the surface; from upper flanks to margin densely covered by projecting **hairs** */†(20–)30–50(–60)((–93)) × (3.5–)4–6(–7)((–8.5)) µm {21}, (1–)2–6(–8)-septate {13}, irregularly flexuous, partly ± moniliform, often coherent to form ± distinct teeth; thick-walled (with an outer and inner refractive delimiting membrane), entire wall *0.6–1.3(–2) µm thick {4}, †(0.5–)0.8–1.8(–2.7) µm {6}, sometimes (sub)apically thickened to 2–8 µm {3} (cap-like, dead terminal hair cells rarely with slightly swollen, low-refractive internal wall layer); **glassy processes** absent. **Anchoring hyphae** very abundant, */†2–3.5(–4) µm wide, walls 0.2–0.8(–1.2) µm thick {11} (including low-refractive gel sheath), distinctly gelatinized, forming a loose or dense t. intricata 20–150 µm thick. **SCBs** in paraphyses and ectal excipulum globose, 1–2.5 µm diam., also crystalloid (filiform, ring-, sickle-, or horseshoe-shaped) {11}, 3–6 µm diam., hyaline to pale orange (especially in excipulum from base to margin). **Exudate** over protruding part of paraphyses 0.2–0.3 µm thick, rough-granulate, firmly attached; over hair surface partly forming scattered, very fine warts. **— ANAMORPH**: vermispora-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** not seen. **Conidia** unbranched, C-shaped, slightly to strongly curved near ends, (straight or) slightly curved in middle part, *67–78 × 5–6.7 µm, 11–15-septate {Luxembourg}; *43–48 × 6.4–6.6 µm, 9–11-septate {Mongolia}.

Habitat: collected (0–)0.3–3 m above the ground, corticated, 8–80 mm thick branches, also 20 cm thick trunks, of *Acer platanoides* {1}, *A. pseudoplatanus* {1}, ?*Carpinus betulus* {1}, ?*Corylus avellana* {1}, *Fagus sylvatica* {1}, *Frangula alnus* {1}, *Fraxinus excelsior* {1}, ?*Populus sp.* {1}, *P. nigra* {2}, *P. tremula* {1/1}, *Salix* sp. {21}, *S. appendiculata* {1}, *S. aurita* × *caprea* {2}, *S. cantabrica* {2}, *S. caprea* {7/1}, *S. cinerea* {3/1}, *S. phylicifolia* {1}, *Sorbus aucuparia* {1}, *S. domestica* {1}, *Tilia* sp. {1}, *Ulmus* sp. {1}, *U. laevis* {1}, indet. angiosperm {2}, textile {1}, on (slightly to) medium, rarely strongly decayed, sometimes entirely detached bark {55} (periderm {10} and bast {25}), exceptionally on wood {4}, often on inner surface of detaching bark, also on edges along large cracks or on outer surface of bast below periderm that curls outwards, or in small holes or narrow crevices by pushing small lobes of periderm aside, ungreyed but sometimes blackened, algae sparse or absent, sometimes on or close to very old pyrenomycetes {5} (*Diatrype*, *Eutypella*, *Rosellinia*, ?*Teichospora*, *Valsa*). **Associated**: *Allophylaria macrospora* {1}, *Brachythecium rutabulum* {1}, *Cistella chlorosticta* {1}, *Crepidotus* sp. {1}, *Cryptocoryneum condensatum* {1}, *Cytidia salicina* {1}, *Diatrype bullata* {3}, *Durella atrocyanea* {1}, *Echinosphaeria strigosa* {1}, *Eutypella sorbi* {1}, *Exidia recisa* {1}, *Flammulina velutipes* {1}, *Frullania dilatata* {1}, *Helicogonium orbiliarum* (parasitic in *O. phragmotricha*) {1}, *Hysteropatella elliptica* {1}, *Lasiosphaeria* sp. {1}, *Merismodes* ?*anomala* {1}, *Metzgeria* sp. {2}, *Neonectria punicea* {1}, *Orbilia aurantiorubra* {4}, *O. auricolor* {1}, *O. carpoboloides* {1}, *O. eucalypti* {3}, *O. phanosoma* {1}, *O. poitevinica* {1}, *O. rubella* {1}, *O. subtrapeziformis* {1}, *O. xanthoguttulata* {5}, *Orthotrichum* sp. {1}, *Parmelia* sp. {1}, *Physcia* sp. {1}, *Propolis farinosa* {1}, *Radula complanata* {1}, *Rosellinia* sp. {1}, *Sclerococcum* sp. {1}, ?*Teichospora* sp. {1}, *Usnea* sp. {1}, *Valsa* sp. {1}. **Desiccation tolerance**: fully tolerant for max. 3.5 months but asci often already dead after 1 month, ascospores still viable after 4.5 months. **Altitude**: 18–470 m a.s.l. (Scandinavia), 260–1200 (central Europe), 900–1780 m (southern Europe), 1070–2400 m (central Asia). **Geology**: Buntsandstein, Muschelkalk, Lower to Middle Jurassic sand- & limestone, Cretaceous limestone, clay & sand, dolomite, Eocene calcareous marl- & sandstone, flysch, Tertiary molasse, Pleistocene moraine; granite, pegmatite, quartz, gabbro basalt, gneiss, schist, serpentinite. **Phenology**: throughout the year (long-lived).

Phenology of *O. phragmotricha*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2	10	4	11	6	4	2	9	2	2	2	3

Taxonomic remarks. *Orbilia phragmotricha* is readily recognized by its very thick-walled, septate hairs without terminal glassy processes, and by small, narrowly fusoid to fusiform ascospores with a short, somewhat geniculate tail. *O. phragmotricha* is very close to the North American *O. paradoxoides*, especially in hair morphology, the latter differing in much wider spores. *O. rubella* deviates in larger spores and in short to long glassy processes on the hair tips. The glassy matrix of these processes appears to be of a nature different from the thick walls of the hairs of *O. phragmotricha*. The hair wall in *O. phragmotricha* seems to be composed of a dense gel matrix which corresponds to the less dense gel on the anchoring hyphae.

Variation. Considerable variation in hair size was noted: length varied from 20–30 µm up to 45–93 µm (mostly 30–50 µm), width from 2.8–4.5 µm up to 6–8.5 µm (mostly 4–6 µm), wall thickness between †0.5–1.3 and †1–2(–2.7) µm, and cell number from (2–)3–4 µm up to 5–7(–9) µm. In *O. paradoxoides* a similar variation was observed within the single known population, somewhat depending on the size of the apothecia (longer and wider hairs in larger apothecia). Although the spores of *O. phragmotricha* show only little variation, they slightly differ among the collections in length and/or width, and vary also in the apices between obtuse and acute. High variation was noted in apothecial colour which was mostly pale to light salmon-rose, but also deep orange.

Nomenclature and type studies. *O. phragmotricha* is proposed here as a nomen novum for *Orbiliaster paradoxus*. This taxon turned out to be conspecific with *Orbilia rubella* s. Karsten (p.p.maj.) and *Hyalinia rubella* s. Nannfeldt (p.p.). Karsten's (1870: 248, 1871: 102) concept of *O. rubella* was found to be quite consistent: six out of seven reviewed collections belonged to *O. phragmotricha*, but one (P. Karsten 4852) to *O. xanthoguttulata*. One (FFE 834) is a mixture of *O. phragmotricha* and *O. auricolor*. The rather long spores (8–12 × 0.5 µm) indicated by Karsten (l.c.) obviously include *O. xanthoguttulata*: his notes on the label of 4852 (apothecia golden yellow, spores 10–12 × 0.5 µm) refer to this species, whereas Karsten's (l.c.) macroscopic diagnosis of *O. rubella* refers to carneous-red apothecia with a lacerate margin, unlike *O. xanthoguttulata*. Later, Karsten (1885: 142) included a specimen of Rehm (Ascomyc. 461, = *O. rehmii* in the present study) in his concept of *O. rubella*.

Nannfeldt (1932: 252) had a rather broad concept of *Hyalinia rubella*. His description, which is restricted to excipular and hair characters, is solely based on FFE 834 (the population of *O. phragmotricha*). Nannfeldt described and illustrated the hairs as 30–40 × 3–5 µm, cylindrical, indistinctly or not at all septate, thin-walled, agglutinated as scale-like teeth. Reexamination of FFE 834 (H) in the present study showed, however, that the hairs are wider (30–55 × 5–7 µm), thick-walled, and up to 6-septate (Pl. 432: 5).

Nannfeldt's broad concept of *H. rubella* is documented by the fact that he accepted Karsten's inclusion of Rehm Ascomyc. 461 in this species. Nannfeldt further added with hesitation two specimens of Roumeguère, which were not revised in the present study. He also believed that the type of *O. coccinella* (herb. UPS) was possibly conspecific with *O. rubella*, and he even included the type of *Peziza rubinella* (= *O. vinosa*) in the scope of this species. Based on Massee's (1894a) redescription of *Peziza cruenta* and its asserted synonyms *P. rufula*, *P. fibriseda*, *P. saccharifera* and *P. regalis*, Nannfeldt referred all these five North American taxa, which are mainly accepted as different species in the present monograph, with some doubt to synonymy with *O. rubella*.

Based on a single recent Finnish collection, Huhtinen (1992) proposed ***Orbiliaster paradoxus*** as a new species. He placed it in the genus *Orbiliaster* because of the presence of long, septate hairs with a cyanophilous wall coating, and uninflated paraphyses, similar as in *Orbiliaster pilosus*. We have not examined the type specimen (TUR 99719) since Huhtinen's detailed description very well concurs with the present concept of *O. phragmotricha*. As the only difference to be mentioned, the paraphyses were described as cylindrical, 2 µm wide (in Huhtinen's drawing a width of 2–2.5 µm can be evaluated), whereas they were in our material */†2.5–4 µm wide and often distinctly lanceolate to spathulate. Because of the brief and

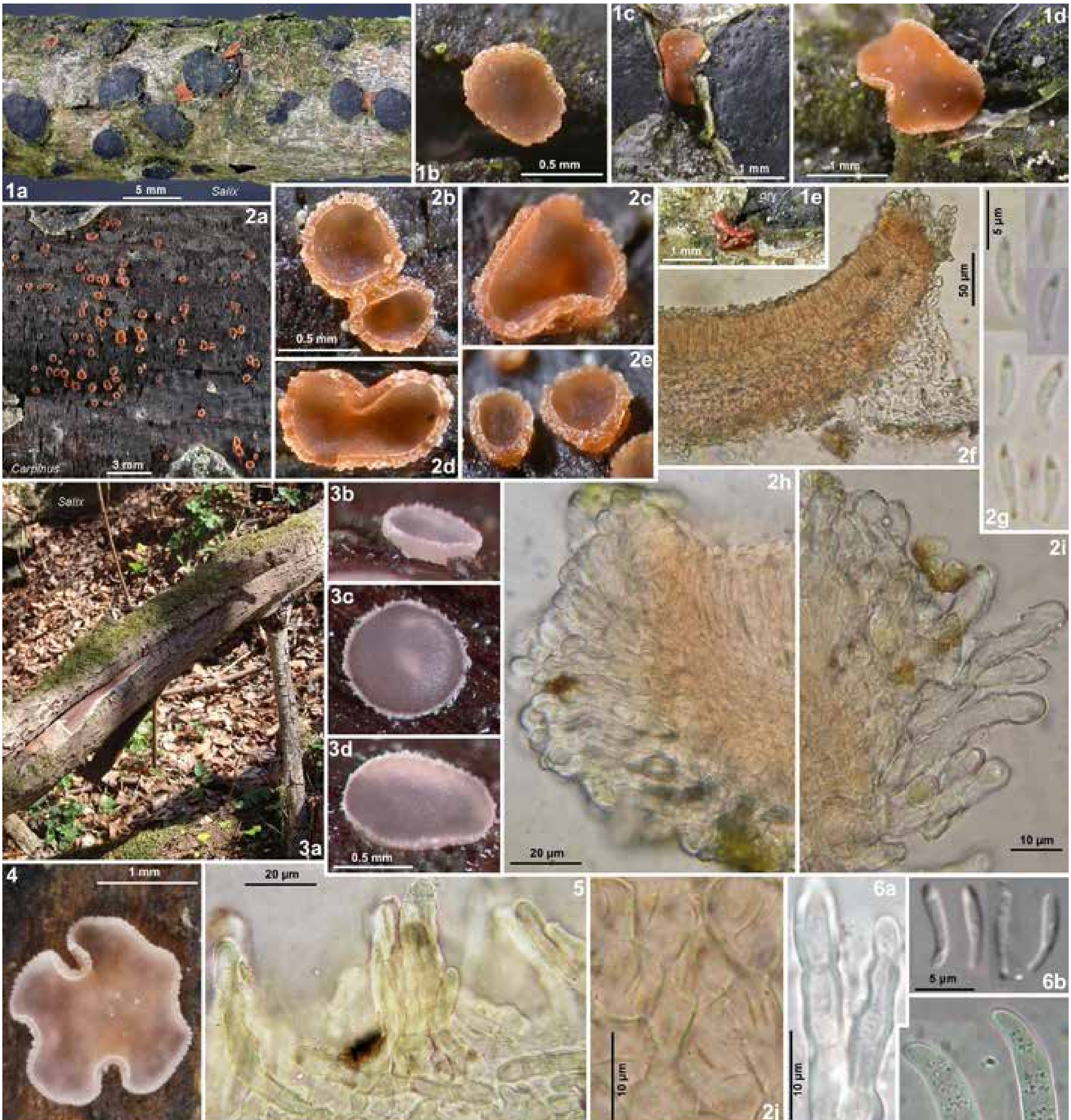


Plate 432. **1–9**: *Orbilia phragmotricha*. – **3a**. corticated, fallen, recently dead *Salix* trunk; **1a–d**, **2a–e**, **3b–d**, 4, **7a**. rehydrated apothecia; **1e**, **7b**. dry apothecia; **2f**. apothecia in median section; **2h–i**. id., marginal ectal excipulum and hairs; **5**. marginal hairs in external view; **2j**. SCBs in basal excipular cells; **6a**. hairs; **7c**. paraphyses; **2g**, **6b**, **8**. ascospores; **7d**, **9**. conidia (**7d** from substrate, **9** from culture). – Living state, except for **2h–i**, **6a**, **6b** (right spores) (in H_2O), **5** (in KOH). – **3a–d**: phot. P. Perz; **6a–b**: phot. E.S. Popov (**b**: DIC); **8**: phot. P. Blank. — **1a–e**. H.B. 8293: Switzerland, Luzern, on *Salix*; **2a–i**. H.B. 8451: France, Hautes-Alpes, on ?*Carpinus*; **3a–d**. P.P. 20070426-4: Poland, unlocalized, on *Salix*; **4**. H.B. 6916: Luxembourg, Ettelbruck, on *Salix*; **5**. P. Karsten FFE 834: Finland, Mustiala, on *Salix*; **6a–b**. 3.VIII.2008: Russia, Altay, on *Salix*; **7a–d**. H.B. 7890b: Mongolia, Altay, on *Salix*; **8**. H.B. 4624: Switzerland, Winterthur, on *Salix*; **9**. H.B. 7535a (epitype): Luxembourg, Dommeldange, on *Salix*.

partly incorrect descriptions in Karsten (l.c.) and Nannfeldt (l.c.), Huhtinen overlooked the presence of *O. phragmotricha* in Karsten's herbarium.

The single specimen of ***O. texticola*** in M (Pl. 431: 3) contains a two-fold handwritten diagnosis. Since the collection was not distributed as exsiccata with copies of the diagnosis, *O. texticola* is to be considered to be an invalid herbarium name.

A specimen from Luxembourg (Dommeldange, on *Salix*, Pls 431: 7, 432: 9, IVV: H.B. 7535a), from which an ascospores isolate (CBS 117017) and a sequence were gained, is herewith designated as **epitype** of *O. phragmotricha*.

Not included collection. A Serbian sample on *Urtica dioica* (IVV: 2.IV.2018) resembles *O. phragmotricha* in the spores, spathulate paraphyses, and crystalloid SCBs, but has ± elongate orange apothecia which lack any hairs or glassy processes. It probably represents an undescribed species, which might belong in series *Rubellae*.

Anamorph. The phragmosporous conidia obtained in pure culture from a sample from Luxembourg (Pls 431: 7j; 432: 9) were only formed when the agar was flooded with water. Those found on the natural substrate in the Mongolian collection are much shorter and with fewer septa (Pl. 432: 7d).

Phylogeny. Sequences of *O. phragmotricha* were gained from cultures of two collections from Luxembourg (on *Salix* and *Fraxinus*) which comprise the S1506 intron, ITS, and LSU, the former also SSU. In the overlapping region they are identical except for 2 gaps in the ITS2. When analysing the ITS region, *O. phragmotricha* clustered strongly supported with a 5.3–5.5 % distance with *O. rubella* (Phyls 14, S15), the lowest distances being otherwise 9–9.3 % to *O. pisciformis*. In the LSU the distance to other members of section *Aurantiorubrae* lies at min. 3–5 %, and in the intron at min. 18–20 %.

Ecology. *O. phragmotricha* occurs on medium rotten, often detached bark (usually on the inner surface) of mainly xeric branches and trunks of different angiosperm trees, predominantly *Salicaceae*. In only two collections a few apothecia grew on decorticated wood: in one of them (H.B. 8238) the majority was on bast, whereas a sparse collection from Asturias (Spain) studied by E. Rubio was said to be exclusively on wood. The species seems to be not uncommon in colline to altimontane subcontinental, supra- to orotemperate central Europe, hemi- to thermoboreal Scandinavia, and oro- (rarely supra-)submediterranean humid southern Europe. Records are so far lacking from cold- to warm-temperate atlantic western and subatlantic or subcontinental northern regions of Europe. The vegetation includes various moist and more or less shady deciduous forests in ravines, near fens, or in floodplains. Two collections were made in continental central Asia on *Salix* in forests near rivulets in the orotemperate (sub)humid (winter-dry), montane to subalpine mountain taiga of the Altay region.

Map 76. Known distribution of *O. phragmotricha* in Europe (cyan = *O.* aff. *phragmotricha*).

Specimens included. **NORWAY**: **Oslo**, 8 km NW of Oslo, 1.8 km NNE of Holmenkollen, N of Frognerseteren, 470 m, branches of *Salix* (?)*caprea*, on bark, 14.VIII.2002, G. Marson (H.B. 7187a). – **Aust-Agder**, 5 km ENE of Arendal, Tromøy, Kvernhuskjerr, 18 m, trunk of *S. caprea*, on bark, 15.IV.2009, T.H. Dahl (T.H.D. 116/09, H.B. 9046c ø, doc. vid.). — **SWEDEN**: **Uppsala**, 11 km NW of Uppsala, 2 km SW of Bälinge, N of Morberga, 35 m, trunk of *Populus tremula*, on bark, 26.IV.1969, K. Holm & L. Holm (UPS, Holm & Nannf. F. exs. Suec. 3449, as *Hyalinia rubella*, H.B. 7329 ø). — **FINLAND**: **North Karelia**, 42 km WNW of Joensuu, 0.8 km WNW of Outokumpu, Raivionmäki, 140 m, branch of *S. caprea*, on bark, 30.I.2011, M. Pennanen (M.P. 110106, doc. vid.). – **Kanta-Häme**, ~8 km E of Forssa, ~1 km N of Tammela, around Mustiala, ~110 m, branch of *S. phylicifolia*, on bark, 28.XI.1868, P.A. Karsten (Karsten 4849, H-6051967; 4853, H-6051954; 4854a, H-6051978, as *Peziza rubella*). – ibid., on bark of *Salix*, XI.1868, P.A. Karsten (herb. Niessl, M, as *O. rubella*). – ibid, branch of *Salix*, on bark, 28.VIII.?1865, P.A. Karsten (Karsten 4850, H-6051955, as *P. rubella*). – ibid., branch of *Populus nigra*, on bark, 25.V.1869, P.A. Karsten (Karsten 4851, H-6051977, als *P. rubella*). – ibid., branch of *P. nigra*, on bark, 8.XII.1869, P.A. Karsten (Karsten 4855, H-6051966, as *O. rubella*). – ibid., branches of *Tilia*, on bark, 5.IV.1870, P.A. Karsten (Karsten 4856, H-6051965, as *O. rubella*, H.B. 7596 ø). – ibid., branch of *Salix*, on bark, IX.?1869, P.A. Karsten (H 6051957, Karsten FFE 834, *as O. rubella* [mixture with *O. auricolor*]). – **Varsinais-Suomi**, 1.7 km SW of Parainen (Pargas), S of Skräbböle limestone quarry, 40 m, bark of ?*Populus tremula* or *Salix*, 19.X.1985, S. Huhtinen (TUR 99719, **holotype**, doc. vid.). — **POLAND**: unlocalized, branch of *Salix*, on bark, 26.IV.2007, vid. P. Perz (P.P. 20070426-4). — **SLOVAKIA**: **Žilina**, 19 km NW of Žilina, SE of Semeteš, 763 m, branch of *Salix*, on wood & bark, 5.II.2018, A. Polhorský (A.P. 18/52, doc. vid.). — **GERMANY**: **Baden-Württemberg**, Schwäbische Alb, 9 km WNW of Ulm, 3.5 km W of Blaustein, Arnegger Ried, 495 m, on bark of *S. cinerea*, 15.IV.1999, L.G. Krieglsteiner (STU, non vid.). – Schwarzwald, 5 km NW of Calw, 0.8 km SE of Oberkollbach, N of Schweinbach rivulet, 540 m, branch of *Salix*, on bark, ~28.II.1994, A. Gminder (ø). – **Bayern**, **Unterfranken**, Rhön, 8 km SE of Gersfeld, 1.3 km N of Bischofsheim, S of Stengerts, Moorwasser, 500 m, trunk of *S. caprea*, on bark, 26.II.2007, L.G. Krieglsteiner (L.K., non vid.). – **Oberpfalz**, 15 km ENE of Weiden, SE of ruin of Flossenbürg, 685 m, trunk of *Ulmus*, on bark, 21.IV.2014, H.O. Baral (H.B. 9876a). – **Oberbayern**, 8.5 km SE of München, 1 km ESE of Neuperlach, 543 m, branch of *Salix*, on bark, 31.XII.2009, B. Fellmann (MAMU 1842, doc. vid.). – ibid., 16. & 17.I.2011 (ø, doc. vid., MAMU 1220, 1533). – Traunstein, 5 km NE of Laufen, 5.5 km SE of Fridolfing, Salzach river, W of Lettensau, 390 m, trunk of ?*Corylus avellana*, on bark, 3.III.1991, T.R. Lohmeyer (H.B. 4357). – 'Oberammergau', on textile, IX.1899, [L.] Marxer (herb. Allescher, M, comm. G. Schnabl, als '*O. texticola* Allescher nov. spec.', H.B. 5076 ø). — **AUSTRIA**: **Niederösterreich**, 28 km W of Wiener Neustadt, 4 km WNW of Puchberg, NW of Sonnleiten, Sebastianfall, 740 m, branch of *Salix caprea*, on bark, 2.V.2004, G. Koller & T. Bardorf (H.B. 7534). – 6.5 km ENE of Wiener Neustadt, 1 km E of Lichtenwörth, Urwackerau 260 m, branch of *Acer platanoides*, on bark, 13. IV.2019, G. Koller (doc. vid.). – 6 km SW of Puchberg Schneeberg, Baumgartnerhaus, 1180 m, branch of *Sorbus aucuparia*, on *Eutypella sorbi*, 1902, F. v. Höhnel (Höhnel A 4952, M, as *O. rubella*). – **Steiermark**, 20 km NNW of Bruck an der Mur, 3 km NNW of St. Ilgen, Karlschütt, 890 m, branch of *Salix*, on bark, 9.V.2009, G. Friebes (G.F. 20090031, doc. vid.). – **Kärnten**, 11 km SE of Klagenfurt, 1.5 km NNW of St. Margareten im Rosental, Drau river, 410 m, branch of *Salix*, on bark and *Diatrype bullata*, 31.XII.2002, W. Jaklitsch (W.J. 2055, H.B. 7277). – 0.5 km NNE of St. Margareten, 582 m, branch of *Frangula alnus*, on bark, 19.II.1994, W. Jaklitsch (WU 13308). — **SWITZERLAND**: **Nidwalden**, 8 km SSW of Luzern, 2.5 km WSW of Hergiswil, Renggeli, Mülibach, 1000 m, branch of *Acer pseudoplatanus*, on bark & wood, 16.VIII.2006, H.O. Baral (H.B. 8238). – 3.2 km W of Hergiswil, N of Gschwänd, 1200 m, branch of *Salix appendiculata*, on bark, 18.VIII.2006, H.O. Baral (H.B. 8293). – **Obwalden**, 3.3 km WNW of Alpnach, 2.3 km NW of Schoried, Gärteli, 900 m, branch of indet. angiosperm, on bark and old pyrenomycete, 28.IV.1979, T. Honermann (NMLU 2804-79 Ho3, as *Rhamnus frangula* [= *Frangula alnus*]). – **Zürich**, 4.2 km S of Winterthur, 0.5 km N of Kyburg, An der Töss, Leisental, 480 m, trunk of *Salix*, on bark, 23.II.1992, R. De Marchi (R.M., H.B. 4624). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 11 km

W of Ettelbruck, 1.8 km NW of Grosbous, W of Bruch, 390 m, branch of *Salix aurita × caprea*, on bark, 26.III.2001, G. Marson (H.B. 6901). – ibid., 24.IV.2001, G. Marson & H.O. Baral (H.B. 6916, G.M., S.H.). – **Gutland**, **Luxembourg**, 4 km NE of Luxembourg, 2 km ENE of Dommeldange, Schlaed, 310 m, branch of *S. caprea*, on bark, 12.V.2004, G. Marson (ex H.B. 7535a, M-0291767, **epitype**, anam. cult., CBS 117017; sq.: KT215259). – 5 km S of Luxembourg, 1.8 km SW of Hesperange, Fennerholz, 292 m, branch of *S. cinerea*, on bark, 6.II.2003, G. Marson (ø). – ibid., branch of *Salix*, on bark, 6. II.2003, G. Marson (ø). – 4 km ENE of Luxembourg, NW of Kalchesbrück, E of Findel, 333 m, trunk of *Fraxinus excelsior*, on bark, 4.IV.2013, G. Marson (G.M. 2013-04-04.1; sq.: KT380081). – **Esch-sur-Alzette**, 4.7 km SE of Esch-sur-Alzette, 0.8 km SW of Tétange, Millebierg, 390 m, trunk of *Fagus sylvatica*, on bark, 8.II.2010, G. Marson (ø). — **FRANCE**: **Franche-Comté**, **Jura**, Haut Jura, 35 km NW of Genève, 8 km N of St.-Claude, ENE of Les Prés de Valfin, 850 m, branch of *Salix cinerea*, on bark and *Diatrype bullata*, 20.VIII.2000, D. Triebel & G. Rambold (M-0229703, D. Triebel MFE 462, H.B. 6821 ø). – **Doubs**, 5 km SE of Besançon, E of La Vèze, marais de Saône, ruisseau des Moulins, 385 m, branch of *Salix*, on bark, 6.II.2014, G. Moyne (G.My. 2014 02 01). – ibid., 20.II.2014, G. Moyne, J.M. Moingeon, P. Chaillet (G.My. 2014 02 07/08). – **Rhône-Alpes**, **Savoie**, 6.3 km S of Albertville, 3 km W of Esserts-Blay, Forêt de Darbelay, 1550 m, branch of *Salix*, on bark, 6.V.2005, N. Van Vooren, vid. J.P. Priou (J.P.P. 25126, H.B. 7915a). – **Provence-Alpes-Côte d'Azur**, **Hautes-Alpes**, 30 km ESE of Gap, 4.5 km SSW of Les Crots, SW of Abbaye de Boscodon, 1220 m, branch of ?*Carpinus betulus*, on bark, 8.III.2007, Y. Mourgues (H.B. 8451). – 11.5 km NW of Briançon, 1.6 km SE of Le-Monêtier-les-Bains, NW of les Guibertes, 1445 m, branches of *Salix*, on bark, 14.VII.1994, G. Marson (H.B. 5126a, G.M. 5212). – **Alpes Maritimes**, Mercantour, 3.5 km N of Colmars, 3 km S of Allos, La digue d'Allos, 1350 m, branch of *Salix*, on bark, 6.VI.2010, J.P. Priou (J.P.P. 10123, doc. vid.). – 3.5 km ENE of Allos, Valplane, 1780 m, branch of *Sorbus domestica*, on wood, 7.VI.2010, J.P. Priou (J.P.P. 10128, doc. vid.). – 25 km NNW of Monte Carlo, 6.5 km E of Lantosque, Col du Turini, 1640 m, branch of *Salix*, on bark, 3.X.1993, G. Marson (H.B. 4990a). – **Auvergne**, **Cantal**, 4.5 km WNW of Paulhac, 0.3 km NW of Muratel, 1105 m, branch of *Salix*, on bark, 22.IV.2011, G. Girod, vid. J.P. Priou (ø, doc. vid.). – 9 km SW of St.-Flour, 1.5 km WSW of Sériers, E of Peyrelade, 1000 m, on bark of ?*Populus*, 28.III.2009, G. Girod, vid. J.P. Priou (J.P.P. 29062, doc. vid.). – **Languedoc-Roussillon**, **Aude**, Pyrénées-Orientales, 27 km SW of Limoux, 6 km N of Roquefeuil, maison forestière de la Jasse, 900 m, branch of *Salix* (?)*cinerea*, on bark, 4.V.2007, B. Rivault, vid. M. Hairaud (M.H. 20507, non vid.). — **SPAIN**: **Asturias**, 35 km SSW of Oviedo, 3.8 km SSE of Villa del Sub, Puerto de Ventana, 1180 m, of *S. caprea*, on wood, 28. VIII.2008, E. Rubio (E.R.D. 4564, doc. vid.). – 7 km S of Pola de Somiedo, 1.6 km W of Santa María del Puerto, 1505 m, branch of *S. cantabrica*, on bark, 5. VI.2013, F.J. Balda & M. Tapia (ø). – ibid., 5.VI.2017, M. Pennanen, vid. J.P. Priou (J.P.P. 17123, doc. vid.). – 23 km SW of Pola de Somiedo, 4 km E of Monasterio de Hermo, 1365 m, branch of *Salix caprea*, on bark, 31.VIII.2008, E. Rubio (ø, non vid.). – 10.5 km ESE of Pola de Somiedo, 1.8 km SE of Saliencia, 1240 m, branch of *Salix*, on bark, 4.VII.2009, J. Linde, vid. E. Rubio (ø, non vid.). – **Aragón**, **Huesca**, 2.7 km NE of Benasque, 1245 m, branch of indet. angiosperm, on bark, 14.IV.2018, R. Blasco (doc. vid.). — **RUSSIA (West)**: **Novgorod**, **Borovichi**, 51 km SW of Borovichi, 16.5 km N of Valday, Krasnaja Gorka, 245 m, twig of *Ulmus laevis*, on bark, 24.IX.2011, E.S. Popov (LE 247950, doc. vid.). — **RUSSIA (East)**: **Altay**, **Onguday**, 18.5 km SE of Onguday, 3 km S of Chike-Taman pass, valley of Izyndyk river, 1062 m, on bark of *Salix*, 3.VIII.2008, E.S. Popov (LE 247246, doc. vid.). — **MONGOLIA**: **Bayan Ölgii**, Sagsai, Altay Mts., Tavan Bogd, 25 km SE of Dayan lake, 8 km NE of Chinese border, Songino Gol, 2400 m, branch of *Salix*, on bark, 15.VIII.2005, P. Karasch (H.B. 7890b, anam. substr.).

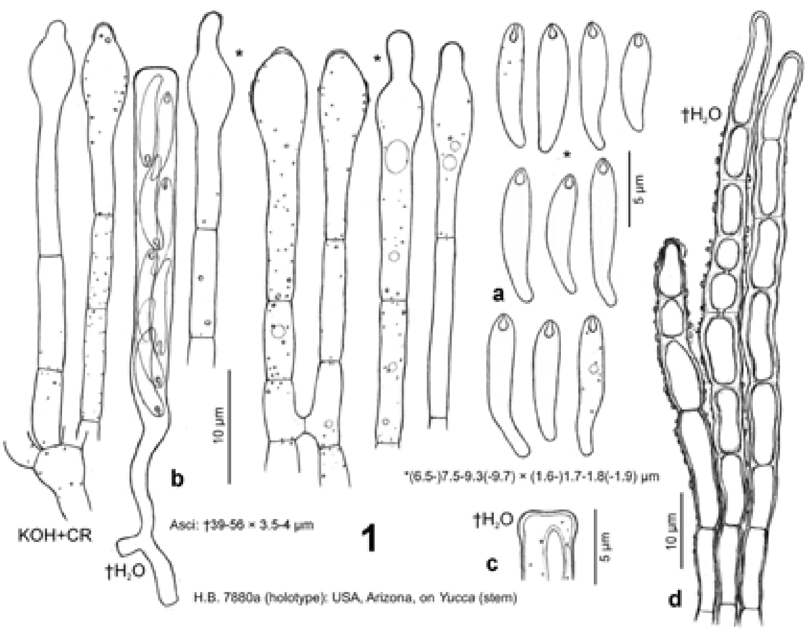


Plate 433. **1**: *Orbilia paradoxoides*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. marginal hairs.

Not included. **SERBIA**: **Vojvodina**, Fruška Gora, 22.5 km WSW of Novi Sad, 2.3 km SW of Grabovo, Ravne, 200 m, stem of *Urtica dioica*, 2.IV.2018, D. Savić (FG-1040, doc. vid.).

Orbilia paradoxoides Baral, **sp. nov.**, MB 813749 — Pls 433–434

Etymology: named after the resemblance to *O. phragmotricha* (≡ *Orbiliaster paradoxus*).

Typification: USA, Arizona, Clifton, inflorescence stem of *Yucca*, 1.VI.2003, G. Marson (ex H.B. 7880a, M-0276551, holotype).

Latin diagnosis: *Apothecia rehydratata 0.3–1.8 mm diam., roseo-aurantiaca, sessilia, margine albido-fimbriato. Ascosporae *6.5–9.7 × 1.6–1.9 µm, subcylindricae ad fusoideo-clavatae, apice obtusae, ad basim modice attenuatae et leniter vel distincte geniculatae, in statu vivo corpusculum refringens minutum lacrimiformem, ad apicem affixum continentes. Paraphyses ad apicem valde inflatae, spathulatae vel lageniformes. Habitat ad caules siccos putridos inflorescentiae* Yuccae *in zonameso temperata semiarida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1.3(–1.8) mm diam., 0.14–0.24(–0.3) mm high (receptacle 0.07–0.13 mm), light to bright rose or orange-rose, not or somewhat translucent, round to elliptical, scattered to (sub)gregarious; disc first slightly to strongly concave, finally flat, margin 0–30 µm protruding (15–60 µm incl. hairs), fimbriate by prominent whitish hairs, partly forming irregular teeth; broadly sessile, slightly to strongly erumpent between fibres, rarely superficial; dry bright orange(-rose), nearly closed. **Asci** *49–54 × 4.5–5 µm, †39–56 × 3.5–4 µm, 8-spored, spores (†) biseriate, ~3–5 lower spores inverted (often mixed), pars sporifera *19–25 µm long; **apex** (†) strongly truncate (slightly indented, laterally sometimes distinctly inflated); **base** with short to medium long, thin, flexuous stalk, T-, L- or Y-shaped. **Ascospores** *(6.5–)7.5–9.3(–9.7) × (1.6–)1.7–1.8(–1.9) µm, †6.4–9.2 × 1.5–1.7 µm, subcylindrical to fusoid-clavate, apex obtuse (to subacute), base medium attenuated in a tail-like end, rarely a distinct tail of 1.5–2.5 × 0.7–1 µm, here mostly slightly to medium geniculate; **SBs** *0.9–1.3 × 0.5–0.7 µm, tear-shaped, apically narrowed to a small to wide point. **Paraphyses** apically medium to strongly spathulate to lageniform or mammiform, terminal cells *13–24 × 3–4(–4.8) µm, †2.5–4(–4.8) µm wide, exceeding the dead asci by 4–7 µm, lower cells *(5–)7.5–16 × 2–2.6 µm, †1.7–2 µm wide; very rarely branched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline, 30–70 µm thick, of dense textura intricata, finally very loose in centre, partly with many inflated cells, medium sharply delimited from ectal excipulum only towards margin. **Ectal excipulum** hyaline, of thin-walled († slightly gelatinized), irregularly to strictly vertically oriented t. globulosa-angularis-prismatica from base to mid flanks or margin, 60–100(–200) µm thick near base, cells *10–24(–34) × 6–14(–18) µm; 20 µm thick near margin (25–35 µm at uppermost margin), of light orange t. (angularis-)prismatica(-porrecta) oriented at a 10–30° angle to the surface, marginal cortical cells *5–13 × 3–4.5 µm, without yellow LBs; **hairs** †30–90 × (3.5–)4–6(–6.5) µm, 3–10-septate, wall †0.5–1.5(–2) µm thick, externally partly tuberculate by granular exudate, ± coherent to form indistinct teeth, **glassy processes** absent. **Anchoring hyphae** abundant, †(2.5–)3–4 µm wide, walls 0.3–0.7 µm

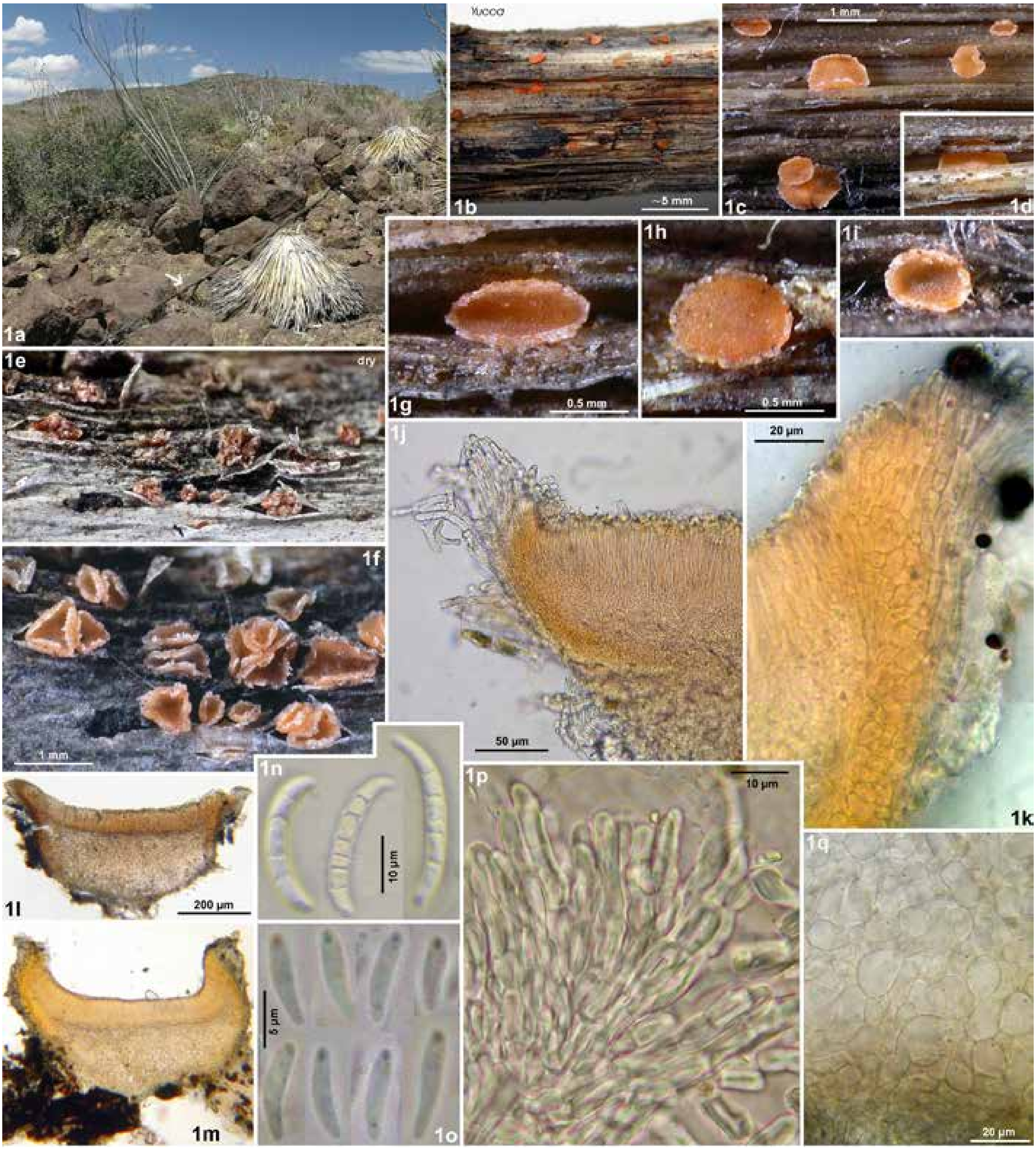


Plate 434. **1**: *Orbilia paradoxoides*. – **1a**. mountainous desert vegetation with *Yucca elata* and *Fouquieria splendens*; **1b**. dead xeric stem of *Yucca*; **1c–d**, **f–i**. rehydrated apothecia; **1e**. dry apothecia; **1l–m**. apothecia in median section; **1j–k**. id., marginal region; **1p**. hairs; **1q**. id., basal excipular cells; **1o**. ascospores; **1n**. conidia from substrate. – Living state, except for **1j**, **n**, **p** (in H_2O). — **1a–p**. H.B. 7880a (holotype): USA, Arizona, on *Yucca*.

thick, forming a thick loose t. intricata. **SCBs** in paraphyses globose, indistinct; in ectal excipulum (near margin) not observed. **Exudate** over paraphyses 0.2–0.3 µm thick, indistinctly rough, firmly attached; over hairs ~0.3–0.8 µm thick, rough-tuberculate. **— ANAMORPH**: vermispora-like (presumed, from natural substrate). **Conidiophores** not seen. **Conidia** unbranched, medium curved (slightly C-shaped), †24–31 × 3.5–4.5 µm, 4–6-septate.

Habitat: collected 0.2–0.6 m above the ground, 10–30 mm thick inflorescence stems of *Yucca* sp., strongly decayed and greyed, on epidermis-free areas or in cracks of epidermis, sometimes on epidermis, green algae very sparse. **Associated**: *Dothideales*, *Orbilia bicknellensis*, *O. denticulata*, *O. lentiformis*, *O. pleiolentiformis*, *Pragmopora* sp. **Desiccation tolerance**: most excipular and medullary cells, in some apothecia also many paraphyses and some mature asci still viable after 28 months. **Altitude**: 1510 m a.s.l. **Geology**: Oligocene to Miocene volcanic rock (basalt, andesite, rhyolite). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia paradoxoides* is very closely related to Eurasian *O. phragmotricha*, from which it differs in the larger, especially wider ascospores with a less distinct, much thicker tail-like base, apically more strongly inflated paraphyses with a more abrupt beak, and in the absence of crystalloid SCBs in the living paraphyses and excipular cells. In hair morphology the two species closely concur.

Anamorph. The medium curved phragmoconidia found on the substrate near apothecia are similar to those of the other species of series *Rubellae* (Pl. 434: 1n).

Ecology. The single very abundant collection was made on strongly decayed xeric inflorescence stems of *Yucca* in a warm-temperate semiarid mixed grass-scrubland adjacent to creosotebush-tarbush desert scrub in a mountainous volcanic area in the Chihuahuan desert of the southwest of Northern America.

Specimens included. **USA**: **Arizona**, Mogollon Rim, 31 km ENE of Safford, 20 km SSE of Clifton, 1510 m, inflorescence stem of *Yucca elata*, 1.VI.2003, G. Marson (M-0276551, **holotype**; **isotype** in H.B. 7880a, anam. substr.).

Series *Aurantiorubrae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Aurantiorubrae*** – Type species: *Orbilia aurantiorubra* Boud.

Etymology: named after the type species, *Orbilia aurantiorubra*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–1(–1.7) mm diam., pale to bright (yellow-)orange, also cream to rose, margin smooth to finely rough or crenulate, sessile or with a short and broad stipe **Asci** *(35–)40–70(–82) × (3.7–)4–5.2(–5.5) µm, 8-spored, lower (or upper) 3–5 spores inverted; **apex** (†) strongly truncate, partly distinctly indented, not or distinctly laterally widened; **base** L-, Y- or h-shaped. **Ascospores** *(9–)10–14 (–17.2) × 1–1.6 µm, narrowly fusiform, apex acute to acuminate, base slightly to strongly narrowed, tail-like or with a distinct tail, medium to very strongly curved near base (± helicoid, upper part falcate), **SBs** *(2–)2.5–5(–5.5) × (0.3–)0.5–1.1 µm, straight, narrowly tear-shaped to subulate, apically narrowed to a small point or sometimes a distinct filum. **Paraphyses** slightly to medium capitate-clavate, terminal cells 1–2.5(–3.5)× longer than lower cells. **Ectal excipulum** cells near base *7–23(–27) × 6–15(–24) µm; **glassy processes** absent or 1–9 µm up to 10–23 µm long. **SCBs** globose mixed with crystalloid ones; **VBs** absent; **LBs** hyaline, sometimes yellow-orange (carotenoids). **Exudate** (0.3–)1–3(–4) µm thick, continuous or cloddy-granular, loosely to firmly attached, hyaline to pale yellowish. — **ANAMORPH**: vermispora-like. **Conidiophores** short (2–10 µm). **Conidiogenous cells** monoblastic or sympodial. **Conidia** phragmosporous, *13–37 × 2.4–5.7 µm (in situ), 3–6(–9)-septate, slightly to strongly curved.

Habitat: bark or rarely wood of angiosperms, humid to semihumid, temperate to submediterranean or subtropical, always desiccation-tolerant.

Recognized species: 3.

Taxonomic remarks. Beside the type species *O. aurantiorubra*, the very closely related *O. jugulospora* is regarded as the only taxon that belongs with certainty to series *Aurantiorubrae*. A third species, *O. binchuanensis*, is tentatively included because of its similar ascospores, although spore orientation within the asci is opposite to the other two species and the vital characters are unknown.

Series *Aurantiorubrae* is characterized by long and narrow ascospores that are gradually attenuated above into an acute to acuminate end which contains a narrowly tear-shaped to subulate spore body, and below into a thin or thick, rounded, distinctly geniculate or hooked end. In fact, the spores exhibit a distinct helicoid curvature mainly towards the base, whilst the upper part is more or less falcate. Although the helicoid curvature is quite obvious, its sense of rotation could not clearly be seen. Similar spores occur in series *Xanthoguttulatae* and *Abutilones*, but their high molecular distance forced us to recognize different series for them. For the morphological differences to series *Abutilones*, *Xanthoguttulatae*, and *Hyalinia* see under these series.

A remarkable feature of series *Aurantiorubrae*, which is also often seen in series *Commatoideae* and *Rubellae*, is the presence of crystalloid SCBs in paraphyses and excipular cells, comprising filiform, rod- to S- or ring-shaped but also rhomboid structures. These three series show a comparatively low molecular distance among each other, except for the only species with available DNA data which lacks crystalloid SCBs (*O. caulicola*), which clustered separate from those with crystalloid SCBs. A possibility would be to include series *Rubellae* and *Commatoideae* in series *Aurantiorubrae*, based on the sequences of *O. rubella*, *O. phragmotricha*, *O. pisciformis*, and *O. comma*, but more molecular data is required to find a good solution.

Species delimitation. *O. aurantiorubra* is possibly a collective species of two very closely related taxa occurring on different hosts, based on slight differences in spore length and molecular data. *O. jugulospora* is genetically sharply separated, nevertheless, it is not easy to recognize this species morphologically, except that its conidia are distinctly narrower than in *O. aurantiorubra*.

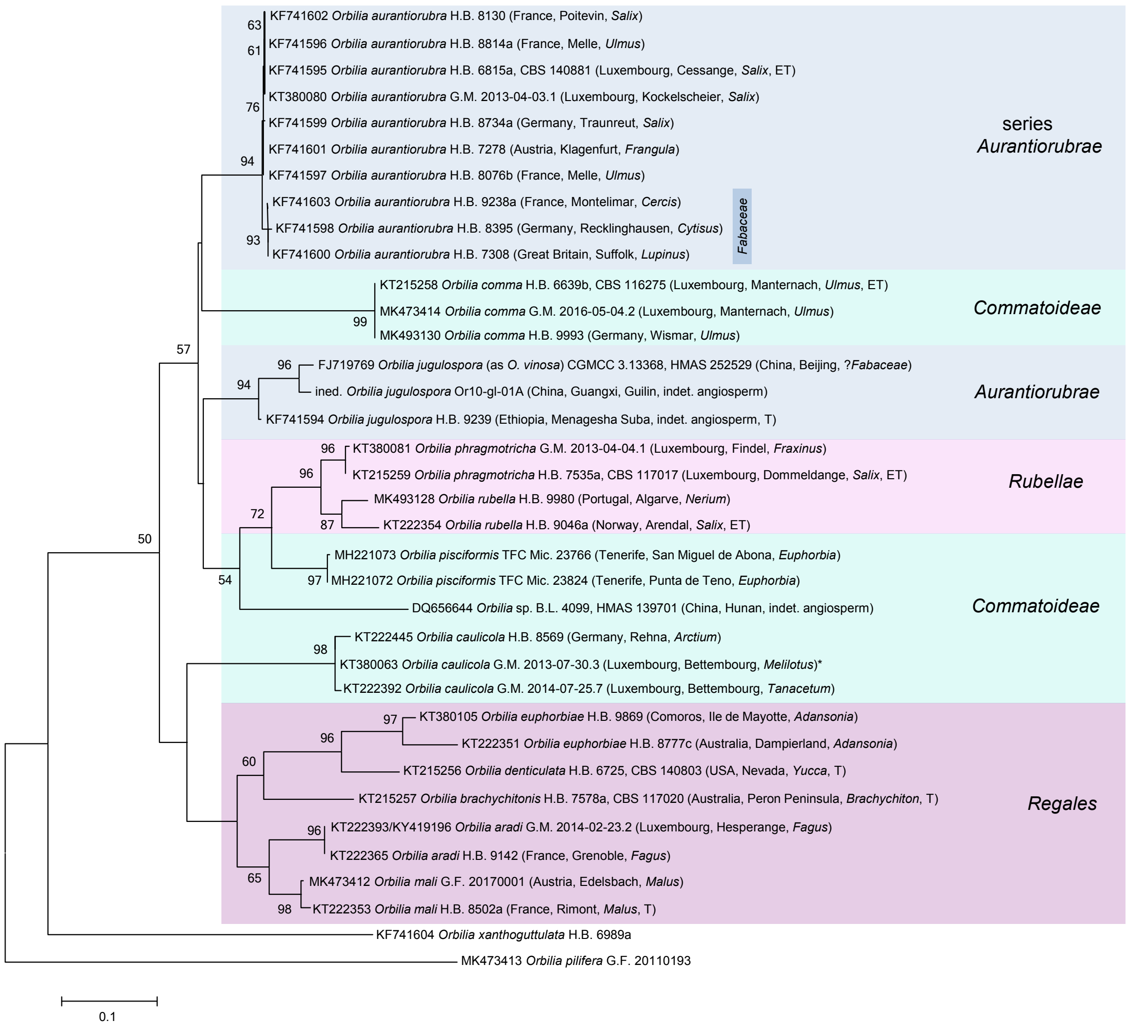
Anamorph. Very similar C-shaped conidia were obtained in pure culture of *O. aurantiorubra* and *O. jugulospora*, which are distinctly shorter and with a tendency to fewer septa compared to the otherwise similar conidia of *O. comma* and *O. phragmotricha*.

Phylogeny. DNA-data were available for *O. aurantiorubra* and *O. jugulospora*, which formed a strongly supported subclade in the analysis of the ITS region by Quijada et al. (2014b), or a medium supported clade in the analyses of ITS+LSU or ITS (Phyls 13, S15), or did not form a clade in Phyls 14 or S16. *O. aurantiorubra* clustered in Baral et al. (2017b, SSU+ITS+LSU) in a strongly supported clade with *O. comma* (series *Commatoideae*) and series *Rubellae*.

O. aurantiorubra was previously considered by us to be closely related to *O. xanthoguttulata* because of rather strong morphological similarities in the teleomorph, although the two species differ in their anamorphs: vermispora-like in the former and dicranidion-like in the latter species. The two species are disposed in different series because they clustered in our molecular analyses always in very different clades. This high molecular distance is also seen in the analysis of Quijada et al. (2014b), who investigated the phylogenetic relationship between members of series *Aurantiorubrae* and *Xanthoguttulatae* based on ITS sequences of 17 strains of series X*anthoguttulatae*, nine of *O. aurantiorubra*, and one of *O. jugulospora*.

Specific nucleotide positions. No molecular motif that unequivocally characterizes series *Aurantiorubrae* has been found. In the LSU D1–D2, pos. 516 is GGA**T**AAA in *O. aurantiorubra* and *O. jugulospora*, which is rather extraordinary within section *Aurantiorubrae* where it is GGA**C**AAA as in most other *Orbilia* spp., but it is GGA**T**AAA also in *O.* (aff.) *farnesianae*, *O. paracaudata*, and *O. amarilla* of series *Piliferae*, a majority of section *Helicoon*, and some species of series *Arthrobotrys*.

Ecology. At least two of the three included species are desiccation-tolerant. All grew on bark of angiosperms, rarely



Phylogenetic analysis 14. Phylogram of series *Aurantiorubrae* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (36 sequences, 648 positions, aligned with MUSCLE) using the T3+G model in MEGA6 (500 replicates). The tree is rooted with *O. pilifera* and *O. xanthoguttulata*. Asci 8-spored in all taxa; T = type, ET = epitype, * = without partial 5.8S and ITS2.

Key to species of series *Aurantiorubrae*

1. Upper spores consistently inverted within asci (acute SB-containing end pointing downwards)........2
1. Lower spores predominantly inverted within asci........3

2. Spores entirely strongly curved (helicoid)........ ***O. pseudobrevistipitata***, p. 863 & ***O. bomiensis***, p. 865 (series *Xanthoguttulatae*)
2. Spores slightly curved (falcate) except for the strongly bent basal end, *9.5–13.5 × 1–1.3 µm; angiosperm bark, subtropical humid eastern Asia........***O. binchuanensis***, p. 844

3. SBs 2–3(–3.3) µm long; paraphysis apices ± ellipsoid; apothecia yellow(-orange), rarely whitish........see ***O. xanthoguttulata*** (series *Xanthoguttulatae*), p. 848
3. SBs (2.7–)3–5 µm long; paraphysis apices clavate-capitate; apothecia (yellowish-)orange(-rose)........4

4. Spores strongly helicoid (basally hooked), *(9.5–)10.5–12(–13) × 1–1.4 µm; SBs mainly 0.4–0.6 µm wide; conidia *2.5–3.5 µm wide, 3(–4)-septate; angiosperm bark, cold-temperate to subtropical humid eastern Asia, northeastern Africa........***O. jugulospora***, p. 843
4. Spores medium helicoid, *9–12.5 up to 12–15(–17) × 1.1–1.6 µm wide; SBs mainly 0.7–1 µm wide; conidia mainly *4–5 µm wide, 4–6-septate; bark (rarely wood) of mainly *Salix*, *Ulmus* and *Fabaceae*, hemiboreal to (oro)temperate humid and mesomediterranean semihumid Europe, Macaronesia, western Asia, eastern North America........***O. aurantiorubra***, p. 834

on wood. *O. aurantiorubra* is known from hemiboreal to mesomediterranean, humid to semihumid Europe and appears to occur also in North America. *O. jugulospora* and *O. binchuanensis* were found in temperate to subtropical humid areas of Asia and Africa.

Orbilia aurantiorubra Boud., Hist. Class. Discom. Eur.: 103 (1907) — Pls 435–438, Map 77

Etymology: named according to the orange-red apothecial colour.

Typification: France, Haute-Marne, Vitry le François, branch of *Salix*, II.1877, D. Richon (herb. Boudier, PC, holotype); Luxembourg, Cessange, Bois de Cessange, branch of *Salix caprea*, 5.XI.2000, G. Marson (ex H.B. 6815a, M-0291763, epitype, designated here, MBT385120, ex-epitype culture: CBS 140881; sq.: KF741595).

Misapplied names: Schweinitz (1832: 177, p.p.), as *Peziza vinosa*; Schröter (1893: 120), as *O. rubella*; Baral (in Baral & Krieglsteiner 1985: 28), as *O. vinosa.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.4–1.2(–1.7) mm diam., 0.14–0.25(–0.35) mm high (receptacle 0.14–0.18 mm), pale or usually light to bright orange-apricot (to brick-red), more rarely yellow-orange, yellowish-cream or salmon-rose(-orange), hardly to medium translucent, round, strongly undulating when large, scattered to often ± densely gregarious in smaller or larger groups; disc slightly concave, soon flat, margin distinct, 0–5 µm protruding, smooth to finely rough; broadly sessile or with a narrow stipe-like base 0.03–0.13 × 0.18–0.2 mm, superficial; dry bright to deep ochraceous-orange or mostly orange-rose-apricot to brick- or blood-red, with thick protruding margin. **Asci** *(45–)52–70(–82) × (4.2–)4.5–5.2(–5.5) µm {15}, †(39–)45–65(–75) × (3.5–)4–4.5(–5.2) µm {12}, 8-spored, spores *4-seriate, 3–5 lower spores inverted {14} (rarely or often mixed: sometimes 1–3 apical spores inverted, sometimes also lower spores not inverted), pars sporifera *22–38 → 18 µm long; **apex** (†) strongly truncate (rarely slightly indented and laterally inflated); **base** with short to often very long, thin, flexuous stalk, L-, Y- or h-shaped. **Ascospores** *9–12.5 {21} or 11–13.5 {19} or (12–)13–15(–17.2) {25} × (1.1–)1.2–1.5(–1.6) µm {60} (in situ, actual length ~11.5–14 µm up to ~14–18 µm), †(9–)9.5–13 {8} or (10.5–)12–14.5(–15) {11} × (1.1–)1.2–1.4(–1.5) µm {19}, narrowly fusiform with (sub)cylincrical middle part, with gradually tapering, acute to acuminate apex, base slightly to medium attenuated (tail-like) or with a tail of 1.5–3 × 0.6–1 µm, often very slightly inflated at the end, distinctly helicoid (looking falcate in profile view), near base medium to mostly strongly geniculate; **SBs** *(2.7–)3–5(–5.5)((–6)) × (0.6–)0.7–1 µm {22} → 2.3–3.7 × 1–1.3 µm, narrowly tear-shaped to subulate, also abruptly narrowed to a filum of ± equal length. **Paraphyses** apically uninflated to slightly or medium (rarely strongly) capitate-clavate, exceptionally spathulate or ± moniliform, (0–)3–6 µm protruding beyond dead asci, terminal cells *(10–)14–30(–35) × (2.2–)2.5–4(–5.3) µm {8}, †1.8–4(–4.7) µm wide {2}, lower cells *(8–)11–18(–22.5) × 1.3–2.7 µm {7}, near base *3–10 × 2–3.5 µm; rarely branched at upper septum, hymenium subhyaline to light orange. **Medullary excipulum** in total 50–170 µm thick, upper part 0–50 µm thick, hyaline to pale rose, of dense textura intricata with globose to angular inflated cells, lower part 50–120 µm thick, of dense to medium loose, large-celled t. globulosa-angularis (cells *7–20 × 6–12.5 µm), irregular to upwards oriented, near margin often forming a distinct, subhyaline to light yellow-orange-rose, horizontal t. porrecta 8–20 µm thick, partly only here sharply delimited. **Ectal excipulum** very pale to light rose or orange, of thin-walled († slightly gelatinized), vertically oriented t. angularis(-globulosa) from base to lower flanks, 25–80(–200) µm thick near base, cells *7–23(–27) × 6–15(–24) µm {6}; 15–20 µm thick at mid flanks and margin, at mid flanks of t. prismatica-angularis oriented at an 80–90° angle to the surface, at margin of t. prismatica-porrecta at 45–90°, marginal cortical cells */†6–15 × (3–)3.5–5(–6) µm {4}, **glassy processes** absent, exceptionally present, 1.5–6 × 3.5–4 µm {1}. **Anchoring hyphae** ± abundant, *2–3.2 µm wide, walls 0.2(–0.3) µm thick {3}, forming a loose or dense hyaline t. intricata-porrecta up to 50 µm thick. **SCBs** in paraphyses globose {11}, 1.2–2(–3) µm diam.; also filiform to S-shaped {12}; excipular cells on lower and mid flanks with inconspicuous to strongly refractive, thin (rarely thick), horseshoe- or often ring- to S-shaped, also rhomboid, hyaline to rarely pale yellow-orange SCBs {18}, marginal cortical cells also with globose SCBs 0.8–3 µm diam; **LBs** in ectal excipulum and paraphyses minute, sparse, hyaline, rarely yellowish. **Exudate** over paraphyses (0.3–)1–2(–4) µm thick, cloddy to granular, also cap-like, hyaline to pale yellowish, firmly attached (large clods also detaching); over margin and flanks rough-cloddy, subhyaline to pale yellow-chlorinaceous, (0.5–)1–5(–7) µm thick. — **ANAMORPH**: vermispora-like (from ascospore isolate {3} and natural substrate {10}). **Conidiophores** reduced, *2–5(–8) × (1–)1.5–2.5 µm {2}, conidia formed terminally or sympodially. **Conidia** phragmosporous, cylindrical with ± tapered ends, slightly to strongly curved (C-shaped), with straight to curved middle part, *(15.5–)19–24(–32.5) {4} or (25–)27–32(–37) {4} × (3.7–)4–5(–5.7) µm {8} (in situ), †(15–)19–29.5 × (2.4–)3–3.7(–4) {4}, ((3–))(4–)5(–6)((–9))-septate {10}, containing a number of minute LBs and a large globose, non-refractive central vacuole, rarely also some large LBs.

Habitat: collected (0.2–)0.5–3(–12) m above the ground, also sometimes on the moist ground, on corticated, (4–)10–50(–100) mm thick branches, more rarely twigs or trunks, of *Acer pseudoplatanus* {1}, ?*Ailanthus altissima* {1}, *Cercis siliquastrum* {2}, *Chamaecytisus proliferus* {1}, *Cytisus scoparius* {14}, *Elaeagnus pungens* {1}, *Euphorbia characias* {1}, *Frangula alnus* {3}, *Fraxinus excelsior* {1}, *Genista florida* {1/1}, *Lupinus arboreus* {2}, *Prunus padus* {1}, ?*Quercus* sp. {1}, *Salix* sp. {33}, *S. alba* {2/1}, *S. aurita* {1}, *S. aurita* × *caprea* {2}, *S. caprea* {20/1}, *S. cinerea* {7/2}, *S. rosmarinifolia* {1}, *Spartium junceum* {1}, *Ulex europaeus* {3}, *Ulmus* sp. {17/3}, *U. laevis* {5}, *U. minor* {4/1}, indet. angiosperm {2}; on slightly to strongly decayed bark {120} (periderm {14} and bast {40}), rarely wood {11}, on exterior of bark but often in small holes or clefts of periderm or on periderm-free areas, also frequently on inner surface of detached hanging bark; rarely on textile {1}; often on or near intact or usually very old pyrenomycetes and coelomycetes (*Chaetosphaeria*, *Cryptodiaporthe*, *Cucurbitaria*, *Diaporthe*, *Diatrype*, ?*Diplodia*, *Eutypella*, *Hypoxylon*, *Karstenula*, *Nectria* etc.), slightly to strongly covered by green algae, rarely in or close to beetle galleries, or in small holes made by ?birds. **Associated**: *Allophylaria macrospora* {1}, *Arthonia cinnabarina* {1}, *Arthrobotrys* sp. {1}, ?*Bacidia* sp. {1}, *Bionectria ralfsii* {2}, *Brachythecium rutabulum* {1}, *Calycina claroflava* {1}, *Calycina* sp. (heterosporous) {1}, *Candelaria concolor* {1}, *Chaetosphaeria phaeostroma* {1}, *Cistella chlorosticta* {1/1}, *Cladonia* sp. {1}, *Cosmospora* sp. {1}, *Cryptocoryneum condensatum* {3}, ?*Cryptodiaporthe* sp. {1}, *Cucurbitaria rhamni* {1}, *Diaporthe syngenesia* {1}, *Diatrype bullata* {12}, *D. stigma* {2}, ?*Diplodia* sp. {1}, *Echinosphaeria* sp. {1}, *Eutypella dissepta* {1/1}, *Exidia recisa* {1}, *Glyphium elatum* {1}, *Helicogonium orbiliarum* (parasitic in *O. aurantiorubra*) {1}, *Hyalorbilia orbiliicola* (parasitic on *O. aurantiorubra*) {12}, *H. fusispora* {1}, *H. subfusispora* {3}, *Hyperphyscia adglutinata* {1}, *Hypoxylon* sp. {1}, *Hysteropatella elliptica* {4}, *Karstenia* sp. {1}, *K. macer* {1}, *K. rhopaloides* {3}, *Karstenula rhodostoma* {1}, *Lachnella alboviolascens* {1}, *Lasiosphaeria* sp. {1}, *Lecanora* sp. {1}, *Lopadostoma gastrinum* {2}, *Melanomma* ?*pulvis-pyrius* {1}, *Metzgeria* sp. {1}, *Micropeziza* sp. {1}, *Nectria* ?*magnusiana* {1}, *N. pseudopeziza* {4}, *Neonectria* ?*coccinea* {1}, *N. punicea* {1}, *Opegrapha* sp. {1}, *Orbilia siculispora* {1}, *O. aristata* {3}, *O. auricolor* {1}, *O. breviaristata* {2}, *O. carpoboloides* {10}, *O. cercidicola* {1}, *O. clavuliformis* {2}, *O. comma* {1}, *O. corculispora* {2}, *O. eucalypti* {3}, *O. mali* {1}, *O. phragmotricha* {4}, *O. pilifera* {5}, *O. pseudoaristata* {1}, *O. subclavuliformis* {2}, *O. trapeziformis* {1}, *O. xanthoguttulata* {4}, *Orthotrichum affine* {1}, *Patellaria atrata* {1}, *Physcia* sp. {2}, *P. adscendens* {1}, *P.* ?*stellaris* {1}, *Psammina* sp. {1}, ?*Pyrenopeziza* sp. {1}, *P. caespiticia* {1}, *Sclerococcum* sp. {1}, *Stictis radiata* {1}, *Taeniolella stilbospora* {1}, *Trichopeziza perrotioides* {1}, *Unguiculariopsis* sp. {3}, *U. ilicincola* {1}, *Xanthoria parietina* {3}, *Xerombrophila crystallifera* {1}, *Xeropilidium dennisii* {1}; acrocarpous mosses, various further crustose lichens. **Desiccation tolerance**: fully viable for at least 2 months (Luxembourg), after 23 months some ascospores and excipular cells still alive, after 32 months some conidia (from mediterranean area). **Altitude**: 1–470 m a.s.l. (northern Europe), 2–750 m (central & western Europe), 31–1561 m (southern Europe), -7–185 m (far eastern Europe). **Geology**: Cambrian, Ordovician & Devonian sediments, Carboniferous silt & greywacke, Buntsandstein, Muschelkalk, Keuper, Jurassic & Cretaceous clay-, sand-, marl- & limestone, gypsum, Minette, Tertiary molasse, Quaternary sand, clay, till & chalk; granite, migmatite, rhyolitoid, mica schist, basaltic breccia. **Phenology**: throughout the year (long-lived, especially from autumn to spring).

Phenology of *O. aurantiorubra*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
18	19	17	20	8	8	1	5	5	11	14	12

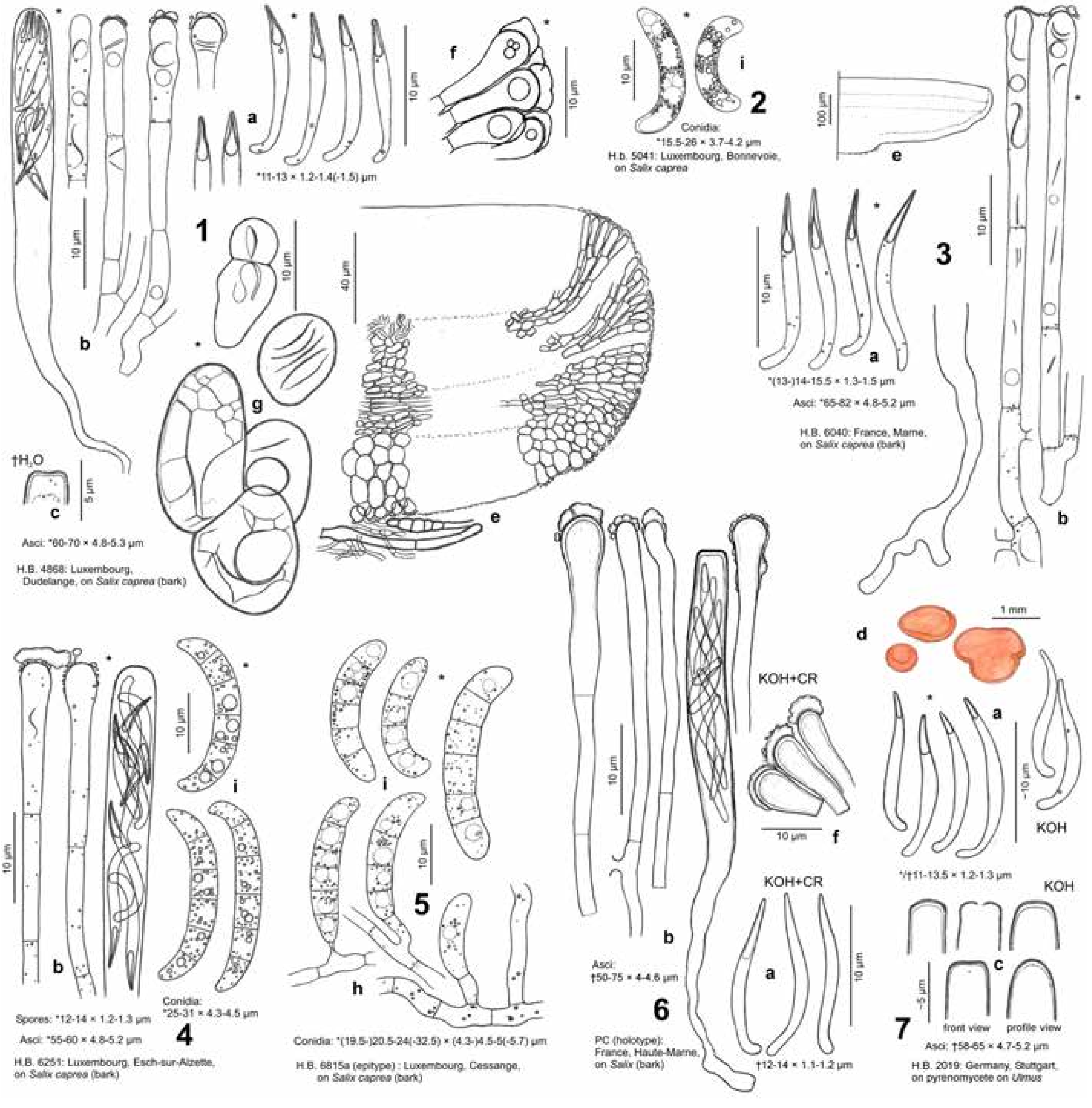


Plate 435. **1–7**: *Orbilia aurantiorubra* (on *Salix* and *Ulmus*). – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecia (fresh); **e**. apothecia in median section; **f**. id., margin; **g**. basal cells of ectal excipulum with SCBs; **h**. conidiophores; **i**. conidia (**4** from substrate; **2**, **5** from culture).

Taxonomic remarks. *Orbilia aurantiorubra* is well characterized by its rather distinctly though not strongly helicoid ascospores with geniculate, rather thick bases and acute subulate apices that contain long, narrowly tear-shaped to subulate SBs. The species resembles *O. xanthoguttulata* and *O. succulenticola* in having almost the same spore shape and size, except that the attenuated part of the spore apices tends to be longer and the included SBs are distinctly longer by hardly overlapping in their length (3–5 µm vs. 2–3 µm). *O. aurantiorubra* further differs in (rose-)orange apothecia that consistently lack a distinct stipe, clavate-capitate paraphysis apices, the presence of crystalloid SCBs and almost consistent absence of both yellow LBs and glassy processes, and an anamorph with unbranched (phragmosporous) conidia. For two very similar subtropical species, the Afro-Asian *O. jugulospora* (p. 843) and the Chinese *O. binchuanensis* (p. 844), see there.

Variation. Rather high variation in length of the ascospores and spore bodies is observed within the present concept of *O. aurantiorubra*. In a majority of the collections (including the type) the spores measured 11–14 µm in length (in situ), especially on the favourite substrates *Salix* and *Ulmus* (Pl. 435: 1, 4, 6–7, Pl. 437: 3f). Yet, a number of specimens showed spores of only 9–12(–13) µm, especially when growing on *Fabaceae* (Pls 436, 438) or rarely extraordinarily long spores of (12–)14–16(–17) µm (on *Salix* and *Ulmus*, see Pls 435: 3; 437: 2d, 6). Also a collection on *Elaeagnus* from England showed spores 14–15 µm long (J.P. Priou pers. comm.). The SBs vary in length from 2.7–3.5 µm up to 4.7–5.5 µm by showing a rather

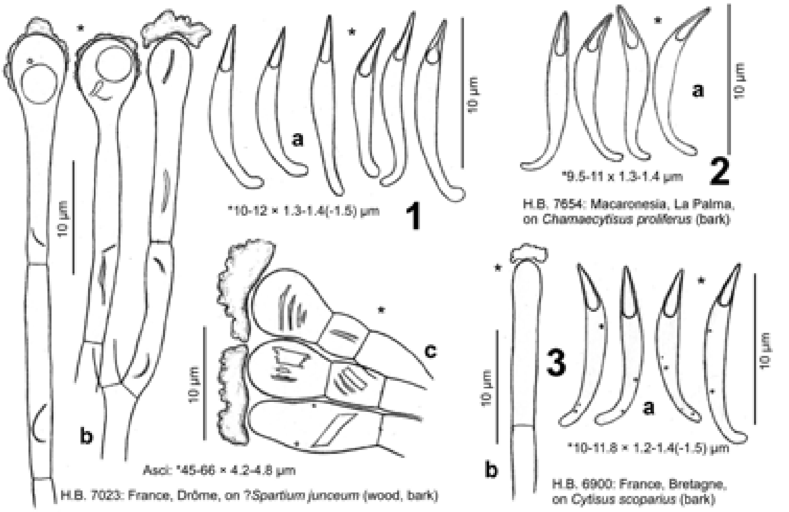


Plate 436. **1–3**: *Orbilia aurantiorubra* (on *Fabaceae*). – **a**. ascospores; **b**. paraphyses; **c**. marginal ectal excipulum in median section.

strict correlation with spore length. Whether different taxa are involved in this variation is not clear.

Typically, the crystalloid SCBs are thin and look as if filiform though they are in fact like a membrane, but in two collections, on *Cytisus* (Pl. 438: 2c–e) and *Ulmus* (Pl. 437: 7b–c), they were partly thicker and semicircular to keyhole-shaped. The latter collection showed short glassy processes at the margin (Pl. 437: 7a) and also some minute yellowish LBs in the excipular cells, according to photographs by I. Wagner, features which were not seen in any of the here studied specimens.

Apothecial colour varied rather considerably between orange-red, yellow-orange and pinkish, but this variation is sometimes observed within a collection (Pl. 437: 3a–e).

Taxa concept. When sorting all records according to spore length, fabaceous substrates remarkably accumulate at the shorter-spored end of the list. In addition to this, short-spored collections on *Fabaceae* predominantly derive from warmer and milder, atlantic to mediterranean climatic regions where the recorded host genera preferably occur (see Map 77). However, several exceptions break this rule. For instance, two records on *Ulmus* from Austria (G.F. 20090147) showed spores of only *9.5–12 µm (G. Friebes pers. comm.), and in four specimens on *Fabaceae* (*Cercis*, *Cytisus*, *Genista*, *Lupinus*) the spores measured *10–13 or 11–13 µm. A collection on *Salix* from a subcontinental montane region (Pl. 437: 3f) showed spores of mainly *10.5–12.5 µm length, while one on *Lupinus* from an atlantic lowland region (H.B. 7298a) had slightly longer spores (*11–13 µm). Rather long spores (up to 15–17 µm) were not only seen in records from subatlantic to continental regions but also from submediterranean areas in western France and northern Spain where *Ulmus* and *Salix* occur. Sharp limits in spore length could not be drawn, because specimens on *Salix* and *Ulmus* not infrequently showed a spore length of *(10–)11–13 µm.

A remarkable situation in northwestern France (Bretagne) confirms a correlation between spore size and substrate. J.P. Priou (pers. comm.) collected here frequently on *Fabaceae* (*Cytisus* and *Ulex*) but also sometimes on *Euphorbia*, *Frangula*, *Salix*, and *Ulmus* (Map 77): all specimens on *Fabaceae*, *Euphorbia* and *Frangula* had short spores (*9–11, 10–12, rarely 11–13 µm), whereas those on *Ulmus* and *Salix* but also *Elaeagnus* had longer spores of *11.5–14 or 13–14 µm. On the other hand, the three available samples on *Frangula* differed in spore length between *9–11 µm (France), *11 µm (Belgium), and *12–13.2 µm (Austria).

A few literature reports also appear to confirm a certain correlation between spore size and substrate (Boudier 1904–10: on *Salix* from Champagne, drawn with a length of (11.5–)13–16.5 µm; Spooner 2001: on *Ulmus* from Surrey and *Acer pseudoplatanus* from Devon, *11–14 × 1–1.5 µm; Priou 2005: on *Cytisus scoparius* in Bretagne and Portugal, *9–13 × 1.2–1.6 µm).

The single studied specimen from North America (atlantic lowland, on ?*Quercus*, IVV: H.B. 7726) showed a spore length at the lower range (†9–11 × 1.2–1.5 µm). In spore shape it is similar to *O. xanthoguttulata*, with subacute apices and the widest part often closer to the apex, but the shape of the paraphyses seems to exclude that species.

Type studies. To the group of long-spored specimens belongs also the holotype of *O. aurantiorubra* (on *Salix*), for which Boudier (1907: 103, 1904–10: 268) gave a spore size of 15–18 × 2 µm. Yet, his values are undoubtedly too large, a frequent phenomenon in his work. From the magnification of his drawing (Boudier 1908 [1904–10]: pl. 464, see Fig. 150: 1) a spore size of (11.5–)13–16.5 × 1.2–1.4 µm can be evaluated, which much better corresponds to the present study of the holotype (Pl. 435: 6). Boudier described the spores as elongate-cylindrical, vermiform, but largely overlooked that one end is acute. Obviously, he depicted dead spores since his illustration is devoid of spore bodies and the upper spore end rarely recognizable.

Boudier (l.c.) measured the asci as 60–80 × 5–6 µm. From his plate a size of 60–78 × 4.2–5.5 µm can be evaluated (the figured asci appear to be dead). This is slightly above measurements found here in the holotype. The width of the paraphysis apices he gave as 5–7 µm (?living state). We have evaluated 4.5–6.5 µm from the plate but only †2–4.7 µm in the type material. Boudier described and depicted 'one or several oil drops' in the paraphysis apices, which do not seem to have been yellow, since they are colourless on his drawing and the paraphyses were described as 'white'. This allows to exclude identity with *O. xanthoguttulata*, in addition to the orange apothecial colour and the clavate paraphysis apices, which did not contain LBs in the holotype (see Pl. 435: 6b). Very probably, these hyaline drops were globose SCBs which disappear when mounting in KOH. According to its wood anatomy, the substrate of the holotype is *Salix*, not *Ulmus* as stated in the protologue. That this material represents the holotype is obvious from the fact that the studied branch fragment with the associated *Xanthoria* (IVV: H.B. 6894) is exactly the fragment that Boudier depicted (Fig. 150: 1).

A specimen from Luxembourg (Cessange, on *Salix*, Pl. 435: 5, IVV: H.B. 6815a) from which an ascospore isolate (CBS 140881) and a sequence were gained is designated here as **epitype** of *O. aurantiorubra*.

Misapplication. Undated and unlocalized specimens in the Schweinitz Herbarium (925-182, PH, BPI) under the name *Peziza vinosa* might correspond to Schweinitz's (1832: 177) report of *Peziza vinosa* from North America. They contained *O. tenuispora* with straight spores (section *Helicoon*, on wood, Pl. 562: 3), and the two in PH also abundantly *O. aurantiorubra* with helicoid spores (on bark, IVV: H.B. 7726b). Schröter's

Plate 437. **1–10**: *Orbilia aurantiorubra* (on *Salix* and *Ulmus*). – **4**. wet *Salicetum* with living and dead *Salix* branches; **1a–c**, **2a–c**, **3a–b**, **d–e**, **5a**. rehydrated apothecia; **3c**. dry apothecia; **1d**. apothecium in median section; **2d**. ascus with ascospores (SBs stained in CRB); **5b**. paraphysis apices; **3f**, **6**. ascospores; **7a**. glassy processes at margin, **7b–c**. ring- to S-shaped crystalloid SCBs in ectal excipulum (flanks); **8–10b**. conidia from natural substrate (**8–9**) and pure culture (**10**). – Living state (**2d**, **10b** in CRB), except for **7a** (in CRB), ascus in **2d**, **9b** (in H_2O). – **2c–d**: phot. M. Hairaud, **5a–b**: phot. P. Perz, **6**: phot. E. Rubio, **7**: phot. I. Wagner, **8**: phot. M. Bemmann. — **1a–d**. H.B. 8130: France, Poitou, Marais Poitevin, on *Salix*; **2a–d**. H.B. 8076b: ibid., Clussais-la-Pommeraie, on *Ulmus*; **3a–f**. H.B. 8734a: Germany, Bayern, Traunreut, on *Salix*; **4**. H.B. 8805a: France, Marais Poitevin, on *Salix*; **5a–b**. P.P. 20061106: Poland, Bystrzyca Kłodzka, on *Salix*; **6**. E.R.D. 4578: Spain, Asturias, on *Salix*; **7a–b**. 6.I.2013: Austria, Wiener Neustadt, on *Ulmus*; **8**. 4.I.2013: Germany, Heidelberg, on *Salix*; **9a–b**. H.B. 9087a: France, Aix-en-Provence, on *Ulmus*; **10a–b**. G.M. 2013-04-03.1: Luxembourg, Kockelscheier, on *Salix*.

Table 69. Nine nucleotide positions in the ITS1 (pos. 1–189) and ITS2 rDNA (pos. 345–545) that vary in the alignment of available *Orbilia aurantiorubra* sequences (Y = C or T). The three specimens on *Fabaceae* (*Cytisus*, *Cercis*, *Lupinus*) consistently differ in 2 nucleotides and 3 gaps from those on non-*Fabaceae*.

Herbarium	Host	Locality	35	61	62	92	98	99	132	369	405
H.B. 8734a	*Salix*	Germany, Traunstein	C	–	–	C	T	A	C	–	A
H.B. 7278	*Frangula*	Austria, St. Margareten	C	–	–	C	T	A	C	–	G
H.B. 8076b	*Ulmus*	France, Melle	C	–	–	C	T	A	C	–	G
H.B. 8814a	*Ulmus*	France, Melle	C	–	–	C	C	A	C	–	G
H.B. 8130	*Salix*	France, Niort	C	–	–	C	C	A	C	–	G
H.B. 6815a	*Salix*	Luxembourg	C	–	–	C	C	A	C	–	G
G.M. 2013-04-03.1	*Salix*	Luxembourg	C	–	–	C	Y	A	C	–	G
H.B. 8395	*Cytisus*	Germany, Recklinghausen	T	T	A	T	T	C	T	C	G
H.B. 9238a	*Cercis*	France, Montélimar	T	T	A	T	T	A	C	C	G
H.B. 7308	*Lupinus*	Great Britain, Dunwich	T	T	A	T	T	A	C	C	G

(1893: 120) report as *O. rubella* (on bark of *Salix*, *Populus*, *Ulmus*) from Silesia (Goszczowice, Lubiąż, Wrocław, Zielona Góra in Poland; Niesky in Germany) undoubtedly refers to *O. aurantiorubra*, according to the description and substrate. At the time when Baral (in Baral & Krieglsteiner 1985: 28) applied the name *O. vinosa* to two samples of *O. aurantiorubra* from Stuttgart (Maierwald, on *Ulmus*), *O. vinosa* in the present sense was still unknown to the author.

Anamorph. The conidia of *O. aurantiorubra* resemble those described for *Chionomyces ponapensis* Matsush. (on bark from tropical Micronesia), a species mentioned under *Vermispora* (see p. 247). In most cases, including our pure cultures, conidia were observed in collections on *Salix*, but a few were also seen on *Ulmus*, *Cytisus*, and *Cercis*.

Conidial size varied between the populations especially in length, also in the number of septa. Short conidia (~19–24 µm) were seen, e.g., in pure culture (Pl. 435: 2, with 3 septa) but also on natural substrate (Pl. 437: 8, with 5 septa, both examples on *Salix*). Conidia of the longer type (~22–33 µm) were mostly 5-septate, while conidia of *34–37 µm with 9 septa were occasionally seen in pure culture (Pl. 437: 10b right, on *Salix*) and on natural substrate (J.P.P. 29004, on *Cytisus*).

Phylogeny. Sequences of a total of nine specimens were gained during Quijada et al.'s (2014b) study, and a tenth later (G.M. 2013-04-03.1). Three of them were on *Fabaceae*, one on *Frangula*, two on *Ulmus*, and four on *Salix* (Tab. 69). All sequences comprise the ITS region, but three also LSU (H.B. 6815a and G.M. 2013-04-03.1 on *Salix*, H.B. 9238a on *Cercis*) and two also SSU (H.B. 6815a, 9238a). Most of them were taken from apothecia, mainly by L. Quijada, but two originate from pure culture (H.B. 6815a, G.M. 2013-04-03.1). In all 10 sequences the absence of the S1506 intron could be verified.

Based on these data, *O. aurantiorubra* shows a rather high distance to the morphologically similar *O. jugulospora* (ITS 9–11.5%, LSU D1–D2 2.9–3.2%, SSU V8–V9 2.4%). Both species differ from *O. xanthoguttulata*/*O. succulenticola* by ~25–26% in the ITS and 6–8% in the LSU.

Variance in the entire ITS region among samples on non-fabaceous hosts was 0–2 nucleotides (0–0.4%) and no gaps. Both the high molecular similarity and the lack of correlation between nucleotides and substrate or geographical origin support the present species concept of a single species. For instance, the specimen on *Frangula* from eastern Austria shows full identity with one of the *Ulmus* samples from western France, whereas three samples on *Salix* are identical with the other on *Ulmus*. The two on *Ulmus* are from the same collection area in western France, but deviate by 1 nt at pos. 98 in ITS1. At this position three samples have C, three T, and one is ambiguous (Tab. 69). The deviation at pos. 405 is unequivocal according to the chromatogram.

Also among the three fabaceous hosts ITS variance was only 0–0.4% without gaps. Thereby, the specimen on *Cytisus* from Germany unequivocally deviates by 2 nt from those on *Cercis* from southern France and *Lupinus* from England, which are identical (Tab. 69). The distance between fabaceous and non-fabaceous hosts ranges at 0.4–0.9%, thereby 2 nucleotides consistently deviate between the two groups (pos. 35 & 92, T vs. C), and 3 consistent gaps occur in the non-fabaceous group (pos. 61–62 & 369, Tab. 69).

Although the three strains on *Fabaceae* formed a strongly supported subclade within the clade of *O. aurantiorubra* (Phyl. 14), the observed ITS distance lies within the currently accepted range of variation of a single species. Among the three available LSU sequences, the two on *Salix* are identical (D1–D2, 554 nt) whereas that on *Cercis* differs by 0.3%. The two available SSU sequences (V8–V9, 363 nt) concur between *Salix* and *Cercis*.

Ecology. *O. aurantiorubra* was found on varyingly decayed bark (rarely wood) of xeric twigs, branches, and trunks of angiosperm trees and shrubs, predominantly *Salix* {70}, less often *Ulmus* {27} and *Fabaceae* {25}, rarely other plant families, exceptionally ± woody herbaceous stems (*Euphorbia*). The collections are mainly from planar to montane altitude and include cold- to warm-temperate, atlantic to continental, but also orotemperate, hemi- to thermoboreal, orosub- to mesosubmediterranean, and supra- to mesomediterranean, humid to semihumid regions. A single record from warm-continental humid North America (Pennsylvania) suggests a circumpolar distribution in the northern hemisphere. The vegetation includes thermophilous and shady forests (e.g., *Salicetum cinereae*, *Alno-Ulmion*, *Fraxino-Aceretum pseudoplatani*). The single Macaronesian collection was in a thermomediterranean semihumid *Chamaecytisus* (tagasaste) plantation at the foot of the laurel and pine forest.

Specimens included. **GREAT BRITAIN**: **West Midlands**, **West Midlands**, 14 km NNW of Birmingham, 1 km N of Walsall, Mill Lane, 128 m, 10.X.2015, P. Thompson (P.T. 10/10/2015-9, doc. vid.). – **East England**, **Suffolk**, 4 km ESE of Halesworth, NNW of Wenhaston, Bicker's Heath, 15 m, branch of *Cytisus scoparius*, on bark, 22.II.2006, S.M. Francis (E.B. 4667, K(M) 227420, doc. vid.). – ibid., branch of *C. scoparius*, on bark, 30.XI.2006, S.M. Francis (H.B. 8379a). – 4.5 km NE of Leiston, Minsmere Haven, S of Sluice, 1 m, twig of *Lupinus arboreus*, on wood, 15.II.2003, E. Batten (E.B. 4391-2 ø, H.B. 7298a). – 5 km SW of Southwold, 1.8 km NNW of Dunwich, Dunwich Forest, 15 m, stems of *L. arboreus*, 7.III.2003, E. Batten & S.M. Francis (E.B. 4394, K(M) 227463, H.B. 7308; sq.: KF741600). – **Cambridgeshire**, 11 km N of Huntingdon, 6 km E of Sawtry, Woodwalton Fen, branch of *Salix cinerea*, on bark, 7 m, 17. IV.2017, H.O. Baral (ex H.B. 10064, K(M) 263138). – **South East England**,

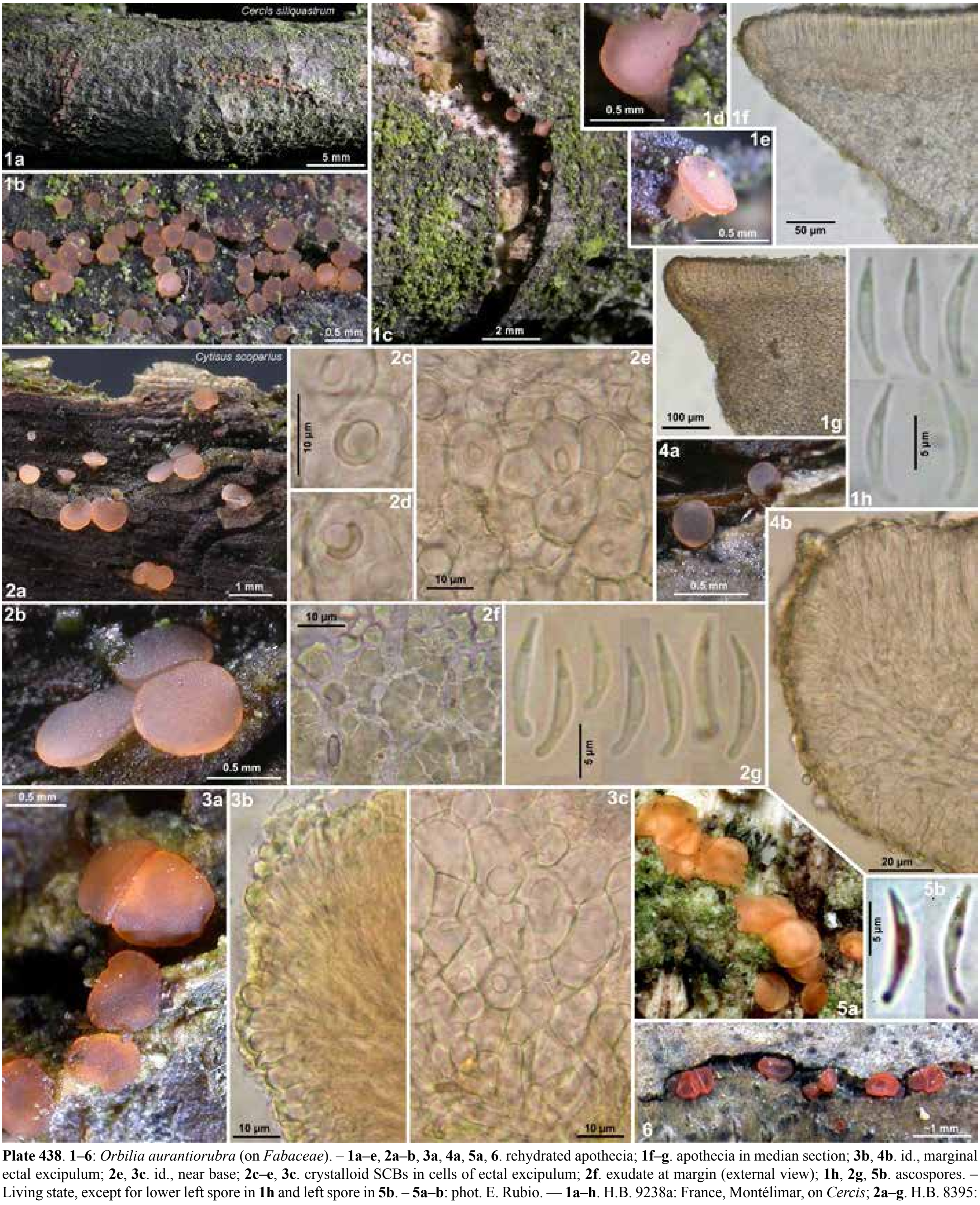
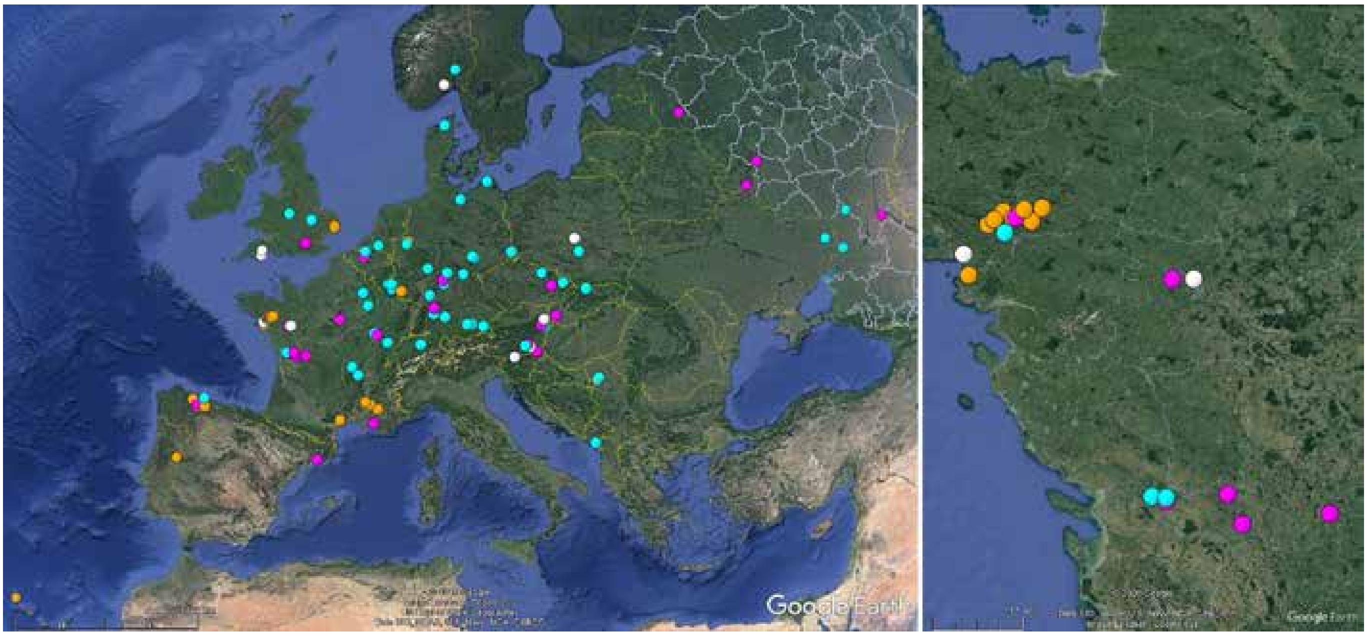


Plate 438. **1–6**: *Orbilia aurantiorubra* (on *Fabaceae*). – **1a–e**, **2a–b**, **3a**, **4a**, **5a**, **6**. rehydrated apothecia; **1f–g**. apothecia in median section; **3b**, **4b**. id., marginal ectal excipulum; **2e**, **3c**. id., near base; **2c–e**, **3c**. crystalloid SCBs in cells of ectal excipulum; **2f**. exudate at margin (external view); **1h**, **2g**, **5b**. ascospores. – Living state, except for lower left spore in **1h** and left spore in **5b**. – **5a–b**: phot. E. Rubio. — **1a–h**. H.B. 9238a: France, Montélimar, on *Cercis*; **2a–g**. H.B. 8395: Germany, Recklinghausen, on *Cytisus*; **3a–c**. H.B. 7654: La Palma, on *Chamaecytisus*; **4a–b**. H.B. 8379a: Great Britain, Suffolk, on *Cytisus*; **5a–b**. E.R.D. 4387: Spain, Asturias, on *Ulex*; **6**. 17.IV.2004: Germany, Weiskirchen, on *Cytisus*.

Surrey, 26 km SW of London, 2.5 km SW of Esher, Winterdown Wood, 40 m, branch of *Ulmus*, on old ?*Thyridaria*, 14.III.1999, B.M. Spooner (K(M) 60614, non vid.). – ibid., 1.5 km SSE of Esher, Arbrook Common, 35 m, branch of *Ulmus*, on old stromata, 21.III.1999, B.M. Spooner (K(M) 60823, non vid.). – **South West England**, **Devon**, ~3.5 km N of Torquay, Watcombe Woods, ~50 m, branch of *Acer pseudoplatanus*, 7.I.1996, P. Roberts (K(M) 33380, non vid.). – 1.3 km NNW of Exeter, St. David's Hill, 25 m, trunk of *Elaeagnus pungens*, on bark, J.P. Priou, 23.II.2014 (J.P.P. 14037, doc. vid.). — **NORWAY**: **Oslo**, 8 km NW of Oslo, 1.8 km NNE of Holmenkollen, N of Frognerseteren, 470 m, branch of *Salix* (?)*caprea*, on bark, 14.VIII.2002, G. Marson (H.B. 7187b). – **Telemark**, 3.8 km NE of Skien, Lensmannseter, 250 m, branch of *Fraxinus excelsior*, on bark, 4.IV.2008, T.H. Dahl & K. Homble (ø, doc. vid.). — **DENMARK**: **Nordjylland**, 24 km NNW of Aalborg, NNW, 7 km NNE of Aabybro, Store Vildmose, S of Blokhusvej, 6 m, branch of *Salix*, on bark, 16.V.2005, B.M.

Spooner (ø). — **POLAND**: **Lower Silesia**, 7 km SSE of Bystrzyca Kłodzka, 2 km SW of Wilkanów, 435 m, branch of *Salix*, on bark, 6.XI.2006, P. Perz (P.P. 20061106-001, doc. vid.). – **Łódź**, 6 km SE of Radomsko, 1.5 km W of Orzechówek, 245 m, branch of *Salix*, on bark, 21.II.2010, J. Nowicki, vid. P. Perz (P.P. 20100221 JN, doc. vid.). – 3.5 km WSW of Pabianice, Cechło Pierwsze, Wąska street, 186 m, on rope, 13.VI.2015, P. Perz (P.P. 20150613-1, doc. vid.). — **CZECHIA**: **Moravia-Silesia**, Northern Moravia, 17 km SW of Ostrava, 2.5 km SE of Studénka, NE border of Albrechtičky, 243 m, branch of *Salix caprea*, on bark, 17.X.2009, M. Chlebická (PRM 915866, doc. vid.). – **Olomouc**, 3.2 km NNE of Olomouc, 1 km NE of Černovír, Černovírske slatiniste, 225 m, branch of *Ulmus*, on bark, 10.III.2019, V. Halasů (V.H. 1044, doc. vid.). — **SLOVAKIA**: **Bratislava**, 23 km NE of Bratislava, 3 km NNW of Senec, 148 m, branch of *Ulmus*, on bark, 12.V.2019, A. Polhorský (A.P. 19/17, anam. substr., doc. vid.). – **Žilina**, 7.7 km W of Tvrdošín, 1.2 km SE of Brezovica, 750 m, branch of *Salix*, on bark, 31.XII.2017, A. Polhorský (A.P. 18/45, anam. substr., doc. vid.). — **GERMANY**: **Mecklenburg-Vorpommern**, 26 km N of Stralsund, Hiddensee, 2.8 km S of Vitte, 5 m, branch of *Salix* ?*cinerea*, on bark, 31.III.2018, T. Richter (ø). – 6 km SSW of Rehna, Borner Moor, 60 m, branch of *Salix cinerea*, on bark, 2.I.2017, T. Richter, vid. I. Wagner (doc. vid.). – **Nordrhein-Westfalen**, 20 km NNW of Recklinghausen, 5.5 km NNW of Haltern am See, NW of Lavesum, Geisheide, 80 m, branch of *Cytisus scoparius*, on bark, 30.XII.2006, F. Kasparek (ex H.B. 8395; sq.: KF741598). – 11 km NW of Recklinghausen, 3 km NW of Marl, Lipper Höhe, 45 m, branch of *Salix*, on bark, 24.IV.2011, U. Lindemann & D. Wieschollek (ø, doc. vid.). – **Sachsen-Anhalt**, 2.5 km S of Naumburg, Buchholz, branch of *S. caprea*, on bark, 8.X.2018, W. Huth (W.H., non vid.). – 14.5 km SE of Naumburg, 2 km E of Waldau, 270 m, branch of *S. cinerea*, on bark, 22.XI.2017, W. Huth (W.H., doc. vid.). – **Sachsen**, 15 km W of Niesky, 2.3 km WNW of Wartha, Gleinsche Heide, 157 m, branch of *S. caprea*, on bark, 21.IX.2018, W. Huth (H.B. 10180 ø). – **Thüringen**, 2.5 km SW of Sonneberg, S of Hönbach, 355 m, branch of *S. caprea*, on bark, 13.XII.2011, I. Wagner (ø, doc. vid.). – **Hessen**, 3 km WSW of Gießen, 1.5 km SSE of Heuchelheim, Silbersee, 160 m, branch of *Salix*, on bark & wood, 6.II.2016, R. Freitag, vid. W. Schößler & I. Wagner (doc. vid.). – **Saarland**, 3 km SE of Weiskirchen, 2 km ENE of Thailen, Bildchen, 310 m, branch of *Cytisus scoparius*, on bark, 17.IV.2004, A. Gminder (ø). – **Baden-Württemberg**, 9.5 km E of Heidelberg, Neckargemünd-Kleingemünd, 122 m, branch of *Salix alba*, on bark & wood, 4.I.2013, M. Bemmann (ø, anam. substr., doc. vid.). – 6 km NW of Stuttgart, 1.5 km NE of Weilimdorf, Maierwald, 335 m, branch of *Ulmus*, on bark, 27.I.1974, H.O. Baral (H.B. 1235b, STU: H.H. 10407). – ibid., branch of *Ulmus*, on bark and old pyrenomycete, 27.IV.1977, H.O. Baral (H.B. 2019). – 3.5 km NE of Tübingen, 1.3 km SW of Pfrondorf, Bitzle, 420 m, branch of *Salix caprea*, on bark, 6. III.1996, F. Baral-Weber & H.O. Baral (H.B. 5421). – ENE of Pfrondorf, Tiefenbach, 410 m, branch of *S. caprea*, on bark, 7.XI.2004, H.O. Baral, E. Weber & F. Arenal (ø). – 9 km WNW of Ulm, 3.5 km W of Blaustein, Arnegger Ried, 495 m, branch of *S. cinerea*, on bark, 15.IV.1999, L.G. Krieglsteiner (ø). – **Bayern**, **Unterfranken**, 17 km NW of Würzburg, 2 km W of Zellingen, Hügelspitz, 260 m, branch of *S. caprea*, on bark, 11.XI.1995, H.O. Baral (ø). – 13 km NNW of Karlstadt, 3 km NNE of Gemünden am Main, W of Schönau, Nonnenpfad, 190 m, trunk of *Ulmus*, on bark, 18.II.1995, L.G. Krieglsteiner (L.K.). – 8 km SE of Gersfeld, 1.3 km N of Bischofsheim, S of Stengerts, Moorwasser, 500 m, trunk of *S. caprea*, on bark, 26.II.2007, L.G. Krieglsteiner (L.K., non vid.). – **Oberbayern**, 8.5 km SE of München, 1 km ESE of Neuperlach, 543 m, branch of *Salix*, on bark, 28.XII.2011, B. Fellmann (MAMU 1907, doc. vid.). – 3 km NW of Gauting, 2 km NE of Pentenried, Birkenholz, 580 m, branches of *S. caprea*, on bark, 17.XII.2004, P. Karasch (MAMU 225, doc. vid.). – 16 km NNE of Prien am Chiemsee, 1 km SE of Großbergham, between Brunnen- and Griessee (Seeon-Seebruck), 545 m, branch of *Salix*, on bark, 27. III.2010, T.R. Lohmeyer (ø, doc. vid.). – 6.5 km W of Traunreut, ~1 km NE of Truchtlaching, Alz river, 535 m, branch of *Salix*, on bark, 31.XII.2007, T.R. Lohmeyer (T.R.L. 2007/81, H.B. 8734a; sq.: KF741599). — **SWITZERLAND**: **Luzern**, 15 km NNW of Luzern, WSW of Baldegg, Baldegger See, 464 m, trunk of *Salix*, on bark, 25.I.2014, U. Graf (ø, doc. vid.). — **AUSTRIA**: **Wien**, ~14 km ESE of Wien, Lobau at Donau river, 155 m, branch of (?)*Ailanthus altissima*, on bark, 10.IV.1994, W. Jaklitsch (WU 13306). – **Niederösterreich**, 11 km NE of Wiener Neustadt, SW of Haschendorf, 228 m, branch of *Ulmus*, on bark, 6.I.2013, Z. Jorgovanovic, vid. I. Wagner (I.W., doc. vid.). – **Steiermark**, 12 km SSE of Graz, 1.2 km SW of Fernitz, Mur, Kalsdorfer Au, 320 m, branch of *Ulmus*, on bark, 16.I.2010, G. Friebes (G.F. 20100026, -029, -031, -037–039, doc. vid.). – ibid., trunk of *Prunus padus*, on bark, 1.IV.2010, G. Friebes (G.F. 20100100, doc. vid.). – 10 km WNW of Graz, 2 km E of St. Oswald, Burg Plankenwarth, 600 m, branch of *Ulmus*, on bark, 15.II.2014, G. Friebes (G.F. 20140023). – 8 km WNW of Bad Radkersburg, 4 km W of Halbenrain, SW of Unterpurkla, Donnersdorfer Au, 218 m, branch of *U. laevis*, on bark, 24.I.2009, G. Friebes (G.F. 20090006, doc. vid.). – ibid., branch of *U. laevis*, on wood, 12.XII.2009, G. Friebes (G.F. 20090147, doc. vid.). – 2.8 km S of Voitsberg, 1.3 km WSW of Teigitschgraben, W of power plant Arnstein, 396 m, branch of *Salix*, on bark, 15.XII.2017, G. Friebes (GJO 88896, doc. vid.). – **Burgenland**, 2.5 km SSE of Eisenstadt, 2 km NW of Trausdorf, 150 m, branch of *Salix* ~*cinerea*, on bark, 27.I.2013, Z. Jorgovanovic, vid. I. Wagner (I.W., doc. vid.). – **Kärnten**, 12 km SE of Klagenfurt, NW of St. Margareten im Rosental, 565 m, branch of *Salix*, on bark, 11.VI.1993, W. Jaklitsch (WU 13305). – 1.5 km NNW of St. Margareten im Rosental, Drau river, 410 m, branches of *S.* (?)*alba*, on bark, 15.X.2000, W. Jaklitsch (H.B. 6798). – ibid., branch of *Frangula alnus*, on bark, 31.XII.2002, W. Jaklitsch (W.J. 2054; ex H.B. 7278; sq.: KF741601). — **NETHERLANDS**: **Noord-Brabant**, 5 km SW of Tilburg, NE of De Kaaistoep, 11 m, branches of *Salix*, on bark, 9.XI. & 30.XII.2012, L. Rommelaars (L.R. 12-168, doc. vid.). — **BELGIUM**: **Vlaanderen**, **Oost-Vlaanderen**, 6 km NNE of Aalst, 1 km NW of Wieze, Valleibos, 7 m, branch of *Ulmus minor*, on bark, 20.IV.2013, B. Declercq (B.D. 13/29, doc. vid.). – 24 km W of Antwerpen, 4 km NNW of Kemzeke, Stropersbos, 8 m, branch of *Frangula alnus*, 2.I.2014, B. Declercq (B.D. 14/001, non vid.). – 19 km W of Antwerpen, 2 km SSW of Meerdonk, Paneweel, 2 m, *Salix* branch, on *Diatrype stigma*, 19.X.2013, B. Declercq (B.D. 13/090, non vid.). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 11 km W of Ettelbruck, 1.8 km NW of Grosbous, W of Bruch, 390 m, branch of *Salix*, on bark, 24.IV.2001, G. Marson & H.O. Baral (ø). – ibid., branch of *S. cinerea*, on bark, ~26.III.2001, G. Marson (H.B. 6991a). – **Gutland**, **Redange**, 10 km W of Mersch, W of Kapweiler, Rouer, 260 m, branches of *S. cinerea*, on bark & wood, 24.VII.1993, G. Marson (H.B. 4925, G.M. 5003, M). – **Diekirch**, 3.5 km ESE of Ettelbruck, 1.7 km SE of Ingeldorf, Jongeboesch, Béibert, 353 m, branch of *Salix*, on bark, 18.VI.2001, G. Marson (ø). – **Luxembourg**, 4 km NE of Luxembourg, 2 km ENE of Dommeldange, Schlaed, 310 m, branch of *S. caprea*, on bark, 12.V.2004, G. Marson (H.B. 7535b). – 7 km NE of Luxembourg, 1.5 km WSW of Senningerberg, Gréngewald, Kuelebierg, 395 m, of *Salix*, on bark, 27. XI.2004, G. Marson (ø). – 2.5 km S of Luxembourg, 1 km SW of Bonnevoie, railway depot, 282 m, twig & branch of *S. caprea*, on bark, wood & old (?) *Cryptodiaporthe*, 14.V.1998, G. Marson (H.B. 6142a). – 1 km E of Bonnevoie, S of Itzigersté, Kappbierg, 285 m, branch of *S. caprea*, 5.II.1994, G. Marson (H.B. 5041 dry culture, anam. cult.). – 5 km S of Luxembourg, 1.8 km SW of Hesperange, Fennerholz, 292 m, branch of *Salix*, on bark, 6.II.2003, G. Marson (ø). – 1 km W of Hesperange, Géisselbierg, 290 m, trunk of *S. caprea*, on bark, 3.I.2004, G. Marson (ø). – 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, branch of *S. caprea*, on bark, 5.XI.2000, G. Marson (ex H.B. 6815a, M-0291763, **epitype**, anam. substr., anam. cult., CBS 140881; sq.: KF741595). – branch of *Salix*, on bark, 14.XI.2000, G. Marson (ø). – **Esch-sur-Alzette**, 5 km SSW of Luxembourg, 0.7 km N of Kockelscheier, Haus der Natur, 305 m, branch of *S. aurita* × *caprea*, on bark, 10.XI.2000, G. Marson (H.B. 6835 ø). – ibid., branch of *Salix*, on bark, 3.IV.2013, G. Marson (G.M. 2013-04-03.1 ø, anam. cult.; sq.: KT380080). – ibid., Weier, 300 m, branch of *S. cinerea*, on bark, 15.IX.1998, G. Marson (H.B. 6244b). – ibid., branch of *S. aurita* × *caprea*, on bark, 13.X.2010, G. Marson (ø). – 0.7 km SE of Esch-sur-Alzette, Neudorf, railway station, 310 m, branch of *S. caprea*, on bark, 19. VIII.1998, G. Marson (H.B. 6251, anam. substr.). – 4.5 km SSE of Esch-sur-Alzette, 3 km W of Rumelange, Héisingerbierg, 415 m, branches of *S. caprea*, on bark & wood, 24.IV.2002, G. Marson (ø). – 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, branch of *S. caprea*, on bark, 27. IV.1993, G. Marson (H.B. 4868, G.M. 4973). – 2 km SE of Dudelange, Bloklapp, 290 m, branches of *S. caprea*, on bark, 13.III.2001, G. Marson (H.B. 6882b, anam. substr.). – 2 km NNE of Dudelange, 1.5 km S of Bettembourg, railway, 275 m, branch of *S. caprea*, on bark, 20.VI.1998, G. Marson (H.B. 6173c). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 5.3 km NE of Pipriac, NE of Courbouton, 38 m, branch of *Ulex europaeus*, on bark, 27.XI.2007, J.P. Priou (J.P.P. 27133 ø, doc. vid.). – 12 km E of La Gacilly, 1 km W of St.-Just, Moulin de Cojoux, 67 m, branch of *Cytisus scoparius*, on bark, 26.III.2001, J.P. Priou (J.P.P. 21066, H.B. 6900). – **Morbihan**, 9.5 km SE of Malestroit, 2.7 km WNW of St.-Martin-sur-Oust, Beauvais, Rieux, 8 m, stem of *Euphorbia characias*, 20.IV.2014, J.P. Priou (J.P.P. 14083, doc. vid.). – 3 km SW of Muzillac, SE of Tissac, 10 m, branch of *Frangula alnus*, on *Karstenula rhodostoma*, 13.XII.2009, J.P. Priou (J.P.P. 29241, doc. vid.). – 8.5 km WNW of Redon, 2 km E of St.-Jacut-les-Pins, Moulin de Calléon, 19 m, branch of *Salix*, on bark, 5.II.2006, J.P. Priou (J.P.P. 26030, doc. vid.). – 2 km NE of La Gacilly, Lieuvy, 10 m, trunk of *Ulmus*, on bark, 30. III.2013, J.P. Priou (J.P.P. 13061, doc. vid.). – 9.5 km SE of Malestroit, 2.7 km WNW of St.-Martin-sur-Oust, Beauvais, 8 m, branch of *Cytisus scoparius*, on bark, 3.III.2009, J.P. Priou (J.P.P. 29038, doc. vid.). – ibid., on bark of *C. scoparius*, 23.III.2007, A. Delannoy, vid. J.P. Priou (J.P.P. 27068, non vid.). – 33 km ENE of Vannes, 3 km NE of Pluherlin, NNE of le Gachot, 70 m, branch of *C. scoparius*, on wood, 29.I.2009, J.P. Priou (J.P.P. 29004, anam. substr., doc. vid.). – 9 km NE of La Gacilly, 1.2 km ENE of Quelneuc, 17 m, branch of *Ulex europaeus*, on bark, 20.I.2006, J.P. Priou (J.P.P. 26016, doc. vid.). – 4 km NE of La Gacilly, 1.5 km NE of La Chapelle-Gaceline, La Gibaudáel, 39 m, branch of *C. scoparius*, on bark, 16.I.2006, J.P. Priou (J.P.P. 26010, doc. vid.). – 1 km N of La Gacilly, Yves Rocher, 27 m, branch of *C. scoparius*, 22.I.2004, J.P. Priou (J.P.P. 24029, non vid.). – 8 km WNW of La Gacilly, S of St.-Nicolas-du-Tertre,



Map 77. Known distribution of *O. aurantiorubra* in Europe and Macaronesia (right: closeup of western France); magenta = *Ulmus*, cyan = *Salix*, orange = *Fabaceae*, white = other hosts, indet. angiosperms, textile.

Etang près La Croix, 47 m, branch of *C. scoparius*, 25.XII.2003, J.P. Priou (J.P.P. 23146, doc. vid.). – **Pays-de-la-Loire**, **Loire-Atlantique**, 2 km NE of Kercabellec, 4.2 km WSW of Assérac, S of Mesquéry, Pen-Bé, 5 m, branch of *C. scoparius*, 10.XI.2006, J.P. Priou (J.P.P. 26174, non vid.). – **Maine-et-Loire**, 8 km NNW of Angers, 1 km NW of Cantenay-Épinard, Parc de la Roche, 25 m, branch of indet. angiosperm, on bark, 9.II.1985, M. Galand (J.M. 8502A). – 16 km WNW of Angers, W of St.-Clément-de-la-Place, Château des Brosses, branch of ?*Ulmus* ('*Laurus*'), on bark, 17.II.1985, M. Galand (J.M. 8504A). – **Poitou-Charentes**, **Deux-Sèvres**, 13 km ESE of Melle, Coudré, centre ville, 158 m, trunk of *Ulmus* (?)*minor*, on bark, 4.III.2006, M. Hairaud & B. Coué (ex H.B. 8076b; sq.: KF741597). – 13.5 km N of Melle, 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 103 m, branch of *Ulmus*, on bark, 17.IV.2008, H.O. Baral (ex H.B. 8814a; sq.: KF741596). – 14 km WSW of Niort, 1.2 km NNE of Amuré, Marais Poitevin, Port Goron, 5 m, branch of *Ulmus*, on bark, 15.IV.2008, J.P. Priou (ø). – 1 km ENE of Le Vanneau-Irleau, Marais Poitevin, 3 m, branches of *Salix*, on bark, 15.IV.2008, H.O. Baral & J.A. Camy (H.B. 8805a ø). – 4 km NW of St.-Hilaire-La-Palud, Marais Poitevin, 4 m, branches of *S. aurita*, on bark, 25.IV.2006, H.O. Baral (H.B. 8130; sq.: KF741602). – **Vienne**, 6.5 km NW of Adriers, 1 km S of Nérignac, E of Les Aimardières (farm), 160 m, trunk of *Ulmus*, on bark, 19.III.2006, B. Coué (ø, non vid.). – **Centre**, **Loiret**, 10 km N of Montargis, 4 km NNE of Cepoy, E of les Ricordelles, Loing river, 75 m, twig and branch of *Ulmus*, on bark & old pyrenomycete, 28.II.1998, A. Reynaud (H.B. 6062). – **Champagne-Ardenne**, **Marne**, 16.5 km NE of Reims, N of Isles-sur-Suippe, 80 m, branch of *Salix caprea*, on bark, 2.II.1998, M. Langlois (H.B. 6040). – **Haute-Marne**, Champagne, ~9 km N of Vitry le François, St.-Amand-sur-Fion, branch of *Salix*, on bark and *Diatrype bullata*, 110 m, II.1877, D. Richon (herb. Boudier, PC, **holotype**, H.B. 6894 ø). – **Franche-Comté**, **Doubs**, 5 km SE of Besançon, E of La Vèze, marais de Saône, ruisseau des Moulins, 385 m, branch of *Salix*, on bark, 11.IV.2013, G. Moyne (ø). – **Bourgogne**, **Côte-d'Or**, 32.5 km NNE of Dijon, 2.3 km NW of Selongey, SE of Foncegrive, Ruisseau de la Venelle, 310 m, branch of *Salix*, on bark and *D. bullata*, 30.X.2009, J.P. Priou (J.P.P. 29210, doc. vid.). – 33 km NE of Dijon, NW of Fontaine-Française, Étang Pagosse, 230 m, branch of *Ulmus*, on bark, 26.X.2009, J.P. Priou (J.P.P. 29203, non vid.). – **Rhône-Alpes**, **Loire**, 19 km WSW of Roanne, 4 km WSW of Arcon, Forêt de l'Assise, le Gué de la Chaux, 1060 m, branch of *Salix*, on bark, 7.V.2010, J.P. Priou (H.B. 9301 ø). – 26 km NNW of St.-Étienne, Montrond-les-Bains, at river Loire, 340 m, *Ulmus*, on bark, 3.I.1994, A. Ayel (doc. vid.). – ~2 km ENE of Montrond-les-Bains, St.-André-le-Puy, 360 m, branch of *Salix*, on bark, 30.V.1994, A. Ayel (ø). – **Drôme**, 13 km SE of Montélimar, SW of Abbaye d'Aiguebelle, 215 m, branch of *Cercis siliquastrum*, on bark, 22.IX.2009, G. Marson (H.B. 9238a; sq.: KF741603). – 1 km NNW of Nyons, W of Col du Pontias, 400 m, branch of *C. siliquastrum*, on bark, 13. VIII.2009, G. Marson (only conidia, anam. substr.). – **Provence-Alpes-Côte d'Azur**, **Bouches-du-Rhône**, 3 km SW of Aix-en-Provence, La Baume, Chemin de la Blaque, branch of *Ulmus minor*, on bark, 145 m, 1.XI.2006, H. Aeberhard (H.B. 9087a ø, anam. substr.). – **Alpes-de-Haute-Provence**, 10 km ESE of Sederon, W of Curel, 765 m, branch of *Spartium junceum*, on bark & wood, 17.VIII.2001, G. Marson (H.B. 7023). – **Languedoc-Roussillon**, **Hérault**, ~13 km SE of Bédarieux, ?2.5 km NW of Neffiès, ?SSE of Vailhan, Le chateau d'eau, ~150 m, branch of *Cytisus scoparius*, on bark, 6.V.2005, G. Garcia (G.G. 05050604, doc. vid.). — **SPAIN**: **Asturias**, 10 km WSW of Gijón, 1 km ESE of Serín, San Andrés lake, 31 m, branches of *Salix*, on wood, 9.IX.2008, E. Rubio (E.R.D. 4578, doc. vid.). – 3.7 km NE of Pola de Somiedo, SW of La Falguera, 1170 m, branch of *Ulmus minor*, on bark, 20.IV.2013, E. Rubio (E.R.D. 5826, doc. vid.). – 11 km SE of Pola de Somiedo, 6 km SE of Valle de Lago, 1560 m, on twig of ?*Genista florida*, on bark and stromata of *Geejayessia*, 4.VI.2013, J.P. Priou (J.P.P. 13124, doc. vid.). – 55 km WSW of Avilés, NE of Orrea, 500 m, branch of *Ulex europaeus*, on wood, 29.II.2008, E. Rubio (E.R.D. 4387, doc. vid.). – 30 km SE of Oviedo, 3 km SSW of Cabañaquinta, Mirador de Cotobello, 1175 m, branch of *Genista florida*, on bark, 26.VI.2019, J. Díaz (ø, doc. vid.). – **Cataluña**, **Barcelona** 25 km NNW of Barcelona, 4.8 km NE of Terrassa, 322 m, branch of *Ulmus*, on bark, 1.II.2014, J. Bometón (J.B. 0448/14). — **PORTUGAL**: **Guarda**, Beira Interior Norte, 26 km SE of Guarda, 3.5 km NE of Sabugal, SW of Rendo, 820 m, branch of *Cytisus scoparius*, on bark, 1.I.2005, J.P. Priou (J.P.P. 25007, non vid.). – ibid., 2.3 km S of Rendo, Quinta dos Prados, 843 m, branch of *Salix*, on bark, 23.XI.2019, M.A. Ribes (doc. vid.). — **SERBIA**: **Vojvodina**, 3 km NW of Novi Sad, 75 m, branch of *Salix alba*, on bark, 21.III.2015, D. Savić (FG-372, doc. vid.). – Fruška Gora, 12 km SW of Novi Sad, 1 km SSW of Beočin, Erdelj, 235 m, branch of indet. angiosperm, on bark, 2.III.2015, D. Savić (FG-371, doc. vid.). — **MONTENEGRO**: 17 km SSW of Podgorica, 1 km W of Bistrice, 8 m, branch of *Salix*, on bark, 20.II.2016, B. Perić (B.P. Dgf/C7D-20-02-16, doc. vid.). — **UKRAINE**: **Lugansk**, 11 km NNW of Slavyanoserbsk, 4.5 km NW of Trehizbenka, 55 m, branch of *Salix rosmarinifolia*, on bark, 8.V.2011, A.Y. Akulov, vid. S. Helleman (CWU Myc AS4407, S.H. 740, anam. substr., doc. vid.). — **RUSSIA (West)**: **Pskov**, **Loknya**, 42.5 km NNW of Velikiye Luki, 9 km N of Nasva, N of Bashovo, 126 m, branch of *Ulmus laevis*, on bark, 17. VIII.2011, E.S. Popov (E.S.P. 11-0043, doc. vid.). – **Bryansk**, **Suzemka**, Bryanskiy Les, 95 km SSW of Bryansk, 14 km SSE of Trubchevsk, NW of Chukhrai, Nerussa river, 138 m, twig of *U. laevis*, on bark, 23.X.2012, E.S. Popov (LE 248007, non vid.). – **Oryol**, **Znamenskoye**, Orlovskoye Polesiye, 75 km ENE of Bryansk, 63 km NW of Oryol, 2.3 km NE of Elenka, Vytebet river, 174 m, twig of *U. laevis*, on bark, 19.X.2012, E.S. Popov (LE 248003, 248004, non vid.). – **Rostov**, **Krasny Sulin**, 90 km NNE of Rostov-on-Don, 15 km NE of Krasny Sulin, Osinovka river, 185 m, on bark of *Salix*, 17.VI.2001, Y.A. Rebriev (LE, non vid.). – **Sholokhovsky**, 230 km WNW of Volgograd, 1 km SW of Veshenskaya, 57 m, bark of *Salix*, 7.X.2006, E.S. Popov (LE 247258, doc. vid.). – **Volgograd**, **Svetly Yar**, Volga-Akhtuba, 33 km SE of Volgograd, 9 km NE of Svetly Yar, E of Sotovo lake, -7 m, twig of *Ulmus minor*, on bark, 21.IX.2012, E.S. Popov (LE 248300, non vid.). — **MACARONESIA**: **Canary Islands**, **La Palma**, Cumbre Nueva, 3.5 km SSW of San Pedro, W of Las Ledas, 700 m, branch of *Chamaecytisus proliferus*, on bark, 5.I.2005, P. Karasch (P.K. LP 012005-17, H.B. 7654a). — **USA**: **Pennsylvania**, Bethlehem, Salem, ?100 m, branch of ?*Quercus*, on bark, undated, collector unknown (herb. Schweinitz 925-182, PH 01029282, 01029283, H.B. 7726 ø).

Orbilia jugulospora Baral, in Quijada et al., Phytotaxa 175: 10 (2014) — Pls 439–440

Etymology: named after the very acute, spiky spore apex.

Typification: Ethiopia, Addis Ababa, Menagesha Suba, branch of indet. angiosperm, 22.XII.2009, U. Lindemann (ex H.B. 9239, M-0257566, holotype; sq.: KF741594)

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–0.7(–0.9) mm diam., 0.12–0.2 mm high (receptacle 0.07–0.11 mm), bright orange(-ochraceous) [T] or rose(–pink) {1}, (semi)translucent, round, scattered to gregarious; disc flat, margin distinct, not protruding, smooth; sessile or with a broad stipe 0.02–0.05 × 0.28 mm, superficial; dry bright orange-rose. **Asci** *46–50 × 4–4.2 {T} or 5.5 µm {1}, †42–67 × 3.8–4.2 µm {1}, 8-spored, spores *4-seriate in two bundles, 3–5 lower spores inverted {3} (often strongly mixed, sometimes some upper spores inverted), pars sporifera *25 µm long; **apex** (†) strongly truncate (never distinctly indented, laterally not or distinctly inflated), hemispherical in side view, thin-walled; **base** with short to very long, thick or thin, flexuous stalk, L-shaped. **Ascospores** *(9.5–)10.5–12(–13) × 1–1.4 µm {4} (~12–16 µm actual length), †10–12 × 0.9–1.1 µm {T}, narrowly fusiform, apex acute to acuminate, base gradually narrowed in a tail-like end or in a tail of 2–3.5 × 0.4–0.7 µm with rounded, partly very slightly inflated end, strongly curved (helicoid), near base hook-like; **SBs** *3–4.5 × (0.3–)0.4–0.6(–0.8) {4}, subulate, straight. **Paraphyses** apically slightly to medium clavate-capitate, terminal cells *26–27 × 3–4 µm {T}, †17.5–20 × 3–4 µm {1}, lower cells *5.5–13 × 1.5–2 µm {2}; unbranched at upper septum, hymenium pale orange. **Medullary excipulum** hyaline to pale orange, 30–50 µm thick, of loose to dense textura intricata with inflated cells, sharply delimited from ectal excipulum (at mid flanks by a t. porrecta). **Ectal excipulum** pale orange, of (*) thin-walled, vertically oriented textura globulosa-angularis(-prismatica) from base to margin, 70–110 µm thick near base, cells *9–14 × 6–10 µm {T}; 20 µm thick at flanks, 15–20 µm at margin, oriented at a 50–80° angle to the surface, marginal cortical cells *7.5–10 × 3.5–5 µm {T}; **glassy processes** absent. **Anchoring hyphae** medium abundant, *1.8–2.5 µm wide, walls 0.2 µm thick {T}. **SCBs** globose, in paraphyses 1.5–2.4 µm diam., in basal and marginal ectal excipulum 2.5–3 µm diam., here also rod- to sickle- (half-moon) or ring-shaped {T}, medium to strongly refractive, subhyaline; **LBs** in ectal excipular cells at lower flanks 0.2–0.4 µm diam., in groups, bright yellow-orange (carotenoids). **Exudate** over paraphyses 0.2–2 µm thick, cloddy-continuous to granular, very pale yellowish, firmly attached, over margin and flanks 1–2.5 µm thick, cloddy. **— ANAMORPH**: vermispora-like (from ascospore isolate {2}. **Conidiophores** reduced, *2.5–10 × 1.5–3.5 µm, at first cylindrical, later moniliform (bulbous) by proliferation. **Conidia** *((10.3–))(13–)16–28(–31) × ((2.2–))(2.4–)2.6–3.4 µm, ((1–))3(–4)-septate {2}, slightly to strongly curved, either entirely or more towards the ends, containing a number of minute or up to ~0.5–1 µm large droplets (probably LBs) near the walls of each cell.

Habitat: standing, or lying on dry ground, corticated, 9–?30 mm thick branches of ?*Fabaceae* sp. {1}, indet. angiosperms {3}, on slightly to medium decayed bark {4} (periderm {4} or inner surface of bark {1}), ± close to old pyrenomycete {T}, partly darkened, without algae. **Associated**: foliose liverwort, *Stilbella* sp. {1}. **Desiccation tolerance**: ± fully viable for 3 weeks. **Altitude**: 2520 m a.s.l. (northeastern Africa), 1250 m (northeastern China), 20–?500 m (southern China). **Geology**: Proterozoic metamorphic rock. **Phenology**: V, IX, XII (probably throughout the year).

Taxonomic remarks. *Orbilia jugulospora* is very similar to the more temperate, mainly European *O. aurantiorubra*. It differs only gradually in somewhat narrower, partly apically more acuminate and basally more hook-like ascospores, and in a tendency to narrower SBs. In the holotype the presence of yellow-orange LBs and hyaline half-moon-shaped (crystalloid) as well as globose SCBs in the ectal excipulum is remarkable. Stronger differences are seen in the anamorph and molecular data.

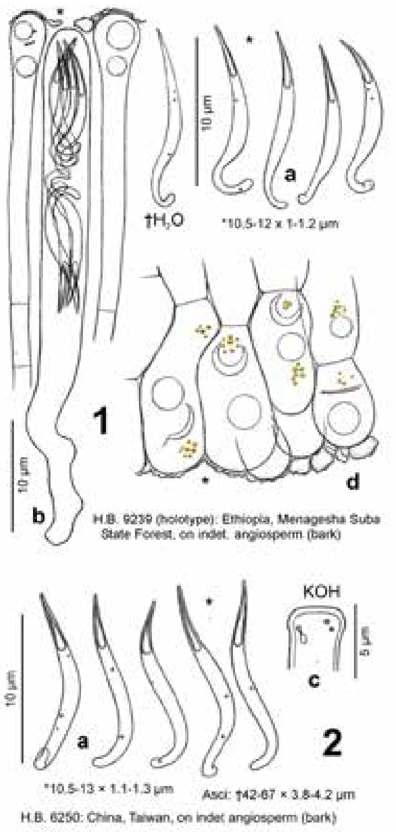


Plate 439. **1–2**: *Orbilia jugulospora*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. median section of ectal excipulum at lower flanks (cells containing SCBs and yellow-orange LBs).

Variation. The abundant paratype collection from Taiwan differs from the holotype in slightly wider asci and spores, distinctly wider SBs, and gregarious apothecia with a rose-pinkish colour. Only the spores were alive when this specimen was studied. Also in the specimen fom Beijing the ascospores are slightly wider (*10.5–12.5 × 1.2–1.4 µm, Pl. 440: 3a), while in that from Guangxi spore size (*~11–12.5 × 1–1.1 µm) concurs with the holotype. In both the colour of the fresh apothecia was orange(-red). Only the spores and the elements of the culture are alive on the photos of these two records, therefore, the presence of SCBs or LBs is unknown in all of the Asian samples.

Type studies. In the protologue, the holotype in M was erroneously given by the first author as isotype and 'herb. Baral' as holotype, also the H.B. number 9239 was wrongly ascribed to U. Lindemann. In fact, a duplicate of the holotype does not exist, nor does a duplicate of the paratype exist in the herbarium of R. Kirschner. The sparse holotype consisted of only seven apothecia, all of which were used up during microscopic and molecular study.

Anamorph. In pure culture of the samples from Beijing and Guangxi, conidia very similar to *O. aurantiorubra* developed, though distinctly narrower and with mainly 3 instead of 5 septa (X.Z. Jiang pers. comm., Pl. 440: 3b–d, 4b). No conidia could be found near apothecia of the holotype.

Phylogeny. A sequence taken from apothecia of the holotype from Ethiopia comprises SSU (without S1506 intron), ITS and LSU, and sequences from two Chinese cultures include ITS and LSU (also here the intron is clearly absent in one of them). The two Chinese cultures differ from the holotype by 5 % in the ITS, and between each other by 2.5 % (all deviating 13 nt are in the ITS1), which seems to indicate that the present concept of *O. jugulospora* is too wide. In the LSU D1–D2 the distance within *O. jugulospora* is 1.2 % between the Chinese strains and the holotype and 0.4 % within China.

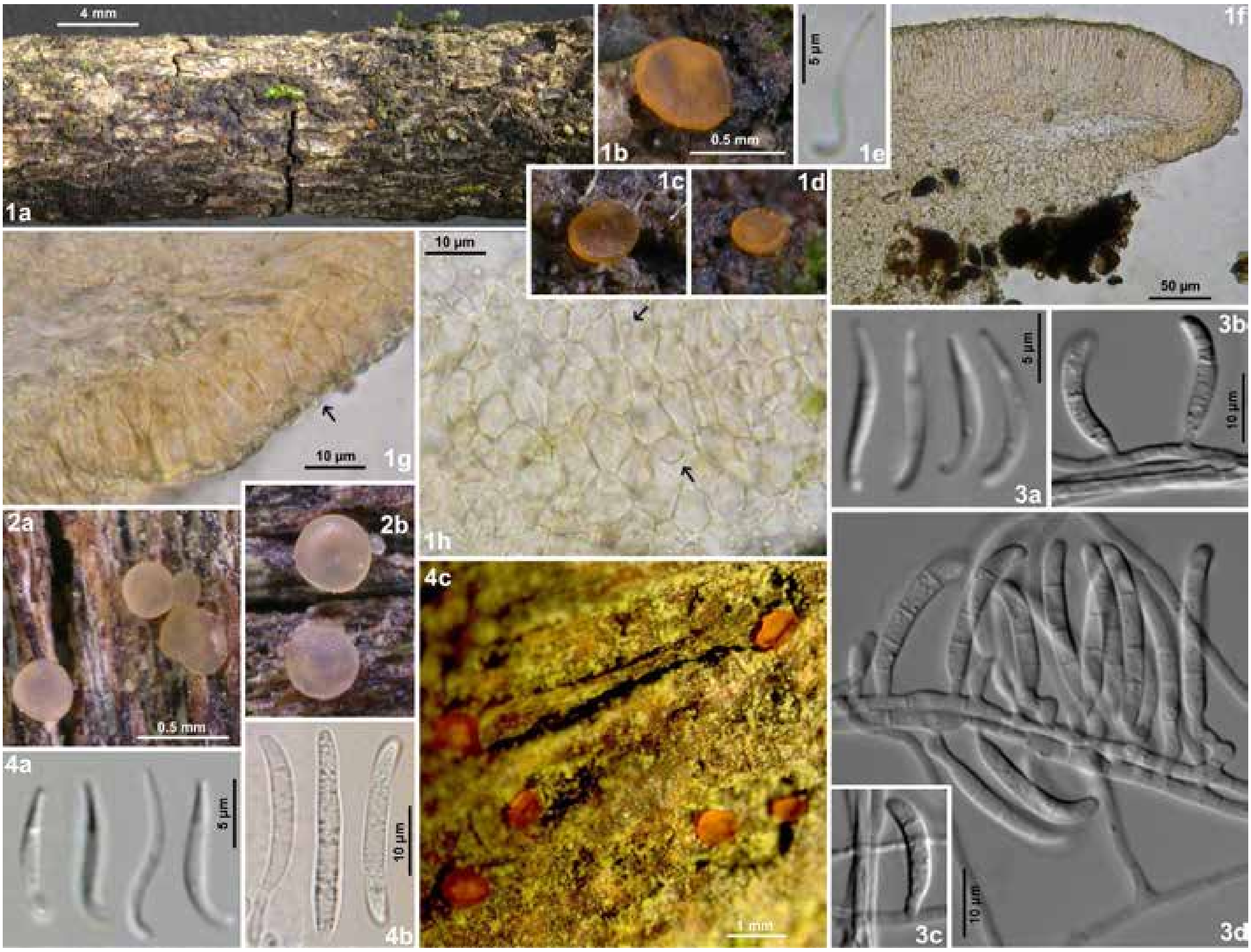


Plate 440. **1–3**: *Orbilia jugulospora*. – **1a**. corticated mesic branch; **1b–d**, **2a–b**, **4c**. rehydrated apothecia (**2**: after 12 years); **1f**. apothecium in median section; **1g–h**. id., ectal excipulum (base and lower flanks), some cells with crystalloid SCBs (arrows); **1e**, **3a**, **4a**. ascospores; **3b–d**, **4b**. conidiophores and conidia, from pure culture. – Living state, except for **1e**, **2c** (in H_2O). – **3a–d**, **4a–c**: phot. X.Z. Jiang (**3a–d**, **4a**: DIC). — **1a–h**. H.B. 9239 (holotype): Ethiopia, Menagesha Suba, on indet. angiosperm; **2a–c**. H.B. 6250: Taiwan, Taipei, on indet. angiosperm; **3a–d**. HMAS 252529: China, Beijing, on ?*Fabales*; **4a–c**. Or10-gl-01A: China, Guangxi, on indet. angiosperm.

The three samples of *O. jugulospora* form in our analyses of ITS+LSU, ITS, or LSU a strongly (Phyls 13–14, S15) or medium (Phyl. S16) supported clade which clustered in the LSU and combined tree sister to *O. aurantiorubra*. For the distances to *O. aurantiorubra* see under that species (p. 839).

Ecology. *O. jugulospora* was found on medium decayed bark of ± xeric, corticated branches of unidentified angiosperms. The holotype was from a warm-temperate humid though somewhat winter-dry, evergreen, afromontane, predominantly broad-leaved forest at the western slope of an old volcano in the central plateau of the Ethiopian highlands, and the paratypes from orotemperate eastern and subtropical humid (monsoon-influenced) southeastern humid Asia.

Specimens included. **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, southern part of Menagesha Suba State Forest, 2520 m, branch of indet. angiosperm, on bark, 22.XII.2009, U. Lindemann (ex H.B. 9239, M-0257566, **holotype**; sq.: KF741594). — **CHINA**: **Beijing**, **Mentougou**, 98 km W of Beijing, NE of Sujiancun, Lingshan Scenic Area, ~1250 m, branches of ?*Fabales*, on bark, 18.V.2008, X.Z. Jiang (jx-2000a, HMAS 252529, CGMCC 3.13368, anam. cult., doc. vid.; sq.: FJ719769 as *Orbilia* sp., HQ110696 as *O. vinosa*). – **Guangxi**, **Guilin**, Longsheng, forest along G321 state road (unlocalized), 200–800 m, branch of indet. angiosperm, on bark, IX.2010, X.Z. Jiang (Or10-gl-01A, anam. cult., doc. vid., sq.: ined.). – **Taiwan**, **Taipei**, 5 km SE of Taipei, 2 km NW of Wen Shan, Xianyan rd., near Ping An church, 20 m, branch of indet. angiosperm, on bark, 27.IX.1998, R. Kirschner (R.K. 405 ø, H. B. 6250).

Orbilia binchuanensis Baral & Hong Y. Su, sp. nov., MB 813761 — Pls 441–442

Etymology: named after the county Binchuan in the province of Yunnan.

Typification: China, Yunnan, Binchuan, branch of indet. angiosperm, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (ex H.B. 8979c, M-0276443, holotype).

Latin diagnosis: *Differt ab* Orbilia aurantiorubra *ascosporis superioribus inverse orientatis, cellulis marginalibus excipuli processis vitreis praeditis, apotheciis minoribus. Habitat ad corticem putridum rami uvidi arboris angiospermae in zona subtropica humida Asiae meridio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–0.5 mm diam., 0.1 mm high (receptacle 0.08 → 0.06 mm), light cream(-orange), translucent, round, scattered; disc flat, margin not protruding, finely crenulate, with teeth of 15 × 30 µm; sessile on a narrowed base, superficial; dry brownish. **Asci** †(28–)31–36 × 3.3–4.2 µm, 8-spored, spores †~4(–8)-seriate, ± 4 upper spores inverted (not mixed), pars sporifera †20–26 µm long; **apex** (†) strongly truncate (sometimes very slightly indented, laterally not inflated), hemispherical in side view, thin-walled; **base** with very short to medium long, ± thick, flexuous stalk, L- or Y-shaped. **Ascospores** *(9.5–)11–12.7 × 1–1.3 µm, †10–11.5(–13.5) × (0.8–)0.9–1.1(–1.3) µm (~11–15 µm actual length), narrowly (cylindric-)fusoid, apex subacute to acute, base medium attenuated, with rounded end, main part (very) slightly (to medium) curved, tail-like base or tail of 1.5–2 × 0.7–0.8 µm, (very) strongly bent, falcate or very slightly helicoid; **SBs** *2–3.5 × 0.7–1 µm, subulate, straight. **Paraphyses** apically slightly clavate, terminal cells †13–18 × 1.7–2.5 µm,

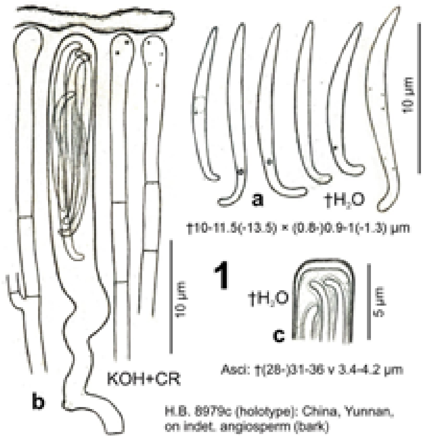


Plate 441. **1**: *Orbilia binchuanensis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex.

lower cells *5.5–9 × 1.5–2 µm, †6–7 × 1.2–1.5 µm; unbranched at upper septum. **Medullary excipulum** 25 µm thick, of medium dense textura intricata-angularis, indistinctly delimited from ectal excipulum. **Ectal excipulum** of (†) thin-walled, irregularly oriented t. angularis-globulosa at base and flanks, 50 µm thick near base, cells †8–12 × 7–9.5 µm; 25 µm thick at flanks, 12 µm at margin, mid flanks abruptly of t. prismatica oriented at a 10–20° angle to the surface, marginal cortical cells †7–10 × 2.5–3 µm; **glassy processes** 10–23 × 2.5–3.3 µm, medium refractive, distinctly stratified, pale yellow-ochre, distinctly outwards curved, coherent to form small teeth. **Anchoring hyphae** sparse, †2–3 µm wide, walls 0.2 µm thick. **SCBs** and **VBs** unknown. **Exudate** over paraphyses 1.5–3 µm thick, continuous, pale yellowish, loosely attached, over glassy processes 0.2–0.5 µm thick, rough. **— ANAMORPH**: unknown.

Habitat: on corticated, ~25–30 mm thick branch of unidentified angiosperm lying on moist ground, on very decayed bark (bast), strongly darkened, without algae. **Associated**: *Hyalorbilia japonica*, *H. multiguttulata.* **Desiccation tolerance**: dead in all parts when examined after 3 months. Altitude: 2700 m a.s.l. **Geology**: mafic volcanic rock. **Phenology**: X.

Taxonomic remarks. *Orbilia binchuanensis* differs from *O. aurantiorubra* and *O. jugulospora* in the upper spores being consistently inversely oriented, in much shorter asci, and in the presence of glassy processes which provoke a crenulate margin. The apothecia are thinner and less pigmented.

Ecology. The very sparse collection was on the outside of rotten bark of a hygric branch of an unidentified angiosperm in an evergreen broad-leaved forest with *Castanopsis*, *Cinnamomum*, *Lithocarpus*, *Quercus*, *Rhododendron* etc. in the subtropical humid (winter-dry) highlands of southeastern Asia. The apothecia grew in close neighbourhood of two *Hyalorbilia* species.

Specimens included. **CHINA**: **Yunnan**, **Dali**, Binchuan, 42 km NNE of Dali, Jizushan, ~2700 m, branch of indet. angiosperm, on bark, 20.X.2008, X.M. Gao, H.Y. Su & X.J. Su (ex H.Y.S. jz-3/H.B. 8979c, M-0276443, **holotype**).

Series *Xanthoguttulatae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Xanthoguttulatae*** Baral, Quijada & E. Weber, **ser. nov.**, MB 815011 **–** Type species: *Orbilia xanthoguttulata* Baral

Etymology: named after the type species, *O. xanthoguttulata*.

Latin diagnosis: *Series* Xanthoguttulatae *sensu stricto seriei* Aurantiorubrae *similis sed conidia staurospora (typo* Dicranidion*), paraphyses apice ellipsoideae ad spathulatae, corpuscula crystalloidea carentia, guttulae luteae minutae plerumque copiose praesentes differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.3–1(–2) mm diam., whitish or pale to bright pinkish, yellow, ochraceous-orange or red-brown, margin smooth to distinctly crenulate, sessile or with ± distinct short stipe. **Asci** *(26–)30–74(–82) × 3.3–5.4 µm, 8-spored, lower or upper (2–)3–5(–6) spores inverted; **apex** (†) slightly to strongly truncate, sometimes slightly to distinctly indented, laterally rarely slightly inflated; **base** T-, L-, Y- or h-, never H-shaped. **Ascospores** *8–16 × 0.7–1.8 µm, (very) narrowly fusoid to fusiform(-clavate), apex subacute to acuminate, rarely obtuse, base slightly to strongly narrowed to an often ± distinct tail, medium to strongly curved towards base or entirely (falcate or mostly helicoid, right- or left-handed), **SBs** *1–6 × 0.4–1.2 µm, straight, tear-shaped to subulate, rarely ellipsoid to globose, apically narrowed to a point or ± short filum. **Paraphyses** not or slightly to strongly inflated at the apex, capitate-clavate or ellipsoid-spathulate to lageniform, terminal cells 0.8–7× longer than lower cells. **Ectal excipulum** cells near base *(8–)10–25(–28) × (6–)8–15(–20) µm (on ± xeric substrate) or */†(15–)20–50(–70) × (10–)15–40(–60) µm (on hygric substrate), near margin of t. angularis to t. prismatica-porrecta; **glassy processes** absent or 1–10 µm up to 40–70 µm long. **SCBs**

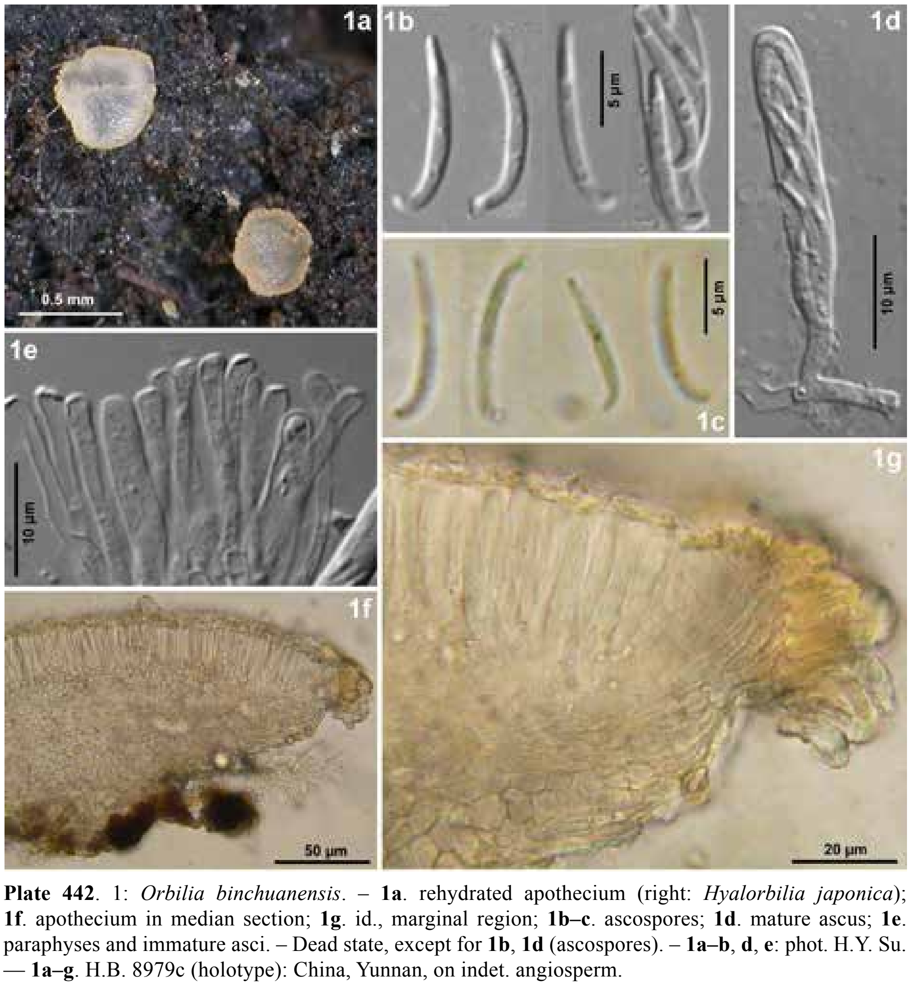


Plate 442. 1: *Orbilia binchuanensis*. – **1a**. rehydrated apothecium (right: *Hyalorbilia japonica*); **1f**. apothecium in median section; **1g**. id., marginal region; **1b–c**. ascospores; **1d**. mature ascus; **1e**. paraphyses and immature asci. – Dead state, except for **1b**, **1d** (ascospores). – **1a–b**, **d**, **e**: phot. H.Y. Su. — **1a–g**. H.B. 8979c (holotype): China, Yunnan, on indet. angiosperm.

absent or globose to elongate, sometimes crystalloid; **VBs** absent or present; yellow **LBs** (carotenoids) absent or present. **Exudate** 0.1–2.5 µm thick, cloddy-granular to cap-like, loosely or firmly attached, hyaline or pale yellowish. **— ANAMORPH**: dactylella- or dicranidion-like. **Conidiophores** mostly unbranched, 2–200 µm long, 2–4 µm wide at the base, 1.8–2.4 µm at the tip. **Conidiogenous cells** monoblastic or sympodial. **Conidia** either phragmosporous, cylindric(-clavate), *15–42 × (3.8–)5–7(–8) µm, straight, (0–)1–3(–5) septate, or staurosporous, 2-armed, without stipe (U-shaped), *18–37 × 9–11 µm.

Habitat: bark and wood, temperate to mediterranean or tropical, humid to semiarid, desiccation-tolerant or -sensitive.

Recognized species: 8, plus 1 unnamed species ('affinis').

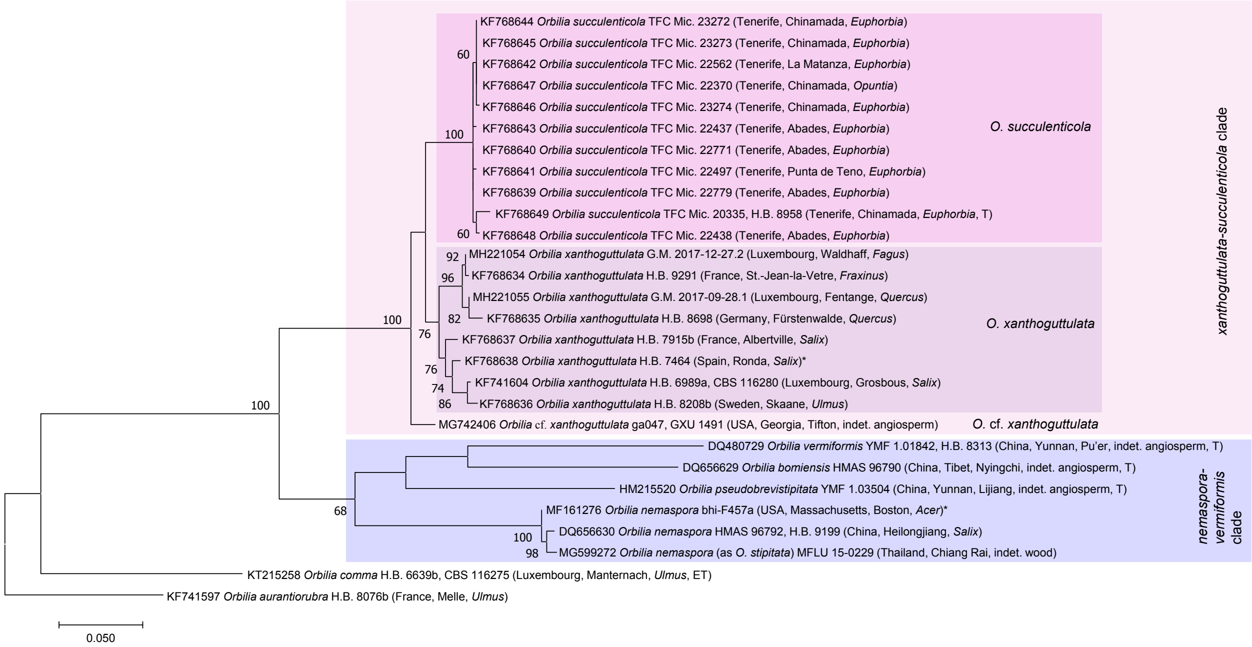
Taxonomic remarks. Series *Xanthoguttulatae* is segregated from series *Aurantiorubrae* and *Hyalinia* mainly because of its molecular data, which group *O. xanthoguttulata* and the very similar *O. succulenticola* (*xanthoguttulata-succulenticola* clade) close to taxa around *O. nemaspora* (*nemaspora-vermiformis* clade). Despite this strong phylogenetic result, members of the *nemaspora-vermiformis* clade closely resembles series *Hyalinia* morphologically as well as in their predominantly desiccation-sensitive apothecia. On the other hand, *O. xanthoguttulata* and *O. succulenticola* resemble species of series *Aurantiorubrae* morphologically as well as in their high desiccation tolerance. Also a certain correlation between different conidial types and desiccation tolerance is observed: more or less desiccation-intolerant species of series *Hyalinia* and series *Xanthoguttulatae* (*nemaspora-vermiformis* clade) have straight phragmoconidia, desiccation-tolerant species have C-shaped (series *Aurantiorubrae*) or staurosporous conidia (*O. xanthoguttulata*). Based on this character correlation, we originally distinguished only two series, *Aurantiorubrae* and *Hyalinia*.

Further differences between these groups were found in the type of SCBs, the presence of yellow LBs (carotenoid), and in the shape of paraphysis apices. A combination of globose and crystalloid SCBs is typical of series *Aurantiorubrae* and *Hyalinia*, whereas in the *xanthoguttulata-succulenticola* clade crystalloid SCBs are consistently absent and globose SCBs rare. In the *nemaspora-vermiformis* clade crystalloid SCBs were only occasionally seen and globose SCBs sometimes (however, several species were mainly studied in the dead state). The paraphyses and marginal excipular cells of *O. xanthoguttulata* and *O. succulenticola* contain varying amounts of yellow LBs. *O. bomiensis* resembles species of the *xanthoguttulata-succulenticola* clade in its yellow apothecia, but the location of the pigment is unclear because living cells were not studied. In the *xanthoguttulata-succulenticola* clade the paraphysis apices are ellipsoid-spathulate, whereas series *Aurantiorubrae* and *Hyalinia*, and also the *nemaspora-vermiformis* clade feature capitate-clavate (or uninflated), the latter also lageniform apices (*O. pseudobrevistipitata*).

In ascospore and SB morphology the four groups are rather similar in their helicoid spores with a strongly tapered base and a usually acute apex that contains an elongate tear-shaped spore body. Slight differences are noted in spore curvature: members of series *Hyalinia* and the *nemaspora-vermiformis* clade have usually strongly helicoid spores, whilst those of series *Aurantiorubrae* and the *xanthoguttulata-succulenticola* clade tend to have only slightly helicoid spores. In *O. bomiensis* the distinctly wider spores are twisted left-handed and have only slightly tapered bases, and the SBs are globose, whereas in other members of the *nemaspora-vermiformis* clade and in series *Hyalinia* the spores are twisted right-handed. In *O. crenatofalcata* and one collection of *O. crenatonemaspora* (series *Hyalinia*), however, the spores are falcate or only very slightly helicoid.

O. binchuanensis, *O. bomiensis*, *O. pseudobrevistipitata* and *O. spirillospora* deviate from the remaining species of series *Xanthoguttulatae* and *Hyalinia* in the upper spores being inverted within the asci, also in growing on more xeric substrate. *O. spirillospora*, *O. crenatonemaspora*, and also *O. nemaspora* p.p. are outstanding in their rather long SBs.

Species delimitation. *O. xanthoguttulata* and *O. succulenticola* are morphologically very similar but genetically and geographically distinct. Likewise, *O. vermiformis* and *O. nemaspora* are easily confused, differing mainly in spore width. *O. crenatonemaspora*



Phylogenetic analysis 15. Phylogram of series *Xanthoguttulatae* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (28 sequences, 646 positions, aligned with MUSCLE) using the T3+I model in MEGA7 (500 replicates). The tree is rooted with *O. aurantiorubra* and *O. comma*. Asci 8-spored in all taxa; T = type, ET = epitype, * = without partial ITS2.

Key to species of series *Xanthoguttulatae*

1. Lower spores inverted within asci (SBs pointing towards base); SBs tear-shaped to subulate 2
1. Upper spores inverted within asci (SBs pointing towards base); SBs globose to subulate 8

2. Paraphyses with ellipsoid to spathulate(-mammiform) apex, usually containing yellow LBs; substrate xeric 3
2. Paraphyses with capitate (± globose) apex or uninflated, without yellow LBs; substrate hygric 4

3. Spores *(10–)11–14.5(–16) × (1.2–)1.3–1.6(–1.8) µm; SBs 1.8–3.3 µm long; marginal cortical cells *(4–)7–11(–14) × (3–)4–7(–9) µm, oriented at a 70–90° angle, terminated by 0–9 µm long glassy processes; bark (rarely wood) of various angio-, rarely gymnosperms, boreal humid to thermomediterranean semihumid Europe .... ***O. xanthoguttulata***, p. 848
A collection from subtropical North America is morphologically identical but its DNA data place it between this and *O. succulenticola* (p. 851).
3. Spores *(9–)9.5–11(–12) × (1–)1.2–1.5(–1.6) µm; SBs 1.7–2.6 µm long; marginal cortical cells *8–13 × (3–)4–5(–6) µm, oriented at a 30–80° angle, terminated by 8–18 µm long glassy processes; wood of *Euphorbia*, *Opuntia*, inframediterranean semihumid to arid Macaronesia .... ***O. succulenticola***, p. 853
A collection on *Chamaecytisus* from the upper mesomediterranean semihumid caldera de Teide (> 2000 m) is without a sequence but morphologically identical.

4. Spores falcate or only very slightly helicoid 5
4. Spores consistently medium to strongly helicoid; wood & bark of angiosperms, also bamboo 6

5. Spores *8–9.5(–9.8) × 0.8–0.9(–1) µm, asci †25–30 × 2.8–3.2 µm; wood of *Populus*, supra(sub)mediterranean (semi)humid southern Europe .... ***O. crenatofalcata*** (series *Hyalinia*), p. 883
5. Spores *9.5–13.7 × 1–1.2 µm, asci †25–45 × 3–4.5 µm .... see under 6 (*O. crenatonemaspora*)

6. Marginal cortical cells †2.7–5 µm wide, tipped by 7–35 µm long glassy processes; apothecial margin distinctly denticulate; spores *(9.5–)10–12(–13.7) × 1–1.1(–1.2) µm; SBs 2.5–5.5 µm long; subtropical humid southern China .... ***O. crenatonemaspora***, p. 862
6. Marginal cortical cells †(3–)5–10(–13) µm wide, without glassy processes; apothecial margin smooth or denticulate; spores *8–11.3 µm long; SBs 1.5–3.7 µm long 7

7. Spores *(8.8–)9.5–11.3 × 1–1.1(–1.3) µm, fusoid, with distinct thin tail; SBs 1.5–1.8 µm long; (sub)tropical humid eastern Asia, Carribean region, Madagascar .... ***O. vermiformis***, p. 856
7. Spores *(8–)8.5–10(–11) × 0.7–0.8 µm, narrowly fusoid, tail often indistinct; SBs 1.6–2(–3.7) µm long; cold-temperate to tropical humid America, Europe, Comoros, eastern Asia .... ***O. nemaspora***, p. 858

8. Spores *10–13.5 × 1.5–1.7 µm, twisted like a left-hand thread, base only slightly tapered to a rounded end; SBs ± globose; apothecia bright yellow-orange, margin crenulate by long glassy processes; hygric wood of indet. angiosperm, orotemperate, cold-continental humid central Asia .... ***O. bomiensis***, p. 865
8. Spores max. *1.1 µm wide, twisted like a right-hand thread, base strongly tapered; SBs elongate tear-shaped to subulate; apothecia pale cream to light orange-ochre 9

9. Spores *13–14 × 1–1.1 µm, twisted by 1.5 turns; margin smooth, without glassy processes; xeric bark of *Hibiscus*, tropical humid northeastern Australia .... ***O. spirillospora***, p. 866
9. Spores *8–11 × 0.7–0.9 µm, twisted by only 1 turn; margin smooth to distinctly crenulate or dentate; xeric or hygric wood & bark of indet. angiosperms, (sub)tropical humid eastern Asia 10

10. Apices of paraphyses slightly capitate, covered by thick exudate; apothecial margin with 5–10 µm long cortical cells tipped by (8–)20–40(–50) µm long glassy processes; spores †9–11 × 0.7–0.8 µm .... ***O.* aff. *pseudobrevistipitata***, p. 864
10. Apices of paraphyses spathulate to lageniform, covered by thin exudate; apothecial margin with (10–)13–20 µm long hair-like cortical cells tipped by 0–5(–13) µm long glassy processes; spores *8–10.3 × 0.8–0.9 µm .... ***O. pseudobrevistipitata***, p. 863

is not easily delimited from *O. scolecospora* of series *Hyalinia*. The remaining species of series *Xanthoguttulatae* were too rarely collected in order to know their variability.

Anamorph. The two recognized clades differ in the anamorph: dicranidion-like in the *xanthoguttulata-succulenticola* clade, dactylella-like in the *nemaspora-vermiformis* clade (but anamorphs are unknown in some taxa).

The dicranidion-like conidia of *O. xanthoguttulata* are characterized by the lack of a stipe. They are quite extraordinary within section *Aurantiorubrae*, but resemble those of series *Orbilia*. Despite this similarity, a phylogenetic relationship was not supported. Similar conidia but with a distinct short stipe occur in *O. siculispora* (series *Abutilones*, with often more than two arms), and in the rather unrelated *O. ovalis* (section *Lentiformes*). We have observed this anamorph only in *O. xanthoguttulata*, while that of *O. succulenticola* still needs to be detected.

Within the *nemaspora-vermiformis* clade, ascospore isolates have been gained from *O. vermiformis* (Yu et al. 2007a), *O. nemaspora* (Liu 2006), and *O. pseudobrevistipitata* (Qin et al. 2011). Their dactylella-like, 1–5-septate, cylindric-clavate conidia are formed on short to very long conidiophores. Trapping organs were not observed when nematodes were added.

Phylogeny. DNA-data were available for two species of the *xanthoguttulata-succulenticola* clade (*O. xanthoguttulata*, *O. succulenticola*) and four of the *nemaspora-vermiformis* clade (*O. bomiensis*, *O. pseudobrevistipitata*, *O. nemaspora*, *O. vermiformis*). They comprise mainly the ITS region, in two species of each clade also LSU and in *O. xanthoguttulata* SSU. The S1506 intron occurred in one species of the former clade and three of the latter.

In different phylogenetic analyses (Quijada et al. 2014b, Baral et al. 2017b, Phyls 7, 13, S15), the two clades clustered together with high support but also high distance. The strongly supported *xanthoguttulata-succulenticola* clade includes two very closely related species, whereas the four species of the *nemaspora-vermiformis* clade formed a medium, weakly, or strongly supported sister group with a high distance among the species (Phyls 13, 15, S15). Because of their obvious molecular similarity and the low support of the *nemaspora-vermiformis* clade we here include both clades in a single series, although their different anamorphs would support recognition of more than one series. The above-mentioned morphological similarities between the *xanthoguttulata-succulenticola* clade and series *Aurantiorubrae* on the one hand, and between the *nemaspora-vermiformis* clade and series *Hyalinia* on the other hand are problematic regarding unsequenced taxa which are difficult to place in the proper group. The phylogenetic position of series *Xanthoguttulatae* is rather isolated and unresolved, showing a high molecular distance to other groups. For further discussion see under series *Hyalinia* (p. 868).

In a most parsimonious analysis of the ITS region by Yu et al. (2007a), *O. vermiformis* clustered with 93 % bootstrap support with taxa belonging to series *Drechslerella* of section *Arthrobotrys*. Therefore, the authors wondered why *O. vermiformis* did not produce any nematode-trapping organs. However, the tree does not show the distances between the sequences, also it contains mainly members of section *Arthrobotrys* but not any of subgenus *Habrostictis* other than *O. vermiformis*.

Specific nucleotide positions. One position in the LSU D1 is highly characteristic of series *Xanthoguttulatae* in comparison to other members of section *Aurantiorubrae*: pos. 159 is AGAGG**T** vs. AGAGG**A** in most other *Orbiliomycetes* (never **T**). Two further positions are characteristic only when excluding *O. nemaspora*: pos. 127 CTGGA**T** vs. CTGRR**G** (rarely CTGGT**G** or CTGGG**A**), pos. 135 GG**A**TT vs. **C** (rarely **T**); except for a few exceptions, also these 2 nucleotides are unique within the genus *Orbilia*.

The *xanthoguttulata-succulenticola* clade has a unique motif at pos. 160–180 of LSU D1 (**G**GCTTCGGTTGT**A**GC**T**CCGG**T**) in which it deviates from the majority of related groups at the positions in bold, pos. 160 being even unique within *Orbilia*. Pos. 180 is also T in the *O. nemaspora* clade, series *Hyalinia*, and section *Ovoideae*, but C in any other *Orbilia* spp. (with rare exceptions having T). The *xanthoguttulata-succulenticola* clade is further characterized at pos. 292 (CTC**T**AA) in contrast to all other *Orbilia* spp. which have CTC**A**AA, except for section *Lentiformes* and *Gamsylella arcuata* (and most basal orbiliaceous genera) which also have CTC**T**AA.

Ecology. *O. xanthoguttulata* and *O. succulenticola* are desiccation-tolerant species. The former occurs in temperate to subalpine humid and mediterranean semihumid Europe mainly on bark of various angiosperms, whereas the latter is only known from inframediterranean semiarid Macaronesia on wood of succulents. Members of the *O. nemaspora* clade are desiccation-sensitive or slightly -tolerant and were recorded in (sub)tropical humid to semihumid Asia, Australia, Africa, and South America, and in warm- to cold-temperate humid North America, Europe, and Asia, also in cold-continental altimontane central Asia (*O. bomiensis*).

1. Xanthoguttulata-succulenticola clade

Orbilia xanthoguttulata Baral, in Quijada et al., Phytotaxa 175: 12 (2014) — Pls 443–444, Map 78

Etymology: named according to the yellow lipid bodies in both paraphyses and marginal excipular cells.

Typification: Spain, Guadalajara, Cantalojas, branch of *Genista* (?)*florida*, 30.X.1991, A. Raitviir & R. Galán (AH 6796, holotype).

Misapplied names: Baral (1987: 428), as *O. comma*; Karsten (1870: 248, 1871: 102, p.p. [P. Karsten 4852]), as *O. rubella*; Rehm (1891: 447, fig. 9–10; 458), as *O. curvatispora*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–1(–1.5) mm diam., 0.19–0.31 mm high (receptacle 0.11–0.15(–0.22) mm), pale to light yellowish-cream or mostly golden yellow, also ochraceous-orange, sometimes turning deep orange to blood-red with age, rarely whitish; somewhat translucent, round, lobate when large, scattered to gregarious; disc slightly concave to flat, margin ± thick, 0–15 µm protruding, smooth; often with a distinct, cylindrical to obconical stipe 0.05–0.2(–0.3) × 0.2–0.4(–0.8) mm, superficial or slightly erumpent from bast; dry light to deep honey-yellow-ochre to yellow-orange, orange-apricot-red, or vermilion-red. **Asci** *(47–)53–74(–82) × (4–)4.2–5(–5.3) µm {10} → 5.7–5.8 µm wide, †(40–)44–67(–79) × (3.5–)3.8–4.6(–5) µm {7}, 8-spored, spores *4-seriate, ± helicoidally twisted, (2–)3–5(–6) lower spores inverted {14} (not or rarely mixed), pars sporifera *23–30(–35) {8} long (†20–30 µm), rarely *30–36(–39) µm {1} (†30–40 µm); **apex** (†) strongly truncate (sometimes distinctly indented, laterally not widened); **base** with short to very long, thin, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *(10–)11–15(–16) ((–18)) × (1.2–)1.3–1.6(–1.8) µm {24} (~12–17 µm actual length), †(9.2–)10.5–14(–14.7) × (1–)1.1–1.3(–1.5) µm {10}, narrowly fusiform with (sub)cylindrical middle part, apex acute (to acuminate), base slightly to strongly attenuated, falcate to mostly distinctly helicoid, medium to strongly curved especially near base; **SBs** *(1.5–)2–3(–3.3) × 0.7–1.1 µm {18}, tear-shaped to subulate, apically narrowed to a point, rarely to a short filum. **Paraphyses** apically (slightly to) medium or strongly inflated, spathulate (to submammiform), terminal cells *11–31 × (2.5–)3–4.5(–5.7) µm {9}, †2.5–4.2 µm wide {2}, exceeding the living or dead asci by 2–8 µm, lower cells *9–15 × 1.3–2.1 µm {4}, †1–1.7 µm wide {3}; never branched at upper septum; hymenium (pale to) light to bright yellow. **Medullary excipulum** hyaline, 20–70 µm thick, sometimes up to 150 µm in centre, of medium loose to dense textura intricata with many inflated cells, very sharply delimited from ectal excipulum by a parallel 10–20(–30) µm thick layer of dense or loose t. porrecta. **Ectal excipulum** hyaline, towards margin usually light to bright yellow-orange, of thin-walled, vertically oriented t. globulosa-angularis-prismatica, 50–100(–180) µm thick at base, 30–100 µm at lower flanks, cells *10–25(–28) × 6–17(–20) µm {7}; 15–30 µm thick at mid flanks and margin, at margin of t. angularis-globulosa oriented at a 70–90° angle {8}, marginal cortical cells clavate to subglobose, *(4–)7–11(–14) × (3–)4–7(–9) µm {5}; **glassy processes** present, (0–)1–5(–9) × 3–5(–7) µm {~15}, conical, low to high refractive, sometimes stratified, hyaline to pale yellowish, ± curved outwards if not very short, also ± absent {5}, often difficult to distinguish from exudate. **Anchoring hyphae** sparse or abundant, *(1.5–)2–3(–4) µm wide, walls 0.2–0.3(–0.4) µm thick {4}, with or without scattered yellowish LBs 0.3–1.5 µm diam., sometimes forming a dense t. intricata up to 40–50 µm thick, partly gradually intergrading with excipular cells. **SCBs** in paraphyses, margin and flanks usually absent, rarely globose, very low-refractive; **LBs** bright to deep golden yellow(-orange) (carotenoids), near apex and in lower half of paraphyses 0.2–1(–2) µm diam., scattered or mostly rather abundant {~57}, rarely absent {2}; in medullary excipulum 1–2.5 µm diam., sparse; in ectal excipulum near margin scattered or abundant, small to large; deep blue-green-olive when applying IKI to water mount. **Exudate** over paraphyses forming individual, conical to convex or truncate glassy caps on nearly all apices, (0.3–)0.5–2 µm thick {~22}, smooth to warted, firmly attached, hyaline, rarely absent, over margin and flanks 0.2–0.5 µm thick. — **ANAMORPH**: dicranidion-like (from ascospore isolate {1} and natural substrate {1}). **Conidiophores** not seen. **Conidia** U-shaped, 2-armed, *18–37 × 9.2–11 µm {2}, arms *4.2–5 µm wide, 2–5-septate, base truncate or conical, stipe absent or nearly so.

Habitat: collected 0–5 m above the ground, on 9–80 mm thick, ± corticated branches (also thick trunks) of *Abies alba* {1}, ?*Betula* sp. {1}, *Carpinus betulus* {1}, *Castanea sativa* {1}, *Cercis siliquastrum* {2}, *Cornus sanguinea* {1}, *Crataegus* sp. {1}, *Eucalyptus*

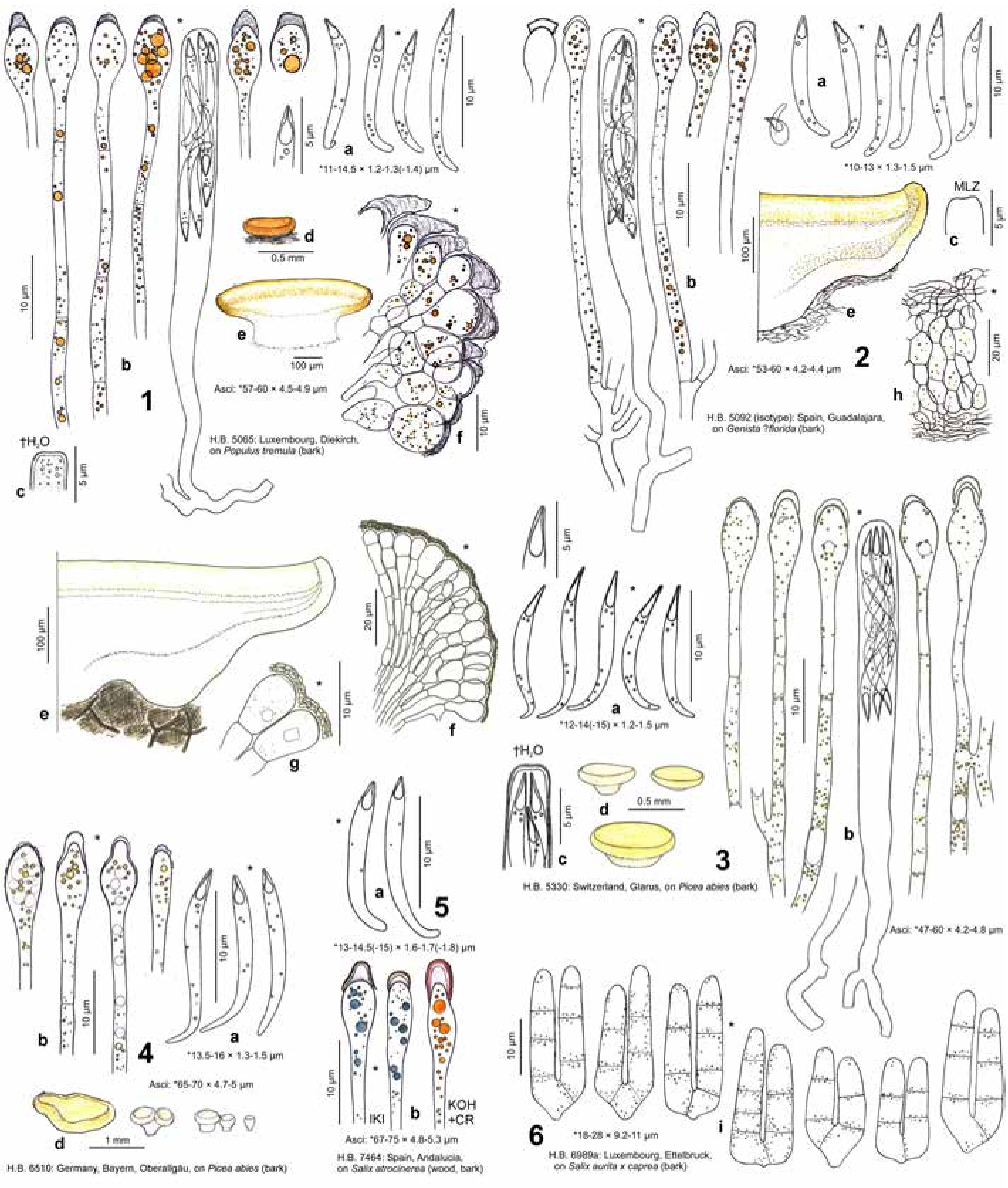


Plate 443. **1–6**: *Orbilia xanthoguttulata*. – **a**. ascospores; **b**. asci and paraphyses (**5b**: yellow-orange LBs stained blue-green in IKI, covering layer of cap-like matrix stained rose-red in CR); **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecia in median section; **f**. id., marginal ectal excipulum, cortical cells bearing glassy processes; **g**. id., cortical cells covered by exudate; **h**. id., ectal excipulum near base; **i**. conidia from culture.

gomphocephala {1}, *Fagus sylvatica* {3}, *Fraxinus excelsior* {2}, *Genista* (?)*florida* {1}, *Liriodendron tulipifera* {2}, *Picea abies* {4}, *Pistacia lentiscus* {1}, *P. terebinthus* {1}, *Populus* sp. {2}, *P. tremula* {3/1}, *Prunus avium* {1}, *Quercus* sp. {7}, *Q. petraea* {1}, *Q. robur* {1}, *Salix* sp. {10}, *S. alba* {1}, *S. atrocinerea* {1}, *S. aurita* × *caprea* {1}, *S. breviserrata* {1}, *S. caprea* {7}, *Tilia* sp. {1}, *T. cordata* {2}, *Ulmus* sp. {5}, *U. glabra* {2}, on slightly to strongly decayed bark {60} (on bast, sometimes periderm), rarely on wood {9}, in cracks or holes of periderm, on small to large periderm-free areas, also completely hidden by overlying periderm, on edge and inner surface of detaching or hanging bark, also in old beetle galleries, here partly on boring dust of bark beetle {4} (sometimes close to their dead imagines), sometimes greyed, green algae sparse or abundant, sometimes closely associated with old pyrenomycetes (partly growing on old *Diatrype* or

Plate 444. **1–14**: *Orbilia xanthoguttulata*. – **5**. southwest-exposed border of lowland boreal broad-leaved forest; **1a–c**, **2a**, **3a–d**, **4a–d**, **6a–b**, **7**, **8a**, **9**, **11**. rehydrated apothecia (**11**: whitish form, 9 years after collecting); **3e–g**. dry apothecia; **2b**. apothecium in median section; **2d**. id., basal ectal excipulum; **1d**, **2c**, **8b**, **10a**, **13a**. asci and paraphyses (with LBs containing carotenoids); **2e**, **10b**, **12**, **13b**. ascospores; **14**. conidia from substrate. – Living state (**10a** fully turgescent). – **4a–d**, **5**, **7**, **12**: phot. P. Perz; **10**: phot. R. Tena. — **1a–d**. H.B. 8698: Germany, Fürstenwalde, on *Quercus*; **2a–e**. H.B. 8208b: Sweden, Skåne, on *Ulmus*; **3a–g**. H.B. 7915b: France, Savoie, on *Salix*; **4a–d**. P.P. 20060625: Poland, Griewoszow, on *Salix*; **5**. H.B. 9366b: Sweden, Gävleborg, on *Populus*; **6a–b**.

?*Diaporthe*). **Associated**: ?*Calycellina* sp. {1}, *Cistella chlorosticta* {1}, *Cosmospora* sp. {1}, *C. episphaeria* {1}, *Diatrype bullata* {4}, *D.* ?*decorticata* {1}, *D. stigma* {1}, *Exidia* sp. {1}, *Episphaeria fraxinicola* {1}, ?*Exidia thuretiana* {1}, *Glyphium elatum* {1}, *Graphis scripta* {1}, *Grovesiella abieticola* {1}, *Helicogonium orbiliarum* (parasitic in *O. xanthoguttulata*) {1}, *Hyalorbilia orbiliicola* (parasitic on *O. aurantiorubra*) {1}, *H. juliae* {1}, *H. subfusispora* {1}, *Hysteropatella elliptica* {2}, *Hypogymnia physodes* {1}, *Ionomidotis fulvotingens* {1}, *Karstenia* sp. {1}, *Lasiobelonium belanense* {1}, *Lecanora* sp. {2}, *Lecidella elaeochroma* {1}, *Melanohalea exasperata* {1}, *Merismodes* ?*anomala* {2}, *Mollisia* ?*oblonga* {1}, ?*Monodictys* sp. {1}, *Orbilia aradi* {2}, *O. aristata* {1}, *O. aurantiorubra* {4}, *O. comma* {1}, *O. eucalypti* {2}, *O. fraxini* {1}, *O. mali* {1}, *O. myriosphaera* {1}, *O. phragmotricha* {5}, *O. pilifera* {2}, *O. navicularis* {1}, *O. pleiogambelii* {1}, *O. pseudoaristata* {1}, *O. rubella* {3}, *O. subclavuliformis* {1}, *O. vinosa* {1}, *O.* ?*vitalbae* {1}, *Peniophora* ?*lyci* {1}, *Physcia* sp. {1}, *P. adscendens* {1}, ?*Pyrenopeziza* sp. {1}, *Unguicularìopsis* sp. {1}, *U. rehmii* {1}, *Xanthoria parietina* {1}, acrocarpous mosses. **Desiccation tolerance**: some immature asci still viable after 4 months (central Europe), some mature asci and excipular cells still viable after 31 months (Spain). **Altitude**: 5–140 m a.s.l. (Scandinavia), 20–1200 (central and atlantic Europe), 4–1755 m (southern Europe). **Geology**: Paleozoic greywacke, Ordovician sand- & siltstone, Permian mud- & sandstone, Buntsandstein, Muschelkalk, Triassic dolomite, Keuper, Lower Jurassic & Cretaceous marl, sandstone & shale, Minette, flysch, Tertiary clay, Pleistocene till; granite, granitoid, pegmatite, gneiss, mica schist, ophiolite serpentinite, pyroxenite, gabbro, basalt. **Phenology**: throughout the year (long-lived).

Phenology of *O. xanthoguttulata*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
4	6	10	10	9	6	2	5	5	5	5	4

Taxonomic remarks. *Orbilia xanthoguttulata* is readily recognized by its spathulate paraphysis apices which mostly contain many small to large yellow LBs, which also occur in the lower half of paraphyses and in the ectal excipulum at mid flanks and margin, and give the distinct yellow colour to the apothecia. With its helicoid spores with tear-shaped SBs in the acute apices, *O. xanthoguttulata* closely resembles *O. aurantiorubra* (series *Aurantiorubrae*) but also *O. vermiformis* (*nemaspora-vermiformis* clade), which both differ not only in colour but also in having uninflated to capitate-clavate paraphysis apices without abundant LBs, and the margin consistently without glassy processes. *O. xanthoguttulata* further differs from these two species in its dicranidion-like anamorph, and from *O. aurantiorubra* in lacking crystalloid SCBs.

Variation. The length of ascospores and especially of SBs varies to a considerable extent. Depending on the population, spore length ranges from *10–12 µm up to *13.5–16 µm (mainly 11–14 µm), and SB length from 1.8–2.4 µm up to 2.8–3.3 µm. Spore width is usually *1.3–1.5 µm, rarely 1.2–1.3 µm (Pl. 443: 1) or 1.6–1.8 µm (Pls 443: 5; 444: 10). Spores of 10–13 µm were observed at mediterranean sites (e. g., Pls 443: 2; 444: 10) as well as in northern France and Scandinavia, and spores of the longer range occurred likewise across Europe.

Two collections on *Picea* bark from Glarus and Oberallgäu (Pls 443: 3–4; 444: 11) showed almost unpigmented apothecia besides light yellow ones. In one of them (443: 3) the ascospores were a bit more spirally twisted, with more attenuated basal ends and longer SBs, also glassy processes were not seen at the margin. However, glassy processes were in specimens on angiosperm hosts also often very short (around 1–3 µm), and sometimes predominantly absent, also difficult to distinguish from exudate. Three further samples on conifers (on wood, boring dust and bark of *Abies* and *Picea*) had bright yellow-orange apothecia, and also here one on *Picea* showed more strongly helicoid spores and that on *Abies* (IVV: 21.IV.2018) extraordinarily long spores of *(14–)16–17(–18) × 1.4–1.6 µm. Apothecial pigmentation was found to depend on the intensity of illumination: apothecia growing exposed possessed abundant yellow LBs whereas those below the bark were quite unpigmented. No molecular data were available for samples on conifers.

Misapplication. During revision of *O. rubella* in P. Karsten's herbarium, one of the specimens turned out to belong to *O. xanthoguttulata*. Also Rehm's (1891) description of *O. curvatispora* (spores worm-shaped, helicoid, apices of paraphyses egg-shaped inflated, with a yellowish oil drop; Germany, Bayern, Sugenheim, on dry-rotten hanging twigs of *Quercus*) very probably refers to a specimen of *O. xanthoguttulata*. Baral (1987b) misapplied the name *O. comma* to the pesent species when reporting yellow LBs with a blue-green IKI reaction.

Not included collection. Although the only known North American collection, described in Shao et al. (2018), fits very well European *O. xanthoguttulata* in morphology of both teleomorph and anamorph it was not included in the present description because of deviating molecular data (see below).

Anamorph. Despite morphological similarities between *O. xanthoguttulata* and *O. aurantiorubra*, the two species strongly differ in their anamorphs. The conidia of *O. xanthoguttulata* (Pls 443: 6; 444: 14) resemble *Dicranidion amazonense* (on palm leaves from Peru) in size and absence of a stipe. However, a broadly truncate base which we have seen in many conidia of *O. xanthoguttulata* is not reported for *D. amazonense*. Conidia of *O. eucalypti* and *O. tremulae* have also a very similar shape but are distinctly smaller.

Phylogeny. Sequences of eight European samples of *O. xanthoguttulata* were available, all comprising the S1506 intron and the ITS region, five also LSU and four SSU. One of them was gained from pure culture (H.B. 6989a) by G. Hagedorn and seven from apothecia by L. Quijada, M. Weiß, and G. Marson. From pure culture of the sample from Georgia (North America), ITS (intron region not covered) and LSU were obtained (Shao et al. 2018).

Within the European strains, variation of 0.6–3.5 % was observed in the entire ITS region, but no correlation between these distances and the geographical origin within Europe or the spore size if available could be noted. However, a correlation with the host is seen when retrieving a phylogeny from the ITS region (Phyl. 15, see also Quijada et al. 2014b): samples on *Quercus*, *Fagus*, and *Fraxinus* formed a strongly supported clade, while those on *Salix* and *Ulmus* clustered in a medium supported sister clade.

In the LSU D1–D2 domain the European sequences differ only at pos. 539 (C in H.B. 7915b and 7464, both on *Salix*; T in H.B. 6989a on *Salix*, G.M. 2017-12-27.2 on *Fagus*, and 2017-09-28.1 on *Quercus*). The American ga047 and Macaronesian *O. succulenticola* also have T. In the four available SSU sequences *O.*

H.B. 8170a: France, Melle, on *Ulmus*; **7**. P.P. 20070426-5: Poland, unlocalized, on *Salix*; **8a–b**. H.B. 9182b: France, Nyons, on *Quercus*; **9**. H.B. 7464: Spain, Málaga, on *Salix*; **10**. 17.III.2011: Spain, Alicante, on *Ulmus*; **11**. H.B. 5330: Switzerland, Glarus, on *Picea*; **12**. P.P. 20070825: Poland, Śrem, on *Crataegus*; **13a–b**. H.B. 9291: France, Loire, on *Fraxinus*; **14**. H.B. 7884b: Luxembourg, Junglinster, on *Fagus*.

xanthoguttulata showed no variation in the (V7–)V8–V9 region. In the intron it varies by 1–4 %, and also here the strains on *Salix* and *Ulmus* clustered in an unsupported separate clade (Phyl. S14). For the differences to *O. succulenticola* see below.

The sample from Georgia clustered distantly from *O. xanthoguttulata* and *O. succulenticola* when analysing the ITS and/or LSU region (Phyls 13, 15, S15, S16, Shao et al. 2018), though in the combined analyses in a medium supported clade with *O. succulenticola*. Here an ITS distance of 3.3–5.5 % is observed to *O. xanthoguttulata* and 5–5.5 % to *O. succulenticola*, the 3.3 % distance being to the Spanish strain from Málaga. The Georgia sample also differs in having an insert of 11 nt in the ITS2. The S1506 intron appears to be absent, considering the used ITS5 primer and a high signal at the 3'-end of SSU. In the LSU this sample deviates from *O. xanthoguttulata* and *O. succulenticola* by 2 nt in the D1 and 2 nt in the D2 domain (pos. 132, 160, 456, 471), but due to 1–2 variable nt in European *O. xanthoguttulata* and 1 in *O. succulenticola* the distance ranges at 0.6–1.5 %. The D3 domain was not available in *O. succulenticola*; also here 1 nt (pos. 936, GT**C**C) deviates from *O. xanthoguttulata* (G.M. 2017-09-28.1, GT**T**C). All these deviations are unequivocal in the available chromatograms, and they suggest that the sample from Georgia belongs to a different, cryptic taxon.

Ecology. *O. xanthoguttulata* shows a remarkably diverse ecology. The species was collected on undecayed to decayed bark (rarely wood) of xeric branches or sometimes trunks of angiosperm trees and shrubs, predominantly *Salicaceae* {26}, *Ulmus* {7}, and *Quercus* {9}, rarely gymnosperms. The collections are from humid to semihumid, atlantic to subcontinental sites in thermo- to hemiboreal northern Europe, meso- to orotemperate western and central Europe, and orosub- to thermomediterranean southern Europe. In mediterranean samples a much higher desiccation tolerance than in central European samples was observed. The vegetation includes *Querco-Fagetum*, *Fraxino-Aceretum pseudoplatani*, *Abieto-Fagetum*, *Picea-Vaccinietum*, *Salix-Betula-Populus*-pioneer vegetation in quarries, floodplain forests, thermophilous shrubs, and mediterranean maquis. The not included sample from eastern North America was in a subtropical humid angiosperm forest.

Map 78. Known distribution of *O. xanthoguttulata* in Europe.

Specimens included. **NORWAY**: **Aust-Agder**, 5 km ENE of Arendal, Tromøy, Kvernhuskjerr, 18 m, trunk of *Salix caprea*, on bark, 15.IV.2009, T.H. Dahl (T.H.D. 116/09, H.B. 9046b ø, doc. vid.). – ibid., S of Alvekilen, 5 m, on bark of *Ulmus glabra*, 9.IV.2009, T.H. Dahl (T.H.D. 98/09, non vid.). — **SWEDEN**: **Gävleborg**, 12 km SSW of Hudiksvall, 3.5 km SSW of Iggesund, NE of Njutånger, 18 m, branch of *Populus tremula*, on bark, 23.VII.2010, H.O. Baral & P. Perz (H.B. 9366b ø). – **Skåne**, Söderåsen, 6 km WNW of Röstånga, Kohagahus, Kvärkabäckens ravine, 135 m, branch of *Ulmus glabra*, on bark, 3.VI.2006, T. Læssøe & H.O. Baral (H.B. 8208b; sq.: KF768636). — **FINLAND**: **North Karelia**, 42 km WNW of Joensuu, WNW of Outokumpu, Raivionmäki, 140 m, branch of *Salix caprea*, on bark, 30.I.2011, M. Pennanen (M.P. 110106, doc. vid.). – **Kanta-Häme**, ~8 km E of Forssa, ~1 km N of Tammela, around Mustiala, 110 m, branch of *Salix*, on bark, 6.XI.1868, P.A. Karsten (Karsten 4852, as *O. rubella*, H-6051976). – **Uusima**, 49 km ENE of Helsinki, 4 km ESE of Porvoo, 33 m, branch of *Populus tremula*, on bark, 2.IV.2020, J. Äikäs (doc. vid.). — **POLAND**: unlocalized, branch of *Salix*, on bark, 26.IV.2007, vid. P. Perz (P.P. 20070426-5). – **Greater Poland**, 40 km S of Poznań, 9 km WSW of Śrem, 2 km ENE of Rąbiń, Uroszysko Rąbiń, 103 m, branch of *Crataegus*, 25.VIII.2007, A. Kujawa & P. Perz (A.K., P.P. 20070825-6-Kujawa, doc. vid.). – **Łódź**, 6 km SE of Radomsko, 1.5 km W of Orzechówek, 245 m, branch of *Salix*, on bark, 21.II.2010, J. Nowicki, vid. P. Perz (P.P. 20100221 JN, doc. vid.). – **Lower Silesia**, 11 km SW of Bystrzyca Kłodzka, 1.2 km SE of Gniewoszów, 530 m, on bark of *Salix*, 25.VI.2006, P. Perz (P.P. 20060625, doc. vid.). — **SLOVAKIA**: **Bratislava**, 23 km NE of Bratislava, 3 km NNW of Senec, 148 m, branch of *Quercus*, on wood, 12.V.2019, A. Polhorský (A.P. 19/18, doc. vid.). — **GERMANY**: **Brandenburg**, 8.5 km NW of Fürstenwalde, 3 km NE of Hangelsberg, 55 m, branch of *Quercus robur*, on bark, 24.XI.2007, R.K. Schumacher (R.S. 24.11.2007-076, ex H.B. 8698; sq.: KF768635). – **Sachsen-Anhalt**, 9.5 km WNW of Halle, 2 km WNW of Lieskau, Benkendorfer Grund, 100 m, branch of *Prunus avium*, on bark, 27.XII.2009, G. Hensel (ø, doc. vid.). – **Thüringen**, 4.2 km SSW of Sonneberg, 2.5 km E of Neustadt, Unterlind/Heubisch, 345 m, branch of *Salix*, on bark, 7.III.2009, P. Püwert & I. Wagner (ø, doc. vid.). – 2.5 km SW of Sonneberg, S of Hönbach, 355 m, branch of *S. caprea*, on bark, 31.XII.2012, I. Wagner (ø, doc. vid.). – **Rheinland-Pfalz**, Pfälzer Wald, 15 km WNW of Landau, 5 km NW of Annweiler, NW of Rinnthal, 208 m, branch of *Tilia*, on bark, 27.VI.2002, G. Marson (H.B. 7155b ø). – **Baden-Württemberg**, Tübingen, lake in park N of railway station, 320 m, branch of *Liriodendron tulipifera*, on bark, 20.X.2002, H.O. Baral (ø). – 2.5 km NE of Tübingen, 1.5 km N of Lustnau, Hägnach, 380 m, branch of *Carpinus betulus*, on bark, 4.VIII.2002, H.O. Baral (ø). – 11.5 km SW of Ulm, 2.5 km ENE of Ringingen, 540 m, branch of *Quercus petraea,* on bark, 7.II.2014, U. Seibert (doc. vid.). – **Bayern**, **Oberfranken**, 3.8 km E of Marktredwitz, S of Brand, Kleeschlag, 570 m, branch of ?*Betula*, on wood, 17.III.2019, M. Reul (M.R. 6759 ø, doc. vid.). – **Oberpfalz**, 15 km ENE of Weiden, SE of ruin of Flossenbürg, 685 m, trunk of *Ulmus*, on bark, 21.IV.2014, H.O. Baral (H.B. 9876b). – **Schwaben**, Oberallgäu, 9 km E of Sonthofen, NW of Oberjoch, Ornach Mt., 1200 m, trunk of *Picea abies*, on bark, 30.IX.1999, R. Kirschner (H.B. 6510). – **Oberbayern**, Berchtesgadener Land, 20 km NW of Salzburg, 3 km NW of Laufen, NE of Lebenau-Forstgarten, Salzach, Osinger Wald, 405 m, branch of *Salix*, on bark, 10.III.2012, I. Rößl (H.B. 9666). – 5.5 km N of Bad Reichenhall, S of Aufham, Reitweg, 505 m, trunk of *F. excelsior*, on bark, 7.III.2018, I. Rößl (doc. vid.). — **SWITZERLAND**: **Schaffhausen**, 2 km ENE of Schaffhausen, W of Gennersbrunn, Langegerten, 485 m, branch of *Ulmus*, on bark, 2.I.1987, P. Blank (P.B. 458, as *O. comma*, H.B. 3141b ø). – **Glarus**, 6.5 km SSE of Glarus, 2 km SE of Schwanden, 1100 m, trunk of *Picea abies*, on bark, 6.IX.1995, R. Kirschner (H.B. 5330). – **Schwyz**, 7.7 km E of Einsiedeln, SW of Sattelegg, 1180 m, branch of *Abies alba*, on bark, 21.IV.2018, U. Graf (doc. vid.). — **AUSTRIA**: **Steiermark**, 17 km NNW of Graz, 1.7 km W of Semriach, Römergrab, 865 m, branch of *P. abies*, on wood (boring dust) & bark, 18.IV.2011, G. Friebes (G.F. 20110043, doc. vid.). – 9.5 km WNW of Graz, NNW of Plankenwarth, Luttengraben, 540 m, log of *Populus*, on wood, 7.XII.2014, I. Wendelin, vid. G. Friebes (GJO 73803, doc. vid.: Friebes 2017: 24, figs 23r). – 14 km SW of Hartberg, W of Herberstein, 520 m, branch of *Quercus*, on wood, 2.III.2013, G. Friebes (G.F. 20130028, doc. vid.). – 16 km SW of Leoben, 3 km NE of Feistritz, Gulsen, Mittagskogel, 850 m, branch of *Picea abies*, on wood, 12.X.2013, G. Friebes (G.F. 20130151, doc. vid.). – **Burgenland**, 5.5 km WNW of Rechnitz, 1.5 km N of Althodis, Baumwipfelweg, 550 m, branch of *Quercus*, on bark, 27.II.2016, G. Friebes (G.F. 20160018, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 12.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, N of WWII memorial, 430 m, log of *Ulmus*, on bark, 7.V.2019, D. Savić (FG-1061, doc. vid.). – 12 km SSE of Novi Sad, N of TV tower, 511 m, branch of *Salix alba*, on bark, 26.VI.2019, D. Savić (FG-1097, doc. vid.). — **LUXEMBOURG**: **L'Oesling**, **Redange**, 11 km W of Ettelbruck, 1.8 km NW of Grosbous, W of Bruch (an der Wark), 390 m, branch of *Salix aurita* × *caprea*, on bark, 26.III.2001, G. Marson (H.B. 6989a, CBS 116280, anam. cult.; sq.: KF741604). – **Gutland**, **Diekirch**, 3.5 km E of Diekirch, 1.7 km SW of Bettendorf, Schoofsboesch, Carrières de Gilsdorf, 310 m, branch of (?)*Populus tremula*, on bark, 26.IV.1994, G. Marson (H.B. 5065). – **Luxembourg**, 6 km

NNE of Luxembourg, 1.2 km WNW of Waldhaff, Gréngewald, Stafelter, 419 m, trunks of *Fagus sylvatica*, on bark, 27.XII.2017, G. Marson (G.M. 2017-12-27.2; sq.: MH221054). – 6 km S of Luxembourg, 1.7 km WSW of Fentange, Mierchesfeld, 302 m, branch of *Quercus*, on wood, 28.IX.2017, G. Marson (G.M. 2017-09-28.1; sq.: MH221055). – **Grevenmacher**, 13.5 km NE of Luxembourg, 1.7 km WNW of Junglinster, S-end of Bierger, 350 m, trunk of *Fagus sylvatica*, on bark, 21.VIII.2005, G. Marson (H.B. 7884b ø, anam. substr.). – 3.5 km N of Grevenmacher, 1.7 km ENE of Manternach, Syre river, WNW of Fielsmillen, 185 m, branch of *Liriodendron tulipifera*, on bark, 22.IV.1995, G. Marson & H.O. Baral (H.B. 5260). – **Esch-sur-Alzette**, 4.5 km SW of Luxembourg, 1.5 km SW of Cessange, Bois de Cessange, 305 m, branch of *Populus tremula*, on bark, 10. XI.2000, G. Marson (ø). – 5 km SSW of Luxembourg, 0.7 km N of Kockelscheier, Haus der Natur, 305 m, branch of *Salix caprea*, on bark, 10.XI.2000, G. Marson (H.B. 6831). – 9.5 km ESE of Esch-sur-Alzette, 2 km SE of Dudelange, Bloklapp, 288 m, branch of *S. caprea*, on bark, 13.III.2001, G. Marson (ø). – 3 km E of Esch-sur-Alzette, 2 km NW of Kayl, Brucherbierg, 375 m, branch of *S. caprea*, on bark, 7.VI.1998, G. Marson (H.B. 6152b). — **FRANCE**: **Haute-Normandie**, **Seine-Maritime**, 14 km SW of Rouen, SW of Les Essarts, Forêt de la Londe, 128 m, branch of *Quercus*, on bark and old pyrenomycete, 20.III.2005, A. Delannoy (J.P.P. 25068, doc. vid.). – **Bretagne**, **Morbihan**, 8.5 km WNW of Redon, 1.9 km E of St.-Jacut-les-Pins, Moulin de Calléon, 20 m, branch of *Salix*, on bark and *Diatrype bullata*, 5.II.2006, J.P. Priou (J.P.P. 26033 doc. vid.). – 1 km WNW of La Gacilly, rue de Picardie, 38 m, branch of *Castanea sativa*, on bark, 5.VI.2012, J.P. Priou (J.P.P. 12135, doc. vid.). – 0.4 km NNE of La Gacilly, S of La Bouère, 11 m, branch of *Populus*, on bark, 6.V.2013, J.P. Priou (J.P.P. 13099, doc. vid.). – **Poitou-Charentes**, **Deux-Sèvres**, 18.5 km ESE of Melle, 2 km N of Mairé l'Evescault, 135 m, trunk of *Ulmus*, on bark, 1.V.2006, B. Coué (H.B. 8170a). – **Alsace**, **Haut-Rhin**, 25 km W of Basel, 2 km E of Bisel, direkt E (W?!) v. Rehhof, nahe Fischweiher, 425 m, branch of *Quercus*, on wood, 19.IX.1999, H.O. Baral (H.B. 6462). – **Bourgogne**, **Côte-d'Or**, 32.5 km NNE of Dijon, 2.3 km NW of Selongey, SE of Foncegrive, Ruisseau de la Venelle, 310 m, branch of *Salix*, on bark and *Diatrype bullata*, 30.X.2009, J.P. Priou (J.P.P. 29211, doc. vid.). – **Franche-Comté**, **Doubs**, 5 km SE of Besançon, E of La Vèze, marais de Saône, ruisseau des Moulins, 385 m, branch of *Salix*, on bark, 6.II.2014, G. Moyne (G. My. 2014 02 02). – **Midi-Pyrénées**, **Ariège**, 12 km ENE of St.-Girons, 2 km NNE of Rimont, Las Muros, 475 m, trunk of *S. caprea*, on bark, 24.V.2006, M. Hairaud (M.H., doc. vid.). – **Rhône-Alpes**, **Drôme**, 10 km ENE of Nyons, 1 km N of Curnier, 383 m, branch of *Cercis siliquastrum*, on boring dust, 12.IX.2009, G. Marson (H.B. 9182b). – **Loire**, 16 km WNW of Boën, 1.5 km S of St.-Jean-la-Vêtre, Ventuel, Village de Vacances, 880 m, branch of *Fraxinus excelsior*, on bark, 6.V.2010, P. Chaillet (ex H.B. 9291; sq.: KF768634). – **Savoie**, 19 km ENE of Albertville, 4.5 km ESE of Beaufort, N of Lac de Roseland, ~1320 m, branch of *Salix*, on bark, 4.VIII.1995, G. Marson (ø). – 6.3 km S of Albertville, 3 km W of Esserts-Blay, Forêt de Darbelay, 1550 m, branch of *Salix*, on bark, 6.V.2005, N. Van Vooren (J.P.P. 25125, H.B. 7915b; sq.: KF768637). — **SPAIN**: **Asturias**, 12.5 km ESE of Somiedo, 5 km SE of Saliencia, S of Lago Cerveiriz, Picos Albos, 1755 m, branch of *Salix breviserrata*, on bark, 14.VII.2012, J.A. Sánchez (E.R.D. 5613, doc. vid.). – **Castilla-La Mancha**, **Guadalajara**, Sierra Norte de Guadalajara, ~15 km N of Sigüenza, ~E of Tobes, 1200 m, on bark of *Quercus*, 2.XI.1991, M. de la Cruz (AH 6797). – Sierra de Guadarrama, 9.5 km W of Cantalojas, 7.5 km ESE of Riofrío de Riaza, Hayedo de Tejera Negra, 1625 m, branch of *Genista* (?)*florida*, on bark, 30.X.1991, A. Raitviir & R. Galán (AH 6796, **holotype**; **isotype** in H.B. 5092). – **Navarra**, 11 km NE of Pamplona, SSE of Sarasibar, 520 m, branch of *Cornus sanguinea*, on bark, 26.I.2013, F.J. Balda (F.J.B. 2376, doc. vid.). – **Aragón**, **Huesca**, 16.5 km E of Sabiñánigo, E of Bergua, 1028 m, log of *Fagus sylvatica*, on bark, 12.V.2017, J. Castillo (doc. vid.). – **Cataluña**, **Barcelona**, 25 km NNW of Barcelona, 4.8 km NE of Terrassa, 322 m, branch of *Ulmus*, on bark, 1.II.2014, J. Bometón (J.B. 0449/14). – **Com. Valenciana**, **Valencia**, 14 km SSE of Valencia, El Saler, Gola de Pujol, 4 m, trunk of *Eucalyptus gomphocephala*, on bark, 6.III.2011, J. Ormad (ø, doc. vid.). – **Alicante**, 43 km NNW of Alicante, 1 km SW of Banyeres de Mariola, Molí de l'Ombría, 705 m, branch of *Ulmus*, on bark, 17.III.2011, F. García Alonso (ø, doc. vid.). – **Andalucía**, **Málaga**, Sierra de Grazalema, 11 km ENE of Grazalema, 9 km WNW of Ronda, Venta de la Vega hotel, 663 m, branch of *Salix atrocinerea*, on bark & wood, 6.I.2004, F. Prieto & A. González (AH 7580, H.B. 7464; sq.: KF768638). – **Jaén**, Sierra de Ventisqueros, 18.5 km SSE of Jaén, 7 km ENE of Valdepeñas de Jaén, 1.9 km S of El Parrizoso, 1130 m, branch of *Pistacia terebinthus*, on boring dust and bark, 18.IV.2017, S. Tello (ex S.T. 18041702, H.B. 10113b). – 22 km SSW of Jaén, 4.7 km S of Fuensanta de Martos, 4 km SE of Vadohornillo, 740 m, branch of *P. lentiscus*, on bark, 5.IV.2014, S. Tello (JA-CUSSTA 7930, doc. vid.). — **RUSSIA (West)**: **Pskov**, **Loknya**, 41 km NW of Velikiye Luki, 8.5 km N of Nasva, W of Bashovo, 135 m, branch of *Tilia cordata*, on bark, 18.VIII.2011, E.S. Popov (LE 247565, E.S.P.-11-0047, doc. vid.). – **Bryansk**, **Suzemka**, Bryanskiy Les, 95 km SSW of Bryansk, 14 km SSE of Trubchevsk, NW of Chukhrai, Nerussa River, 138 m, branch of *T. cordata*, on bark, 23.X.2012, E.S. Popov (LE 248006, non vid.).

Not included. **USA**: **Georgia**, 7 km NNW of Tifton, Black Shank Farm, 105 m, branch of indet. angiosperm, on bark, 16.IX.2015, Y.Y. Shao (UGA ga047, GXU 1491, anam. cult., doc. vid.; sq.: MG742406, MG742407).

Orbilia succulenticola Quijada, Baral & Beltrán-Tej., in Quijada et al., Phytotaxa 175: 13 (2014) — Pls 445–446, Map 79

Etymology: named after the inhabited branches of succulent plants.

Typification: Macaronesia, Tenerife, Punta Hidalgo, branch of *Euphorbia canariensis*, 20.X.2008, L. Quijada & E.V. Rodríguez (TFC Mic. 20335, holotype; sq.: KF768649).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.6–1(–1.2) mm diam., (0.18–)0.23–0.3(–0.37) mm high (receptacle 0.14–0.15 → 0.1–0.12 mm), light yellowish-ochraceous, slightly translucent, ± round, scattered to gregarious in small groups; disc flat to slightly convex, margin thin, not protruding, very finely crenulate; sessile on an obconical stipe up to 0.07 × 0.35 mm, superficial; dry slightly concave, deep ochraceous-brownish(-orange). **Asci** *(51–)55–63(–67) × (4–)4.2–4.8(–5.4) µm {7}, †42–57 × 3.4–4 µm {10}, 8-spored, spores *2–4-seriate, (2–)3–4(–5) lower spores inverted {6} (sometimes slightly mixed), pars sporifera *20–23 µm long; **apex** (†) strongly truncate (not or very slightly indented, laterally never inflated); **base** with medium to long, thin, flexuous stalk, T-, L- or h-shaped. **Ascospores** *(9–)9.5–11(–12) × (1–)1.2–1.5(–1.6) µm {8} (~10–13 µm actual length), †(8.3–)9–10(–10.4) × (0.9–)1–1.3 µm {10}, fusiform-clavate, apex acute, base medium to strongly attenuated in a ± distinct, sometimes swollen tail of 1.7–3.5(–5) × 0.5–0.7(–1) µm (ca. 1/4–1/3 of spore length), inequilateral to slightly curved in upper part, medium (to strongly) so in region of tail, slightly helicoid; **SBs** *(1.7–)2–2.4(–2.6) × (0.6–)0.8–1(–1.2) µm {8}, tear-shaped, apically narrowed to a short, hardly visible filum. **Paraphyses** apically slightly to medium (rarely strongly) clavate-spathulate(-ellipsoid), terminal cells *(16.5–)22–28(–34) × (2.5–)3–4(–5) µm {7}, (†) 1–8 µm longer than dead asci, lower cells *(5–)7–11(–14) × 1.5–2 µm {6}; rarely branched at upper septum, hymenium pale yellowish-ochraceous. **Medullary excipulum** hyaline, 70–125 µm thick, of medium loose to dense textura intricata with many inflated cells, sharply delimited by a t. porrecta mainly at flanks. **Ectal excipulum** hyaline, of (†) thin-walled, vertically oriented t. prismatica-angularis at base and flanks, 50–75 µm thick near base, cells *(8.5–)10–23(–28) × (6.5–)9–13(–18.5) µm {6}; 20 → 10 µm thick near margin, of light yellowish-ochraceous t. prismatica oriented at a 30–80° angle to the surface, marginal cortical cells *8–13 × (3–)4–5(–6) µm {7}; **glassy processes** 8–18 × 3–5 µm {6}, at flanks 2–10 × 4–6 µm, medium refractive, indistinctly

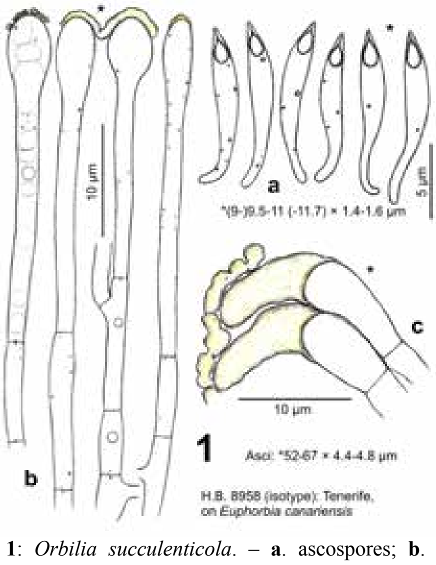


Plate 445. **1**: *Orbilia succulenticola*. – **a**. ascospores; **b**. paraphyses; **c**. marginal cortical cells with glassy processes in median section.

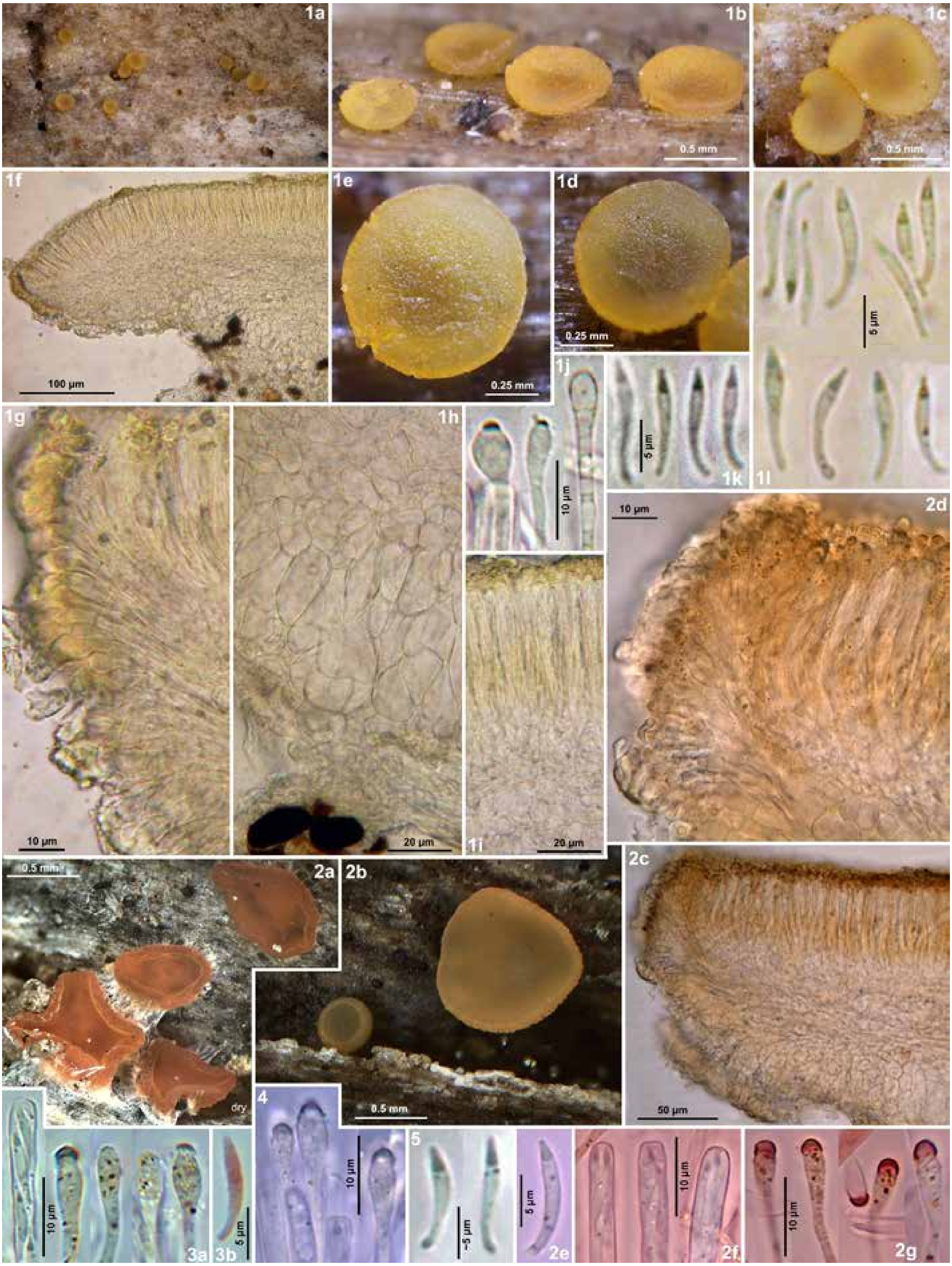


Plate 446. **1**, **3–5**: *Orbilia succulenticola*; **2**: *O.* cf. *succulenticola*. – **1a–d**, **2b**. rehydrated apothecia; **2a**. dry apothecia; **1f**, **2c**. apothecia in median section; **1g**, **2d**. id., ectal excipulum at margin; **1h**. id., near base; **1j**, **2f–g**, **3a**, **4**. asci and paraphyses; **1k–l**, **2e**, **3b**, **5**. ascospores. — Living state, except for **2g** (in CR), **3b** (in CR), ascus in **3a**. – **1j–k**, **2–5**: phot. L. Quijada (**1b**, **1l**: from Quijada et al. 2014b). — **1a–l**. H.B. 8958 (TFC Mic. 20335, **1a–i**, l: isotype, **1j–k**: holotype): Tenerife, Anaga, Punta Hidalgo, on *Euphorbia canariensis*; **2a–g**. TFC Mic. 23292: Vilaflor, on *Chamaecytisus*; **3a–b**. TFC Mic. 23229: La Matanza, on *E. canariensis*; **4**. TFC Mic. 22119: Punta de Teno, on *E. balsamifera*; **5**. TFC Mic. 22822: Güímar, on *E. atropurpurea*.

stratified, consistently outwards curved, covered by yellowish exudate. **Anchoring hyphae** very abundant, *2.2–2.8(–3.5) µm wide, walls 0.2(–0.3) µm thick {1}, forming a medium dense, hyaline, not or medium gelatinized t. intricata ~10–20(–60) µm thick. **SCBs** in paraphyses and ectal excipulum absent but sometimes indistinct small globose SCBs seen in paraphyses. Bright to deep golden yellow(-orange) **LBs** (carotenoids) absent {T} or scattered to abundant near apex and in lower half of paraphyses and in marginal ectal excipulum {9}, 0.4–0.7 µm diam. **Exudate** over paraphyses (0.3–)1–1.5(–2) µm thick, granular-cloddy, sometimes cap-like, pale yellowish-ochraceous, firmly attached, over margin and flanks 1.5–3.5 µm thick, cloddy. — **ANAMORPH**: unknown.

Habitat: collected on the ground (but not in close soil contact), 2–7 cm thick decorticated xeric branches of *Euphorbia atropurpurea* {1}, *E. balsamifera* {2}, *E. canariensis* {5}, *E. lamarckii* {2}, *Opuntia maxima* {1}, on strongly decayed wood (inner and outer surface) {10}, slightly greyed, no algae. **Associated**: none observed. **Desiccation tolerance**: ectal and medullary excipulum, also some paraphyses and mature asci viable after 1 month. **Altitude**: 45–402 m a.s.l. **Geology**: basaltic flows and pyroclasts, ignimbrite. **Phenology**: I–II, VII–VIII, X–XI (throughout the year, long-lived).

Taxonomic remarks. *Orbilia succulenticola* closely resembles *O. aurantiorubra* (series *Aurantiorubrae*) in ascospore features, especially samples on *Fabaceae* (Pl. 436) which show about the same spore size. It differs in distinctly shorter SBs, more ellipsoid (spathulate) apices of paraphyses, the absence of S-shaped SCBs, the presence of short glassy processes, and in apothecial colour.

Based on its yellow apothecial pigment located in small LBs, ellipsoid paraphysis apices, and glassy processes, *O. succulenticola* is obviously much more closely related to *O. xanthoguttulata*, which mainly differs in longer spores and slightly longer SBs, also in slightly shorter and wider marginal cortical cells oriented at a higher angle, and in shorter glassy processes. However, most of these features overlap to some extent, for instance, only those spore length values given in brackets overlap while the predominant ones lie in the range of */†9–11 and */†11–14.5 µm, respectively.

O. succulenticola may be confused with *O. euphorbiae* (series *Regales*) and *O. pseudeuphorbiae* (series *Neodactylella*), though mainly because of the same substrate. The two species differ in shorter spores with rounded to obtuse apices and less tail-like bases, in much smaller SBs (0.8–1.8 × 0.3–1 µm), and in the paraphyses with usually more distinctly spathulate to lageniform apices, some of which containing yellow LBs in the lower but never in the apical part.

Variation. *O. succulenticola* shows only little variation in the length of spores and SBs, thus rather sharply permits separation from the similar *O. xanthoguttulata* based especially on spore length. The type collection of *O. succulenticola* further differs in virtually lacking yellow LBs in paraphyses and excipular cells (Pls 445: 1; 446: 1f-j), and in more ellipsoid than spathulate paraphysis apices without prominent exudate caps. However, the nine paratype collections of *O. succulenticola* show sparse to rather abundant bright yellow LBs in the lower and upper part of paraphyses, and the inflated apices are often more elongate and sometimes spathulate and often covered by thick caps of exudate (Pl. 446: 2g, 3–4).

Not included collection. A more recent sample not mentioned in Quijada et al. (2014b) grew at high altitude (2083 m) on a different host (*Chamaecytisus*, IVV: TFC Mic. 23292). Nevertheless, it matches *O. succulenticola* quite well in the length and shape of spores (*10.5–11.3 × 1.2–1.5 µm) and SBs (2–2.5 µm) and in the yellow-orange LBs occurring in abundance especially in the paraphyses.

Map 79. Known distribution of *O. succulenticola* in Tenerife (Macaronesia, yellow = not included collection).

Phylogeny. From apothecia of *O. succulenticola*, B. Liu obtained ITS and LSU D1–D2 from the isotype (H.B. 8958), and L. Quijada ITS sequences of ten samples from eight collection sites other than the type locality. The observed variation in the ITS region within these sequences lies in the range of 0–1 %. This relatively low variation could be explained by the fact that *O. succulenticola* is so far only known from lowland regions of Tenerife. Regrettably, no DNA was taken from the rather lately collected sample on *Chamaecytisus* from the Canary pine woodland.

The distance to *O. xanthoguttulata* lies in the range of 4–6 % in the entire ITS region, whereas in the LSU only 1 nt differs from the majority of *O. xanthoguttulata* sequences (pos. 611: TG**T**TG vs. TG**C**TG), but further 1–2 nt (pos. 539, 553) deviate depending on the strain and completeness of the sequences. In all 11 sequences of *O. succulenticola* the S1506 intron is absent, in contrast to all six sequences of European *O. xanthoguttulata* in which the intron is present. All this confirms that the two morphologically similar species are sharply separated, reflecting their different geographical distribution and host spectrum.

Ecology. *O. succulenticola* appears to be restricted to the inframediterranean, semihumid to arid xerophytic scrubland of Macaronesia, where it was mainly collected in the cardonal (*Periploco laevigatae-Euphorbietum canariensis*), but also in the tabaibal dulce (*Ceropegio fuscae-Euphorbietum balsamiferae*), *Launaeo arborescentis-Schizogynetum sericeae*, and *Ceropegio dichotomae-Euphorbietum aphyllae* (L. Quijada & E. Beltrán-Tejera pers. comm.). It occurs on dead, xeric, decorticated branches of different succulent *Euphorbia* species, particularly *E. canariensis*, also *Opuntia*, always close to the ground. The not included record on a xeric branch of *Chamaecytisus* was from an upper mesomediterranean semihumid summit broom-scrub in the Canary pine woodland (*Sideritido solutae-Pinetum canariensis*) on phonolite of Vilaflor at the south-exposed slope of the southern rim around the caldera of the volcano Teide.

Specimens included (always on decorticated branches). **MACARONESIA**: **Canary Islands**, **Tenerife**, Buenavista del Norte, 4.8 km WSW of Buenavista del Norte, Punta de Teno, El Tosconito, 216 m, *Euphorbia lamarckii*, 8.XI.2009, leg. L. Quijada (TFC Mic. 22497, non vid.; sq.: KF768641). – ibid., Cuchillo el Balo, 115 m, *E. balsamifera*, 16.XI.2009, leg. L. Quijada (TFC Mic. 22115 doc. vid., 22118 non vid., 22119, doc. vid.). – San Cristóbal de La Laguna, Anaga, 6 km NE of Tegueste, 2.3 km E of Punta Hidalgo, 1.2 km NW of Chinamada, 345 m, *E. canariensis*, 20.X.2008, L. Quijada & E.V. Rodríguez (TFC Mic. 20335, **holotype**; H.B. 8958, **isotype**; sq.: KF768649); – ibid., sendero a Chinamada, 402 m, *E. canariensis*, 21.VIII.2011, leg. L. Quijada (TFC Mic. 23272, 23273, non vid.; sq.: KF768644, KF768645); – ibid., *E. lamarckii*, (TFC Mic. 23274, non vid.; sq.: KF768646). – ibid., 362 m, *Opuntia maxima*, 11.X.2009 (TFC Mic. 22370, non vid.; sq.: KF768647); – La Matanza de Ajentejo, 8.5 km NE of Puerto de la Cruz, 1.2 km W of La Matanza de Acentejo, NW of Jagre, Puntillo del Sol, 45 m, *E. canariensis*, 27.VII.2011, L. Quijada (TFC Mic. 23229, 22557, 22562, doc. vid.; sq.: KF768642). – Fasnia, 7.5 km SSW of Güímar, 1.5 km NE of Fasnia, Barranco de Herques, *E. atropurpurea*, 346 m, 5.II.2010, L. Quijada (TFC Mic. 22837 non vid., 22822, doc. vid.). – Tacoronte, 2.7 km NNE of El Sauzal, SSW of Mesa del Mar, Hoya las Higueras, 90 m, *E. canariensis*, 26.XI.2009, L. Quijada (TFC Mic. 22632, non vid.). – Arico, 2.2 km NW of Abades, Montaña Centinela, 160 m, *E. canariensis*, 23.I.2010, L. Quijada (TFC Mic. 22771, non vid.; sq.: KF768640; 22779, doc. vid.; sq.: KF768639). – 1 km WSW of Abades, Barranco la Vera, 50 m, *E. balsamifera*, 17.X.2009, L. Quijada (TFC Mic. 22434; 22437, sq.: KF768643; 22438, sq.: KF768648; doc. vid.).

Not included. **MACARONESIA**: **Canary Islands**, **Tenerife**, Adeje, 5 km NW of Vilaflor, 9.5 km SSW of Teide, Lomo el Dornajito, 2083 m, branch of *Chamaecytisus proliferus*, on wood, 12.XII.2012, L. Quijada (TFC Mic. 23292, doc. vid.).

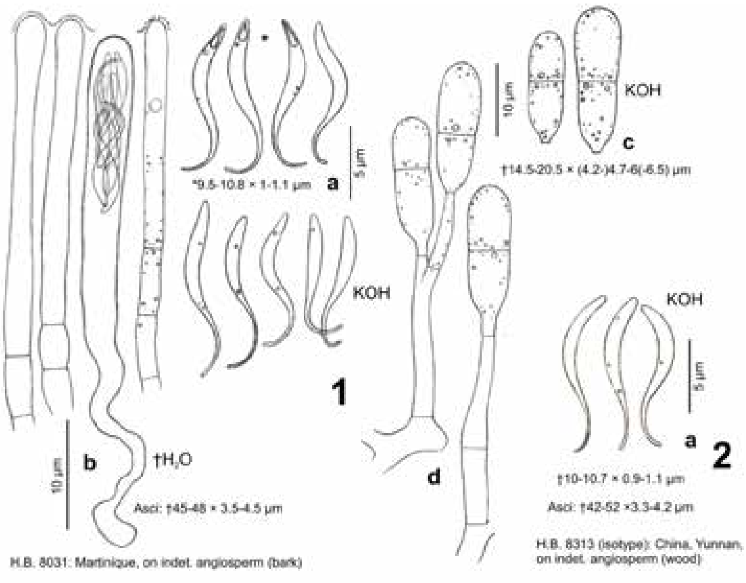


Plate 447. **1–2**: *Orbilia vermiformis*. – **a**. ascospores; **b**. ascus and paraphyses; **c–d**. conidia and conidiophores from substrate (on older apothecia).

2. *Nemaspora-vermiformis* clade

Orbilia vermiformis Baral, Z.F. Yu & K.Q. Zhang, in Yu et al., Mycotaxon 99: 272 (2007) — Pls 447–448

= *Dactylella vermiformis* Z.F. Yu, Ying Zhang & K.Q. Zhang, in Yu et al., Mycotaxon 99: 275 (2007).

Etymology: named according to the worm-shaped ascospores.

Typification: China, Yunnan, Xiaoheijiang, root of indet. angiosperm, 3.IX.2005, M. Qiao (YMFT 1.01842, holotype of teleomorph; YMF 1.01842, holotype of anamorph; sq.: DQ480729).

Description: — **TELEOMORPH**: **Apothecia** moist/rehydrated 0.4–2 mm diam., 0.18–0.4.5 mm high (receptacle 0.13–0.26 → 0.09–0.1 mm), whitish to pale yellowish-cream, turning light carneous with age, slightly to medium translucent, round, (densely) gregarious in medium to large groups; disc slightly concave to slightly convex, margin distinct, 5–10(–30) µm protruding, (very) finely crenulate; sessile on a broad base or with a hidden stipe 0.08–0.1 × 0.3–0.35 mm, superficial. **Asci** */†39.5–62 × 3.3–5 µm {T}, †40–53 × 3.3–4.2(–4.5) µm {3}, 8-spored, spores *4-seriate, (2–)4 lower spores inverted {2} (rarely mixed); **apex** (†) medium to strongly truncate (not or slightly to strongly indented, laterally not inflated); **base** with short to long, medium thin, flexuous stalk, L- to Y-shaped. **Ascospores** *(8.8–)9.5–11.3 × 1–1.1(–1.3) µm {2} (~10–13 µm actual length), †(8–)9–11(–12) × 0.9–1.1(–1.2) µm {3}, narrowly fusoid to fusiform, apex obtuse to subacute or acute, base strongly attenuated in a ± indistinctly differentiated narrow tail of 2.5–5 × 0.15–0.4 µm, strongly helicoid (always twisted like a right-hand thread {2}); **SBs** (1.3–)1.5–1.8 × 0.4–0.8(–1) µm {1}, tear-shaped, apically narrowed to a very short filum. **Paraphyses** apically uninflated or only very slightly clavate, terminal cell †21–32 {1} × 2–3 µm {2}, lower cells †4–6 × 1.8–2.8 µm {1}; unbranched at upper septum. **Medullary excipulum** 20–30 µm thick, of dense textura intricata-angularis-porrecta, medium to very sharply delimited from ectal excipulum. **Ectal excipulum** of (†) thin-walled, indistinctly oriented t. angularis(-prismatica) from base to margin, 100–300 µm thick near base, cells †20–45 × (10–)15–35 µm {2}; 100 → 40 µm thick at flanks, 20–40 µm thick at margin, oriented at a 70–80° angle to the surface, marginal cortical cells †(6–)9–14(–17) {3} × (4.5–)5–7 {1} or (6–)8–12(–13) {2} µm; **glassy processes** absent {3}. **Anchoring hyphae** abundant, †2–4(–5) µm wide, walls 0.2(–0.3) µm thick {2}, forming a dense hyaline, not or slightly gelatinized t. intricata-angularis 40–150 µm thick {2}. **SCBs** in paraphyses globose to elongate, crystalloid SCBs absent; **VBs** ?absent. **Exudate** over paraphyses 0.1–0.2 µm up to 0.3–1 µm thick, granular-cloddy or ± continuous, not loosely attached; over margin and flanks absent. — **ANAMORPH**: dactylella-like (from ascospore isolate {1, Yu et al. 2007a} and natural substrate {1}). **Conidiophores** septate, erect, simple, sometimes branched, 70–150 µm long, 3 µm wide at base and 1.8–2 µm wide at tip {Yunnan}, †22–30 µm long, 2.7–3.6 µm wide at base, 1.2–1.8 µm at tip {Martinique}, conidia formed terminally, singly or often on sparsely sympodially proliferating branches. **Conidia** cylindrical to cylindric-clavate, rounded at the distal end, narrowed and truncate at the proximal end, here often with a distinct basal protrusion, straight, sometimes slightly curved, (0–)1-septate, *20–30(–37) × 5.8–8 µm {Yunnan}, †14.5–20.5 × 4.2–6.5 µm {Martinique}.

Habitat: lying on moist ground, corticated or decorticated, ~6–15 cm thick branches and roots of indet. angiosperm {2}, ?*Mangifera indica* {1}, on ± deeply slightly to strongly decayed wood {2} and bark {1} (periderm), somewhat blackened, without algae. **Associated**: none observed. **Desiccation tolerance**: only a few spores still viable after 1 month. **Altitude**: 90–1100 m a.s.l. **Geology**: China: Jurassic-Cretaceous sedimentary rock; Comoros: volcanic igneous rock. **Phenology**: V, IX, XII (in tropical belt possibly throughout the year).

Taxonomic remarks. *Orbilia vermiformis* is very similar to *O. nemaspora*, from which it mainly differs in the ascospores being wider in their upper part in contrast to the thin tail-like lower part, perhaps also in less inflated paraphyses and in the anamorph (see below). Whether differences in the presence of VBs exist remains unclear due to lack of studies on living specimens.

Variation. The collection from Martinique differs from specimens from southern China and the Comoros in distinctly narrower marginal cortical cells.

Anamorph. The conidia in the type culture of *O. vermiformis* as reported by Yu et al. (l.c.) are somewhat larger and more clavate than those observed on the natural substrate in the collection from Middle America, in which also the conidiophores were shorter. Nevertheless, we think that the American specimen belongs to *O. vermiformis*. *O. nemaspora* has a very similar anamorph: the conidia of *O. vermiformis* are slightly shorter and (0–)1-septate, whereas those of *O. nemaspora* were sometimes 2–3(–4)-septate when formed in pure culture.

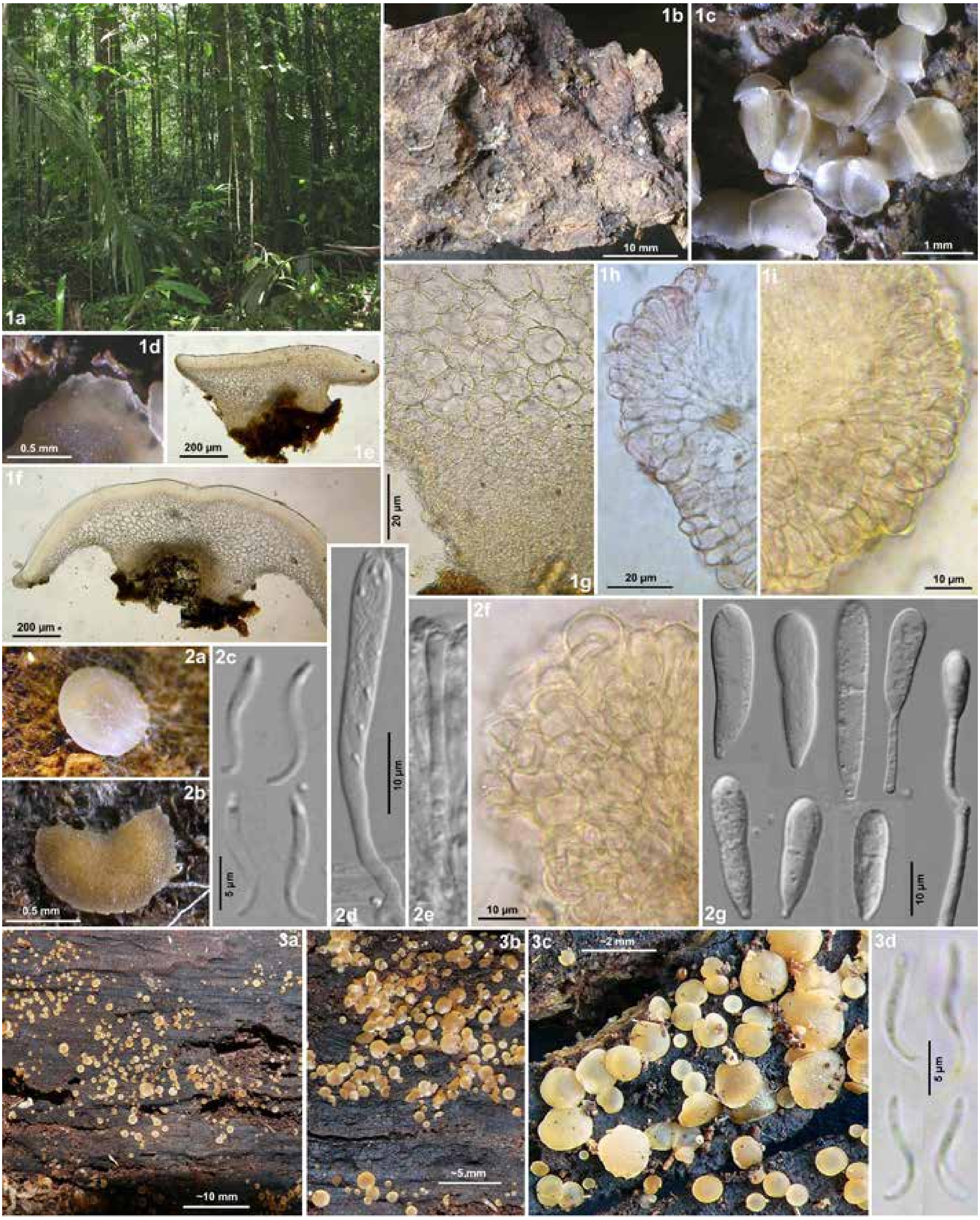


Plate 448. **1–3**: *Orbilia vermiformis*. – **1a**. tropical rainforest; **2a**, **3a–c**. fresh apothecia; **1c–d**, **2b**. rehydrated apothecia; **1e–f**. apothecia in median section; **1g**. id., basal ectal excipulum with dense layer of anchoring hyphae; **1h–i**, **2f**. id., marginal ectal excipulum; **2d**. mature ascus, **2e**. paraphysis; **2c**, **3d**. ascospores; **2g**. conidia and conidiophores from culture. – Living state, except for **1e–i** & **2f** (in KOH), **3d** & ascus in **2d** (in H_2O). – **1a**: phot. C. Lechat; **2a**, **c–e**, **g**: from Yu et al. (2007a, DIC); **3a–c**: phot. M. Pélissier. — **1a–i**. H.B. 8031: Martinique, on indet. angiosperm; **2a–g**. YMF 1.01842 (holotype): China, Yunnan, on indet. angiosperm; **3a–d**. H.B. 9747: Comoros, on ?*Mangifera*.

Yu et al. (2007a) compared *Dactylella vermiformis* with other species of *Dactylella* with 1-septate conidia. Accordingly, *Arthrobotrys* (‘*Dactylella*’) *pseudoclavata* has larger conidia and forms 3-dimensional networks, *D. arrhenopa* and *D. polyctona* have smaller conidia. *Dactylellina entomopaga*, a springtail capturing species, has similar 1-septate, 15–28 × 4.5–5.5 µm large conidia, which are, however, formed on denticles in a loose capitate arrangement (Drechsler 1944b).

Phylogeny. The ITS sequence gained from the type culture by Yu et al. (2007a) clustered in our analysis in the weakly (ML) or strongly (NJ) supported *nemaspora-vermiformis* clade of series *Xanthoguttulatae* (Phyls 15, S15) but with a high distance to other species, the closest percentage being to *O. nemaspora* (12.5 %). The S1506 intron is present and likewise shows a high distance to other species, the lowest percentage being to *O. nemaspora* (12 %), with which it formed only here a strongly supported clade (Phyl. S14).

Ecology. The type of *O. vermiformis* grew on rather undecayed wood of an angiosperm root in a subtropical humid (winter-dry) evergreen broad-leaved mountain forest at the southern end of Hengduan Shan, the southeastern extension of Himalaya. The collections from Martinique (Caribbean region) and Mayotte (Comoros, northwest of Madagascar) were on rotten angiosperm bark or wood in tropical humid and wet and dry rainforests at low altitude.

Specimens included. **CHINA**: **Yunnan**, **Pu'er**, Ning'er, 64 km N of Pu'er, Xiaoheijiang, ~1100 m (2100 m in protologue is erroneous), root of indet. angiosperm, on wood, 3.IX.2005, M. Qiao (YMFT 1.01842, **holotype** of *O. vermiformis*; H.B. 8313, **isotype**; YMF 1.01842, **holotype** of *D. vermiformis*, anam. cult.; sq.: DQ480729). — **LESSER ANTILLES**: **Martinique**, 5 km SE of La Sérénité, 3 km ENE of Petit Bourg, Le St.-Esprit, Le Bois La Charles, ~100 m, branch of indet. angiosperm, on bark, 8.XII.2005, C. Lechat (H.B. 8031, C.L.L. 5610, anam. substr.). — **COMOROS**: **Mayotte**, 14.5 km WSW of Mamoudzou, 1 km W of Chiconi, N of Baie de Chiconi, 90 m, branch of ?*Mangifera indica*, on wood, 23.VI.2012, M. Pélissier (J.P.P. 12186, H.B. 9747).

Orbilia nemaspora Baral, Bin Liu, A.I. Romero, Healy & Pfister, **sp. nov.**, MB 813762 — Pls 449–450, Map 80

Etymology: referring to the ascospores resembling nematodes.

Typification: USA, Massachusetts, Concord, log of *Acer*, 26.VII.1995, D.H. Pfister (ex D.H.P. 135 & ex H.B. 5308, M-0276538, holotype).

Misapplication: Ekanayaka et al. (2018), as *Orbilia stipitata* (p.p.).

Latin diagnosis: *Similis* Orbiliae vermiformi *sed ascosporae angustiores, paraphyses ad apicem saepe leniter ad valde capitatae, status anamorphicus conidiis 1–3-septatis. Habitat ad lignum putridum, raro corticem ramorum vel truncorum uvidorum arborum angiospermarum in zona tropica ad supratemperata humida Americae, Africae et Asiae.*

Description: — **TELEOMORPH**: **Apothecia** moist/rehydrated 0.3–0.8 or often 0.5–1.8(–3) mm diam., 0.18–0.38 mm high (receptacle 0.13–0.17 → 0.09–0.12 mm), fresh white or pale carneous to light yellow-ochre, rehydrated (dead) light yellowish-ochraceous to rose-orange or brick-red or reddish-brown with distinct dark translucent centre, round, slightly undulating when large, gregarious; disc flat, eventually medium convex, margin distinct, 0–5 µm protruding, smooth {1} or (very) finely to distinctly crenulate or denticulate {9}; sessile on a broad base or often stipitate, stipe sometimes hidden, obconical to cylindrical, 0.1–0.35 × 0.3–0.6 mm, superficial; dry bright (dirty) yellow-ochre-orange. **Asci** *36–45 × 3.3–3.8(–4) {2}, †(29–)31–45(–54) × 2.8–3.4 µm {11}, 8-spored, spores ± 4-seriate, 4(–5) lower spores inverted (sometimes mixed) {3}, pars sporifera *14–22 → 9–10 µm long; **apex** (†) strongly truncate (not or slightly indented, laterally not widened); **base** with medium to very long, thin, flexuous stalk, T- to L-, Y- or h-shaped. **Ascospores** *(8–)8.5–10(–11) × 0.7–0.8 µm {7} (~11–13 µm actual length), †(7.5–)8.5–9.5(–10)((–12)) × (0.5–)0.6–0.7(–0.8)((–0.9)) µm {12}, very narrowly fusoid to fusiform, apex (*) subacute to acuminate, (†) more obtuse, base ± strongly attenuated in an indistinctly differentiated narrow tail of 2–3.5 × 0.2–0.3 µm, strongly helicoid (always twisted like a right-hand thread), strongly curved especially near base; **SBs** *1.6–2 {4} or 3–3.7 {1} × 0.4–0.5(–0.7) µm {5}, narrowly tear-shaped to subulate, apically narrowed to a (very) short filum. **Paraphyses** apically uninflated or often slightly to medium, sometimes strongly (clavate-) capitate, terminal cell *21–28 × 2–3.3 µm {2}, †24–30 × (1.5–)2–3.3(–4) µm {5}, lower cells *4–7 × 2.2–3.7 µm {1}, †4.5–7 × 1.4–2.2 µm {1}; partially branched at upper septum. **Medullary excipulum** hyaline to pale cream, 15–40 µm thick, of irregularly horizontal textura intricata-porrecta, not or slightly to medium gelatinous, without or with many inflated cells, (very) sharply delimited from ectal excipulum. **Ectal excipulum** hyaline, of (†) thin-walled t. globulosa-angularis from base to margin (orientation indifferent or vertical), 120–300 µm thick at base, cells */†(15–)20–50(–70) × (10–)15–45(–60) µm {8}; 30–100 µm thick at lower flanks, cells at mid flanks *15–23 × 9–17 µm, 15–45 µm near margin, oriented at 45–90°, marginal cortical cells *(8–)10–17 × (5–)7–10(–14) µm {2}, †8–15 × (3–)5–8.5(–10) µm {4}, globose to broadly clavate, thin-walled, mostly forming 10–30 × 10–40 µm large teeth-like protrusions, **glassy processes** absent {11}. **Anchoring hyphae** sparse to often abundant, */†1.5–3(–4.5) µm wide, walls 0.2–0.3 µm thick {5}, usually forming a dense, 20–50 µm thick t. intricata(-angularis) at base and on stipe surface, not or sometimes strongly gelatinous. **SCBs** at flanks and margin (also in the inflated cells of medullary excipulum) brick-shaped {2}, ± low-refractive, 2–4 × 0.7–1.4 µm, or absent {2}; **VBs** in paraphyses medium refractive, globose to elongate {2}. **Exudate** abundant or sparse to almost absent, over paraphyses 0.2–1.5(–2.5) µm thick, rough-continuous or granular to cloddy, loosely attached or forming firmly attached caps, hyaline; over margin and flanks (0.2–)0.5–2 µm thick, granular to rough-cloddy, hyaline (to yellow-brown). — **ANAMORPH**: dactylella-like (from ascospore isolate {1, Liu 2006} and natural substrate {2}). **Conidiophores** (mainly after Liu 2006) ?unbranched, 20–206 µm long, 3–4 µm wide at the base, 1.8–2.4 µm at the tip. **Conidiogenous cells** monoblastic or sympodial. **Conidia** cylindric-clavate, *22.5–42 × 5–8 µm {China}, †17.5–23.5 × 5.3–6.3 µm {Puerto Rico} or †18–19 × 4 µm {Comoros}, rounded above, attenuated and truncate below, 1-septate {2} or (0–)1–3(–4)-septate {China}.

Habitat: lying on moist ground, sometimes in mud in the flooding zone of rivulets, corticated or decorticated, 5–30 cm thick branches or thick logs and cut stumps of *Acer* sp. {3}, *Alnus glutinosa* {1}, *Betula pendula* {1}, *Eucalyptus viminalis* {1}, *Salix* sp. {1}, *Ulmus* sp. {1}, indet. angiosperm trees {8}, stem of bamboo (*Dendrocalamus giganteus*) {1}, on deeply (slightly to) medium or strongly decayed wood {15} or bark {2}, on upper or lateral side, sometimes with many green algae and brown hyphae, partly in or near old beetle galleries (also on boring dust) {4}. **Associated**: *Brachysporium nigrum* {1}, ?*Cacumisporium capitulatum* {1}, *Hyalorbilia fagi* {1}, *H. puertoricensis* {1}, *Hypoxylon* sp. {1}, *Orbilia* ?*brochopaga* {1}, *O.* ?*clavispora* {1}, *O. latispora* {1}, *O. sarraziniana* {1}, *O. sinensis* {1}, *Sclerococcum* sp. {1}, indet. pyrenomycete {2}, acro- and pleurocarpous mosses {1}. **Desiccation tolerance**: obviously desiccation-sensitive, a few spores still viable after 22 months. **Altitude**: 5–430 m a.s.l. **Geology**: Cretaceous flysch, Miocene sand- & limestone, Quaternary sediments; granite, felsic plutonic rock. **Phenology**: VI–XI (temperate northern hemisphere), I–III (southern hemisphere), in tropical belt perhaps throughout the year.

Taxonomic remarks. *Orbilia nemaspora* is characterized by narrowly fusiform (worm-like), strongly helicoid ascospores and desiccation-sensitive, rather large apothecia with a very finely crenulate margin but without glassy processes. For the very similar *O. vermiformis* see p. 856. Morphologically very similar are *O. crenatomarginata* and *O. scolecospora* (series *Hyalinia*), which differ in narrower marginal cortical cells tipped by glassy processes and in ring-shaped crystalloid SCBs, the former also in shorter asci and spores. *O. nemaspora* further resembles *O. aurantiorubra*, from which it differs in less pigmented, desiccation-sensitive apothecia and a large celled, very thick basal ectal excipulum which sometimes contains brick-shaped SCBs, also in smaller spores. The slightly desiccation-tolerant *O. pseudobrevistipitata* differs mainly in lageniform paraphyses and the upper spores being inversely oriented in the asci. The

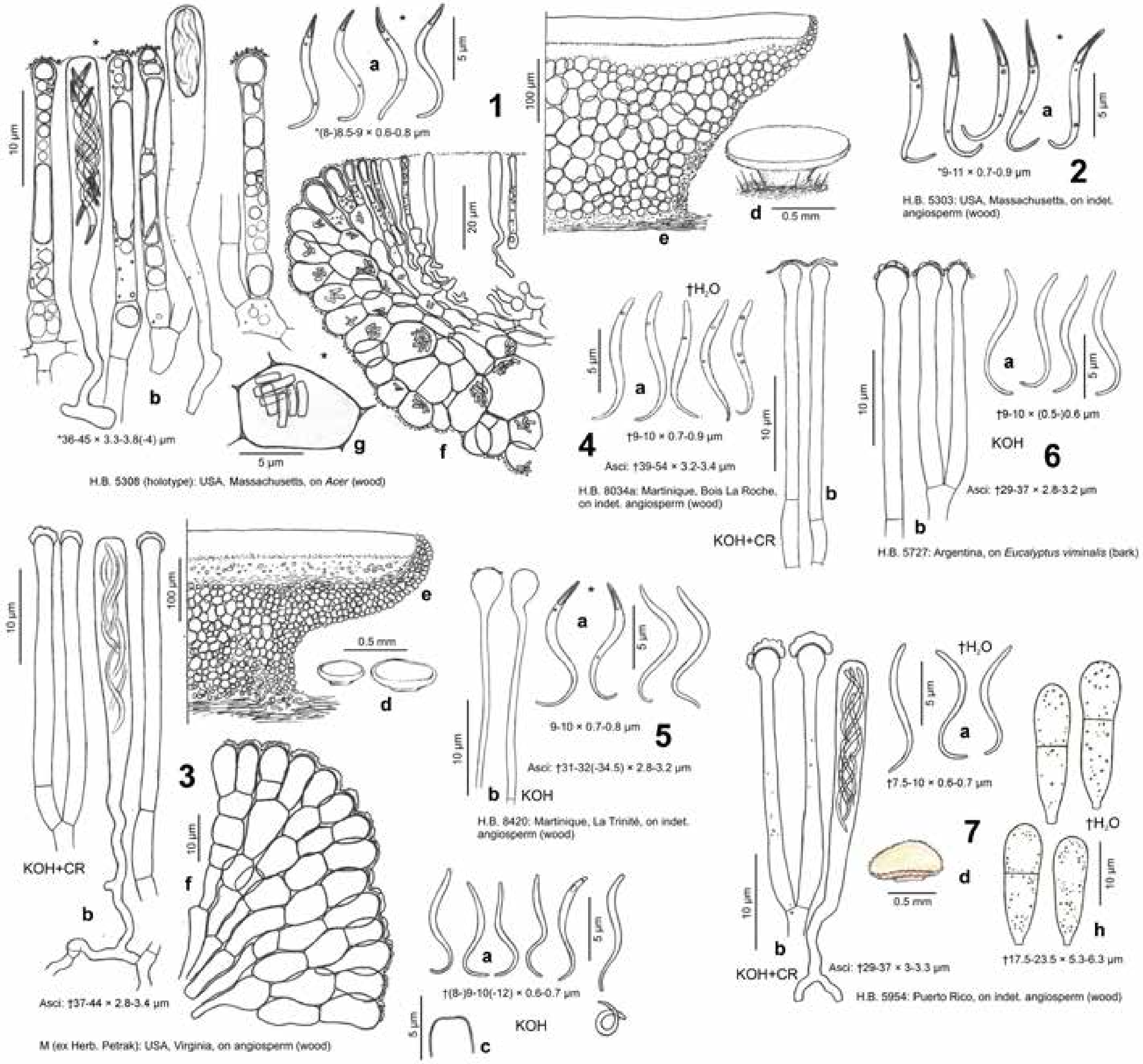


Plate 449. **1–7**: *Orbilia nemaspora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apex; **d**. fresh or rehydrated apothecia; **e**. apothecia in median section; **f**. id., ectal excipulum at margin and mid flanks; **f–g**. living excipular cells with brick-shaped crystalloid SCBs; **h**. conidia from substrate (formed on apothecium).

latter peculiarity is also one of the distinguishing features against *O. bomiensis* and *O. spirillospora*.

The Chinese *O. crenatonemaspora* deviates in marginal teeth made up of narrower, elongate cortical cells tipped by 7–35 µm long glassy processes, and in larger, especially wider spores containing larger SBs (2.5–5.5 × 0.6–0.9 µm).

Variation. Significant variation within *O. nemaspora* was observed in the apical inflation of the paraphyses ranging from uninflated to strongly capitate. Three specimens with not or only slightly inflated paraphyses showed a tendency to longer asci (Pl. 449: 1, 3–4, also in H.B. 5314). SBs are generally rather short but in one collection they were distinctly longer (Pl. 449: 2). The margin is almost always ± crenulate by forming small teeth, but in a collection from Virginia it is smooth (3). Also the thickness of the exudate over the paraphyses is very different among the collections, forming firmly attached caps on 3 and 7 and in H.B. 5314, but a mostly thinner granular layer in the other collections. In a sample from Martinique (Pl. 449: 4) the anchoring hyphae were strongly gelatinized (Pl. 450: 1f), and the marginal cortical cells showed a tendency to be rather narrow, characters not seen in the other specimens. The presence of brick-shaped SCBs in the ectal excipulum was observed in two samples on *Acer* from Massachusetts (holotype and the unillustrated D.H.P. 172), and their absence in the two samples on *Alnus* and *Betula* from Serbia; all other samples lack data on SCBs as their excipula were studied in the dead state. The apothecia much vary in size: in one collection some attained 2–2.8 mm (Pl. 450: 1c), but in another they measured only 0.3–0.5 mm (Pl. 449: 3d).

Literature reports. Romero (1994: 114) described *O. nemaspora* (as *Orbilia* sp.) with sessile apothecia with a bright orange colour and a smooth and slightly undulating margin. The asci are given much wider (35–40 × 5–7 µm), perhaps by artificial flattening, also the paraphysis apices abruptly thickened to 4–5 µm. However, one of her specimens was examined (Pl. 449: 6) and found to have narrow asci and paraphyses, and apothecia with distinct though hidden stipes.

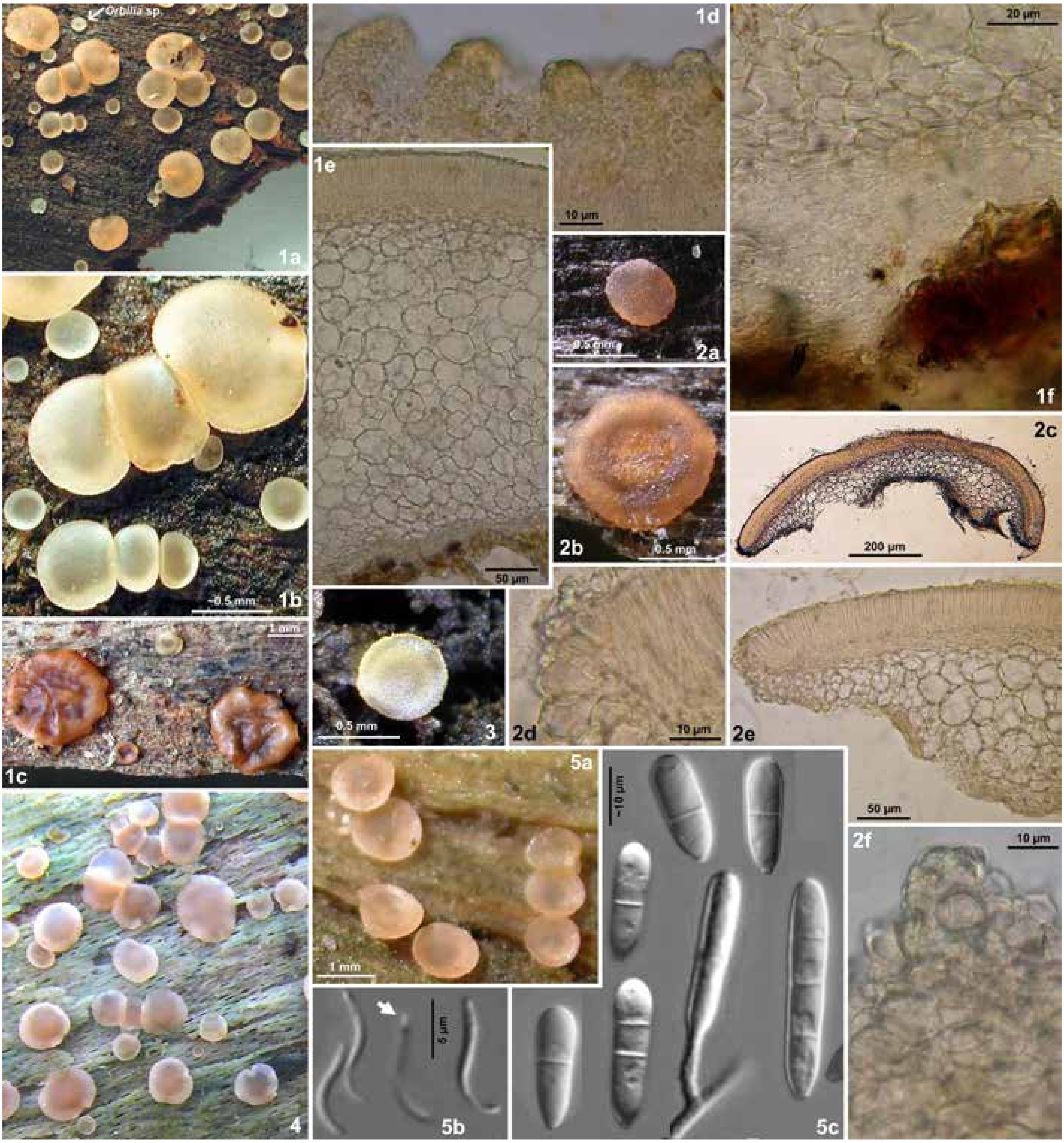


Plate 450. **1–5**: *Orbilia nemaspora*. – **1a–b**, **4**, **5a**. fresh apothecia (**1a–b** mixed with *Orbilia* sp. ?*brochopaga* H.B. 8034b); **1c**, **2a–b**, **3**. rehydrated apothecia; **2c**, **e**. apothecia in median section; **1e**, **2d**. id., ectal excipulum at flanks and margin; **1d**, **2f**. marginal teeth; **5b**. ascospores; **5c**. conidia and conidiophore from culture. – **1a–b**: phot. C. Lechat; **4**: phot. M. Pélissier; **5**: from Liu (2006, fig. 46, DIC). — **1a–e**. H.B. 8034a: Martinique, Bois La Roche, on indet. angiosperm; **2a–f**. H.B. 8420: ibid., La Trinité, on indet. angiosperm; **3**. H.B. 5727: Argentina, Buenos Aires, on *Eucalyptus*; **4**. J.P.P. 13073: Comoros, Mayotte, on indet. angiosperm; **5a–c**. HMAS 96792 (H.B. 9199): China, Heilongjiang, on *Salix*.

A collection from northern China under the name *Orbilia* sp. (Liu 2006: 114, figs 46–47; Pl. 450: 5) fits well *O. nemaspora*, according to the present reexamination. The evaluated spore size (†8–9.5 × 0.6–0.8 µm) concurs with Liu's measurement whereas the scale on his microphoto yields too high values. Bayliss Elliott (1916: 417) reported under the name *O. curvatispora* a collection on branches of *Quercus* from Warwickshire, Great Britain, with 'spirally curved' (helicoid) spores 10–15 × 1 µm, which excludes a species of series *Arthrobotrys*. The spores are reminiscent of *O. nemaspora*, a species so far only known from extra-European regions.

Anamorph. The anamorph of *O. nemaspora* is very similar to that of *O. vermiformis*. In the Chinese ascospore isolate reported by Liu (2006) the conidia tend to be distinctly longer than on the natural substrate in the collections from Puerto Rico and the Comoros, possessing often 2–3(–4) septa, a feature not observed so far in *O. vermiformis*.

Phylogeny. From pure culture of the Chinese sample, Liu et al. (2006a) gained a sequence (ITS+LSU D1–D2), which clustered in their analyses in a clade with *O. bomiensis*, though with high distance and low (ITS) or medium support (LSU). An ITS sequence from apothecia of a North American collection (Boston, bhi-F457a) is incomplete in the ITS2 but, unlike the Chinese one, covers also the 3'-end of SSU where it includes the S1506 intron. For this strain also SSU (V3–V5) and LSU (D2–D3) were available. In the ITS region it differs from the Chinese strain merely by 1 nt in ITS1, and also in the LSU 1 nt differs in D2. When reexamined, this sample contained only *Hyalorbilia fagi* (H.B. 10000), therefore, the sequence is assumed here to originate from a mixed population.

Another strain from Boston (bhi-F166 = H.B. 9994) was sequenced by R.A. Healy (D. Haelewaters pers. comm.), but its sequence was not available. Sequences of four samples from Florida under the name *Orbilia* sp. gained by R.A. Healy et al. also belong to *O. nemaspora* from their rDNA. All four sequences comprise almost the entire intron and ITS1, one also ITS2. In the ITS1 two of them fully concur with bhi-F457a, while the other two deviate from them by 1–2 nt. Also in the intron the North American strains differ by only 0–1 %.

Orbilia stipitata as described by Ekanayaka et al. (2018) from Northern Thailand on unidentified wood appears to be a mixture of 2–3 species. The authors compared their sequence with *O. nemaspora* (strain B.L. 4201) as closest match, though differing in '15 base pairs in ITS and LSU'. However, we see only 7 nt difference between them, 3 in ITS and 4 in LSU, therefore, it seems that this sequence belongs to *O. nemaspora*. However, the illustrated asci and spores appear to belong to two other species (see p. 1685). Surprisingly, the sequence deviates from *O. nemaspora* in the S1506 intron by ~ 10–12 % (and from *O. vermiformis* by 8 %), suggesting a chimere, but BLAST search for the intron alone yields also *O. nemaspora* and *O. vermiformis* as best hits.

The lowest distance of *O. nemaspora* is found to *O. vermiformis*, ranging at 12.5 % in the ITS and at 12 % in the S1506 intron. In the LSU (D1–D2) the lowest distance was to *O. xanthoguttulata* and *O. succulenticola* (6 %). In comparison, the distance to *O. bomiensis* is 14.5 % (ITS) and 7.3 % (LSU). *O. nemaspora* and *O. vermiformis* form a strongly supported clade only in the analysis of the intron (Phyl. S14).

Ecology. *O. nemaspora* is known from rotten, hygric wood, exceptionally bark, of angiosperm trees (mainly unidentified). The examined collections either derive from tropical humid (± wet and dry) Middle America and southeastern Africa (Comoros), subtropical humid (winter-dry) South America, cold-temperate humid (winter-dry) northeastern China, tropical humid (winter-dry) northern Thailand, and continental cold-temperate to subtropical humid eastern North America. Remarkable is the absence of *O. nemaspora* in Europe, except for two very recent records in the humid Fruška Gora in northern Serbia, one at low altitude (subprasubmediterranean) at a rivulet (with *O. sarraziniana*), the other on top of the mountain (cold-temperate) away from water and on the upper, exposed side of the branch.

According to D. Pfister (1995 in litt.), the species is 'one of the most common Orbilias at my study site this July and August'. During her study of micromycetes on logs of *Eucalyptus viminalis*, Romero (1994) likewise found the species very frequently and during most of the year (II, V, VIII, XI). All the here included collections were on wood, only that from South America on *Eucalyptus* was on bark, and one from the Comoros on bamboo. Yet, Romero reported her collections to grow always on bark, on both the outer and inner surface.

Map 80. Known distribution of *O. nemaspora* in Northern and Middle America.

Specimens included. **USA**: **Massachusetts**, Middlesex, 27 km NW of Boston, 2.8 km NNE of Concord, Punkatasset Hill, Hutchins Pond, 45 m, log of *Acer*, on wood, 26.VII.1995, D.H. Pfister (D.H.P. 170 [O.135], FH, **isotype**; ex H.B. 5308, M-0276538, **holotype**); – ibid., log of *Ulmus*, on wood, 12.VII.1995, D.H. Pfister & S.H. Goldbarg (D.H.P. O.128, FH 00458179; H.B. 5303). – 4.3 km N of Concord, Estabrook Woods, 65 m, log of *Acer*, on wood, 2.VIII.1995, D.H. Pfister (D.H.P. 172 [O.136], FH; H.B. 5314). – 6.5 km SE of Boston, Boston Harbor Islands, Thompson Island, 5 m, log of *Acer*, on wood, 30.VII.2014, E. Franck, D. Haelewaters, L. Millman & S. Verhaeghen (bhi-F166, FH, H.B. 9994; sq.: unavailable [R.A. Healy]). – 12.5 km SE of Boston, Peddocks Island, East Head, 10 m, log of *Acer*, on wood, 29.VIII.2015, D. Haelewaters, L. Millman & J. Warfel (bhi-F457a, FH, soc. H.B. 10000 [*Hyalorbilia fagi*], non vid., sq.: MN339158, MF161276, MN339162). – **Virginia**, Arlington Cemetry, ~50 m, branch of indet. angiosperm, on wood, VI.1927, C.L. Shear (herb. Petrak, M, as *O. coccinella*; H.B. 5053 ø). – **Florida**, 2.5 km SSE of Gainesville, Sweetwater Preserve, 40 m, indet. tree, on wood, 6.VIII.2017, R. Healy (FLAS-F-61268, non vid., sq.: MH211847). – 6.3 km E of Melrose, E of Ashley Lake, 33 m, indet. tree, 8.VIII.2017, B. Kaminsky & M.E. Smith (FLAS-F-60767, non vid., sq.: MH488712). – 3.5 km SE of Melrose, NE of Lake Suggs, 40 m, indet. tree, 14.VI.2017, R. Healy, B. Kaminsky, D. Borland & N. Kraisitudomsook (FLAS-F-60881, non vid., sq.: MH488714). – 4 km SSE of Melrose, Ordway-Swisher Biological Station, 40 m, indet. tree, 17.XI.2017, no collector (FLAS-F-60781, non vid., sq.: MH281859). — **PUERTO RICO**: 2.5 km SSW of Luquillo, near Rio Sabana, hill above chicken farm, 20 m, log of indet. angiosperm, on wood, 17.I.1996, D.H. Pfister, F.A. Harrington, D.J. Lodge & S.M. Hundorf (D.H.P. PR 28, FH 00458094; D.H.P. PR 31, FH 00458095). – ibid., near Rio Sabana, Rte. 983 & 991, stump of indet. angiosperm, on wood, ~20 m, 26.I.1996, F.A. Harrington & M. Liftik (D.H.P. PR 148, FH 00304897; H.B. 5954 ø, anam. substr.). – ?5 km SE of Isabela, Reserva Forestal Guajataca, ~250 m, branch of indet. angiosperm, on wood, 23.I.1996, D.H. Pfister et al. (D.H.P. PR 130, FH 00304896). — **LESSER ANTILLES**: **Martinique**, 4.5 km NNW of Case-Pilote, 4 km SE of Le Carbet, Bois La Roche, ~300 m, branch of indet. angiosperm, on wood, 27.VIII.2005, C. Lechat & R. Courtecuisse (H.B. 8034a, C.L.L. 5132). – 6 km SE of La Trinité, 4.5 km NE of Le Robert, Pointe Bateau, ~30 m, branch of indet. angiosperm, on wood, 3.XII.2006, C. Lechat (H.B. 8420, C.L.L. 6168). — **ARGENTINA**: **Buenos Aires**, 21.5 km NW of San Pedro, 7.5 km N of Gobernador Castro, SW of Rio Paraná, 32 m, stump of *Eucalyptus viminalis*, on bark, 9.II.1983, A.I. Romero (BAFC 34210, H.B. 5727). — **CHINA**: **Heilongjiang**, **Yichun**, ~60 km S of Yichun, Liangshui, 400 m, branch of *Salix*, on wood, 14.IX.2004, B. Liu (as indet. wood, B.L. 4201, HMAS 96792, anam. cult.; sq.: DQ656630, DQ656700; H.B. 9199 ø). — **THAILAND**: **Northern Thailand**, **Chiang Rai**, ~23 km W of Chiang Rai, Khun Korn waterfall, ~700 m, indet. tree, on wood, 20.I.2015, A.H. Ekanayaka (MFLU

15-0229, ?mixture in holotype of *O. stipitata*; sq.: MG599272, MG599275). — **COMOROS**: **Mayotte**, 11.5 km SW of Mamoudzou, 2.2 km E of Chiconi, 98 m, stem of *Dendrocalamus giganteus*, 16.I.2013, M. Pélissier, vid. J.P. Priou (J.P.P. 13024, anam. substr., doc. vid.). – ~6 km NW of Bandrele, ~2.8 km NE of Poroani, Crête de Benara, ~340 m, branch of indet. angiosperm, on wood, 22.III.2013, M. Pélissier (J.P.P. 13073, doc. vid.). — **SERBIA**: **Vojvodina**, 17 km SW of Novi Sad, 6 km WSW of Beočin, Testera, 160 m, branch of *Alnus glutinosa*, on bark, 2.X.2019, D. Savić (doc. vid.). – Fruška Gora, 12 km S of Novi Sad, 6 km NNW of Irig, W of WWII memorial, 430 m, log of *Betula pendula*, on bark, 20.IX.2019, D. Savić (doc. vid.).

Orbilia crenatonemaspora Baral & Hong Y. Su, **sp. nov.**, MB 813763 — Pls 451–452

Etymology: named after the denticulate (crenate) apothecial margin and the similarity to *Orbilia nemaspora*.

Typification: China, Yunnan, Jinguangsi, ?log of indet. angiosperm, 25.X.2008, H.Y. Su, X.M. Gao & Y.G. Yan (ex H.B. 8926, M-0276462, holotype).

Latin diagnosis: *Similis* Orbiliae nemasporae *sed apothecia margine crenata, ascosporae longiores, corpuscula refringentia longiora, excipulum cellulis marginalibus processis vitreis praeditis. Habitat ad lignum vel corticem putridum uvidum in zona subtropica humida Asiae meridio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1.4 mm diam., 0.1–0.18 mm high (receptacle 0.1 → 0.07 mm), greyish-white to pinkish-isabelline or carneous-brownish, translucent, round, ± gregarious; disc flat to medium convex, margin 0–10 µm protruding, dentate, with distinct hyaline teeth 25–60 × 30–50 µm; broadly sessile or with a distinct stipe 0.05–0.1 × ?0.2 mm, superficial, dry cream to yellowish. **Asci** †(25–)30–40(–45) × (3–)3.2–4(–4.5) µm {5}, 8-spored, spores *4-seriate, ~4 lower spores inverted {4}, pars sporifera †16–25 µm long; **apex** (†) strongly truncate (not indented, laterally uninflated); **base** with short to long, ± thin, flexuous stalk, T-, L-, Y- to h-shaped. **Ascospores** *(9.5–)10–12(–13.7) × 1–1.1(–1.2) µm {2} (~12–18 µm actual length), †(9.5–)10.5–12.5(–13.5) × (0.7–)0.8–1(–1.1) µm {5}, narrowly fusoid-clavate, apex subacute to acute, base gradually attenuated, medium to strongly curved (helicoid, twisted like a right-hand thread), rarely falcate; **SBs** *~2.5–3.7 × 0.6 {2} or 3.5–5.5 × 0.6–0.9 µm {T}, subulate, apically narrowed to a small point, straight. **Paraphyses** apically slightly to medium (clavate-)capitate, terminal cell †13–16 {1} or 18–24 {T} × (2–)2.5–3.5(–4) µm {2}, lower cells †3–5 × 1.5–1.8(–2) µm wide {1}; unbranched. **Medullary excipulum** 70 µm thick, of ± dense, small-celled textura globulosa-angularis, sharply delimited from ectal excipulum only at flanks (here of t. intricata with inflated cells). **Ectal excipulum** of (†) thin-walled to slightly gelatinized, irregularly oriented t. globulosa-angularis(-prismatica) from base to mid flanks or margin, 70 µm thick near base, cells *12–25(–29) × 9–19 µm {2}; 20–40 µm thick at flanks, 15–30 µm at margin, of. t. globulosa, or of t. prismatica oriented at a 45° angle to the surface, marginal cortical cells */†7–14(–20) × (2.7–)3.3–4(–5) {3}; **glassy processes** 7–17 {1} or 20–35 {T} × 3–4 µm {2}, low to medium refractive, not stratified, coherent to form distinct teeth. **Anchoring hyphae** sparse at base, †1.8–2.7 µm wide, walls 0.2 µm thick {1}. **SCBs** in apices of paraphyses short-cylindrical, refractive, in ectal excipulum at flanks and margin globose, ~3–4 µm diam., here also crystalloid, filiform SCBs {1}; **VBs** not observed. **Exudate** over paraphyses 1–2 µm thick, cloddy, loosely attached, over margin 0.1–0.2 µm thick loose granules. — **ANAMORPH**: unknown.

Habitat: on the moist ground, decorticated or corticated, 15 mm thick branches, also ?logs of indet. angiosperm trees {3}, on medium to strongly decayed wood {2} and bark {1}, sometimes blackened, no algae. **Associated**: *Orbilia scolecospora* {1}, small mosses. **Desiccation tolerance**: after 3 weeks only some ascospores viable. **Altitude**: 1750–2730 m a.s.l. **Geology**: Jurassic & Paleogene sedimentary rock, metamorphic rock. **Phenology**: VII–VIII, X.

Taxonomic remarks. *Orbilia crenatonemaspora* differs from *O. vermiformis* and *O. nemaspora* in the presence of glassy processes which emerge from narrower marginal cortical cells, furthermore in a tendency to longer ascospores and SBs. From *O. nemaspora* it differs also in distinctly wider spores, and from *O. vermiformis* in a less distinct spore tail.

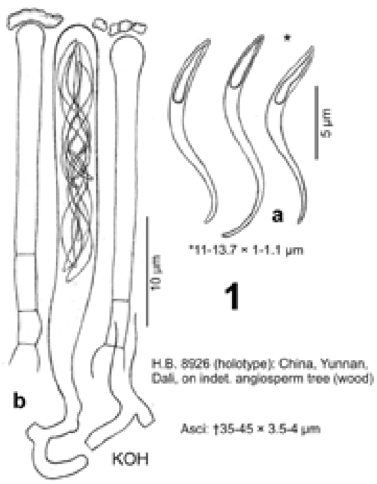


Plate 451. **1**: *Orbilia crenatonemaspora*. – **a**. ascospores; **b**. ascus and paraphyses.

Although they look like VBs, the elongate bodies in the apices of living paraphyses closely concur with those of *O. crenatomarginata* (series *Hyalinia*) and are, therefore, quite probably SCBs. The combination of globose/elongate and crystalloid SCBs is so far unknown within series *Xanthoguttulatae*, therefore, it might well be that molecular data would place *O. crenatonemaspora* in series *Hyalinia*. This view is supported by a strong similarity in the spores to *O. laevimarginata*, especially Pl. 462: 2b, though being much smaller there. Two collections are mentioned under *O. scolecospora* (series *Hyalinia*: Caucasus, Pl. 463: 2; Argentina, see Fig. 164) because their spore length better fits that species, but they are only known in the dead state.

Variation. The five included collections are only tentatively placed together. In the holotype and the topotype (H.B. 8931) the asci, spores and SBs are slightly longer than in the other samples. In the samples from Dali the spores are only slightly helicoid (ljs-2) and or even falcate (ljs-3, Pl. 452: 4b, 5b), resembling those of *O. crenatofalcata* though being distinctly longer. The presence of glassy processes was not tested in these two samples, but the distinct marginal teeth are probably composed of them. In H.B. 8694a the glassy processes are shorter than in the holotype, but the cortical cells are longer, hence the marginal teeth have a similar size. Differences were also noted in the size of the terminal cells of paraphyses (longer and narrower in the type compared to H.B. 8694a). The delimitation from *O. nemaspora* is not very sharp, because also here distinct small teeth generally occur, though glassy processes could never be confirmed (see Pl. 450: 1d).

Ecology. *O. crenatonemaspora* inhabits rotten, hygric wood and bark of unidentified angiosperm trees. Collections are from subtropical humid (winter-dry) evergreen mountain forests at the eastern extension of Himalaya in southern China.

Specimens included. **CHINA**: **Yunnan**, **Dali**, Yongping, 35 km ENE of Baoshan, virgin forest around Golden Light temple (Jinguangsi), 2730 m, ?log of indet. angiosperm, on wood, 25.X.2008, H.Y. Su, X.M. Gao & Y.G. Yan (H.Y.S. jgs-28, ex H.B. 8926, M-0276462, **holotype**); – ibid., branch of indet. angiosperm, on bark, 25.X.2008, H.Y. Su et al. (H.Y.S. jgs-27, CBCD, H.B. 8931). – **Dali**, Dali, 59 km WSW of Lijiang, NW of Jinmugu, Laojunshan, 2700 m, branch indet. ?angiosperm, on bark, 15.VIII.2008, H.Y. Su, X.J. Su & X.N. Zhao (H.Y.S. ljs-2, ljs-3, CBCD, doc. vid.). – **Yuxi**, Yimen, 54 km NW of Yuxi, 3 km NW of Fangtunxiang, Dalongkou, 1750 m, branch of indet. angiosperm, on wood, VII.2007, S.F. Li & J.W. Guo (J.W.G. ym3-7, YMFT, H.B. 8694a).

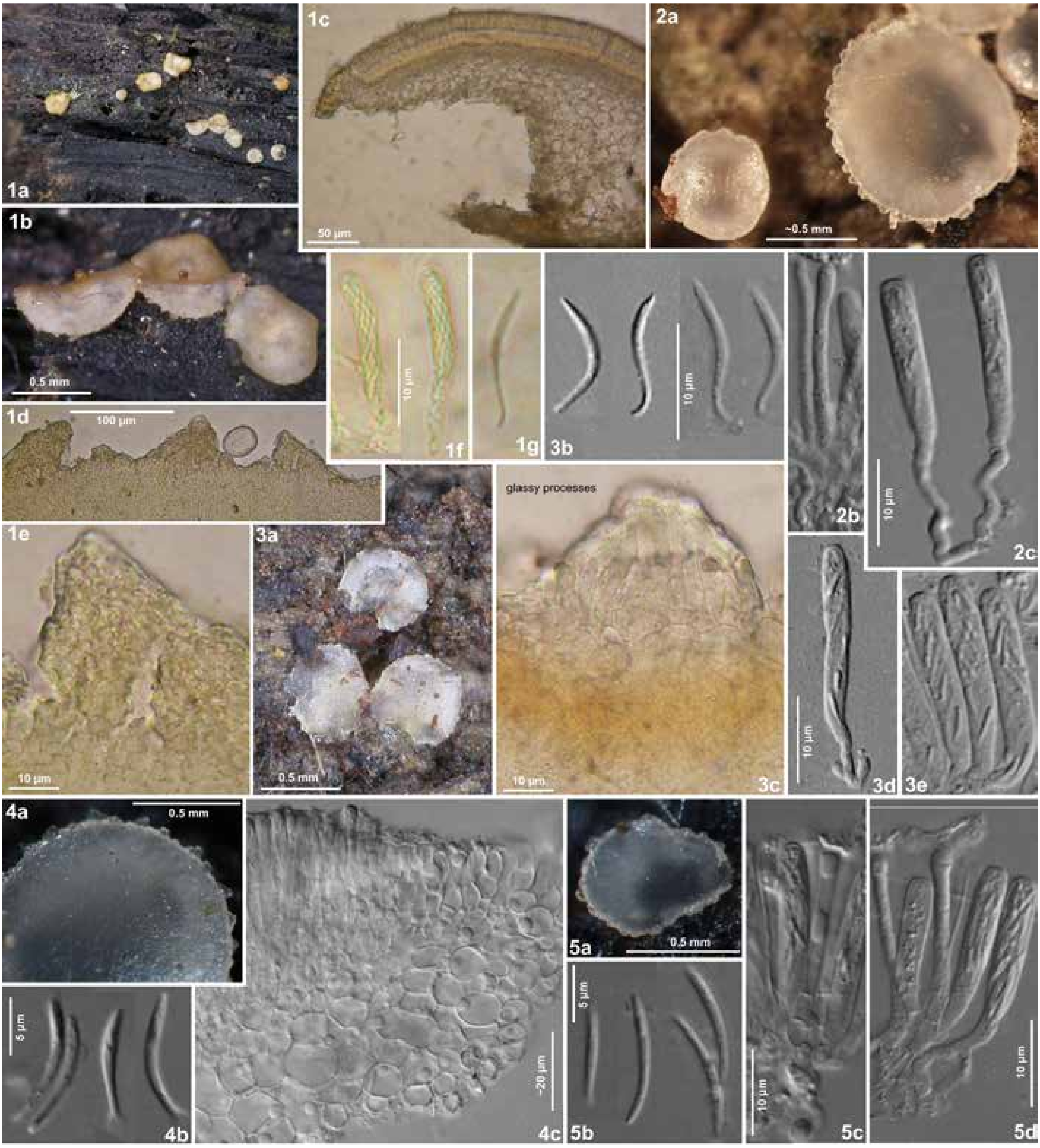


Plate 452. **1–5**: *Orbilia crenatonemaspora* (all on indet. angiosperms). – **2a**, **4a**, **5a**. fresh apothecia; **1a–b**. rehydrated apothecia; **1c**. apothecium in median section; **4c**. id., ectal excipulum near margin, with globose and crystalloid SCBs; **1d–e**, **3c**. marginal teeth; **1f**, **2b–c**, **3d–e**, **5c–d**. asci and paraphyses; **1g**, **3b**, **4b**, **5b**. ascospores. – Dead state (**1c–e** in KOH, **1f** in KOH+IKI), except for **4c**, paraphysis in **5c**, ascospores in **3d–e**, **4b**, **5b** (p.p.). – **2a–c**, **3b**, **d–e**, **4a–c**, **5a–d**: phot. H.Y. Su (DIC). — **1a–g**. H.B. 8694a: China, Yunnan, Yuxi, Yimen; **2a–c**: H.B. 8931: ibid., Dali, Yongping; **3a–e**: H.B. 8926 (holotype): ibid., (holotype); **4a–c**. H.Y.S. ljs-2: ibid., Dali, Laojunshan; **5a–d**. H.Y.S. ljs-3: ibid.

Orbilia pseudobrevistipitata (L. Qin, M. Qiao & Z.F. Yu) Baral & E. Weber, in Zhang et al., Phytotaxa 203: 251 (2015) — Pls 453–454

≡ *Dactylella pseudobrevistipitata* L. Qin, M. Qiao & Z.F. Yu, in Qin et al., Ann. Microbiol. 63: 594, fig. 2 (2011)

Etymology: named after the very short conidiophores similar as in the unrelated *Hyalorbilia brevistipitata*.

Typification: China, Yunnan, Lijiang, indet. angiosperm bark, 18.IX.2009, L. Qin (YMF 1.03504, holotype; sq.: HM215520).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.5(–0.9) mm diam., 0.17 mm high (receptacle 0.1 mm), pale to light cream- or orange-ochre, round, slightly undulating when large, singly or in pairs; disc slightly concave to flat, margin distinct, slightly protruding, finely powdered; with an indistinct hidden stipe 0.08 × 0.06 mm slightly immersed in detritus; dry light cream-orange. **Asci** *(26–)30–36 × (3.2–)3.6–4 µm {1}, †30–35(–40) {1} or 38–44 {T} × 3–3.4 µm {2}, 8-spored, spores 4-seriate, 4 upper (very rarely lower) spores inverted (not mixed) {2}, pars sporifera †16–25 µm; **apex** (†)

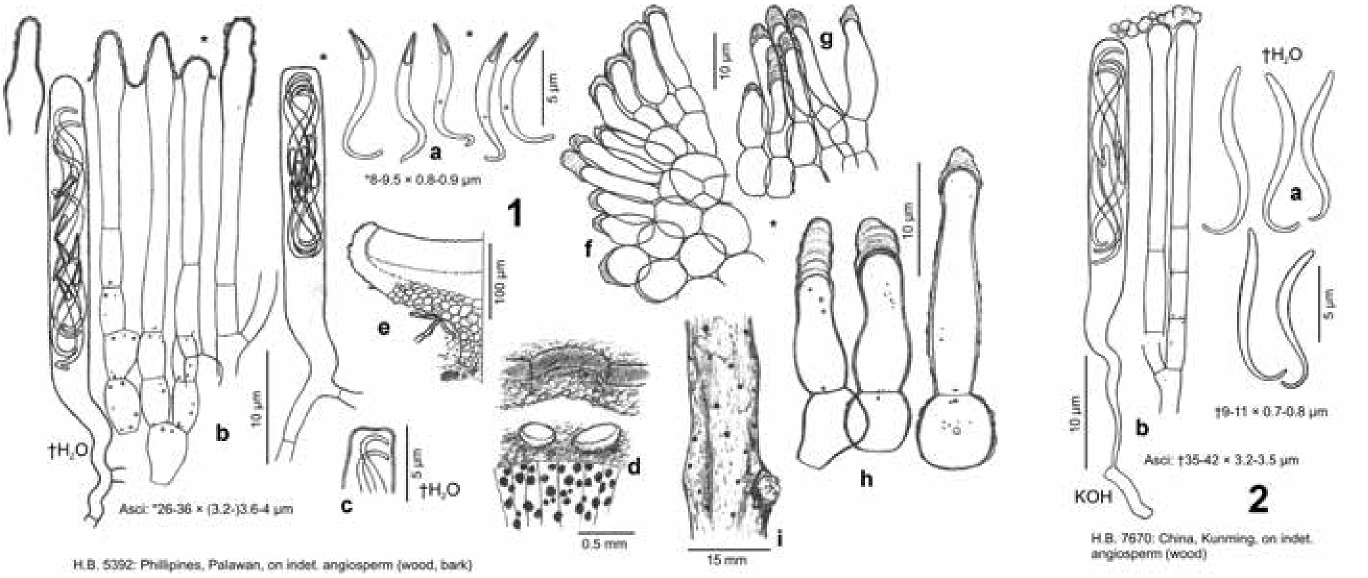


Plate 453. **1**: *Orbilia pseudobrevistipitata*; **2**: *O.* aff. *pseudobrevistipitata*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apex; **d**. rehydrated apothecia on boring dust over wood surface, positioned below emergence hole in detached bark; **e**. apothecia in median section; **f**. id., ectal excipulum and hair-like cortical cells with short glassy processes at margin; **g–h**. id., external view; **i**. corticated branch perforated by emergence holes.

strongly truncate (not indented, laterally not or slightly inflated); **base** with short to long, ± thin, flexuous stalk, L- to Y-shaped. **Ascospores** *8–9.5 {1} or 9–10.3 {T} × 0.8–0.9 µm {2} (~10–13 µm actual length), †(0.7–)0.8 µm wide {1}, narrowly fusiform, apex acute to acuminate, base strongly attenuated in a thin, indistinctly differentiated tail of 1.7–3.5 × 0.3–0.5 µm, strongly helicoidally twisted especially near base (like a right-hand thread, exceptionally falcate); **SBs** 2.2–3 × 0.5–0.6 µm {1}, ~3.5–3.8 × 0.7 µm {T}, narrowly tear-shaped to subulate. **Paraphyses** apically obtusely lanceolate to (sub)lageniform, exceptionally slightly clavate, terminal cell †17–28 {2} × 2–2.3 {T} or 2.4–3(–3.5) {1} µm, exceeding the dead asci by 3–7 µm, lower cells *4–6 × 2.5–3 µm {1}; unbranched at upper septum. **Medullary excipulum** light orange, 30 µm thick in centre, of small-celled indistinct texture, sharply delimited from ectal excipulum. **Ectal excipulum** ± hyaline, of thin-walled textura globulosa-angularis from base to margin, indistinctly oriented at a 45° angle, 40 µm thick near base of receptacle, cells *14–20 × 11–15 µm; 30 µm thick at lower flanks, 20 µm at mid flanks and margin, marginal cortical cells *(10–)13–20 × 3.5–5.3 µm, somewhat free (hair-like) or ± agglutinated to form small teeth, tipped by highly-refractive, pale yellow-orange, distinctly stratified **glassy processes** 0–5(–13) × 3–3.7 µm. **Anchoring hyphae** very sparse, 2–3 µm wide, walls 0.2–0.3 µm thick. **SCBs** and **VBs** apparently absent. **Exudate** over paraphyses 0.2–0.4 µm thick, continuous, slightly rough, firmly attached, covering the inflated protruding part; over margin and flanks absent. **— ANAMORPH**: dactylella/vermispora-like (from ascospore isolate {1, Qin et al. 2011}). **Conidiophores** formed as short lateral outgrowths, *(2–)4–7(–11) × 2–3 µm, aseptate. **Conidiogenous cells** monoblastic {T}. **Conidia** *(18–)22–36(–39) × (3.8–)5–6(–6.7) µm, (1–)2–**3**–4(–5)-septate, cylindrical with rounded ends, straight or sometimes slightly curved, sometimes constricted at septa, containing quite a few distinct LBs at septa and lateral wall {T}. **Chlamydospores** and **trapping organs** not observed in pure culture (with nematode *Panagrellus redivivus*).

Habitat: hanging (?1.5 m above the ground, 13–15 mm thick) or on the moist ground, branches of indet. angiosperm trees {2}, on red-brown boring dust between slightly decayed bark and wood {1} or on bark {2}, on blackened patches, no algae. **Associated**: ?*Opegrapha* and other crustose lichens (on periderm) {1}. **Desiccation tolerance**: asci still viable after a few weeks, ectal excipulum, basal cells of paraphyses, and ascospores viable after ~2 months {1}. **Altitude**: 2–450 m a.s.l. **Phenology**: IX, XI.

Taxonomic remarks. *Orbilia pseudobrevistipitata* resembles, e.g., *O. crenatomarginata* or *O. laevimarginata* (series *Hyalinia*) in its helicoid ascospores. Further characteristic features of this species are ± lageniform paraphyses reminiscent of series *Abutilones*, and an inverse orientation of the upper spores like in some other species of the *nemaspora-vermiformis* clade (*O. bomiensis*, *O. spirillospora*) and of series *Abutilones* (e.g., *O. milinana*).

Variation. Based on unpublished data of the teleomorph of the collection from Yuxi (Pl. 454: 2), from which the holotype was obtained in culture, *O. pseudobrevistipitata* is considered here to be conspecific with the unsequenced specimen from Philippines (Pls 453: 1; 454: 1). The specimen from Yuxi deviates in slightly longer spores that contain larger SBs, also in longer asci and narrower paraphyses, while the excipular characters were not studied by Qin et al. (2011). Only two apothecia were present on the natural substrate, which were used up when obtaining the pure culture, therefore, the authors did not describe the teleomorph in their paper (Z.F. Yu pers. comm.). However, besides the anamorph (Pl. 454: 2e), also apothecia developed in culture which show a smooth margin (2a).

Not included collection. A more montane specimen from southern China (Kunming, Pls 453: 2; 454: 3) seems to represent a species of its own: it differs in the tips of paraphyses being slightly capitate instead of lageniform, covered by a thicker exudate, also in much shorter marginal cortical cells (†5–10 × 3–4.7 µm) tipped by much longer and narrower glassy processes of (8–)20–40(–50) × 2(–2.5) µm forming distinct teeth. In the length of the SBs this resembles the specimen from Yuxi, but the spores are slightly longer.

Anamorph. *Dactylella pseudobrevistipitata* was described by Qin et al. (2011) based on the ascospore isolate of the Yuxi sample. It is characterized by cylindrical, not or slightly curved phragmoconidia with rounded ends formed on very short conidiophores. These strongly reduced conidiophores and the somewhat vermispora-like conidia are quite untypical for a dactylella-like anamorph but reminiscent of series *Aurantiorubrae*.

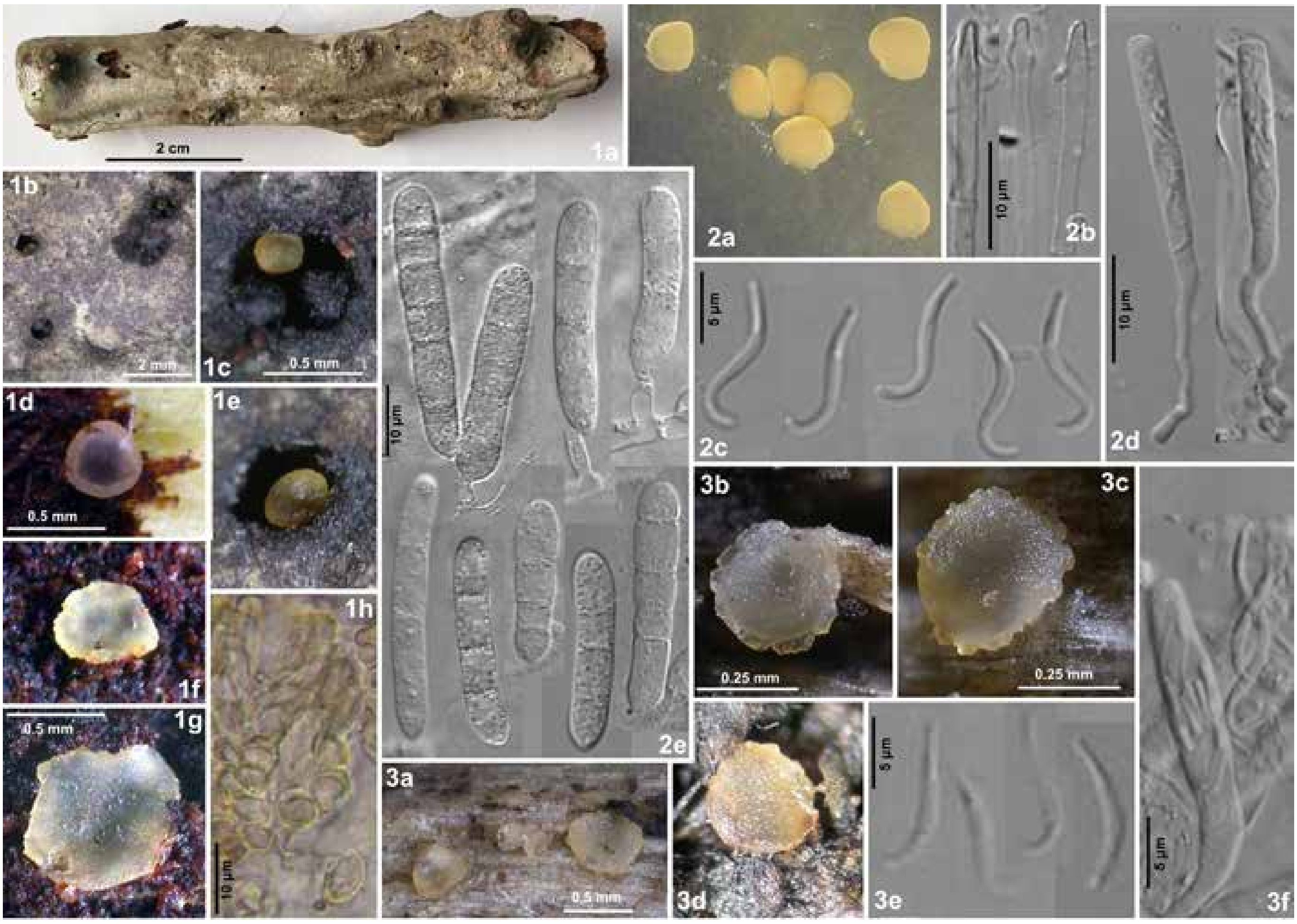


Plate 454. **1–2**: *Orbilia pseudobrevistipitata*; **3**: *O.* aff. *pseudobrevistipitata*. – **1a**. corticated branch perforated by small emergence holes; **1b–g**, **3a–d**. rehydrated apothecia (**1b–c**, **e** in emergence holes); **2a**. fresh apothecia grown on agar; **1h**. marginal ectal excipulum (external view); **2b**. paraphyses; **2d**, **3f**. asci; **2c**, **3e–f**. ascospores; **2e**. conidia and conidiophores from culture. – Living state, except for **1h**, **2b**, asci in **2d**, **3f** (in H_2O). – **2e**: from Qin et al. (2011), **2a–d**, **3d–f**: phot. Z.F. Yu (DIC). — **1**. H.B. 5392: Philippines, Palawan; **2**. YMF 1.03504 (holotype): China, Yunnan, Yuxi; **3**. H.B. 7670: ibid., Kunming (all from indet. angiosperms).

Phylogeny. An ITS sequence obtained by Qin et al. (2011) from the ex-type strain comprises S1506 intron and ITS. It shows a high distance in the ITS region to other species, e.g. 12 % to *O. nemaspora*, 14.5 % to *O. vermiformis* and *O. bomiensis*. The intron shows a high distance to members of series *Hyalinia* (~20 %) but also to *O. vermiformis* and *O. nemaspora* (18–19 %) and *O. xanthoguttulata* (17 %).

Ecology. The holotype of *O. pseudobrevistipitata* was collected on hygric bark of an angiosperm branch in a valley near a brook (Y. Zhang pers. comm.) in a subtropical humid (winter-dry) evergreen forest in southern China. The not included sample from Kunming was on decorticated wood in a similar forest (with *Quercus*). The specimen from Philippines grew on rotten boring dust and bark of a corticated xeric branch of an angiosperm tree at a sandy river bank of the sea shore at the tropical humid (winter-dry) west coast of Palawan island (Philippines, southeastern Asia). The apothecia occurred mostly in small groups on a thin layer of red-brown boring dust between bark and wood in the abundant galleries of a bark beetle, hidden below the loosely attached bark, always below the scattered, round, 0.6–0.75 mm large emergence holes, ca. 1 mm beneath their upper rim, rarely on bark at the edge of the emergence hole. Therefore, the branch seemed to be devoid of apothecia at first glance.

Specimens included. **CHINA**: **Yunnan**, **Yuxi**, Yuanjiang, 100 km SW of Yuxi, 3 km NNW of Lijiang, near Thermal Spring (Reshuitang), ~450 m (‘500 m’), indet. angiosperm bark, 18.IX.2009, L. Qin (YMF 1.03504, **holotype**, permanent slide, anam. cult., doc. vid.; sq.: HM215520, as *Brachyphoris brevistipitata*). — **PHILIPPINES**: **Palawan**, 55 km NNE of Puerto Princesa, 3.5 km E of Sabang, St. Paul Subterranean National Park, Underground River, 2 m, branch of indet. angiosperm tree, on wood, bark and boring dust, 20.XI.1995, P. Wagner (H.B. 5392).

Not included. **CHINA**: **Yunnan**, **Kunming**, ~12 km NE of Kunming, Songhuaba, ~2000 m, branch of indet. angiosperm, on wood, 18.X.2004, Z.F. Yu (Z.F.Y. shb-1, YMFT, H.B. 7670).

Orbilia bomiensis Bin Liu, Xing Z. Liu, W.Y. Zhuang in Liu et al., Fungal Diversity 22: 109 (2006) — Pl. 455

Etymology: named after the collection site (Bomi, Tibet).

Typification: China, Tibet, Bomê, wood of indet. angiosperm, 16.VII.2004, B. Liu & X.Z. Liu (HMAS 96790, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–2 mm diam., up to 0.26 mm high (receptacle 0.13 → 0.07 mm), bright yellow-orange, semitranslucent, round, scattered; disc slightly concave to flat, margin 20 µm protruding, distinctly crenulate with hyaline ± conglutinate hairs; broadly sessile or with a stipe 0.15 × 0.15–0.17 mm, superficial; dry deep reddish-orange. **Asci** †38–45(–63) × (3.1–)3.5–4.7 µm, 8-spored, spores ± 4-seriate (spirally twisted), 4 upper spores inverted (not mixed); **apex** (†) slightly truncate; **base** with short, medium thick, flexuous stalk, T- to L-shaped. **Ascospores** *10–13.5 × 1.5–1.7 µm (actual length ~15–17 µm), narrowly fusoid, apex strongly attenuated, subacute, base moderately narrowed, rounded; very strongly curved (helicoid, twisted like a left-hand thread), less so near apex; **SBs** 0.7–1 µm diam., ± globose, very close to apex. **Paraphyses** apically uninflated to only slightly clavate, terminal cell

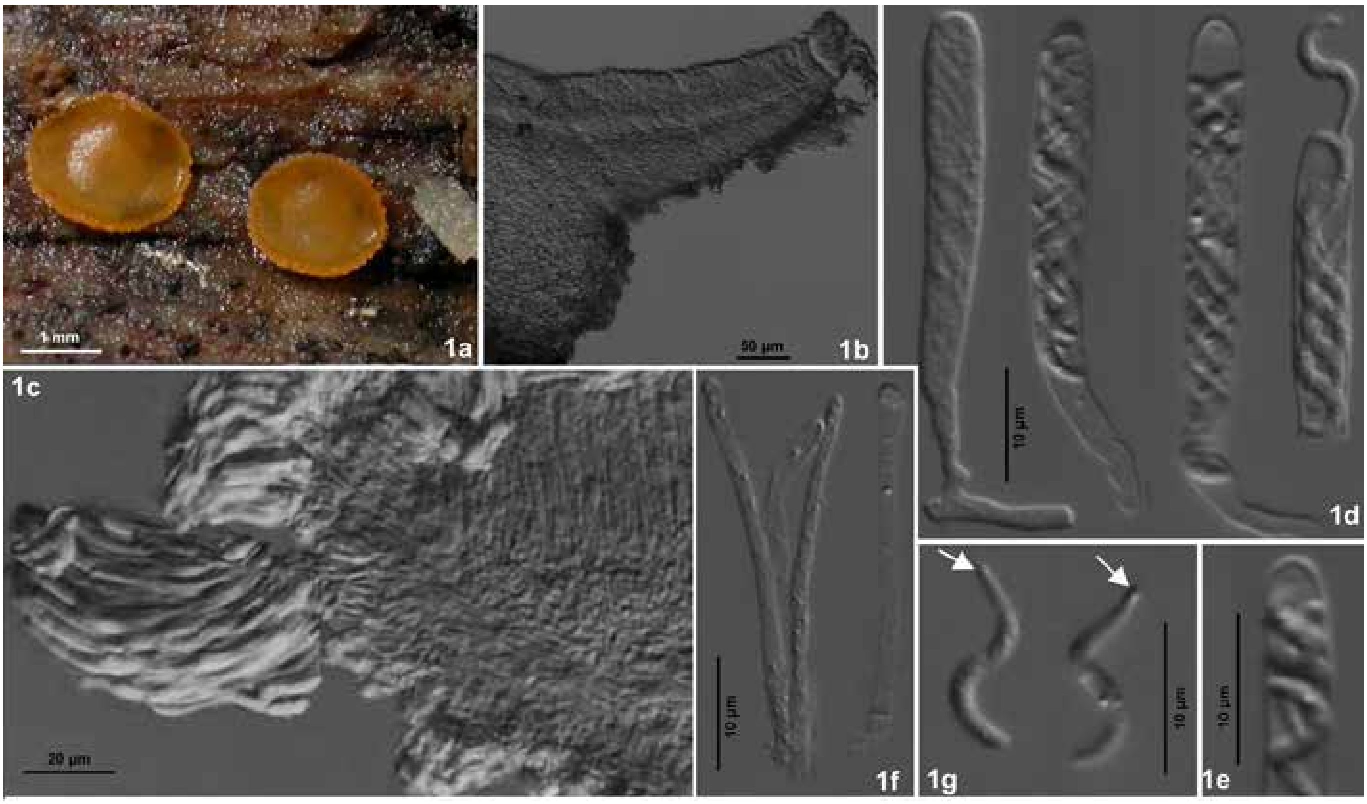


Plate 455. **1**: *Orbilia bomiensis* (holotype). – **1a**. fresh apothecia; **1b**. apothecium in median section; **1c**. id., ectal excipulum near margin, with long glassy processes; **1d**. asci and liberated ascospore; **1e**. ascus apex; **1f**. paraphyses; **1g**. ascospores. – Dead state (in H_2O), except for spores (?). — **1a–g**. from Liu et al. (2006b, DIC), HMAS 96790: China, Tibet, on indet. angiosperm.

†~29–33 × (1.5–)1.8–2.5 µm, lower cells †?7 × 1.5–2 µm; unbranched at upper septum. **Medullary excipulum** 15–25 µm thick, of textura intricata-angularis. **Ectal excipulum** of thin-walled slightly gelatinized, t. globulosa-angularis(-prismatica) from base to mid flanks, ± vertically oriented, 20–150 µm thick near base, cells †13–25 × 7–10 µm; 20 µm thick near margin, of t. porrecta oriented at a 50° angle to the surface, marginal cortical cells †~10–15 × 3.5 µm; **glassy processes** (15–)40–70 × 3–5 µm, highly-refractive, slightly stratified, coherent to form irregular teeth. **Anchoring hyphae** not examined. **SCBs** and **VBs**: no data available. **Exudate** over paraphyses very thin, firmly attached, over margin and flanks not seen. **— ANAMORPH**: unknown.

Habitat: on rotten wood of indet. angiosperm tree lying on moist ground. **Associated**: none mentioned. **Desiccation tolerance**: unknown. **Altitude**: 3100 m a.s.l. **Phenology**: VII.

Taxonomic remarks. *Orbilia bomiensis* was not examined in the present study, and the here presented description is based on the protologue. The species is characterized by very strongly helicoid ascospores, which are obviously twisted like a left-hand thread, judging from the available photographs, given that the photo is not mirror-inverted (Pl. 455: 1d, right ascus). They are only moderately tapered towards base, and contain a short, ± globose SB in the strongly attenuated, ± acute apex. An uncertainty about the SBs as described in the protologue remains, however, because the spores are possibly not alive on the photos, although they were said to have been studied in the living state. A striking feature is also the bright yellow-orange colour of the rather large apothecia. As in *O. pseudobrevistipitata* and *O. spirillospora*, the upper spores are inversely oriented within the asci.

The species appears to be related to *O. spirillospora*, *O. crenatomarginata*, and *O. scolecospora*. However, these and all the other species of series *Xanthoguttulatae* and *Hyalinia* differ in the spores being twisted like a right-hand thread. The three mentioned species deviate in narrowly tear-shaped to subulate SBs, the latter two in the lower spores being inversely oriented within the asci, and *O. scolecospora* in smaller asci and spores.

Phylogeny. From apothecia of the holotype Liu et al. (2006a) gained a sequence (ITS+LSU, S1506 intron absent) which clustered in their analyses in a clade with *O. nemaspora* (see above). *O. bomiensis* shows a high distance to other species of series *Xanthoguttulatae*, the lowest percentage being 14.5% in the ITS to *O. pseudobrevistipitata* and 3.3–4% in the LSU D1–D2 to the *xanthoguttulata-succulenticola* clade (but 6.5% to *O. nemaspora*). In our analyses it clustered in the ITS+LSU tree (Phyl. 13) in the medium supported *nemaspora-vermiformis* clade, but in the LSU tree (Phyl. S16) strongly supported with the *xanthoguttulata-succulenticola* clade.

Ecology. *O. bomiensis* was collected on rotten hygric wood of an unidentified angiosperm tree in an orotemperate (altimontane) humid (winter-dry), continental floodplain forest in the eastern part of Himalaya.

Specimens included. **CHINA**: **Tibet**, **Nyingchi** (Linzhi), 36 km ESE of Bomê (Bomi), 1.3 km ENE of Songzong, 3100 m, wood of indet. angiosperm, 16.VII.2004, B. Liu & X.Z. Liu (B.L. X033, HMAS 96790, **holotype**, doc. vid.).

Orbilia spirillospora Baral & G. Marson, **sp**. **nov**., MB 813764 — Pls 456–457

Etymology: named after the strongly helicoid ascospores resembling members of *Spirillaceae* (*Proteobacteria*).

Typification: Australia, Queensland, Cape Tribulation, branch of *Hibiscus tiliaceus*, 30.VIII.2006, G. Marson (ex H.B. 8487a, BRI AQ799192, holotype).

Latin diagnosis: *Apothecia rehydratata 0.25–0.6 mm diam., pallide luteolo-cremea, sessilia, margine laevi. Ascosporae *13–14 × 1–1.1 µm, anguste fusiformes, apice acuminatae, basi valde attenuatae, conspicue helicoideae, dextrorsum convolutae sesqui-anfractae, corpusculum refringens anguste lacrimiformem ad subulatum, ad apicem filo longo affixum continentes,*

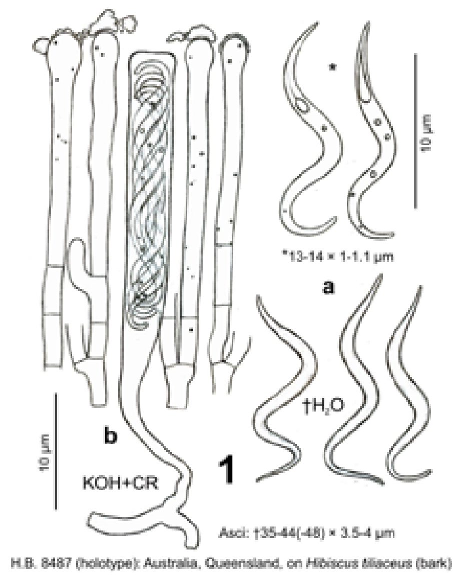


Plate 456. **1**: *Orbilia spirillospora*. – **a**. ascospores; **b**. ascus and paraphyses.

superiores inverse orientates. Paraphyses ad apicem leniter clavato-capitatae, exsudato valido tectae. Excipulum marginale absque processis vitreis. Habitat ad corticem putridum rami sicci Hibisci tiliacei *in zona tropica humida Australiae septentrio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.25–0.5(–0.6) mm diam., 0.09–0.1 mm high (receptacle 0.07–0.08 mm), pale to light (yellowish-)cream, ± translucent, round to slightly undulating, very scattered; disc (slightly concave to) flat, margin distinct, not protruding, smooth; sessile, superficial; dry light cream to rosaceous. **Asci** †35–44(–48) × 3.5–4 µm, 8-spored, spores 4-seriate (spirally twisted), 4 upper spores inverted (not mixed), pars sporifera †23–25 µm long; **apex** (†) medium to strongly truncate (not indented, laterally rarely slightly inflated); **base** with short and thick to mostly long and thin, flexuous stalk, Y-shaped. **Ascospores** *13–14 × 1–1.1 µm, †11.5–14 × 0.9–1 µm (~16–20 µm actual length), very narrowly fusiform (acicular), apex acuminate, base attenuated in a narrow tail-like base or tail of 2.5–3 × 0.2–0.3 µm, strongly helicoid (twisted by ~1.5 turns, always like a right-hand thread); **SBs** 5–6 × 0.7 µm in situ (~5.5–7 µm actual length), narrowly tear-shaped or subulate, rarely ellipsoid, apically narrowed to a short, rarely long filum. **Paraphyses** apically slightly (to medium) clavate-capitate, terminal cell †18–24 × 2–3 µm, lower cells †(3–)4–5(–9) × 1.2–1.6 µm; rarely branched at upper septum. **Medullary excipulum** 10–15 µm thick, of dense textura intricata, sharply delimited from ectal excipulum. **Ectal excipulum** of thin-walled, indistinctly vertically oriented t. angularis from base to margin, 35–45 µm thick near base, cells */†6–19 × 5–13 µm; 10–15 µm thick near margin, oriented at a 40–80° angle to the surface, marginal cortical cells †6–8 × (3–)4–6 µm; **glassy processes** absent. **Anchoring hyphae** abundant, †1.5–2.5 µm wide, walls 0.2 µm thick. **SCBs** and **VBs** unclear. **Exudate** over paraphyses 0.3–2 µm thick, granular-cloddy, hyaline, loosely or often firmly attached; over margin and flanks 0.5–1 µm thick, cloddy to continuous. **— ANAMORPH**: unknown.

Habitat: collected 2–3.5 m above the ground, corticated, 13–20 mm thick, hanging branches of *Hibiscus tiliaceus*, on strongly decayed bark (on periderm and especially in small holes on bast), greyed, no algae. **Associated**: *Orbilia* ?*subfabacearum*. **Desiccation tolerance**: some basal excipular cells and some spores still viable after 8.5 months. **Altitude**: 15 m a.s.l. **Geology**: Devonian sedimentary rock. **Phenology**: probably rather long-lived.

Taxonomic remarks. *Orbilia spirillospora* is readily recognized by its comparatively long, narrowly fusiform, strongly helicoid ascospores with consistently 1.5 turns or slightly more, the upper 4 spores being inversely oriented, and by lacking glassy processes at the margin. Species with similar spores and spore orientation (*O. bomiensis*, *O. pseudobrevistipitata*, *O. scolecospora*) clearly differ in spore size and in showing hardly more than 1 turn, also in the presence of glassy processes. *O.*

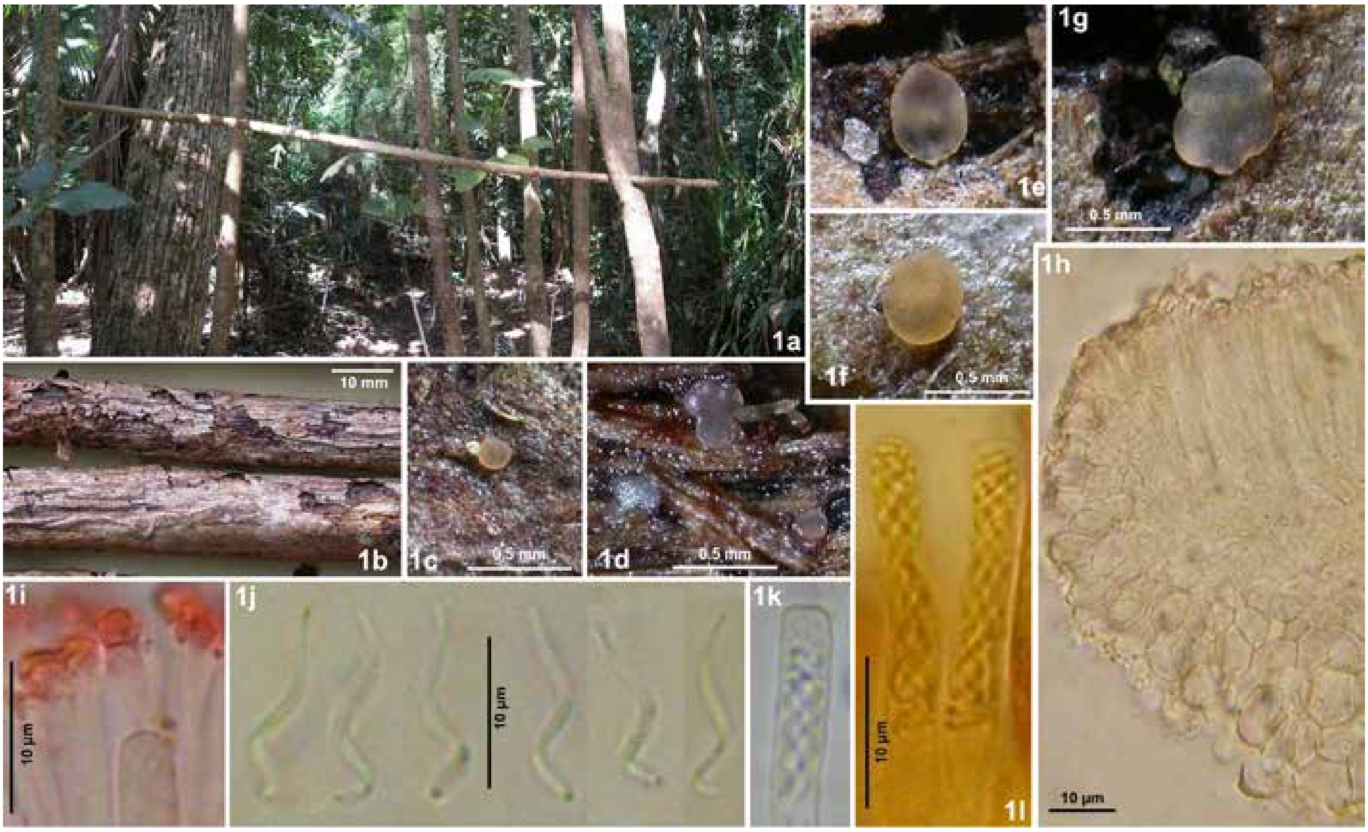


Plate 457. **1**: *Orbilia spirillospora* (holotype). – **1a**. tropical rainforest, the inhabited branch was vertical before it was drawn in this position; **1b**. dead branches of *Hibiscus tiliaceus*; **1c–g**. rehydrated apothecia; **1j**. ascospores; **1k–l**. asci; **1k**. ascus apex; **1i**. paraphyses; **1h**. ectal excipulum in median section (flanks and margin). – Dead state (**1k** in H_2O, **1h**, **j** in KOH, **1i** in KOH+CR, **1l** in KOH+IKI). — **1a–l**. H.B. 8487a: Australia, Queensland, on *Hibiscus*.

pseudobrevistipitata also differs in paraphysis shape, and *O. bomiensis* in the spores being only slightly narrowed at base and in being twisted like a left-hand thread, in much shorter, ± globose SBs, and in larger, bright orange-yellow apothecia.

Ecology. *O. spirillospora* was collected on rotten xeric bark of a climber (*Hibiscus tiliaceus*, Cottonwood) in a tropical, humid, monsoon-influenced (winterdry) evergreen forest with a very high precipitation during summer, at the coastline of northeastern Australia.

Specimens included. **AUSTRALIA**: **Queensland**, Wet Tropics, border of Daintree forest, 47 km N of Port Douglas, 5 km N of Cape Tribulation, 15 m, branch of *Hibiscus tiliaceus*, on bark, 30.VIII.2006, G. Marson (ex H.B. 8487a, BRI AQ799192, **holotype**).

Series *Hyalinia*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Hyalinia*** Baral & E. Weber, **ser. nov.**, MB 815012 –
Type species: *Hyalinia crystallina* (Quél.) Boud.
[= *Orbilia crenatomarginata* (Höhn.) Sacc. & Trotter]

= *Hyalinia* Boud., Bull. Soc. Mycol. Fr. 1: 114 (1885), nom. illegit. (ICN Art. 53.2), non *Hyalina* Stackh. 1809 (*Phaeophyceae*)
≡ *Orbilia* subgroup III *Hyalinia* (Boud.) Velen. Mon. Discomyc. Bohem. p. 102 (1934, unranked).

Etymology: referring to the translucency of the non-pigmented apothecia in the type species.

Latin diagnosis: *Apothecia haud tolerantia ad siccitatem, hyalina ad pallide rosacea vel ochracea, ad marginem partim dentata, dentes e processis vitreis compositi, cellulae excipuli corpusculis crystalloideis hyalinis continentes, ascosporae angustae, falcatae vel helicoideae, in statu vivo corpusculum refringens lacrimiformem vel subuliformem continentes.*

Description: — **TELEOMORPH**: **Apothecia** hydrated 0.15–1.5 mm diam., whitish or pale rosaceous or yellowish-ochraceous, margin smooth or usually finely to distinctly crenulate or dentate, sessile or with an indistinct stipe. **Asci** *23–37 × 3–4 µm, 8-spored, lower ~4 spores inverted; **apex** (†) slightly to strongly truncate in front view, never indented or laterally inflated, thin-walled; **base** never H-shaped. **Ascospores** *6–10.5 × 0.6–1.3 µm, (very) narrowly fusoid to fusiform, apex rounded to acute, base gradually tapered, often tail-like or with a distinct tail, strongly curved (often strongest near base), helicoid (right-handed), also falcate; **SBs** 1.7–3.5 × 0.2–0.5(–0.7) µm, tear-shaped to subulate, with or without a short filum. **Paraphyses** not or only slightly to medium inflated at the apex, clavate-capitate, terminal cells 2–5 × longer than lower cells. **Ectal excipulum** cells near base *9–20(–28) × 7–16(–20) µm, near margin of t. angularis to t. porrecta; **glassy processes** 0–3 µm long or often 4–10 µm up to 60, rarely 100–200 µm long. **SCBs** globose to elongate, always associated with crystalloid ones; **VBs** absent. **Exudate** (0.2–)0.5–2(–3) µm thick, continuous to cloddy-granular, loosely or firmly attached, hyaline to pale yellowish. **— ANAMORPH**: dactylella-like. **Conidiophores** unbranched 40–110 µm long, 3–4.3 µm wide at the base, 1.3–2 µm at the tip. **Conidiogenous cells** monoblastic or sympodial (geniculate or candelabrelloid). **Conidia** phragmosporous, *7.5–50 × 2.8–12 µm, ellipsoid- to cylindric-clavate or cylindrical, straight, (0–)1–6(–7)-septate. **Chlamydospores** and **trapping organs** unknown.

Habitat: Hygric or rarely mesic wood and bark of angiosperms, rarely gymnosperms, temperate to montane or subtropical to tropical, semiarid to humid, desiccation-sensitive.

Recognized species: 4.

Taxonomic remarks. Members of series *Hyalinia* are characterized by very narrowly fusoid, curved ascospores with mostly subacute to acuminate apices containing subulate SBs, and with attenuated or often tail-like, very narrow bases. The spores are typically strongly helicoid and intertwined within the asci, but may also be falcate with an only very slight helicoid twist (*O. crenatofalcata*). Glassy processes which form marginal teeth are typical of this series, though being very short or completely absent in *O. laevimarginata*. Their presence has been considered as a key character of this group by both Höhnel (1907a) and Spooner (1987: 159, 188) who recognized *Hyalinia* at the generic level. Further characteristics are the very long terminal cells of paraphyses in relation to the lower cells, and a dactylella-like anamorph. Hyaline, globose and crystalloid SCBs occur in association in all four included species.

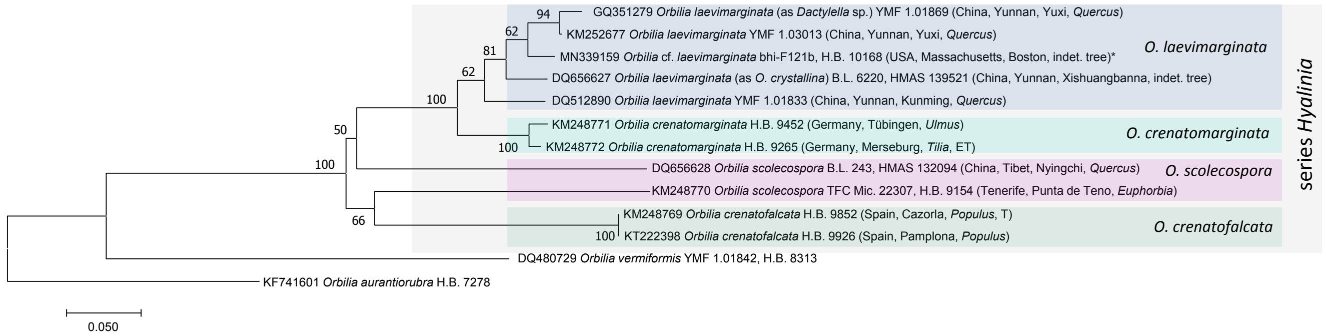
Series *Hyalinia* shows very strong morphological similarities to the *nemaspora-vermiformis* clade of series *Xanthoguttulatae*, from which it can hardly be separated without molecular data. From series *Xanthoguttulatae* s.str. and series *Aurantiorubrae* members of series *Hyalinia* differ in whitish, drought-intolerant apothecia. In the frequent presence of prominent marginal teeth it differs from all of them.

Species delimitation. Among the four included species, merely *O. crenatofalcata* appears to be easily recognizable by its falcate spores. A more or less smooth apothecial margin characterizes the genetically diverse Chinese *O. laevimarginata* which, however, appears to occur also in a form with distinct marginal teeth, while the frequently collected, mainly European *O. crenatomarginata* may rarely have a smooth margin. That species is sharply separated from the similar extra-European *O. scolecospora* by spore and SB size. However, the latter was too rarely collected and sequenced in order to know much about its variability, while molecular data suggests that different taxa are involved (see Phyl. 16).

Anamorph. Ascospore isolates were only gained from *O. laevimarginata* (Y. Zhang et al. 2015). The obtained dactylella-like, 1(–3)-septate, cylindric-ellipsoid conidia were formed on rather short conidiophores, and trapping organs were not observed when nematodes were added. The presumed anamorph of *O. crenatomarginata*, which was rarely observed on the natural substrate, differs hereof in rather long conidiophore and much larger, clavate, multiseptate conidia.

Phylogeny. The phylogenetic position of series *Hyalinia* based on rDNA sequences of *O. crenatomarginata*, *O. laevimarginata*, *O. crenatofalcata*, and *O. scolecospora* remained somewhat unclear. In the combined analysis of section *Aurantiorubrae* it clustered with low support with series *Xanthoguttulatae* (Phyl. 13), whereas in that of the genus *Orbilia* (Phyl. 7) it clustered medium supported sister to the *xanthostigma-tremulae* clade of section *Orbilia*. In the combined analysis in Baral et al. (2017b), series *Hyalinia* clustered unresolved with other members of subgenus *Habrostictis*. The dactylella-like anamorph with its often sometimes conidiophores would suggest a relationship to series *Neodactylella* of section *Arthrobotrys*. However, no such relationship could be deduced from our phylogenetic analyses, and also three morphological features argue against this: distinctly helicoid ascospores and crystalloid SCBs are so far completely absent in section *Arthrobotrys*, and H-shaped ascus bases have never been observed in series *Hyalinia* but frequently so in section *Arthrobotrys.*

The here practised placement of series *Hyalinia* in section *Aurantiorubrae* is supported by strong morphological affinities to the *nemaspora-vermiformis* clade, which includes *O. vermiformis*, *O. nemaspora*, *O. pseudobrevistipitata*, and *O. bomiensis*. This clade did not cluster with series *Hyalinia*, but



Phylogenetic analysis 16. Phylogram of series *Hyalinia* inferred from ML analysis of ITS1-5.8S-ITS2 rDNA dataset (13 sequences, 605 positions, aligned with MUSCLE) using the K2+I model in MEGA7 (500 replicates). The tree is rooted with *O. aurantiorubra* and *O. vermiformis*. Asci 8-spored in all taxa; T = type, ET = epitype, * = without partial ITS2.

formed a sister clade of the *xanthoguttulata-succulenticola* clade. Series *Hyalinia* and series *Xanthoguttulatae* form two strongly supported but rather distant clades, particularly when analysing ITS+LSU or ITS (Phyls 13, S15). The molecular distance between the two series is also obvious when analysing the S1506 intron (Phyl. S14).

Also in the phylogenetic analysis of the ITS region by Liu et al. (2006a), series *Hyalinia* [with *O. crenatomarginata* (as *O. crystallina*) and *O. scolecospora*] clustered distant from series *Xanthoguttulatae* [with *O. bomiensis* and *O. nemaspora* (as *Orbilia* sp.)], but as in our analyses the phylogeny of these two clades remained unresolved. The same result was obtained by Zhang et al. (2015), who named both clades '*Hyalinia*'. In Liu et al.'s (2006a) LSU analysis, series *Xanthoguttulatae* clustered with medium support as a sister group to sections *Aurantiorubrae*, *Helicoon*, and *Arthrobotrys*, while series *Hyalinia* clustered as a sister group to all of them.

Specific nucleotide positions. Several nucleotides being characteristic of series *Hyalinia* in comparison to other series of subgenus *Habrostictis* have been found. In the 5.8S region series *Hyalinia* has at pos. 133 TCCG**G**A vs. TCCG**A**A or TCCG**T**A in other groups (Tab. 68). In the LSU D1 domain it has at pos. 206 TCG**C**GGA (or TCG**A**GGA) vs. TCG**T**AGA in other taxa, though rarely TCG**C**AGA (*O. ebuli*) or TCA**T**AGA (*O. gemma*) (not shown), and at pos. 241 CT**G**C (or TT**G**C) vs. TT**A**C, CT**A**C, TT**T**C, TT**T**T, or TC**T**A in other groups, though rarely TT**G**C (*O. milinana*, *O.* aff. *farnesianae*, *O. tianmushanensis*) (Tab. 68). Also the combination of pos. 171 & 174 is characteristic (G**C**GG**T**C), occurring otherwise only in *O. milinana* (G**C**GA**T**C). A gap at pos. 555 in the D2 domain is very diagnostic: TTA–AG vs. TTA**T**AG or sometimes TTA**C**AG in other *Orbiliomycetes*.

Ecology. All four included species are desiccation-sensitive, except for a slight tolerance in *O. scolecospora*. They occur on wood and bark, mainly of angiosperms. The geographical and climatic distribution includes temperate humid Europe, Asia, and North America (*O. crenatomarginata*), supra(sub) mediterranean semihumid southern Europe, subtropical subhumid eastern Asia (*O. laevimarginata*), and tropical humid Middle America (*O.* cf. *crenatomarginata*).

Key to species of series *Hyalinia*

1. Upper spores inverted within asci; spore apex acute to acuminate .... see **series *Xanthoguttulatae***, p. 845
1. Lower spores inverted within asci (SB-containing end pointing towards ascus base); spore apex rounded to acute 2

2. Spores falcate or only very slightly helicoid 3
2. Spores consistently medium to strongly helicoid 4

3. Spores *8–9.5(–9.8) × 0.8–0.9(–1) µm, asci †25–30 × 2.8–3.2 µm; wood of *Populus*, supra(sub)mediterranean (semi)humid southern Europe .... ***O*. *crenatofalcata***, p. 883
3. Spores *(9.5–)10–12(–13.7) × 1–1.1(–1.2) µm, asci †25–45 × 3–4.5 µm; wood & bark of angiosperms, subtropical humid southern China .... ***O*. *crenatonemaspora*** (series *Xanthoguttulatae*), p. 862

4. Spores predominantly > 9 µm long; SCBs in paraphyses globose to elongate, in excipular cells partly brick- to rod-shaped.. .... see ***O*. *nemaspora***, p. 858 & ***O*. *vermiformis***, p. 856 (series *Xanthoguttulatae*)
4. Spores predominantly < 9 µm long; SCBs in paraphyses and excipular cells globose to elongate, and ring- to keyhole-shaped or rhomboid 5

5. Marginal cortical cells *(2–)4–6 µm wide, sometimes with very short glassy processes (< 3 µm), rarely forming distinct teeth; spores *(6–)7–8(–8.5) × 0.75–0.9(–1) µm, apex subacute to acute; conidia (0–)1(–3)-septate, *7.5–13 × 2.8–3.8 µm, formed in clusters on distinct denticles; wood & bark of *Quercus* etc., subtropical humid China .... ***O*. *laevimarginata***, p. 877
5. Marginal cortical cells *2.2–4 µm wide, generally tipped by 4–10 up to 100–200 µm long glassy processes forming marginal teeth (rarely without teeth); spore apex rounded to subacute; conidia (3–)5–6(–7)-septate, *31–50 × 6.8–12 µm, formed singly at the conidiophore tip (presumed anamorph of *O. crenatomarginata*) 6

6. Spores *7–8.5(–9) × (0.6–)0.7–0.8(–0.9) µm; SBs 1.7–2.2(–2.7) µm long; wood & bark of various angiosperms (often *Tilia*), rarely gymnosperms, hemiboreal to mesosubmediterranean (semi)humid Europe & North America .... ***O*. *crenatomarginata***, p. 870
6. Spores *(7–)8–9(–10.5) × 0.9–1.2(–1.3) µm; SBs 2.2–3.5 µm long; wood and bark of *Eucalyptus*, *Euphorbia*, *Quercus*, cold-continental to subtropical, humid to arid Asia, Australia, Macaronesia, South America .... ***O*. *scolecospora***, p. 879

Orbilia crenatomarginata (Höhn.) Sacc. & Trotter, Syll. Fung. 22: 725 (1913) — Pls 458–460, Map 81

≡ *Hyalinia crenatomarginata* Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. I, 116: 132 (1907).
= *Orbilia crystallina* (Quél.) Baral, Syst. Ascomycetum 13: 120 (1994), nom. illegit., ICN Art. 53.1 [non *Orbilia crystallina* Rodway (1920), *Pezizales*, see p. 1669]
≡ *Helotium crystallinum* Quél., Bull. Soc. Bot. Fr. 24: 329 (1878).
≡ *Hyalinia crystallina* (Quél.) Boud., Icon. Mycol., liste prélim.: 4 (1904).
≡ *Cistella crystallina* (Quél.) Quél., Enchir. Fung.: 319 (1886).
≡ *Cyathicula crystallina* (Quél.) Sacc., Syll. Fung. 8: 307 (1889).
?= *Orbilia tiliacea* Velen., Monogr. Discom. Bohem.: 96, pl. 11 fig. 35 (1934).
= *Orbilia roseohyalina* Velen., Monogr. Discom. Bohem.: 97, pl. 11 fig. 37 (1934).
?= *Orbilia curvatispora* var. *minor* Dennis, Kew Bull. 9: 296 (1954)

Etymology: *crenatomarginata*: according to the denticulate (crenate) margin of the apothecia; *crystallina*: resembling a ‘microscopic crystal candle socket’; *tiliacea*: from the substrate *Tilia*; *roseohyalina*: after the rose colour of the apothecia; *curvatispora* var. *minor*: in all parts smaller than *O. curvatispora* (= *O. auricolor*).

Typification: Austria, Judenau, branch of ?*Tilia*, V.1906, G. Boltmann (FH 00304814, lectotype of ***Hyalinia crenatomarginata***, designated here, MBT202375); Germany, Merseburg, branch of *Tilia*, 5.IV.2010, S. & P. Rönsch (ex H.B. 9265, M-0291776, epitype, designated here, MBT385121; sq.: KM248772). — France, Haut Jura, unlocalized, branch of *Quercus*, L. Quélet (UPS:BOT:F–015652, lectotype of ***Helotium crystallinum***, indirectly designated by Spooner 1987: 188).— Czechia, Karlštejn, wood of *Tilia*, J. Velenovský (PRM 148870, holotype of ***Orbilia tiliacea***). — Czechia, Karlštejn, branch of ?*Salix*, J. Velenovský (PRM 151742, lectotype of ***O. roseohyalina***, designated by Svrček 1954: 20). — Trinidad, Diego Martin, log of indet. angiosperm, E.M. Wakefield (K(M) 36047, holotype of ***O. curvatispora* var. *minor***).

Misapplied name: Boudier (1904–10: 269, pl. 465), as *Hyalinia rosella* (misspelling for *roseola*, see p. 1683).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–1(–1.2) mm diam., in total 0.1–0.2(–0.25) mm high (receptacle 0.05–0.1 mm), watery greyish-white, sometimes with a very faint, rarely distinct rosaceous(-violaceous) or cream-carneous tint, strongly translucent (glassy), round, gregarious; disc flat or slightly convex, margin denticulate to dentate, with ~10–30 small to usually rather large and distinct triangular teeth of 30–100 × 60–120 µm {9}, 0–15 µm protruding beyond disc, rarely smooth in some {1} or all {4} apothecia, always smooth at flanks; broadly sessile or with a broad, obconical, ill-defined stipe 0.05–0.1 × 0.17–0.3 mm, superficial; dry pale to light yellowish-ochraceous-chlorinaceous to rosaceous-orange-brownish. **Asci** *24–34(–37) × (2.9–)3.2–3.8 µm {8}, †20–34 × 2.4–3.3 µm {16}, 8-spored, spores 4–8-seriate, strongly spirally twisted within both the living and dead asci, pars sporifera *9.5–13(–15) µm, †10–19 µm, ~4 lower spores inversely oriented {7} (never mixed); **apex** (†) slightly to strongly truncate (never indented or laterally inflated); **base** with very short to medium long, thick or thin, flexuous stalk, L- or h-shaped. **Ascospores** *7–8.5(–9) × (0.6–)0.7–0.8(–0.9) µm {12} (~9–12 µm actual length), †(6.5–)7–8(–9) × 0.6–0.8(–0.9) µm {18}, very narrowly fusoid(-clavate), upper part almost cylindrical but slightly narrowed towards rounded to subacute apex, base (medium to) strongly attenuated, tail-like or with a distinct tail ~2–3 × 0.2–0.3(–0.4) µm; (*/†) strongly curved especially near base (helicoid, always twisted like a right-hand thread); **SBs** 1.7–2.2(–2.7) × (0.2–)0.3–0.4(–0.5) µm {6}, narrowly tear-shaped (to ellipsoid), apically narrowed to a short filum (but filum sometimes invisible). **Paraphyses** apically cylindrical or very slightly (rarely medium) capitate, terminal cell *11–20 × (1.7–)1.9–2.8(–4) µm {6}, †1.5–2.5 µm wide {2}, lower cells *2.7–5.5 × 1.9–3.3(–4) µm {4}, †2.5–4.5 × 1.3–2.5 µm {2}, rarely branched at upper septum; hymenium hyaline to pale rose. **Medullary excipulum** hyaline, 10–30 µm thick, of dense textura globulosa-angularis(-intricata), not sharply delimited from ectal excipulum. **Ectal excipulum** of thin-walled t. globulosa-angularis from base to margin, (30–)80–110(–150) µm thick near base, cells *10–28 × 8–20 µm {7}, 15–30 µm thick at lower flanks, cells *7–20 × 5–16 µm {2}, 10–15 µm thick at mid flanks and margin, oriented at 30–45°, marginal cortical cells forming a t. porrecta oriented at 0–20°, sometimes running out in free hairs, cells *7–22 × 2.2–4 µm {8}; **glassy processes** 4–10 {3} or (6–)10–50(–62) {16} × (2–)2.5–3.5(–4) {18} µm, low- to high- refractive, sometimes stratified, curved upwards {7}, tightly conglutinate. **Anchoring hyphae** sparse to abundant, */†1.5–3 µm wide (near insertion –4.5 µm), walls 0.2(–0.3) µm thick {5}, without gel or sometimes forming an up to 30 µm thick, glassy-gelatinized t. intricata. **SCBs** in terminal cells of paraphyses and marginal cortical cells globose or elongate-cylindric, (1.2–)1.7–2.3(–3) µm diam., low- to high-refractive, mostly 1 per cell, in lower part of ectal excipulum 1 or more per cell; crystalloid SCBs in terminal and lower cells of paraphyses and in ectal excipulum from base to margin {21}, medium to high-refractive, in paraphyses filiform to S-shaped or rhomboid, in excipulum ring- to keyhole- or horseshoe-shaped, (2–)3–7(–8) × (2–)3–5(–7.5) µm {6}, also plate-like or filiform; **VBs** absent. **Exudate** over paraphyses continuous to cloddy, externally rough to granular, hyaline or pale yellowish, (0.3–)1–2(–3) µm thick, loosely attached; over margin and flanks finely granular or cloddy, 0.3–1 µm thick. — **ANAMORPH**: dactylella-like (presumed, from natural substrate {3}). **Conidiophores** unbranched, septate, erect, up to *~100–110 µm long {1}, 3.5–4 µm wide at the base, 2 µm at the tip, forming a single terminal conidium. **Conidia** *31–50 × (6.8–)8–10.5(–12) µm, ellipsoid-clavate, (3–)5–6(–7)-septate {2}, containing quite a few minute LBs.

Habitat: on underside of decorticated or corticated, 1–10 cm thick branches and much thicker stumps and logs lying on (very) moist but also rather dry ground (never exposed to dry air), of ?*Acer* sp. {1}, *A. pseudoplatanus* {1}, *A. rubrum* {1}, *Betula* sp. {2}, *Carpinus betulus* {8}, *Corylus avellana* {2}, *Eucalyptus globulus* {1}, *Fagus sylvatica* {4}, *Fraxinus excelsior* {1}, *Larix* sp. {1}, *Populus* sp. {2/1}, ?*P. alba* {1}, *P. nigra* {1}, *P. tremula* {1}, *P. tremuloides* {1}, *Prunus avium* {1}, *P. cerasus* {1}, *Quercus* sp. {1/1}, *Q. robur* {1}, *Q. petraea* {1}, *Salix* sp. {6/2}, *S. caprea* {1}, *Tilia* sp. {18/3}, *T. cordata* {2}, *T. platyphyllos* {2}, *T. tomentosa* {1}, *Ulmus* sp. {2}, indet. angiosperms {6}, on 0.5–2 mm or often over 10 mm deep medium to mostly strongly decayed wood {55}, sometimes brown-rotten, also often on bark {27} (periderm {3} or bast {11}), on periderm-free bast or on inner surface of detaching or detached bark, sometimes deep inside large, hollow stumps, green algae absent or sparse, sometimes on black hyphomycetes or subiculum of e.g., *Lasiosphaeria*, or close to old rhizoids of *Armillariella* {1}. **Associated**: *Capronia* sp. {1}, *Collybia cookei* {1}, *Diaporthales* {1}, *Holwaya mucida* {1}, *Hyalorbilia inflatula* {1}, *Lachnum* aff. *virgineum* {1}, *Lasiosphaeria hirsuta* {3}, *Olla transiens* {1}, *Orbilia dryadum* {1}, *O. epipora* {1}, *O. eucalypti* {1}, *O. naumburgensis* {1}, *O. orientalis* {1}, *O.* ?*sarraziniana* {1}, *Pachyella violaceonigra* {1}, *Pleurothecium* sp. {1}, *P. recurvatum* {1}, *Scutellinia* sp. {1}, *Sporidesmium phaeosporum* {1}, *Subulicystidium longisporum* {1}, *Trichia* sp. {1}, *Tulasnella cystidiophora* {1}. **Desiccation tolerance**: after 1 week some excipular cells still viable, but all other elements dead; asci usually dead after half a day, some ascospores rarely viable after 27 months (H.B. 5163); conidia still viable after 2.5 months. **Altitude**: 5–865 m a.s.l. (temperate atlantic to subcontinental Europe), 5–1180 m (± mediterranean Europe), 100–1020 m (continental Europe & Asia). **Geology**: Ordovician silt- & sandstone, Silurian shale, Permian (Rotliegend), Buntsandstein, Muschelkalk, Keuper, Jurassic & Cretaceous sand-, mud-, silt-, marl- & limestone, dolomite, flysch, Tertiary clay, marl & molasse, Pleistocene loess, marl, peat; mica schist, gneiss, serpentinite, ophiolite, basalt. **Phenology**: throughout the year (especially in spring and summer).

Phenology of *O. crenatomarginata*

Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2	6	11	16	10	9	9	8	3	5	3	0

Taxonomic remarks. *Orbilia crenatomarginata* is characterized by small, strongly helicoid, narrowly fusoid, worm-shaped ascospores with ± obtuse apices and gradually tapered, tail-like bases, also by ± long glassy processes being agglutinated to form usually very distinct triangular teeth at the apothecial margin, and by the presence of ring- to horseshoe-shaped crystalloid SCBs, especially in the ectal excipulum (see Pls 458: 1f, 2i; 460: 1). For the morphologically very similar *O. laevimarginata* see p. 877.

The similar, mainly subtropical *O. scolecospora* differs merely in larger, especially wider spores and longer SBs, while the temperate to tropical, extra-European *O. vermiformis* and *O. nemaspora* of series *Xanthoguttulatae* differ, besides slightly larger spores, in the absence of glassy processes and in wider marginal cortical cells, finally in 1–3-septate conidia. The eastern Asian *O. pseudobrevistipitata* (series *Xanthoguttulatae*) differs, e. g., in lageniform paraphyses and in the upper spores inversely oriented, also in very short glassy processes. Ring-shaped crystalloid SCBs also occur in *O. scolecospora* and *O. laevimarginata*, while in *O. nemaspora* brick-shaped SCBs were observed.

Variation. *O. crenatomarginata* was found to show a comparatively low degree of variation. Mainly the length of the glassy processes and consequently that of the marginal teeth varied, resulting in either distinctly denticulate or sometimes almost even margins. Very short to almost absent teeth were only seen in a few collections, e. g., in one from Wienerwald, in which the ca. 10 µm long glassy processes formed an indistinctly crenulate margin (IVV: H.B. 5254). Sometimes, toothed and ± smooth apothecia grew intermingled, e. g., in Pl. 458: 6 and Pl. 459: 9, 11. In any case, the glassy processes were never entirely absent on the marginal cells.

In extra-European collections, distinctly denticulate margins were reported by Spooner (1987: 188, USA) and Raitviir (1991: 362, Russian Far East), and were also observed in the here reported specimens from Middle and Northern America, and central and eastern Russia. Though not explicitly mentioned, marginal teeth were probably also present in a report from Michigan (USA) by Kanouse (1936: 99). The so far single record on coniferous wood (*Larix*, Yakutsk, northeastern Russia, Pl. 459: 9, IVV: H.B. 8705) did not differ in any respect from those on angiosperm substrate.

Slight variation was noted in spore width, ranging from †0.5–0.6 µm (type of *O. crenatomarginata*) up to †0.7–0.8 µm (type of *O. crystallina*). Spore curvature and also shape slightly varies among the here illustrated collections. This variation is particularly obvious when comparing spores in the dead state; it might originate from influences during dying, such as collapsing, or to some degree from inexact observation. A spore size of *8.5–10.5 × 0.8–0.9 µm was observed in a very recent sample from England (N. Aplin pers. comm.), the seemingly first record for the British islands, its length distinctly exceeding the typical values.

Literature reports. The differences which Boudier (1904–10) saw between *H. crystallina* (on *Salix*) and *H. roseola* (on *Tilia*) rely exclusively on macroscopy. He described the apothecia of his *H. roseola* (l.c., p. 269, pl. 465, as *H. rosella*) as pale rose, with obtuse marginal teeth and a very short and broad stipe; those of his *H. crystallina* (l.c., p. 269, pl. 466) were entirely white, with more prominent acute marginal teeth and without a stipe. In the present study no correlation between these features and the inhabited hosts could be observed. The microscopic features always concurred quite well among the specimens from different hosts. As in the type of *H. crystallina* on (?)*Quercus* (Pl. 458: 7) no apothecial stipe could be observed in our study of the *H. roseola* collection, and the marginal teeth were very similar though sometimes absent (Pl. 458: 6).

The dimensions of dead asci and spores in the lectotype of *H. crystallina* as evaluated by Spooner (1987, Pl. 458: 8) and in the present study closely concur with those of the other here studied collections on various substrates, except for a few details: contrary to Spooner's analysis, the paraphyses are branched and densely septate in their lower part. Spooner described the spores as 'laterally flattened', which appears to correspond to a strong constriction a little below the centre in some of the spores drawn by him. This peculiarity was not seen by us in any of the studied specimens, irrespective of whether the spores were alive or dead. Living discharged spores are actually circular in cross section. Since dead spores often become more or less laterally flattened by collapsing during shrinkage, the reported constriction is undoubtedly present only in dead spores.

Inaccurate reports of cylindrical spores without distinctly tapered ends are found in Quélet (1878), Boudier (1904–10: pl. 466), Breitenbach & Kränzlin (1981), and Raitviir (1991: 362). Boudier's description gives a spore size of 10–12 × 2 µm for *H. roseola* and 8–11 × 2 µm for *H. crystallina*. From his plates, however, a size of 8.5–10.5 × 1–1.3 and 8.5–10.2 × 0.9–1.1 µm can be evaluated, respectively (direct distance from end to end). Also Quélet (1878) gave a spore size of '0.012 mm'. Possibly these high values refer to the actual length of the helicoid spores rather than to the length in situ. Under the name *O. crenatomarginata* Velenovský (1934: 102) reported some Bohemian collections with a denticulate margin (on *Alnus*, *Carpinus* and *Quercus*), which appear to fit our present concept, although he figured strongly helicoid spores with often 1.5–2 turns (Fig. 154: 3). Priou & Poncelet (2006) provided a detailed account under the name *O. crystallina*, based on two fresh specimens from Bretagne and Rhône-Alpes. Their illustration includes spore bodies and horseshoe-like crystalloid SCBs in the excipular cells.

Nomenclature and type studies. When transferring *Helotium crystallinum* to *Orbilia*, Baral (1994) overlooked the homonym *Orbilia crystallina* Rodway. Followingly, the combination *Orbilia crystallina* (Quél.) Baral is a nomen illegitimum (ICN 53.1) and the next oldest epithet *crenatomarginata* has to be chosen as basionym of the present species.

Quélet (1878) described ***Helotium crystallinum*** based on two collections, one with white apothecia from bark of *Salix* near Paris (leg. É. Boudier) and 1 with finally rosaceous apothecia from bark of *Quercus*, probably from French Jura (?leg. L. Quélet). A third collection (from bark of *Tilia*, Doubs), had pale rose apothecia and was collected by Quélet shortly after he published *Helotium crystallinum*. Although Quélet (1878) did not mention the difference in colour between the two first samples, he (in sched.) attributed the *Tilia* collection the rank of a variety (as '*Cistella cristallina* Q. v. *roseata*') when transferring *H. crystallinum* to *Cistella*, apparently mainly because of its rose colour. Boudier (1885) described his new genus *Hyalinia* on the basis of the *Salix* collection, but he had also examined Quélet's *Tilia* collection (see Boudier 1904–10: 269, pl. 465). Contrary to Quélet, Boudier distinguished the two collections at the species level by naming the *Salix* specimen *Hyalinia crystallina* and the *Tilia* specimen *H. rosella* (Fr.) Boud. (a misspelling for *roseola*). Boudier's separation into two species was accepted during a reexamination by Nannfeldt (1932: 266), but also by Grelet (1948b: 105) and Moser (1963) who merely copied Boudier's opinion and data.

The 'very abundant' *Salix* collection from Paris was not examined in the present study. It was depicted by Boudier in the fresh state (Boudier 1904–10: pl. 466), and his plate does not leave any doubt about its identity with *O. crenatomarginata*. Boudier stated that both *H. crystallina* and *H. roseola* are rather rare species, and we feel that he saw at that time only these two collections.

According to Nannfeldt (1932: 266), two specimens under the name *Cistella crystallina* are found in UPS, both obviously from Quélet's herbarium. One of them is the *Tilia* collection depicted by Boudier under the name *H. rosella*. This specimen ('Champ. Vallon, on [bark of] *Tilia*, 31.III.1879, L. O.'; the initials refer to Lucien Quélet) is redescribed here (Pl. 458: 6) and confirmed to be *O. crenatomarginata*. The data indicated by Boudier ('Dr Quélet qui l'avait trouvée en mars, dans le Doubs, sur des écorces de Tilleul pourries') undoubtedly refers to the collection from 'Champ. Vallon', according to a handwritten note by Quélet on p. 403 in his personal copy of Quélet (1873) (J.P. Priou pers. comm.).

The other specimen in UPS is undated and unlocalized, and it is the one that was redescribed by Nannfeldt (1932: 252), Spooner (1987: 187), and in the present study (see Pl. 458: 7–8). Though devoid of collection data, Nannfeldt (1932: 252) seems right when stating that L. Quélet is the finder of this specimen, because the included handwritten diagnosis says that the hymenium was 'finally rose', which excludes Boudier's collection. Apart from the rose colour, the diagnosis in this specimen corresponds quite well to the protologue of *Helotium crystallinum*. We conclude that this is the specimen on bark of *Quercus* from Jura. Since the protologue of *Helotium crystallinum* comprises two collections, a lectotype has to be chosen. Spooner (1987: 188) named the *Quercus* collection 'lectotype' in the collection data, which we consider as a valid lectotypification of this species. There is only bark present in the lectotype, and the host genus could not clearly be verified from the bark anatomy.

Obviously, the two illustrations by Boudier (l.c., pls 465–466) are based on authentic material of *Helotium crystallinum*. The *Salix* collection (pl. 466) was mentioned by Quélet in the protologue, thus should be considered as paratype of *H. crystallinum*. The *Tilia* collection (pl. 465) was made by Quélet after he published the taxon, hence it is only authentic material. *Hyalinia roseola* in Fries's sense is a doubtful taxon (see p. 1683).

Four authentic specimens of ***Hyalinia crenatomarginata*** from FH were examined, and the identity with *H. crystallina* is confirmed here, which was also asserted by Svrček (1954: 20) without type study and without any comment. Two of the specimens were mentioned by Höhnel in the protologue and bear handwritten data of his diagnosis. In one (from Haltertal) no apothecia could be found, whereas the other (from Judenau) is very rich and is illustrated here (Pl. 458: 5). Höhnel's notes on the label of the latter specimen have clearly contributed to the data in the protologue. The specimen from Judenau (V.1906, FH) is designated here as **lectotype** of *O. crenatomarginata*, and a specimen from Germany (Merseburg, on *Tilia*, IVV: H.B. 9265), from which a sequence was gained, is designated here as **epitype**.

In the holotype of ***O. tiliacea***, Svrček (1954) found only a single minute apothecium (0.05 mm diam.) with immature asci 24–27 × 2–2.5 µm. Reexamination showed, however, that 12 small apothecia (rehydrated 0.05–0.17 mm) occur along the border of a beetle gallery. These have minute marginal teeth consisting of 15–30 × 2.5–3 µm large glassy processes. No asci were found in the two largest of them. Neither Velenovský nor Svrček saw marginal teeth, although there is no doubt that they were dealing with the same apothecia. Svrček considered *O. tiliacea* as a nomen dubium, but it is tentatively here placed in synonymy with *O. crenatomarginata* due to the teeth and the substrate. The ascospores reported by Velenovský (1–2 µm, ellipsoid, biguttulate) are probably stray spores.

Svrček (1954: 20) revised material of ***O. roseohyalina*** (Karlštejn, X.1926, PRM 151742) and designated it as lectotype, although this collection is not mentioned in Velenovský's protologue. However, it is mentioned on Velenovský's unpublished manuscript plate of that taxon, which contains three collections: two from Karlštejn (on wood of *Cornus*, 14.IV.1923; on wood of indet. angiosperm, X.1926) and one from Mnichovice (on *Robinia*, VII.1926). We assume that it was a lapsus when Velenovský omitted the collection of X.1926 in the protologue of *O. roseohyalina* which now represents the only preserved specimen.

The present study of this lectotype (Pl. 458: 3) on wood of ?*Salix*, according to the wood anatomy) confirms Svrček's result as being conspecific with *Hyalinia crystallina.* However, the material is a mixture: the fragments of a decorticated branch contain seven apothecia with denticulate margins, but also two of *Orbilia* (?)*sarraziniana*. Furthermore, a fragment of a detached bark bears immature *Orbilia ?aurantiorubra*. Velenovský's drawing shows denticulate apothecia and thick exudate which fit well *O. crenatomarginata*, whereas his depicted oblong-ellipsoid spores do not belong to the described *Orbilia*.

The holotype of ***O. curvatispora* var. *minor*** has asci and pars sporifera at the lower end of the length range of *O. crenatomarginata*, and comparatively small apothecia (0.15–0.35 mm) and marginal teeth (10–20 × 25–35 µm, glassy processes 8–20 × 2.8–3.5 µm), but the other characters of this Caribbean collection would fit well (Pl. 458: 4). Dennis' (1954) measurement gives longer and narrower spores than here found (8–10 × 0.3 µm) but his figure of mainly S-shaped spores (see Fig. 159: B) undoubtedly refers to a helicoid curvature, unlike *O. curvatispora* (= *O. auricolor*). Also the paraphyses are figured strongly capitate by Dennis, but they were not enlarged or only slightly to medium so in the present reexamination. Dennis overlooked the small marginal teeth, therefore, he did not compare this taxon with *O. crenatomarginata*. Because of the occurrence in the tropics and the rather small asci, the species should be compared with the subtropical Chinese *O. laevimarginata* or the genetically aberrant collection on *Quercus* bark from cold-temperate Northern America.

Anamorph. The presumed anamorph of *O. crenatomarginata* was two times observed in close association with the apothecia (Pl. 460: 2–3). The conidia differ from those of *O. vermiformis* and *O. nemaspora* (series *Xanthoguttulatae*) in being longer and with many more septa, while they resemble those reported for *O. cardui*, *O. clavispora*, *O. cotoneastri*, and *O. rhopalota* (series *Neodactylella* of section *Arthrobotrys*). They tend to be larger and more distinctly clavate instead of cylindrical as in some of those mentioned species. The conidia of *O. rectispora* (series *Neodactylella*) differ in being longer and narrower and more fusoid. A rather close match is observed to the type of *Dactylella rhopalota* as described by Drechsler (1943b), which differs in sometimes proliferating (geniculate) conidiophore tips and in being isolated from leaf mould. Its conidia fit quite well, especially H.B. 6635, though they tend to be longer in the

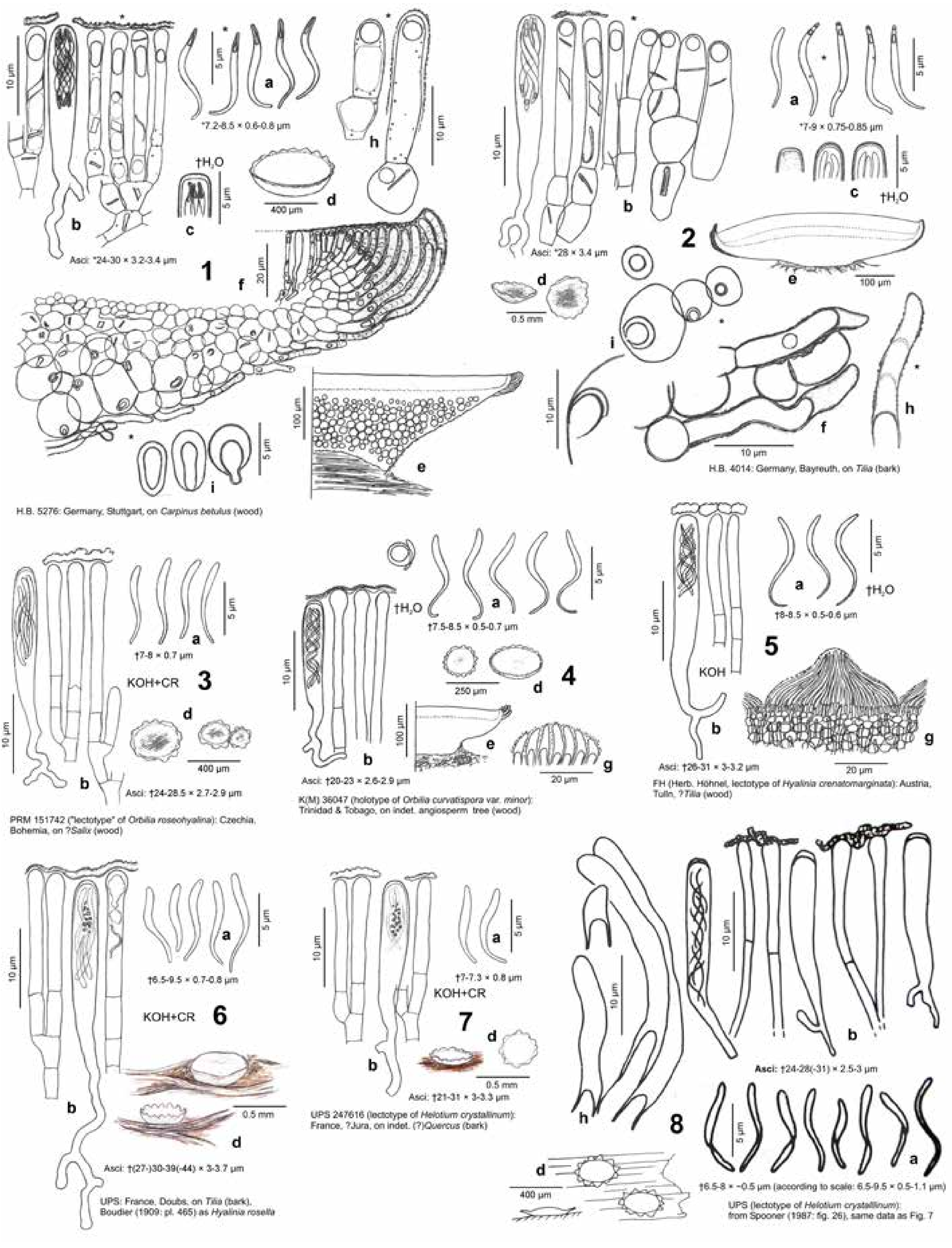


Plate 458. **1–3**, **5–8**: *Orbilia crenatomarginata*; **4**: *O.* cf. *crenatomarginata*. – **a**. ascospores (**4a** in top view); **b**. asci and paraphyses, the latter containing globose/elongate and crystalloid SCBs (**2b** right: transitional marginal elements); **c**. ascus apices; **d**. fresh or rehydrated apothecia with dentate margin; **e**. apothecia in median section; **f**. id., ectal excipulum at flanks and margin, with glassy processes, cells containing ring-shaped crystalloid SCBs; **g**. id., in external view; **h**. glassy processes; **i**. crystalloid SCBs in ectal excipular cells. – **8**. after Spooner (1987).

Plate 459. **1–14**: *Orbilia crenatomarginata*. – **11c**. Thermophilous beech-oak forest with fallen decorticated *Ulmus* log (on upperside below small bark pieces); **1a–b**, **3a**, **4a–b**, **5**, **6**, **9a–b**, **10a**, **11b**, **12**. fresh apothecia; **2**: conidiophores with conidia, associated with apothecia (dry); **3b**. apothecium in median section; **1c**, **4c**, **11a**. id., ectal excipulum at flanks and margin; **3c–g**, **4d–e**. crystalloid SCBs in cells of ectal excipulum; **13**. asci (SBs stained by CRB); **7–8**, **10b**, **14**. ascospores. – Living state, except for asci in **13**. – **4a–b**: phot. J.P. Priou, **6**: phot. J. Labrecque, **7**: phot. P. Perz, **8**: phot. G. Marson (oblique illumination), **10a–b**: E. Rubio, **13**: I. Wagner, **14**: P. Tanchaud. — **1a–c**. H.B. 7916: France, Ain, on *Betula*; **2**. H.B. 7440: Germany, Rhön, on *Tilia*; **3a–g**. H.B. 8146b: France, Niort, on *Carpinus*;

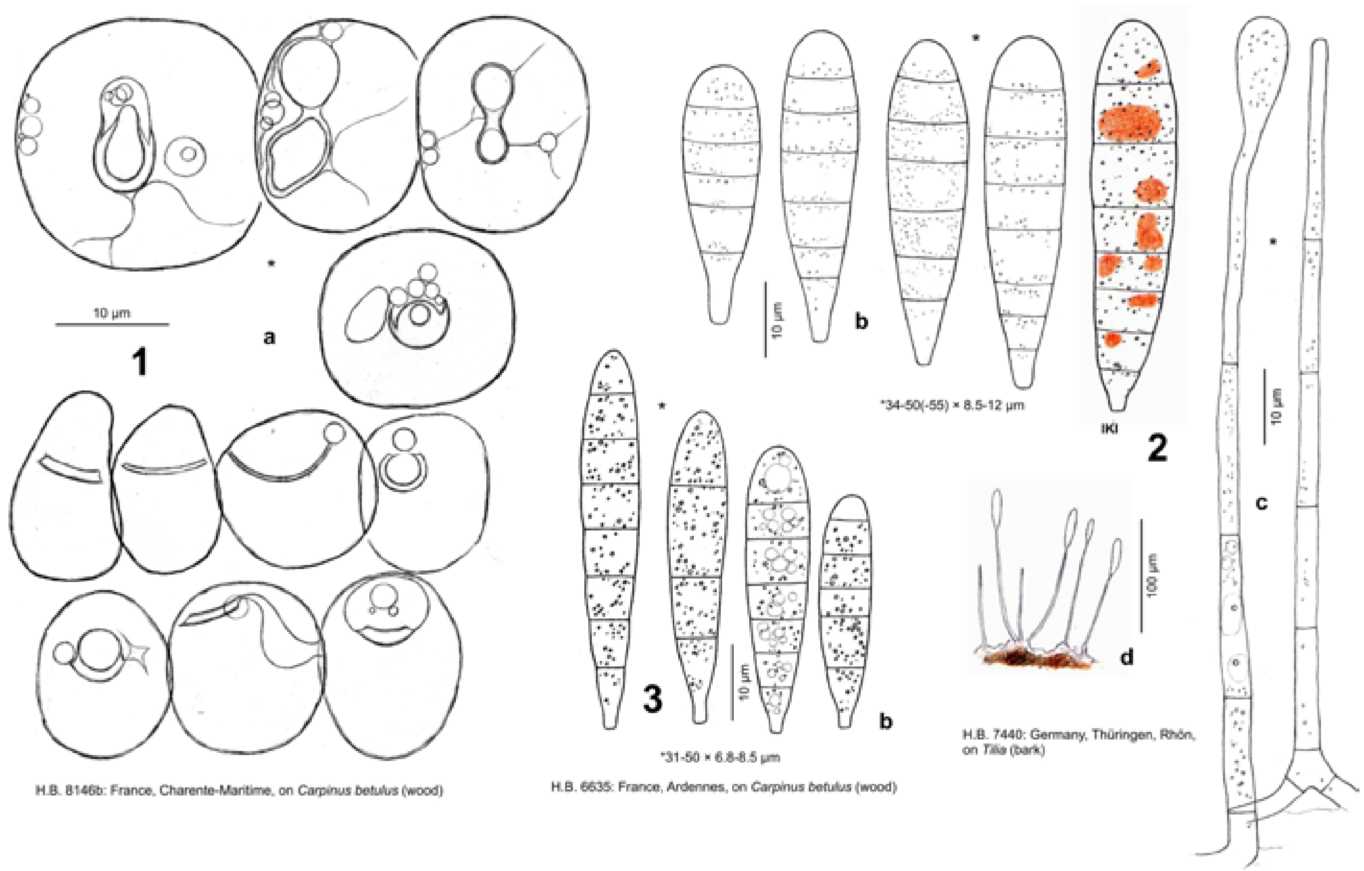


Plate 460. **1–3**: *Orbilia crenatomarginata*. – **a**. ectal excipular cells containing globose and crystalloid SCBs; **b**. conidia from substrate (right conidium in IKI staining glycogen); **c–d**. conidiophores with conidia, from substrate.

protologue (*36–60 × 6.7–9.6 µm) and with up to 10 septa. In H.B. 7440 numerous projecting conidiophores occur over the uneven inner surface of bark (Pl. 459: 2), and the conidia at their tips are distinctly wider than in H.B. 6635 and also wider than in the type of *D. rhopalota* (see Pl. 460).

D. minuta closely resembles the present anamorph in conidial shape, but differs in distinctly larger conidia. Also *O. xinjiangensis* (series *Neodactylella*) has smaller conidia than given for *D. minuta*. Grove (1884) gave the conidiophores of *D. minuta* as 120–150 µm long and the conidia as 60–70 × 14–15 µm. From the magnification of the two figured conidia a size of 60–68 × 13–14 µm can be evaluated, while the sketch under smaller scale shows conidiophores of c. 110–185 µm length and conidia of roughly 60–75 × 16–19 µm. Given that these data are correct, *D. minuta* seems to represent a species different from *O. crenatomarginata*. The type material of *D. minuta* exists in K (Rubner 1996) and consists of a piece of dead wood though without any trace of the fungus. A culture was probably not made by Grove, and further records are unknown.

Phylogeny. The two sequences gained from apothecia of European specimens (H.B. 9265, Merseburg, on *Tilia*; H.B. 9452, Tübingen, on *Ulmus*) comprise SSU, ITS, and LSU. In H.B. 9452 the S1506 intron is present whereas in H.B. 9265 it is absent. The two strains show a distance of 1.6% in the ITS region and 0.5% in the LSU (D1–D2). From Chinese *O. laevimarginata* they deviate by 8.5–12% in the ITS, and by 17.5–18.5% in the intron. *O. scolecospora* differs from *O. crenatomarginata* by 17–18% in the ITS, and *O. crenatofalcata* by 18%.

O. crenatomarginata and *O. laevimarginata* clustered in a strongly supported clade in our analyses of ITS (Phyls 16, S15) or in a weakly supported clade when analysing the intron (S14). *Dactylella rhopalota* as represented in GenBank (strains from Netherlands identified by Rubner 1996) falls in series *Neodactylella* of section *Arthrobotrys*, therefore, *D. rhopalota* is not the anamorph of *O. crenatomarginata*, at least in the sense of Rubner.

Ecology. *O. crenatomarginata* grows on ± strongly rotten wood and bark of hygric branches and logs or stumps of angiosperm trees (mainly *Tilia* {23} and *Salicaceae* {13}), exceptionally gymnosperms (*Larix*). *Tilia* seems to be a favourite substrate, which was also suspected by Engel (1994) who found the species 'very frequently' on that host, mostly on bast, in the northern Frankenalb near Bayreuth (Bayern). Already Svrček (1978) mentioned for Czechia a frequent occurrence on bast of *Tilia*. As more rare substrates he mentioned *Carpinus*, *Sorbus aucuparia*, and *Salix*, and Kotlaba (1981, from Karlštejn) *Betula pendula*. *Quercus* as substrate was indicated by Quélet (1878), Velenovský (1934: 102), and Spooner (l.c.).

O. crenatomarginata was recorded in atlantic to continental, humid to sometimes semihumid, supra- to orotemperate central and eastern, but also in mesotemperate western and suprasub- to mesosubmediterranean southern Europe, very continental oroboreal subhumid (winter-dry) northeastern Asia (Yakutsk), and cold-temperate to hemiboreal humid North America. Also Kanouse (1936: 99, Michigan) and Spooner (1987: 188, Ithaca)

4a–e. H.B. 7683: France, Ille-et-Vilaine, on *Tilia*; **5**. H.B. 9304: France, Essonne, on *Tilia*; **6**. H.B. 9005: Canada, Québec, on *Populus*; **7**. P.P. 20070827: Poland, Kłodzko, on *Tilia*; **8**. 17.III.2007: Luxembourg, on indet. angiosperm; **9a–b**. H.B. 8705: Yakutia, on *Larix*; **10a–b**. E.R.D. 4724: Spain, Asturias, on *Eucalyptus*; **11a–c**. H.B.: 9452: Germany, Tübingen, on *Ulmus*; **12**. H.B. 8704: Yakutia, on (?)*Salix*; **13**. 15.IV.2011: Germany, Grimma, on *Betula*; **14**. 16.V.2015: France, Rochefort, on indet. angiosperm.

reported specimens from the northeast of USA (but see under *O. laevimarginata*, p. 879), and Raitviir (1991: 362) from the far east of Russia (Primorje). It is remarkable that only a single very recent record from Great Britain and Denmark and none from Scandinavia came to our notice. The type of *O. curvatispora* var. *minor* from the Caribbean region represents the only sample from the humid tropics, in case it does not belong to *O. laevimarginata* or a different species.

Map 81. Known distribution of *O. crenatomarginata* in Europe.

The vegetation in central Europe includes various acidic to calcareous deciduous forests in shady valleys and creeks as well as thermophilous slopes. *O. crenatomarginata* is a desiccation-sensitive species that grows on the underside of fallen branches and logs. Although a single collection was made on a dry hanging, 2 cm thick branch in 17 m above the ground, the apothecia were only obtained in a moist chamber several weeks after collection (M. Unterseher pers. comm.), therefore, it is assumed that they grew under constant moisture conditions and were not present when the branch was collected. This deviated from typical specimens merely in very indistinct marginal teeth of very short glassy processes.

Specimens included. **GREAT BRITAIN**: **South East England**, **West Sussex**, 5.5 km E of Haywards Heath, 9 km WNW of Uckfield, Sheffield Park, 51 m, branch of *Carpinus betulus*, on wood, 4.IX.2019, N. Aplin (N.A. 4919, anam. substr., doc. vid.). — **DENMARK**: **Sjælland**, 3 km S of Tibirke, 1.3 km NW of Ramløse, S of Ellemose, 5 m, log of *Salix*, on bark, 2.VIII.2015, T. Læssøe (C [tl-2015-710846], doc. vid.). – 1.8 km ESE of Lillerød, Allerød Sø, 47 m, log of *Salix*, on wood, 2.VIII.2015, R. Riis-Hansen & T. Rønhave Larsen, vid. T. Læssøe (doc. vid.). — **GERMANY**: **Brandenburg**, Märkisch-Oderland, 14 km ESE of Eberswalde, 3.5 km NW of Bad Freienwalde, Räuberlinde, 3 m, branch of *Tilia*, on bark, 15.VIII.1973, D. Benkert (BHU, as *O. curvatispora*). – **Sachsen**, 6 km NNE of Chemnitz, 1 km E of Glösa, Indianerteich, 330 m, log of *Populus*, on wood, 22.VIII.1998, M. Eckel (H.B. 6212b). – 7.5 km SE of Chemnitz, E of Einsiedel, Einsiedler Wald, 390 m, branch of *Tilia*, on wood, 25.IV.2011, B. Mühler (ø, doc. vid.). – 6 km NW of Leipzig, 1 km SW of Wahren, Burgaue, 100 m, branch of *T. cordata*, on wood, 13.VI.2003, M. Unterseher (LZ, H.B. 7431). – 14 km SW of Grimma, 3 km W of Bad Lausick, Schildholz, 155 m, log of *Betula*, on wood, 15.IV.2011, N. Hiller, vid. I. Wagner (ø, doc. vid.). – **Sachsen-Anhalt**, 29.5 km NNW of Magdeburg, 7.3 km NNW of Colbitz, Colbitzer Heide, 86 m, log of *Tilia*, on wood, 1.XI.2018, T. Richter. – 17 km WSW of Merseburg, 2.5 km WSW of St. Micheln, Müchelholz, 190 m, branch of *Tilia*, on bark, 5.IV.2010, S. & P. Rönsch (ex H.B. 9265, M-0291776, epitype; sq.: KM248772). – 5.3 km WSW of Freyburg, ESE of Hirschroda, Balgstädter Lehden, 160 m, branch of *Tilia*, on wood, 13.IX. & 11.X.2008, W., E. & A. Huth (ø, doc. vid.). – 2.7 km WSW of Naumburg, S of Almrich, Sperlingsholz, 195 m, branch of *Fagus sylvatica*, on wood, 24.VIII.2006, W. Huth (ø, non vid.). – 4 km N of Naumburg, 1.5 km E of Großjena, Gerodig, 170 m, branch of *Prunus cerasus*, on wood, 20.V.2007, W. Huth (ø, non vid.). – ibid., log of *Populus tremula*, on wood, 13.IX.2008, W. Huth (ø, non vid.). – 5 km NW of Naumburg, 1.2 km NW of Kleinjena, Poppera-Holz, 200 m, branch of *Fraxinus excelsior*, on wood, 20.IV.1987, W. Huth (JE, non vid.). – ibid., IV.1988, W. Huth (W.H., non vid.). – **Thüringen**, Wartburgkreis (Rhön), 10 km WNW of Meiningen, 1.5 km NNW of Kaltennordheim, Karlsberg, 450 m, branch of *Tilia*, on bark, 24. XI.2003, L.G. Krieglsteiner (L.K., H.B. 7440, anam. substr.). – **Bayern**, **Oberbayern**, 20 km NE of München, 10 km WSW of Erding, Eichenrieder Moos, 470 m, log of *Salix*, on wood & bark, 16.V.1975, A. Einhelliger 128/5 (as *H. crystallina*, M). – **Oberfranken**, 21 km W of Bayreuth, 2.8 km NW of Hollfeld, ESE of Freienfels, Lindenallee, 430 m, branch of *Tilia*, on bark, 24.II.1990, H. Engel (H.E. 12671, H.B. 4014). – ibid., branch of *Tilia*, on bark, 1.V.1990, H. Engel (H.E. 12913, H.B. 4068). – 14 km S of Coburg, 2 km N of Unnersdorf, Heidleite, 330 m, on bark of *Tilia*, 2.IV.1993, H. Engel (H.E. 93/02–13, H.B. 4955). – **Baden-Württemberg**, 3.5 km N of Stuttgart-Vaihingen, 1.8 km NE of Büsnau, N of Pfaffensee, 430 m, log of *Carpinus betulus*, on wood, 30.IV.1995, A. Gminder (H.B. 5276). – 6 km NE of Tübingen, ENE of Pfrondorf, Tiefenbach, N of Einsiedlersteg, 410 m, log of *Tilia cordata*, on wood, 4. VIII.1992, H.O. Baral & K. Siepe (H.B. 4727). – ibid., E of Einsiedlersteg, 420 m, stump of *Tilia*, on wood, 13.X.1996, H.O. Baral (H.B. 5631a). – E of Pfrondorf, Tiefenbach, 385 m, branch of *Fagus sylvatica*, on wood, 24.IX.2018, H.O. Baral (ø). – 1 km SE of Pfrondorf, S of Rauhalde, 345 m, log of *Ulmus*, on bark, 3.II.2002, H.O. Baral (H.B. 7097). – ibid., 14.XI.2010, H.O. Baral (H.B. 9452 ø; sq.: KM248771). — **LUXEMBOURG**: **Gutland**, **Luxembourg**, 1 km NE of Luxembourg, Fort Thüngen, 310 m, on bark of ~*Tilia*, 26.VII.1901, V. Noppeney (LUX 42496, Feltgen as *O. leucostigma*, on *Pinus*). – 7.5 km SE of Luxembourg, 0.8 km NW of Hassel, Louknoeppel, 327 m, on indet. angiosperm, 17.III.2007, B. Schultheis, vid. G. Marson (ø). — **FRANCE**: **Bretagne**, **Ille-et-Vilaine**, 3 km NNE of Guichen, 1 km SW of Le Pont-Réan, La Massaye 62 m, bark of *Tilia*, 15.II.2005, J.P. Priou & A. Poncelet (J.P.P. 25031, H.B. 7683). – **Pays de la Loire**, **Maine-et-Loire**, 3 km NE of La Pommeraye, 0.5 km NW of Chateaupanne, *Salix*, 22.V.1997, J. Mornand (non vid.). – **Poitou-Charentes**, **Charente-Maritime**, 6 km NW of Rochefort sur mer, near St.-Laurent de la Prée, Bois Madame, 5 m, branch of ?*Quercus*, on bark, 18.III.2007, J. Robert (doc. vid.). – 19 km S of Rochefort, 3 km WSW of St.-Gemme, La Grande Vergne, 26 m, branch of indet. angiosperm, on wood, 16.V.2015, P. Tanchaud (ø, doc. vid.). – 25 km SSE of Niort, 2.5 km ESE of la Villedieu, Forêt d'Aulnay, La Borne St.-Léger, 115 m, branch of *Carpinus betulus*, on wood, 28.IV.2006, P. Tanchaud (H.B. 8146b). – **Île de France**, **Val de Marne**, 35 km SE of Paris, 3.5 km WSW of Nandy, Forêt de Rougeau, 74 m, on wood of *Salix*, 3.VI.2006, M. Pellerin & F. Valade, vid. J.P. Priou (J.P.P. 26223, non vid.). – **Val-d'Oise**, Forêt de Montmorency, on bark of *Salix*, III., É. Boudier (as *Hyalinia crystallina*, doc. vid.). – **Essonne**, 35 km S of Paris, near Mennecy, Parc de la Mairie, 90 m, branch of *Tilia*, on bark, 22.IV.2010, R. Chalange (H.B. 9304). – **Hauts-de-Seine**, 15 km SW of Paris, 3 km SE of Versailles, ca. 3 km NW of Jouy-en-Josas, Forêt de Versailles 140 m, branch of *Carpinus betulus*, on wood, 8.IV.2010, R. Dossogne (H.B. 9278a). – **Champagne-Ardenne**, **Ardennes**, 12 km SW of Charleville-Mézières, near Guignicourt-sur-Vence, Bois de Bagnolet, 220 m, branch of *Tilia*, on bark, 10.III.1998, O. Lanfranchi (ø). – 8 km SW of Sedan, 1 km NW of Chéhéry, Bois de la Queue, ~200 m, branch of *Carpinus betulus*, on wood, 2.V.2000, L. Ferry (H.B. 6635, anam. substr.). – **Bourgogne**, **Côte-d'Or**, 26 km NE of Dijon, 2.5 km W of Bourberain, Forêt de Velours, 275 m, log of *C. betulus*, on wood, 7.VII.2008, A. Gardiennet (A.Ga. 08JT5, doc. vid.). – **Saône-et-Loire**, 11 km W of Autun, 1.3 km ESE of La Grande-Verrière, SSW of Sénavelle, 390 m, branch of *Salix caprea*, on wood, 20.I.2011, J.P. Dechaume (doc. vid.). – **Franche-Comté**, **Doubs**, Champ. Vallon [unlocalized], branch of *Tilia*, on bark, 31.III.1879, L. Quélet (UPS, as '*Cistella cristallina* v. *roseata*', type of *Hyalinia roseola*, H.B. 7337 ø). – [Haut Jura], unlocalized, branch of [*Quercus*], on bark, [no date], [?L. Quélet] (UPS:BOT:F-015652, **lectotype** of *Helotium crystallinum*, Spooner 1987 erroneously as 'wood', H.B. 7338 ø). – **Rhône-Alpes**, **Rhône**, 14 km S of Lyon, Sérézin-du-Rhône, Île de la Table

Ronde, 160 m, on wood of *Populus nigra*, 15.IV.2013, N. Van Vooren (N.V. 2013.04.20, doc. vid.). – **Ain**, 1.8 km WNW of Cormaranche-en-Bugey, 2 km SW of Hauteville-Lompnes, Marais de Vaux, 760 m, branch of *Betula*, on wood & bark, 20.IV.2002, N. Van Vooren (H.B. 7916, J.P.P. 25136, Priou & Poncelet 2006 as *Salix*). — **SPAIN**: **Asturias**, 6 km SE of Avilés, SE of Núñez, *Eucalyptus* plantation, 200 m, fragment of *Eucalyptus globulus*, on wood, 21.III.2009, A. Suárez, vid. E. Rubio (E.R.D. 4724, doc. vid.). – **Aragón**, **Huesca**, 4.3 km SW of Benasque, SW of Embalse de Linsoles, 1180 m, branch of *Corylus avellana*, on wood, 15.VII.2018, R. Blasco (doc. vid.). – **Cataluña**, **Barcelona**, Pre-Pyrenees, Sierra del Cadí, 7 km NNW of Guardiola de Berguedà, 4.5 km NNW of Bagà, WNW of Gréixer, l'Estanyet de Gréixer, 1175 m, branch of *Fagus sylvatica*, on wood, 19.VII.2014, J. Bometón (J.B. 516/14, doc. vid.). – ibid., ENE of Gréixer, Riu de l'Hospitalet, 1050 m, branch of *Corylus avellana*, on wood, 19.V.2017, J. Bometón (J.B. 672/17, doc. vid.). — **SWITZERLAND**: **Obwalden**, ~1 km W of Giswil, Lauibach, 500 m, branch of *Salix*, on wood, 22.III.1980, T. Honermann (NMLU 2203–80 Ho1, as *Hyalinia rosella*). – **Luzern**, 2.8 km NE of Luzern, 0.4 km N of Dietschiberg, Hombrig, 585 m, indet. angiosperm, on wood, 2.VII.2011, U. Graf (NMLU). – **Jura**, 6.5 km N of Tramelan, 2.7 km E of Montfaucon, Plain de Saigne, 865 m, branch of *Salix*, on bark, 3.VI.2017, U. Graf (doc. vid.). — **AUSTRIA**: **Niederösterreich** (incl. Wien), Wienerwald, 9 km WSW of Wien, near Lainzer Tiergarten, St. Veiter Tor, 250 m, log of ?*Populus*, on wood, 23.VI.1992, W. Jaklitsch (WU 13302, H.B. 5163). – 6 km NW of Wien, Bellevuestraße, 330 m, branch of *Prunus avium*, on wood, 11.III.1995, W. Jaklitsch (H.B. 5254). – 9 km W of Wien, S of Penzing, Moosgrund [Moosgraben], Haltertal [Halterbachtal], ~250 m, on wood of ?*Acer*, 28.VI.1904, F. v. Höhnel (as '?*Fagus*', no apothecia found). – ~2 km SSE of Pressbaum, [E of Pfalzau,] Hinterer Sattelberg, ~400 m, branch of *Carpinus betulus*, on wood, 17.VII.1907, F. v. Höhnel (FH). – Tulln, ~28 km WNW of Wien, near Judenau, ~190 m, branch of ?*Tilia*, on wood, V.1906, G. Boltmann (FH 00304814, **lectotype** of *Hyalinia crenatomarginata*, H.B. 6286 ø). – 25 km WSW of Wien, S of Pressbaum, Pfalzau, ~400 m, branch of *Carpinus betulus*, on wood, 21.V.1903, F. v. Höhnel (FH 00304816). – 19 km SSW of Wien, 1.4 km WNW of Gumpoldskirchen, Vierjochkogel, 640 m, log of *Tilia*, on bark, 8. III.2014, M. Mann (M.M. 140308-3). – **Kärnten**, 12 km SE of Klagenfurt, NW of St. Margareten im Rosental, 550 m, on wood & bark of indet. angiosperm, 11.VI.1993, W. Jaklitsch (H.B. 5115). – **Steiermark**, 6 km WNW of Feldbach, NE of Rohr a. d. Raab, 360 m, branch of indet. angiosperm, on bark, 20.III.2016, A. Gallé, vid. G. Friebes (G.F. 201600042, doc. vid.). — **CZECHIA**: **Central Bohemia**, near Karlštejn, ~300 m, branch of ?*Salix*, on wood, X.1926, J. Velenovský (PRM 151742, **lectotype** of *O. roseohyalina*, H.B. 6265a ø). – ibid., wood of *Tilia*, X.1926, J. Velenovský (PRM 148870, **lectotype** of *O. tiliacea*, H.B. 6423 ø). – **South Bohemia**, 13.5 km NNW of Písek, 1.3 km NW of Ostrovec, near railway viaduct over Lomnice river, 400 m, branch of *Tilia*, on old stromatic pyrenomycete, 15.VIII.1969, M. Svrček (PRM 684702, as *H. crystallina*, non vid.). — **SLOVAKIA**: **Bratislava**, 23 km NE of Bratislava, 5.3 km NNW of Senec, Martinský les, 149 m, branch of ?*Populus alba*, on wood, 30.IV.2016, A. Polhorský (A.P. 18/49, doc. vid.). — **POLAND**: **Lower Silesia**, Kłodzko, 9 km S of Kłodzko (Glatz), 2 km S of Żelazno, Bielica Mt., 420 m, branch of *Tilia*, on wood, 27.VIII.2007, P. Perz (P.P. 20070827–3, also 1. VII.2007, doc. vid.). – **Lublin**, 7.5 km NNE of Kazimierz Dolny, 1 km E of Parchatka, Kazimierski Park, 160 m, on log of indet. angiosperm, on wood, 18.IV.2009, B. Mazurek (P.P. 20090418-001-BM, doc. vid.). — **UKRAINE**: **Ivano-Frankivsk**, Nadvirna, 55 km W of Kolomyya, 5 km SE of Maksymets, Gorgany forestry, 1020 m, log of *Acer pseudoplatanus*, on bark, 20.VII.2012, A.Y. Akulov (ex CWU Myc 4911, H.B. 9716). – **Kharkiv**, 33 km SE of Kharkiv, NW of Mokhnach, 100 m, wood of *Quercus robur*, 24.IV.2012, I.I. Yatsiuk (CWU Myc D89, Morozova 2015, doc. vid.). — **SERBIA**: **Vojvodina**, Fruška Gora, 7.5 km S of Novi Sad, 4.7 km SE of Ledinci, Paragovo, 203 m, *Tilia tomentosa*, on wood, 18.III.2014, D. Savić (ø, doc. vid.). – ibid., 210 m, *T. platyphyllos*, on wood, 21.II.2007, D. Savić (ø, doc. vid.). – ibid., 235 m, on indet. wood, 17.IV.2015, D. Savić (ø, doc. vid.). – 13 km SSW of Novi Sad, ENE of Brankovac, 392 m, log of *Quercus petraea*, on wood, 9.IV.2019, D. Savić (doc. vid.). – 22.5 km WSW of Novi Sad, 2.3 km SW of Grabovo, Ravne, 200 m, branch of *Fagus sylvatica*, on bark, 5.VI.2014, D. Savić (FG-503, doc. vid.). — **MONTENEGRO**: 21 km NE of Podgorica, SSW of Bolesestra, 935 m, branch of *T. platyphyllos*, on bark, 28.II.2016, B. Perić (B.P. Dgf/C7D-28-02-16, doc. vid.). — **RUSSIA (WEST)**: **Bashkortostan**, **Meleuz**, SW-end of Ural Mts., 35 km ENE of Meleuz, Nugush, ~250 m, branch of ?*Tilia*, on wood, 13.VIII.1974, A. Raitviir (TAAM 63146, as *H. crystallina*, H.B. 8703 ø). — **RUSSIA (East)**: **Sakha** (Yakutia), 17 km NE of Yakutsk, near Tektyur, ~140 m, on wood of *Larix*, 22.VI.1968, H. Remm (TAAM 60461, as *H. crystallina*, H.B. 8705 ø). – ~800 km WSW of Yakutsk, ?25 km NW of Lensk, Zaharovka, ~240 m, branch of (?) *Salix*, on wood, 1.VII.1968, H. Remm (TAAM 60455, as *H. crystallina*, *Alnus*, H.B. 8704 ø). — **CANADA**: **Québec**, 17 km NNW of Québec, near Lac Beauport, 300 m, log of *Populus tremuloides*, on wood, 6.II.2009, J. Cimon, vid. J. Labrecque (J. Cimon 50077, H.B. 9005). – ibid., on wood of *Acer rubrum*, III.2009, J. Cimon (doc. vid.). – **Prince Edward Island**, 16.5 km WSW of Charlottetown, 1.5 km ENE of Bonshaw, log of *Populus*, on bark, 29.V.2019, A. Carter (doc. vid.).

Not included. **Trinidad**, 3 km NNW of Diego Martin, River Estate 45 m, log of indet. angiosperm, on wood, 13.I.1921, E.M. Wakefield (K(M) 36047, holotype of *O. curvatispora* var. *minor*, H.B. 5446 ø).

Orbilia laevimarginata Baral, Y. Zhang & Z.F. Yu, in Zhang et al., Phytotaxa 203: 247 (2015) — Pls 461–462, Map 82

Etymology: named after the typically smooth apothecial margin.
Typification: China, Yunnan, Qinglongzhen, branch of *Quercus*, 3.XI.2004, Z.F. Yu (ex H.B. 7667, M-0276498, holotype).

Description: — **TELEOMORPH**: **Apothecia** fresh (0.14–)0.2–0.5(–1.2) mm diam., 0.08–0.14 mm high (receptacle 0.05–0.06 mm), greyish-white to pale pink, translucent, round, gregarious; disc flat, eventually slightly to medium convex, margin thin, not protruding, smooth {3}, also with prominent broad teeth 25–30 × 60–80 µm, 12–14 per apothecium {1}; sessile on an obconical base, superficial. **Asci** *23–28(–32) × 3.4–3.6 µm {1}, †20–27 × (2.5–)2.9–3.2 µm {2}, 8-spored, spores *~4-seriate, ~4 lower spores inverted {1}, pars sporifera *9–15 µm long; **apex** (†) slightly to medium truncate (not indented, laterally not inflated); **base** with short to long, ± thick, flexuous stalk, L-, h- to Y-shaped. **Ascospores** *(6–)7–8(–8.5) × 0.75–0.9(–1) µm {4} (~9–10 µm actual length), †7.5–9 × 0.7–0.8 µm {3}, narrowly fusiform, apex ± acute, base gradually attenuated, with a thin tail of 1.7–3 × 0.15–0.4 µm, strongly curved (helicoid, twisted like a right-hand thread); **SBs** *1.8–2(–2.2) × 0.3–0.4(–0.5) µm {1}, subulate, apically narrowed to a small point, straight. **Paraphyses** apically uninflated to mostly slightly clavate-capitate, terminal cell *(8–)12–19 × 2–3.2 µm {1}, lower cells *2.5–5 × 1.7–3 µm {1}; branched only in lower part. **Medullary excipulum** hyaline, 10–15 µm thick, of dense textura intricata-angularis, indistinctly delimited from ectal excipulum. **Ectal excipulum** hyaline, of (†) thin-walled textura globulosa-angularis from base to mid flanks, 30–?80 µm thick near base, cells *13–22 × 11–17 µm {1}; 10–13 µm thick near margin, of t. angularis, marginal cortical cells *4.5–8 × 4–6 µm {1}, at uppermost margin of narrow cortical cells *5–8 × 2–3 µm oriented at a 10–20° angle to the surface; **glassy processes** absent or sometimes present, 1.5–2.5 × 2.8–3 µm {1}, high-refractive, somewhat stratified. **Anchoring hyphae** sparse, †2–2.7 µm wide, walls 0.2 µm thick {1}. **SCBs** in paraphyses globose, 1.7–2.6 µm diam., medium refractive, together with filiform to rhomboid or ring-shaped, hyaline crystalloid SCBs {1}; **VBs** absent. **Exudate** over paraphyses 0.2–0.5 µm thick, continuous, with scattered granules, loosely attached, over margin and flanks 0.3–1(–1.5) µm thick, ± cloddy. — **ANAMORPH**: dactylella-like (from ascospore isolate {3}). **Conidiophores** ± unbranched, septate, erect, *41–50 µm long, 3–4.3 µm wide at the

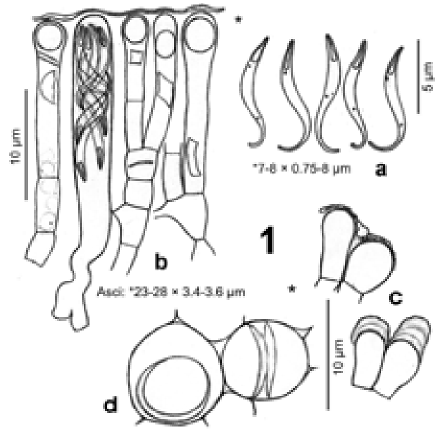


Plate 461. **1**: *Orbilia laevimarginata*. – **a**. ascospores; **b**. ascus and paraphyses (containing globose and crystalloid SCBs); **c**. marginal cortical cells partly tipped by glassy process; **d**. ectal excipular cells containing crystalloid SCBs.

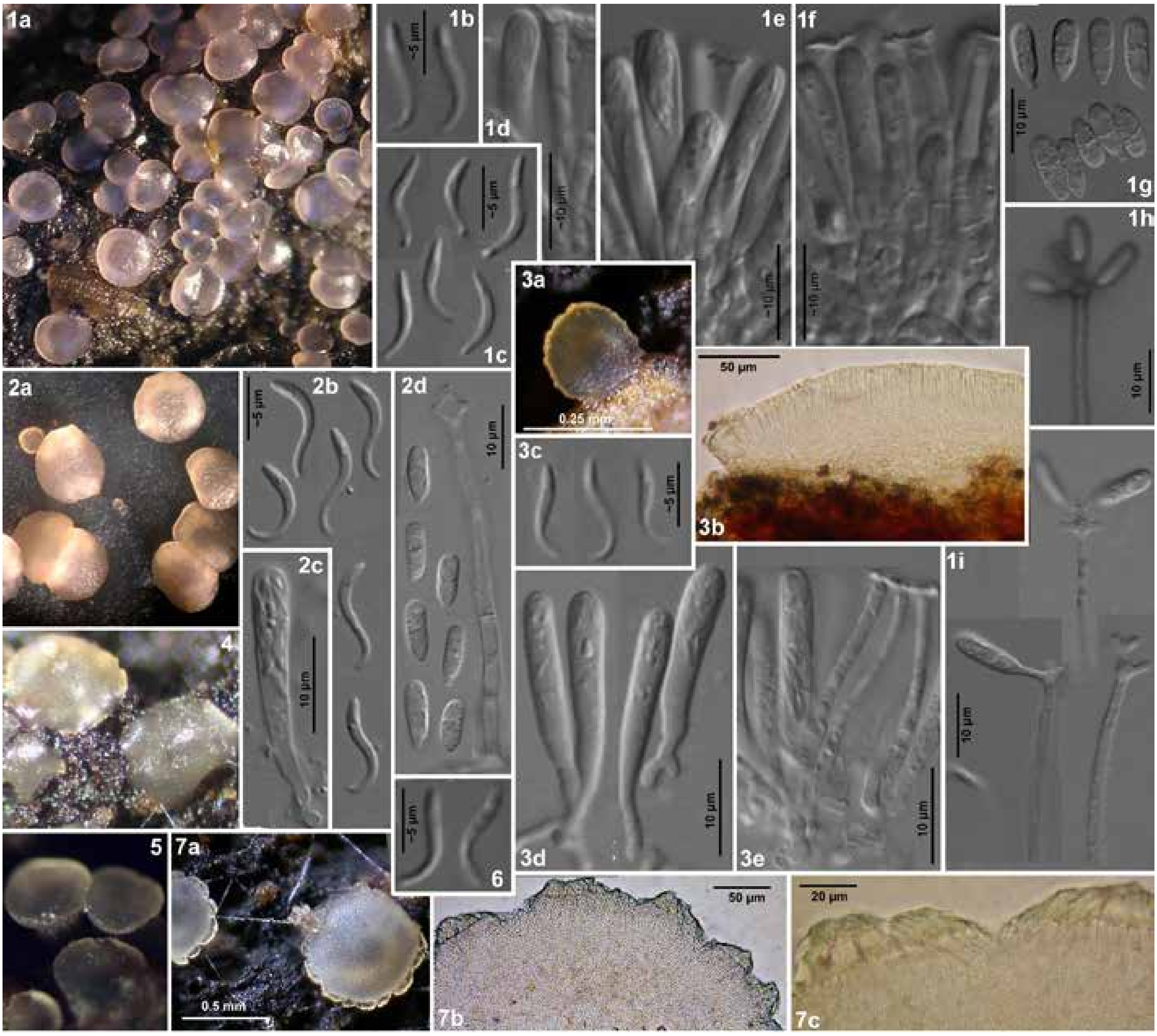


Plate 462. **1–6**: *Orbilia laevimarginata*; **7**: *O.* cf. *laevimarginata*. – **1a**, **2a**, **4**, **5**. fresh apothecia (**2a** on agar); **3a**, **7a**. rehydrated apothecia; **3b**. apothecium in median section; **7b–c**. dentate margin in top view; **1d–f**, **2c**, **3d–e**. asci and paraphyses; **1b–c**, **2b**, **3c**, **6**. ascospores (**1b** & **3c** from substrate, **1c** & **2b–c** from culture); **1g**, **2d**. conidia from culture; **1h–i**, **2d**. conidiophores from culture. – All ascospores and conidia and 2 asci (**1e**, **2c**) in living state. – **1**, **2**, **3c–e**: phot. Y. Zhang (DIC, p.p. from Zhang et al. 2015), **4**, **5**: phot. Z.F. Yu, **6**: from Liu et al. (2007a, DIC). — **1a–i**. YMFT 1.01833: China, Yunnan, Kunming, on *Quercus*; **2a–d**. YMFT 1.03013: ibid., Yuxi, on *Quercus*; **3a–e**. H.B. 7667 (holotype): ibid., Kunming, on *Quercus*; **4**. ?Z.F.Y. xz-1: ibid., Chuxiong, on indet. woody substrate; **5**. H.B. 8978b: China, Yunnan, Dali, on ?*Fagus*; **6**. HMAS 139521: China, Xishuangbanna, on indet. wood; **7a–c**. H.B. 8693: J.W.G. lq2–68: China, Yunnan, Yuxi, on indet. angiosperm.

base, tapering gradually to *1.3–1.6 µm at the tip, here expanded and bearing 1–10 denticles of 2–5 × 1.3–1.6 µm, conidia in capitate clusters (candelabrelloid), occasionally proliferating to form additional clusters. **Conidia** *(7.5–)8.5–12(–13) × 2.8–3.8 µm {3}, (0–)1(–3)-septate, cylindric-ellipsoid with conical to apiculate base, containing several small LBs. **Chlamydospores** absent. **Trapping organs** not observed when nematodes were added.

Habitat: on moist ground, corticated to decorticated, 4–5 cm thick branches of *Quercus* sp. {4}, ?*Fagus* sp. {1}, indet. woody substrate {2}, on entirely strongly decayed wood {4} and bark {2} (periderm and bast), without algae. **Associated**: *Helicogonium hyphodisci* (parasitic in *O. laevimarginata*) {1}. **Desiccation tolerance**: not tested (probably intolerant). **Altitude**: 1000–2700 m a.s.l. **Geology**: Proterozoic, Paleozoic & Jurassic to Cretaceous sedimentary rock; mafic volcanic & metamorphic rock. **Phenology**: VII–XI.

Taxonomic remarks. This taxon is only known from a few records from broad-leaved evergreen forests in Yunnan, southern China. It deviates from *O. crenatomarginata* in a typically ± smooth apothecial margin and a deviating anamorph. Glassy processes were either absent or very short and only occasionally seen. The marginal cortical cells are shorter and wider, also the ascospores tend to be more fusiform by having ± acute apices in comparison to *O. crenatomarginata*. *O. vermiformis* (series *Xanthoguttulatae*) differs in larger spores and conidia, and apparently also in the absence of crystalloid SCBs.

In the collection from Xishuangbanna (HMAS 139521) reported by Liu (2006: 67) and Liu et al. (2007a), the spore apices are less acute, and the marginal cortical cells more elongate (~ 11 × 4–5 µm) by forming a distinct textura porrecta. This texture is reminiscent of *O. crenatomarginata*, though it seemed to lack distinct glassy processes, judging from the photo. However, Liu (l.c.) mentioned glassy processes of 9.5–16 × 2.5–3 µm in his description, and a microphoto that was not included in his thesis shows prominent broad teeth 25–30 × 60–80 µm, 12–14 per apothecium (B. Liu pers. comm.).

Not included collections. Spores and marginal cortical cells similar to the latter specimen were noted in two Chinese records examined by us (H.B. 8693, Pl. 462: 7; H.B. 8744), which possess glassy processes of ~10–20 µm length forming distinct marginal teeth. An anamorph was not observed in these samples with glassy processes and DNA data were not gained, therefore, they are not included in the above description.

A collection on inner surface of *Quercus* bark from Boston, Massachusetts (IVV: bhi-F121b) was only studied in the dead state. It has apothecia with very distinct marginal teeth of 15–30 × 20–80 µm and spores that fit well *O. laevimarginata* or *O. crenatomarginata*. However, its DNA data suggest a species intermediate between both (see below). A not examined, unillustrated collection on *Quercus* bark from Ithaca, New York, identified as *Orbilia crystallina* by Spooner (1987: 188), might belong here. Also the two Canadian collections on *Acer* and *Populus* here included in *O. crenatomarginata* would require molecular investigation.

Anamorph. An anamorph was obtained in pure culture of three samples (no culture was obtained in qlx-1, and B. Liu's culture did not sporulate). In sharp contrast to the presumed anamorph of *O. crenatomarginata*, the conidia are much smaller and possess only 0–3 septa, emerging from 1–10 prominent denticles clustered at the tip of conidiophores (Pl. 462: 1g–i, 2d, Zhang et al. 2015), somewhat similar as in drechslerella-like anamorphs. However, no trapping devices were formed in contact to nematodes.

Phylogeny. Sequences were available for four Chinese samples and one from North America, comprising ITS, four also the S1506 intron (the one from Xishuangbanna did not cover the intron region). In our phylogenetic analyses of the ITS region, *O. laevimarginata* clustered in a weakly supported clade sister to the European *O. crenatomarginata* (Phyls 16, S15, see also Zhang et al. 2015). Rather high distances occur among the four Chinese sequences: the two samples from Dalongkou (ym-87 and ym3-52) differ by a 1.5 % ITS distance from each other (2 % in the intron), the sample from Xishuangbanna (HMAS 139521) deviates from those by 5–6 % in the ITS, and that from Kunming (ya-17) by 7–8 % (3.5–4 % in the intron). The latter two differ from each other by 6.5 % in the ITS. The distance of European samples of *O. crenatomarginata* to all these Chinese strains ranges at 8.5–12 % in the ITS (18–19 % in the intron).

The sample from Massachusetts (bhi-F121b) comprises SSU V2–V5, S1506 intron, and ITS (ITS2 incomplete). It clustered in the ITS region among the variable sequences of *O. laevimarginata* with a 4–6.5 % distance (8.5 % to *O. crenatomarginata*), whereas the S1506 intron suggests a slightly closer relationship to *O. crenatomarginata* (12.5 %, 14.5–15.5 % to *O. laevimarginata*). This high distance in the intron, compared to only 2–4 % among the three *O. laevimarginata* strains, suggests that the North American strain belongs to a different species. Further collections and sequences are needed, in particular from North America and from eastern Asian records in which the apothecia possess distinct marginal teeth.

Ecology. *O. laevimarginata* was found on rotten wood and bark of hygric angiosperm branches in southern China. Collections are predominantly from subtropical humid (winter-dry) broad-leaved evergreen forests, those from Kunming and Yuxi being mainly composed of *Quercus* trees and that from Dali of *Castanopsis* etc. The collection from Xishuangbanna was made in a tropical rainforest. The not included American samples are from cold-temperate humid mixed oak forests on granite and Devonian sediment.

Map 82. Known distribution of *O. laevimarginata* in southeastern Asia.

Specimens included. **CHINA**: **Yunnan**, **Kunming**, 18 km NW of Anning, 6 km NE of Qinglongzhen, Qinglongxia (Yu'an Shan), 1900 m, branch of *Quercus*, on bark & wood, 3.XI.2004, Z.F. Yu (ex Z.F.Y. qlx-1, ex H.B. 7667, M-0276498, **holotype**). – 9 km WNW of Kunming, Bamboo temple (Qiongzhushi, Yu'an Shan), 2150 m, on wood of *Quercus*, VII.2005, Y. Zhang (Y.Z. ya-17, YMFT 1.01833, anam. cult.; sq.: DQ512890). – **Yuxi**, Yimen, 54 km NW of Yuxi, ?3 km NW of Fangtunxiang, Dalongkou, Longquan, ?1750 m, on wood of *Quercus*, VIII.2006, Z.F. Yu & S.F. Li (Z.F.Y. ym-87, YMFT 1.01869, anam. cult.; sq.: GQ351279). – ibid., VIII.2007 (Z.F.Y. ym3-52, YMFT 1.03013, anam. cult.; sq.: KM252677). – **Dali**, 42 km NNE of Dali, Jizushan Nature Reserve, 2700 m, branch of ?*Fagus*, on bark, 20.X.2008, X.M. Gao et al. (Z.F.Y. jz-8, YMFT, H.B. 8978b). – **Chuxiong**, 12.5 km WSW of Chuxiong, S of Jiguang temple, Zixishan, 2155 m, on indet. woody substrate, X.2004, ?Z.F. Yu (?Z.F.Y. xz-1, YMFT ø). – **Xishuangbanna**, around Jinghong, 1000 m, unidentified wood, 9.XI.2002, B. Liu et al. (B.L. 6220, HMAS 139521 incl. culture, doc. vid.; sq.: DQ656627).

Not included (with prominent marginal teeth): **CHINA**: **Yunnan**, **Yuxi**, Yimen, 54 km NW of Yuxi, 3 km NW of Fangtunxiang, Dalongkou, Longquan, 1750 m, branch of indet. angiosperm, on bark, VI.2007, S.F. Li & J.W. Guo (J.W.G. lq2–54, YMFT, H.B. 8744). – ibid., on indet. wood (J.W.G. lq2-68, YMFT, H.B. 8693). — **USA**: **Massachusetts**, 19 km SE of Boston, ~2.5 km NNE of Hingham, World's End peninsula, ~5 m, log of *Quercus*, on bark, 29.IX.2013, D. Haelewaters (bhi-F121b, H.B. 10168; sq.: MN339157, MN339159). – **New York**, 19 km NE of Ithaca, 2 km SW of McLean, Fall Creek, 330 m, *Quercus* bark, 15.V.1894, G.F. Atkinson, vid. B. Spooner (Disc. Exsicc. 22, non vid.).

Orbilia scolecospora (G.W. Beaton) Baral, in Liu et al., Fungal Diversity 22: 117 (2006) — Pls 463–464

≡ *Hyalinia scolecospora* G.W. Beaton, in Beaton & Weste, Trans. Br. Mycol. Soc. 70: 77, fig. 1 (1978) [non *Calloria scolicospora* Rehm 1878, nom. inval.]

Etymology: named after the worm-shaped (scoleciform) ascospores.

Typification: Australia, Victoria, Portland, bark of *Eucalyptus*, 3.V.1964, G. Beaton (Beaton 186, MEL, holotype).

Description: — **TELEOMORPH**: **Apothecia** fresh/rehydrated (0.3–)0.5–1(–1.4) mm diam., 0.1–0.2(–0.3) mm high (receptacle 0.11–0.12 → 0.06–0.08 mm), whitish or cream-dull, to pale yellow-ochre, ± translucent, round, scattered to gregarious; disc slightly concave to flat, margin dentate, with ~7–16 distinct triangular teeth of 30–55 × 80–140 µm with obtuse or blunt ends, teeth protruding ~15–50 µm beyond disc; sessile on a ± narrowed base or obconical stipe (0–60 × 100–250 µm), superficial. **Asci** *28–30 {Yunnan} or 40–56 {Tenerife} × 3.3–4.5 µm {2}, †(24–)27–40(–53) × (2.7–)3–4 µm {4}, 8-spored, pars sporifera *10.5–12.5 µm long (†14–21 µm), spores †2–4-seriate, spirally twisted, ~4 lower spores inverted {3}; **apex** (†) medium truncate (not indented, laterally not inflated); **base** with short to long, ± thin, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *(7–)8–9(–10.5)((–11)) × 0.9–1.2(–1.3) µm {3} (~8–12 µm actual length), †6.5–10 × 0.8–1 µm {3}, narrowly fusoid-clavate, apex obtuse to acute, base strongly attenuated, tail-like or with a distinct tail 0.2–0.6 µm thick, rather strongly curved (helicoid, in profile view S- or sickle-shaped), especially in lower part; **SBs** 2.2–3.7 × (0.2–)0.3–0.5(–0.7) µm {4}, subulate to narrowly tear-

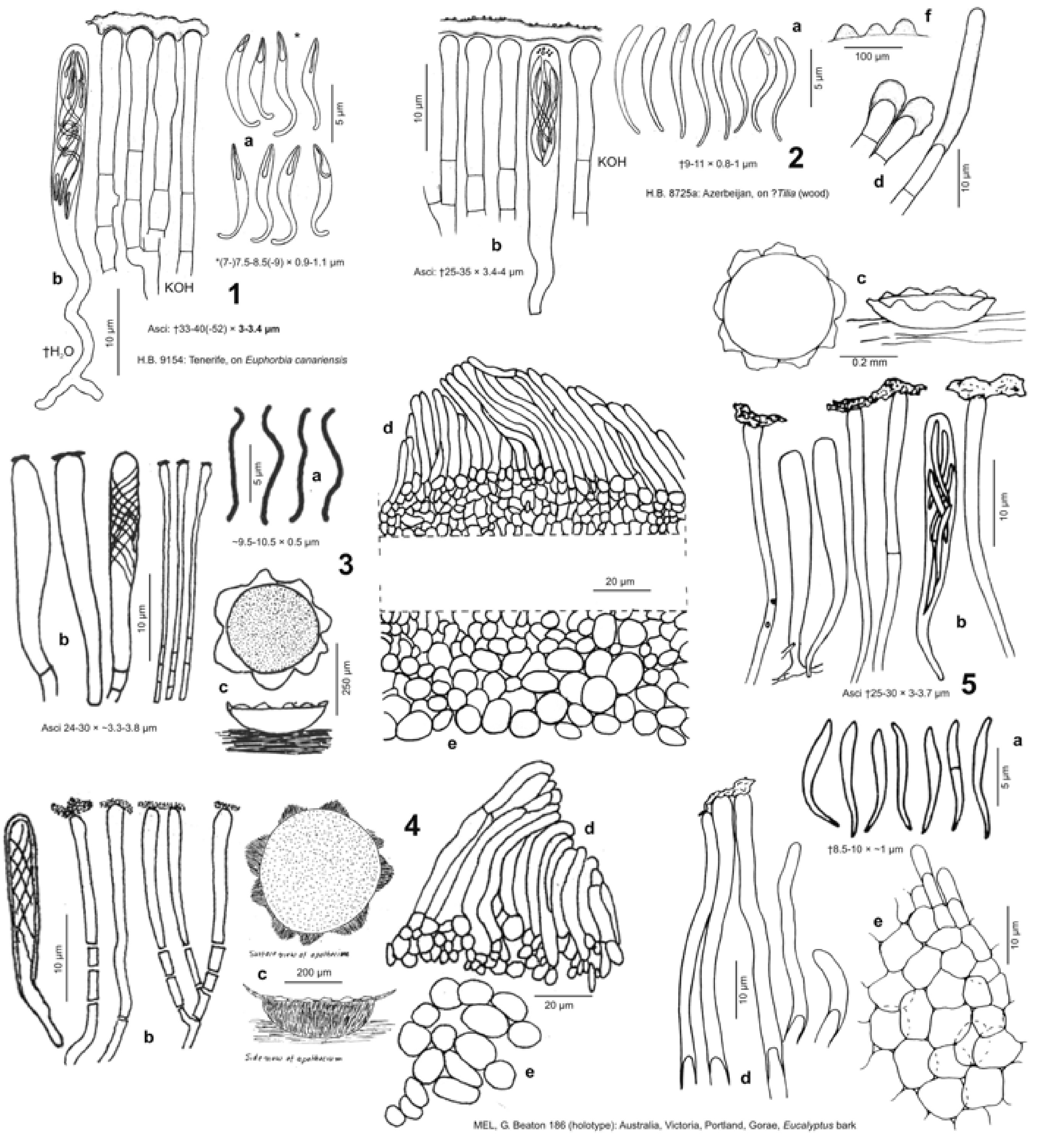


Plate 463. **1**, **3–5**: *Orbilia scolecospora*; **2**: *O.* cf. *scolecospora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. apothecia with dentate margin; **d**. marginal cortical cells with long glassy processes; **e**. excipular cells at flanks; **f**. marginal teeth. — **3–5** from type material: **3**. after Beaton & Weste (1978: 78); **4**. original drawing on herbarium label; **5**. after Spooner (1987: 188).

shaped, apically narrowed to a small point, sometimes slightly flexuous. **Paraphyses** apically uninflated or slightly to medium clavate-capitate, terminal cell †13–21(–24) × (1.7–)2–3.3(–4) µm {3}, lower cells †(2.5–)4–7(–12) × (1.2–)1.5–2.5(–3) µm {2}; never branched at upper septum. **Medullary excipulum** 45–75(–125) µm thick, upper part of small-celled dense textura intricata-angularis, lower part of larger-celled t. globulosa-angularis, indistinctly delimited from ectal excipulum. **Ectal excipulum** of (†) thin-walled to slightly gelatinized, irregularly oriented t. globulosa-prismatica from base to mid flanks, 30–120 µm thick near base, cells *(9–)11–20(–22.5) × (7–)8–14(–16) µm {1}; 20–40 µm thick at flanks, 12–15 µm at margin, inner part of t. angularis oriented at 70–80°, outer part of t. porrecta at 10–20°, marginal cortical cells †9–11 × 2.2–2.8 µm {1}; **glassy processes** 8–55 or 100–200 × (2–)2.5–3.5(–4) µm {2}, refractive, not distinctly stratified, coherent to form distinct, often upwards curved teeth. **Anchoring hyphae** sparse to medium abundant, †1.5–3(–3.5) µm wide, wall 0.2 µm thick. **SCBs** in paraphyses globose to elongate, also crystalloid: filiform to C-shaped, in ectal excipulum ring- to lasso-shaped, 2–5.5 × 2–4 µm {2}. **Exudate** over paraphyses 1–2 µm thick, cloddy-continuous, hyaline to pale yellow, loosely to firmly attached. **— ANAMORPH**: unknown.

Habitat: on the ground, usually on branches and logs of *Eucalyptus* sp. {T}, *Euphorbia canariensis* {6}, *Quercus* sp. {1}, indet. angiosperm {1}, on medium to strongly decayed, fallen bark (detached, inner surface)

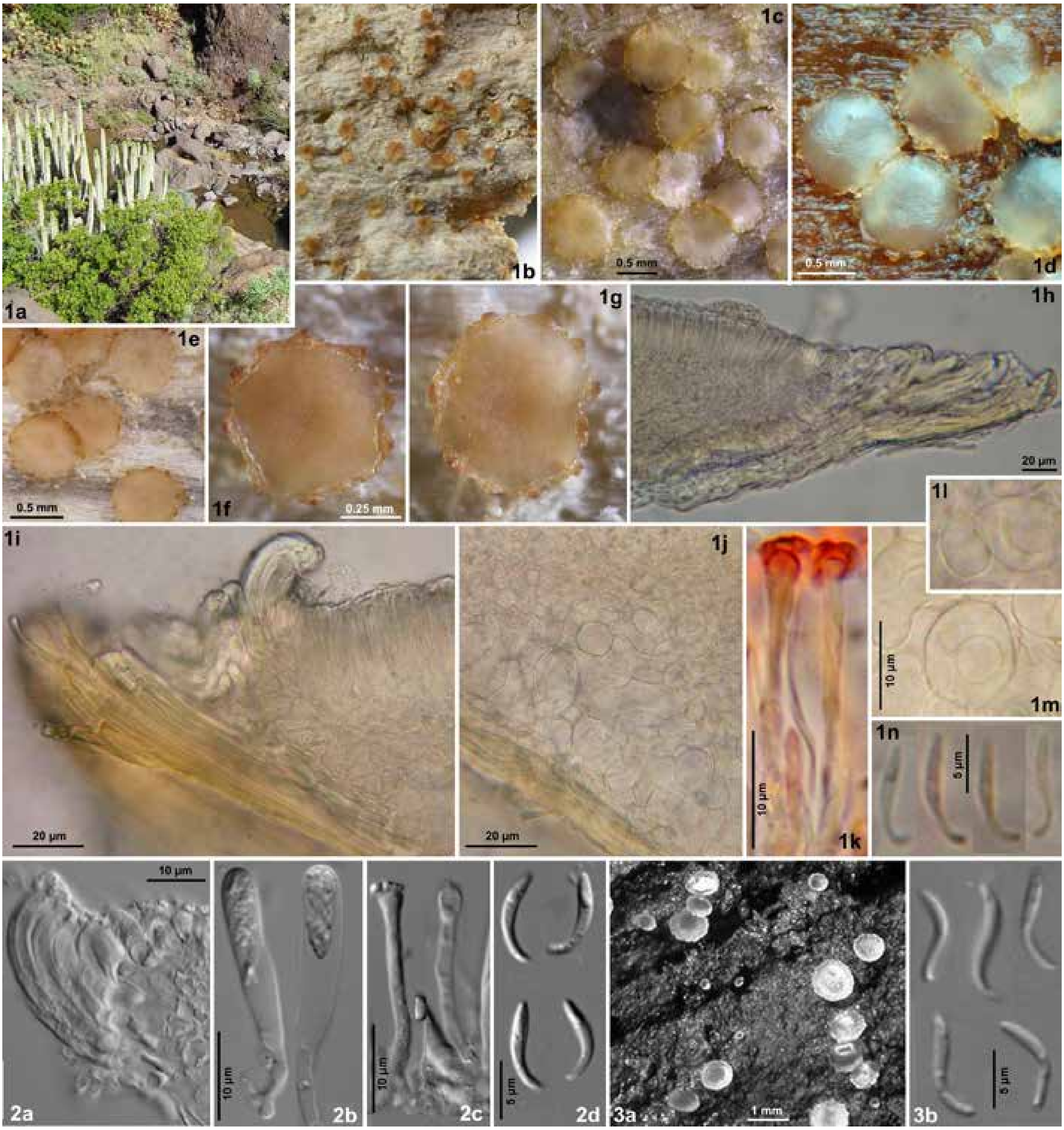


Plate 464. **1–3**: *Orbilia scolecospora*. – **1a**. Tabaibal-Cardonal (*Periploco laevigatae-Euphorbietum canariensis*); **1d**, **3a**. fresh apothecia; **1c**, **e–g**. rehydrated apothecia; **1b**. dry apothecia; **1h–j**, **2a**. ectal excipulum in median section at flanks and margin, with long glassy processes; **1l–m**. ectal excipular cells containing crystalloid SCBs; **2b**. asci (right ascus fully turgescent), **1k**, **2c**. paraphyses; **1n**, **2d**, **3b**. ascospores. – Living state, except for **1k** (in CR), **1n**, **2a**, **3b**. –**1a**, **d**, **h**, **k**, **n**: phot. L. Quijada (**1d**: from Quijada et al. 2016); **2**: phot. Z.F. Yu (DIC); **3**: from Liu et al. 2006b (black & white, DIC). — **1a–n**. H.B. 9154: Tenerife, Teno, on *Euphorbia*; **2a–d**. H.B. 8694b: China, Yunnan, on indet. angiosperm; **3a–b**. HMAS 132094: China, Tibet, on *Quercus*.

{T} or on decorticated wood {5}. **Associated**: *Orbilia crenatonemaspora* {1}. **Desiccation tolerance**: some excipular cells and many spores viable after 3 months. **Altitude**: 120–350 m a.s.l. (Macaronesia), ~80 m (Australia), 1750–3100 m (China). **Geology**: mafic volcanic basaltic & trachybasaltic flow, metamorphic rock. **Phenology**: II, VI–VII, XII (N-hemisphere, perhaps throughout the year).

Taxonomic remarks. *Orbilia scolecospora* is very similar to *O. crenatomarginata*, as already noted by Spooner (1987: 188, the latter as *Hyalinia crystallina*). It differs in slightly longer and distinctly wider ascospores with much longer SBs, also in a more (sub)tropical distribution. *O. vermiformis* (series *Xanthoguttulatae*) differs from *O. scolecospora* in wider marginal cortical cells without glassy processes, and in longer asci and spores. A collection from subtropical China mentioned under *O. pseudobrevistipitata* (series *Xanthoguttulatae*; Pl. 453: 2; 454: 2) differs in narrower spores and in the upper spores being inversely oriented.

Variation. The here figured collections from Macaronesia (Tenerife, on *Euphorbia* wood, treated in detail in Quijada et al. 2016) and China (Tibet, on *Quercus* wood, Liu 2006; Yunnan, on indet. angiosperm wood, Z.F. Yu pers. comm.) included in *O. scolecospora* correspond rather well to the characteristics of the Australian type specimen (on *Eucalyptus* bark) as redescribed by Spooner. Beaton & Weste (1978) and Spooner gave the number of teeth in the type as up to 9, and also Liu et al. (2006b: 108) reported 9 teeth in his Tibetan sample, whereas those from Tenerife have around 9–16 teeth. In the latter, however, the teeth are often confluent to form fewer and larger teeth (see Quijada et al. 2016, fig. 6: 1a–e), for which reason the authors gave only a number of 5–8(–10). The apothecia vary in colour from whitish (Tibet, Tenerife) to yellowish-ochraceous (Australia, Tenerife). In the type the apothecia were smaller (~0.3–0.5 mm diam. fide Beaton & Weste; 0.25–0.45 mm fide Spooner, probably rehydrated) than in the other specimens (mostly 0.5–1 mm). Macaronesian specimens have distinctly longer asci (†33–53 × 2.7–3.5 µm), whereas the Chinese specimens are with †24.5–33 × 3–4 µm in the range of the type and also the two not included samples.

Spore length in the specimens from Tenerife was intermediate between the sample from Yunnan (*6.7–7.6 × 1.1–1.3 µm, Pl. 464: 2d) and that from Tibet (*7.8–10.4 × 1–1.3 µm, Pl. 464: 3b). SB size concurs between those from Tenerife and Yunnan, while the rather short and wide SBs in the Tibet sample (1–1.8 × 0.4–0.6 µm) might refer to overmature spores. In spore shape the Macaronesian specimen has more distinct and narrow tails.

Type studies. The holotype of *O. scolecospora* could not be studied because it was lost during delivery to Europe. N. Middleton (pers. comm.) kindly forwarded a scan of the herbarium label which bears a handwritten description and drawing, also the collection data. These documents deviate from the protologue in several points (Pl. 463: 3–4), and Spooner's (1987: 188) redescription of the holotype again differs hereof. Beaton & Weste (1978) described the spores as 15 × 0.5 µm, narrowly filiform, flexuous (Fig. 3a), and stated that they could not find any free spores. Obviously they measured the actual length, because on their published drawing the spores in situ are only ~9.5–10.5 µm long. The very narrow spore width is in conflict with Spooner's observation of a few free spores which were narrowly clavate-fusoid, often somewhat sigmoid and spirally arranged, sometimes apparently with a median septum (Fig. 5a). We assume that Beaton & Weste's spore description is inexact.

Beaton & Weste (l.c.) and Spooner (l.c.) gave the ascus size as 24–30 × 2.5–3 µm (on the label 20–27.5 × 2–2.5 µm) and 25–30 × 2.5–3(–3.5) µm, but the asci in their drawings are about 3.3–3.8 and 3–3.7 µm wide, respectively. Also the tips of paraphyses were drawn by Beaton & Weste much too narrow (Pl. 463: 3b, evaluated as 0.9–1.2 µm). On the herbarium label paraphysis width is correctly stated as 1.5–2 µm, which fits Spooner's drawing (evaluated as 1.7–2.2 µm).

Not included collections. Two specimens that were only studied in the dead state are not included in the description of *O. scolecospora*. The sparse collection from Caucasus on *Tilia* bark (Pl. 463: 2) differs in slightly longer spores (†9–11 × 0.8–1 µm), apothecia with ± convex, light yellow disc and smaller, especially narrower teeth (20–30 × 40 µm), and a temperate occurrence. The few apothecia in this sample should have possessed around 50–100 teeth according to their large size of 0.8–1.5 mm diam., but were already somewhat distorted when received. This might instead belong in the scope of *O. crenatonemaspora* (series *Xanthoguttulatae*).

A collection from Argentina on bark of *Eucalyptus* (see Fig. 164) could belong in the same relationship. It was reported by Romero (1987, 1994) under the name *Hyalinia scolecospora*, but deviates from the present concept of the species in yellow apothecia and narrowly filiform spores of †10–15 × 0.5 µm (actual length, in situ only ~9 × 0.5 µm as evaluated from drawing). The spores well correspond to the protologue of *H. scolecospora* Pl. 463: 3a, but not to the much wider, heteropolar spores in Spooner's redescription of the holotype (Pl. 463: 5a). The asci measured 25–35 × 3–5 µm (~25 × 3 µm on the drawing), and the spores are intertwined in the asci by forming one bundle (pars sporifera ~9–10 µm long). 14–16 teeth were drawn in the provided illustration. A recent reexamination of Romero's sample by L. Quijada (pers. comm.) confirmed her description of free spores but did not clearly show spores from inside the asci. Also the number of marginal teeth is confirmed, but only when counting confluent aggregates of small teeth as one.

Phylogeny. Sequences gained from apothecia of five samples of *O. scolecospora* were available: four from Tenerife (ITS, once also SSU and LSU) and one from Tibet (ITS+LSU). The four from Tenerife are completely identical except for 1 nt in the ITS1 of TFC Mic. 24450 (L. Quijada pers. comm., not shown in Phyl. 16), while a very high distance of 17.4–17.6 % is observed in the entire ITS region between the Tibetan strain and those from Tenerife. Also in the LSU the distance between the Tibet and Tenerife sample is high (3.5 %, 409 nt), therefore, two different species must be involved. The S1506 intron is absent in the four Macaronesian strains, while the Tibetan strain is incomplete at the 5'-end of ITS1. To *O. crenatomarginata* and *O. laevimarginata* the distance of *O. scolecospora* s.l. lies in the range of 17–22 % in the ITS, and to *O. crenatomarginata* 6–7 % in the LSU.

The two *O. scolecospora* taxa do not even form a clade in our analyses of ITS+LSU, ITS, or LSU (Phyls 13, 16, S15, S16). Whether or not the Australian type of *O. scolecospora* is conspecific with one of these specimens cannot be clarified at present. We assume that the Macaronesian samples belong to a different, undescribed, highly host-specific species. Further molecular data, particularly from other geographical regions, are needed, also from re-collections at the type locality in Australia. The Macaronesian genotype is planned to be described as a new species in a separate paper (Quijada et al. ined.).

Ecology. *O. scolecospora* differs from the desiccation-sensitive *O. crenatomarginata* in a slight drought tolerance of its apothecia, based on observations from the Macaronesian samples. The collective species is at present known from fallen, hygric bark of *Eucalyptus* and wood of *Quercus*, and from mesic branches of *Euphorbia canariensis*. The southeastern Australian collection was from a warm-temperate humid eucalypt open forest in the Victorian Volcanic Plain ecoregion, and the Asian ones from an orotemperate altimontane) humid (winter-dry), continental floodplain forest in eastern Himalaya and from a subtropical humid (winter-dry) mountain forest in Yunnan. Collections from Tenerife (Macaronesia) were in inframediterranean semihumid to mainly lower semiarid to arid xerophytic cardonal scrublands (*Periploco laevigatae-Euphorbietum canariensis*). Here the apothecia developed on *Euphorbia* branches with contact to the soil, mainly on the shaded lower side and only after long periods of rain, though later falling dry for some time. The not included samples are from warm-temperate humid Caucasus and subtropical humid South America.

Specimens included. **MACARONESIA**: **Canary Islands**, **Tenerife**, Buenavista del Norte, 5.2 km WSW of Buenavista del Norte, 3 km NW of Teno Alto, Punta de Teno, 122 m, on branches of *Euphorbia canariensis*, on wood, 16.VI.2009, L. Quijada, C. Quijada & E.V. Rodríguez (TFC Mic. 22307, H.B. 9154; sq.: KM248770; TFC Mic. 22289, 22290, 22297, 22305, non vid.). – ibid., 28.II.2010, L. Quijada, R. Castro & E.V. Rodríguez (TFC Mic. 22872, 22873, non vid.). – ibid., El Draguillo, 130 m, on *E. canariensis*, 5.VI.2009, L. Quijada, C. Quijada & E.V. Rodríguez (TFC Mic. 22235, non vid.). – La Laguna, Anaga, 6 km NE of Tegueste, 1.2 km NW of Chinamada, Andén de la Cruz, 340 m, on *E. canariensis*, 29.XII.2013, L. Quijada & E.V. Rodríguez (TFC Mic. 24450, doc. vid., sq.: UDB0777920). – Fasnia, 7.5 km SSW of Güímar, 1.5 km NE of Fasnia, La Morra los Cardones, 346 m, on *E. canariensis*, 18.XII.2013, L. & C. Quijada (TFC Mic. 24423, doc. vid., sq.: UDB0777921). – ibid. (TFC Mic. 24479, sq.: UDB0777922). — **AUSTRALIA**: **Victoria**, Victorian Volcanic Plain, 12 km NW of Portland, Gorae, State Forest Road, near stream, ~80 m, ?log of *Eucalyptus*, on bark, 3.V.1964, G. Beaton (Beaton 186, MEL, **holotype**, doc. vid., specimen lost). — **CHINA**: **Tibet**, **Nyingchi** (Linzhi), 36 km ESE of Bomê (Bomi), 1.3 km ENE of Songzong, 3100 m, on wood of *Quercus*, 16.VII.2004, B. Liu & X.Z. Liu (HMAS 132094, doc. vid.; sq.: DQ656628, DQ656687). – **Yunnan**, **Yuxi**, Yimen, 54 km NW of Yuxi, 3 km NW of Fangtunxiang, Dalongkou, 1750 m, branch of indet. angiosperm, on wood, VII.2007, S.F. Li & J.W. Guo (J.W.G. ym3-7, YMFT, H.B. 8694b ø, doc. vid.).

Not included. **AZERBAIJAN**: **Shaki-Zaqatala**, Caucasus Mts., ?4 km NE of Zakatala, 'Kordon', 800 m, log of *Tilia*, on wood, 9.VIII.1974, B. Kullman (TAAM 68123, as *Orbilia* sp., H.B. 8725a ø). — **ARGENTINA**: **Buenos Aires**, 21.5 km WNW of San Pedro, 7.5 km N of Gobernador Castro (Rio Paraná), 200 m, on bark of *Eucalyptus viminalis*, XI.1982, A.I. Romero et al. (BAFC 30457, doc. vid.).

Orbilia crenatofalcata Baral & S. Tello, **sp. nov.**, MB 813765 — Pl. 465

Etymology: named after the crenulate margin and falcate ascospores.
Typification: Spain, Andalucía, Cazorla, log of *Populus nigra*, 19.X.2013, S. Tello (JA-CUSSTA 7771, holotype; sq.: KM248769).

Latin diagnosis: Similis Orbiliae crenatomarginatae *sed ascosporis falcatis, dentibus marginalibus apotheciorum minoribus differt. Habitat ad lignum putridum ramorum uvidorum* Populi nigrae *in zona suprasub ad supramediterranea Europae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.27–)0.33–0.6(–0.7) mm diam., in total 0.11–0.16 mm high (receptacle 0.09–0.11 → 0.05–0.07 mm), watery greyish-white to pale cream, strongly translucent, round, subgregarious; disc flat or slightly convex, margin denticulate to dentate, with ca. 30–40 small {T} or 10–20 large teeth {1}; sessile or with a low and broad stipe up to 0.06 × 0.2 mm, superficial; dry pale yellowish-cream or slightly rosaceous. **Asci** *30–33 × 3.2–3.4(–3.7) µm {T}, †25–35 × 2.8–3.3 µm {2}, 8-spored, spores 4–8-seriate, slightly spirally twisted within the living asci, pars sporifera *10–12 µm, †17–18 µm, ~4 lower spores inversely oriented (never mixed); **apex** (†) slightly to strongly truncate (never indented or inflated); **base** with very short to medium long, thick or thin, flexuous stalk, L-, T- or h-shaped. **Ascospores** *8–9.5(–9.8) × 0.8–0.9(–1) µm {T} (~8.5–10 µm actual length), †7.5–10 × 0.6–0.8 µm {2}, very narrowly fusoid, widest part closer to apex, apex subacute, base gradually attenuated, never tail-like; (*/†) slightly to medium curved (falcate, sometimes very slightly helicoid); **SBs** 2–3 × 0.4–0.5 µm, subulate. **Paraphyses** apically cylindrical or very slightly (rarely medium) capitate, terminal cell *11.5–15.5 × 2–2.5 µm, †1.5–2 µm wide, lower cells *3.5–4 × 1.6–2.1 µm, unbranched at upper septum. **Medullary excipulum** ~40–60 µm thick in centre, of dense textura globulosa-angularis, not sharply delimited from ectal excipulum. **Ectal excipulum** of thin-walled t. globulosa-angularis from base to margin, 60–90 µm thick at base, cells *12–17 × 9–16 µm, †10–15 × 9–13 µm, 20–40 µm thick at lower flanks, externally covered by a single layer of hyphoid elements, 20 µm thick at mid flanks and margin, oriented at a high angle, marginal cortical cells †8–12 × 3–7 µm, curved upwards at tip; **glassy processes** 5–10 {T} or 20–40 {1} × 2–4 µm {2}, low- to high-refractive, stratified, conglutinate to form indistinct or distinct teeth. **Anchoring hyphae** sparse, †1.5–3 µm wide, walls 0.2 µm thick. **SCBs** globose, highly refractive, in terminal cells of paraphyses 1 per cell (sometimes cylindrical), in lower part of ectal excipulum 1 or more per cell, 1.2–2.3 µm diam., in apices of marginal cortical cells 1.8–3 µm diam.; crystalloid SCBs in both terminal and lower cells of paraphyses and in ectal excipulum from base to margin {2}, medium to strongly refractive, in paraphyses rhomboid to rod-shaped, in excipulum ring- to C-shaped, 4–7 µm diam., also plate-shaped; **VBs** absent. **Exudate** over paraphyses continuous to cloddy, hyaline or pale yellowish, 0.5–1.8 µm thick, externally rough to granular, loosely attached; over margin and flanks finely granular, ~0.5 µm thick. — **ANAMORPH**: unknown.

Habitat: underside of 15–20 cm thick, decorticated logs of *Populus nigra* {2} lying on moist ground, on very decayed wood {2}. **Associated**: none observed. **Desiccation tolerance**: dead in all parts when examined after 3 weeks. **Altitude**: 490–810 m a.s.l. **Geology**: Jurassic dolomite, Tertiary limestone, marl, clay, sandstone. **Phenology**: VIII, X.

Taxonomic remarks. *Orbilia crenatofalcata* strongly concurs with *O. crenatomarginata* in most features. It differs in consistently falcate ascospores which are only very slightly helicoid and always lack a tail-like base, and contain longer SBs. Macroscopically, the smaller, more numerous marginal teeth might be diagnostic, but in the second collection they were larger and fewer. A similar deviation in ascospore curvature is noted in the possibly heterogeneous Asian *O. crenatonemaspora* (series *Xanthoguttulatae*) which has typically helicoid spores but in some specimens falcate spores very similar to *O. crenatofalcata* though distinctly longer.

Variation. In the specimen from Navarra the apothecia have distinctly longer glassy processes (20–40 vs. 5–10 µm), resulting in larger marginal teeth of only about half the number per apothecium.

Phylogeny. Sequences were taken from apothecia of the holotype from Andalucía and the paratype from Navarra, comprising ITS and in the Navarra strain also LSU (the S1506 intron is absent in both). In the ITS region the two strains are completely identical. *O. crenatofalcata* clustered in the strongly supported *Hyalinia* clade (Phyls 13, S15–S16), though with a high ITS distance of 16–18% to *O. laevimarginata*, *O. crenatomarginata*, and *O. scolecospora*. Also in the LSU the distance to *O. crenatomarginata* and *O. scolecospora* is rather high (5.5–6.5%). 6 deviations in the LSU are unique within section *Aurantiorubrae*: pos. 127 **A** vs. **G** or exceptionally **T**, pos. 178 C**A**GT vs. **G** (**A** only *O. tianmushanensis* of section *Helicoon*), pos. 259 **A**TCGA vs. **T**, pos. 296 AA**C**GG vs. **T**, pos. 317 AA**G**GC vs. **A**, pos. 327 **G**GGC vs. **T** (verified from chromatogram).

Ecology. *O. crenatofalcata* was twice collected on rotten wood of *Populus nigra* in a suprasubmediterranean humid riparian forest with *Populus*, *Salix*, *Alnus*, *Acer*, *Cornus* etc. in the western Pyrenees (Navarra), and in a supramediterranean semihumid forest with *Populus* and *Pinus halepensis* in a valley between Sierra de Cazorla and Sierra de Segura (Andalucía).

Specimens included. **SPAIN**: **Navarra**, western Pyrenees, 12 km NE of Pamplona, W of Akerreta, 490 m, log of *Populus nigra*, on wood, 13.VIII.2014, F.J. Balda (H.B. 9926; sq.: KT222398). – **Andalucía**, **Jaén**, Sierra de Cazorla, 17.5 km NE of Quesada, 8.5 km NE of Cazorla, N of Arroyo frío, 810 m, log of *Populus nigra*, on wood, 19.X.2013, S. Tello (JA-CUSSTA 7771, **holotype**; H.B. 9852, **isotype**; sq.: KM248769).

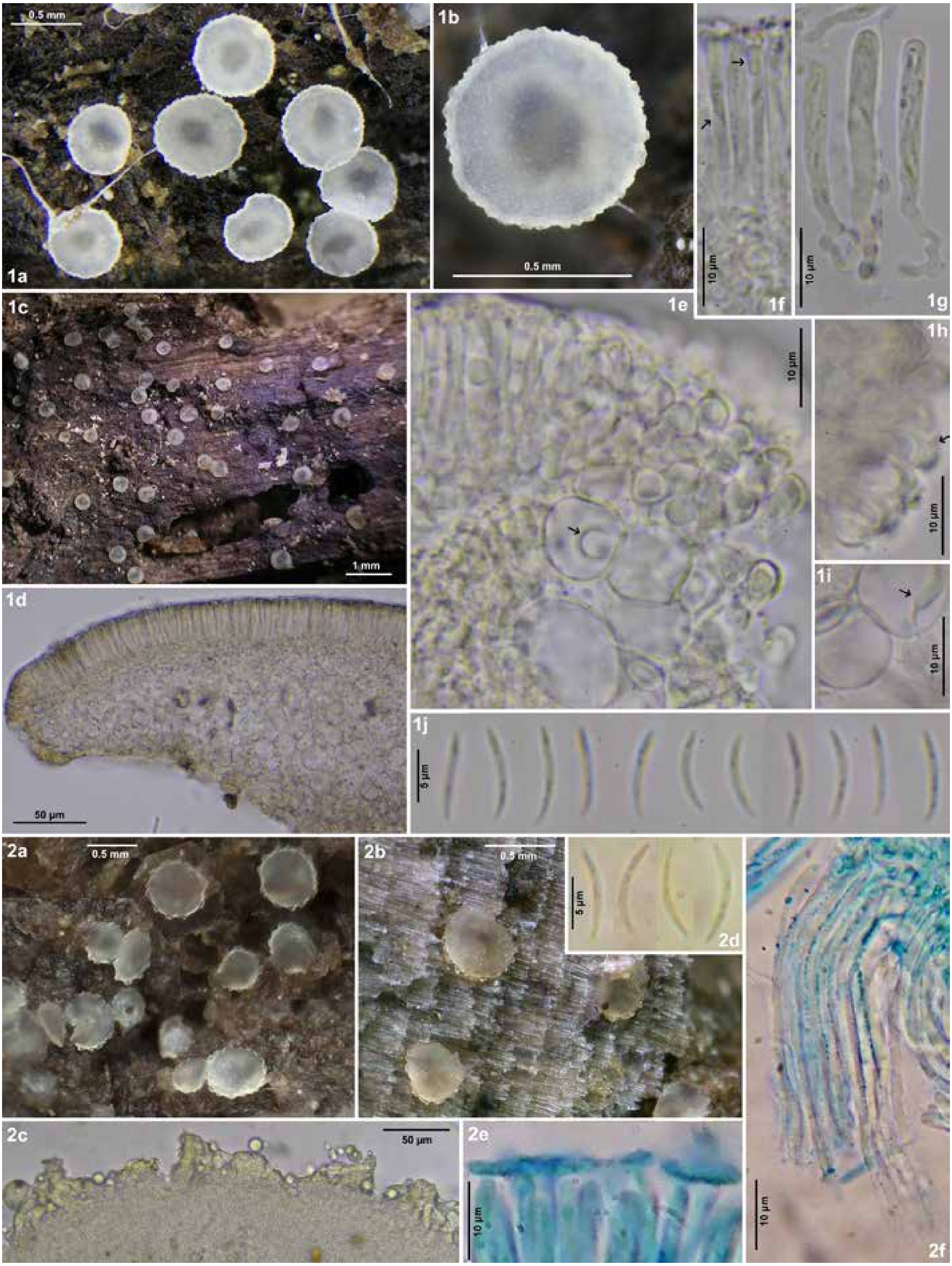


Plate 465. **1–2**: *Orbilia crenatofalcata*. – **1a–b**, **2a**. fresh apothecia; **2b**. rehydrated apothecia. **1c**. rehydrated piece of wood with apothecia; **1d**. apothecium in median section; **1e**. id., marginal region, with crystalloid SCBs (arrow); **1h**. marginal cortical cells with short glassy processes (arrow); **2f**. glassy processes; **1i**. crystalloid SCBs in ectal excipular cells (arrow); **2c**. dentate margin in top view; **2e**. upper part of hymenium with exudate; **1f**. paraphyses with elongate cylindrical SCB (right arrow) rhomboid crystalloid SCBs (left arrow); **1g**. mature asci; **1j**, **2d**. ascospores. – Living state, except for **1h** & 2 asci in **1g** (in H_2O), **2d–f** (**e–f** in CRB). – phot. S. Tello (except for **1c** & **2b–c**). — **1a–j**. JA-CUSSTA 7771, H.B. 9852 (type): Spain, Andalucía, Jaén, on *Populus*; **2a–f**. H.B. 9926: Navarra, Pamplona, on *Populus*.

Series *Abutilones*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Abutilones*** Baral & E. Weber, **ser. nov.**, MB 815013 –
Type species: *Orbilia abutilonis* E.K. Cash

Etymology: named after the type species, *O. abutilonis.*

Latin diagnosis: *Seriei* Aurantiorubrae *similis sed paraphysibus apice pro parte majore spathulatis vel lageniformibus, ascosporis ad basim non raro constrictis et saepe valde geniculatis, conidiis staurosporis (typo* Dicranidion*) differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–1.5(–2) mm diam., pale to bright cream, yellow-ochre to orange- or carmine-rose, margin smooth or pruinose to prominently hairy, sessile or with ± distinct short stipe. **Asci** *37–62(–69) × 3.7–5 µm, 8-spored, lower or upper 3–5(–6) spores inverted; **apex** (†) slightly to strongly truncate, rarely indented, laterally not or sometimes slightly inflated; **base** T-, L- or Y-, h-, rarely H-shaped **Ascospores** *(4.8–)6–11(–12) × (0.6–)0.8–2(–2.3) µm, narrowly (cylindric-)fusoid(-clavate) to fusiform(-clavate), apex acute to acuminate, rarely obtuse to subacute, base hardly to strongly attenuated, sometimes tail-like or with a ± strong subbasal constriction, straight or often slightly to strongly curved (falcate), at base often slightly to very strongly geniculate, sometimes (sub)helicoid; **SBs** 1.5–4(–5.5) × 0.2–1.1 µm, filiform to subulate or tear-shaped, apically narrowed to a small point. **Paraphyses** (uninflated to) slightly to strongly inflated at the apex, spathulate-lageniform or clavate-capitate, terminal cells (1–)1.5–3(–4)× longer than lower cells. **Ectal excipulum** cells near base *(6–)10–20(–30) × (4–)7–15(–20) µm; **glassy processes** absent, rarely 2–15 µm long, **hairs** often present, 15–65 µm long, thin- to thick-walled, septate, also as short, hair-like protrusions. **SCBs** absent, rarely globose or crystalloid; **VBs** absent, rarely present, low-refractive. **Exudate** absent or 0.2–1(–2) µm thick, continuous-rough to cloddy, firmly (or loosely) attached, hyaline or pale yellowish. — **ANAMORPH**: dicranidion-like (*O. abutilonis*, *O. ficicola*, *O. siculispora*). **Conidiophores** short (4–6 µm). **Conidia** staurosporous, maniform, mostly 4-armed by repeated branching, also 2–3-armed, *35–52 × 13–25 µm, arms parallel, in a plane; exceptionally with some unbranched conidia.

Habitat: wood and bark of angiosperms or on herbaceous stems, boreal to tropical, humid to semiarid, always ± desiccation-tolerant.

Recognized species: 14, plus 1 unnamed species ('affinis').

Taxonomic remarks. Morphologically the species of series *Abutilones* resemble those of series *Aurantiorubrae* in having similar ascospores with very acute apices and not or only slightly attenuated, often strongly geniculate bases, but they mainly lack crystalloid SCBs and frequently possess spathulate to mammiform paraphyses and constricted spore bases.

Species delimitation. Many of the species included in series *Abutilones* appear to be easily recognizable, whereas *O. abutilonis*, *O. ficicola*, and *O. siculispora* form a morphologically very difficult species complex. However, *O. abutilonis* and also *O. rosella* would perhaps better be characterized if their vital features were known. *O. milinana* showed some variation which might point to heterogeneity of the included specimens. *O. rosella* and *O. paravitalbae* seem sharply separated from *O. ebuli*, but can be confused with species of other series because the spores lack the basal constriction typical of many species of series *Abutilones*.

This often strong but variable constriction at the more or less geniculate spore base occurs in *O. abutilonis*, *O. ficicola*, *O. siculispora*, and *O. lobeliae*, and less pronounced in *O. subsiculispora*, *O. milinana*, *O. somedana*, and *O. ebuli*. In *O. lobeliae* and *O. milinana* the spore orientation deviates from the others by showing a strong predominance of the upper spores being inverted within the asci. Inverted upper spores were also seen in some asci of *O. abutilonis*, *O. ficicola*, *O. siculispora*, and in *O. carminorosea*.

Six species (*O. abutilonis*, *O. ficicola*, *O. siculispora*, *O. somedana*, *O. suberis*, *O. subsiculispora*) are exceptional in their filiform to narrowly subulate SBs, mostly spathulate-lanceolate to lageniform-mammiform paraphyses (except *O. somedana*), and septate, thin-walled, appressed or projecting marginal hairs (because of lacking vital studies, the SBs of *O. abutilonis* and *O. carminorosea* are unknown, while those of *O. rosella* are probably strongly inflated at their base). *O. ebuli* resembles *O. aurantiorubra* in spore and SB shape, except that the spores of *O. ebuli* are usually not or only slightly curved.

A tendency to short, hair-like projections forming a pruinose to crenulate margin is typical of *O. ebuli*, *O. rosella*, *O. carminorosea*, and *O. rehmii*. Glassy processes are mostly absent or very short, rarely up to 15 µm long (*O. rehmii*). *O. ebuli* and *O. aethiopica* are characterized by tear-shaped SBs with a subulate upper part. *O. milinana*, *O. lobeliae*, *O. ebuli*, *O. rosella*, and *O. somedana* deviate from the remaining species in capitate(-clavate) paraphyses, the former two also in the total absence of marginal hairs. *O. aethiopica* is outstanding in its short and broad, straight spores with a subacute, flat-conical apex, and lanceolate paraphyses. Crystalloid SCBs were only observed in *O. subsiculispora*.

Anamorph. Only from *O. siculispora* an ascospore isolate was gained. It formed (2–)4-armed, maniform, stipitate, dicranidion-like conidia with parallel arms. In *O. abutilonis*, *O. ficicola*, *O. suberis*, and *O. carminorosea* conidia were only found on the natural substrate. They are also 2- or 4-armed but differ in diverging arms and resemble those of *O. fissilis* of series *Orbilia*. In *O. rosella* very different, narrow, vermispora-like conidia were seen on the natural substrate, but their connection to this species, which is only tentatively placed here, is quite uncertain.

Phylogeny. Despite a close morphological similarity to series *Aurantiorubrae*, series *Abutilones* is situated in our analyses unresolved within section *Aurantiorubrae* and very distant from series *Aurantiorubrae*. It forms a strongly supported clade when analysing ITS+LSU or ITS (Phyls 13, S15), though with a high distance among the included species. The concept of series *Abutilones* is mainly based on our sequence data, which were available for *O. aethiopica*, *O. carminorosea*, *O. ebuli*, *O. ficicola*, *O. milinana*, and *O. siculispora*. Placement of *O. aethiopica* in this clade is surprising because of its morphological dissimilarity.

Specific nucleotide positions. Three nucleotides in the 5.8S region are characteristic of series *Abutilones*: pos. 30 is TTC**C**CGC and pos. 140 & 144 A**C**GTC**C**G compared to other members of section *Aurantiorubrae* which have TTC**T**CGC and A**T**GTC**T**G. As an exception, one of the two strains of *O. milinana* (B.L. X098) has TTC**T**CGC, and *O. poitevinica* A**C**GTC**T**G. In the LSU D1–D2 domain pos. 332 is highly diagnostic for the group, showing GGCG**G**GAGAC whereas all other members of subgenus *Habrostictis* have GGCG**A**GAGAC (though also *O. paravitalbae*). However, the motif of series *Abutilones* is shared by the genera *Mycoceros* and *Hyalorbilia*, and within *Orbilia* by section *Ovoideae*, *O. dryadum*, and section *Arthrobotrys* p.p.maj.; pos. 487–491 is G**GG**GG unlike any other *Orbilia* spp. which mostly have G**CA**GG or more rarely G**CG**GG or G**TG**GG (pos. 488 is unique within series *Abutilones*).

Ecology. All included species are more or less desiccation-tolerant. They have been collected on wood and bark of

Key to species of series *Abutilones*

1. Spores *4.8–6.3 × 1.8–2.5 µm, with a flat-conical, subacute apex forming a > 90° angle; paraphyses (sub)lanceolate, also ± uninflated; apothecia yellowish-ochre, margin rough; angiosperm bark, mesotemperate humid northeastern Africa .... ***O. aethiopica***, p. 912
1. Spores *6.5–12 × 0.6–1.8(–2) µm, apex acute to acuminate, rarely obtuse, forming a < 90° angle; paraphyses with rounded apex, cylindrical, capitate or lageniform-mammiform, also lanceolate 2

2. Apices of paraphyses distinctly ellipsoid-spathulate to lanceolate or mammiform, exceptionally uninflated 3
2. Apices of paraphyses clavate-capitate, sometimes ellipsoid or uninflated 8

3. Spores without subbasal constriction, *~ 1–1.3 µm wide 4
3. Spores with slight to strong subbasal constriction, *~ 1.1–1.5(–1.7) µm wide; marginal hairs without glassy processes 5

4. Spores †(6.5–)7–7.5(–8) × (0.9–)1–1.2 µm, fusiform, base strongly attenuated, tail-like; hairs absent or 12–30 µm long, tipped by 1–15 µm long glassy processes; bark of *Malus*, cold-temperate humid central Europe .... ***O. rehmii***, p. 904
4. Spores *6.5–9 × 1–1.2 µm, base not attenuated; hairs 25–65 µm long, without glassy processes; bark of *Quercus suber*, mesomediterranean semihumid southern Europe .... ***O. suberis***, p. 895

5. Spores with slight subbasal constriction, *8.5–10.5 × 1.4–1.7 µm; asci *53–69 µm long; paraphyses with crystalloid SCBs; bark of *Artemisia filifolia*, cold-temperate subhumid western North America .... ***O. subsiculispora***, p. 890
5. Spores with slight to strong subbasal constriction, *6.5–10.5 × 1.1–1.6 µm; asci *37–58 µm long; paraphyses and excipular cells without crystalloid SCBs (unknown in *O. abutilonis*) 6

6. Disc orange-ochraceous; hairs broad up to the apex, upper cell *3–5.5 µm wide, thin-walled; conidia with (2–)4 parallel, 3.8–5.5 µm wide arms; spores *(6.5–)7–9(–10) µm long; bark & wood of *Populus*, *Ulmus*, cold-temperate humid Europe..... ***O. siculispora***, p. 886
6. Disc usually pinkish, rarely ochraceous; hairs partly distinctly narrower in upper part, upper cell *2.5–3.3 µm wide, thin- to thick-walled; conidia with 2–4 strongly diverging, outwards curved, *3.5–4.3 µm wide arms; spores *(7.5–)8–10(–10.5) µm long 7

7. Basal inflation of */†spores max. 2 × thicker than connecting part; hair cells 5–14 µm long; apothecia pinkish; bark of *Ficus*, *Populus*, *Tilia*, *Ulmus* etc., submediterranean semihumid to cold-temperate (thermophilous) humid Europe .... ***O. ficicola***, p. 892
7. Basal inflation of †spores > 4 × thicker than connecting part; hair cells 10–18 µm long; apothecia ochraceous to pinkish; bark of *Abutilon*, tropical semihumid Hawaii .... ***O. abutilonis***, p. 890

8. Upper spores inverted within asci; spore base consistently (very) strongly and sharply reflexed and ± constricted 9
8. Lower spores mostly inverted within asci; spore base straight to strongly curved but not sharply reflexed, rarely constricted 10

9. Spores *7–10.5 × 0.9–1.3 µm, inflated basal part below constriction bent forwards; wood and bark of *Juglans*, *Euphorbia* etc., cold-continental to tropical (semi)humid Asia, Middle America, Macaronesia .... ***O. milinana***, p. 897
9. Spores *7–8 × 0.6–0.8 µm, inflated basal part below constriction bent backwards; bark of *Lobelia*, warm-temperate humid northeastern Africa .... ***O. lobeliae***, p. 899

10. Spores †6.5–7.5(–8) × 1.2–1.3(–1.4) µm, base strongly attenuated (tail-like) and quite strongly curved; apothecia bright carmine-rose, thick-fleshed, margin whitish powdered; wood of *Adansonia*, tropical subhumid western Australia .... ***O. carminorosea***, p. 906
10. Spores straight or only slightly to medium curved; apothecia light rose-orange-cream, margin ± crenulate by short agglutinated hairs; boreal to mediterranean Europe 11

11. Spores */†(7–)7.5–9(–9.8) × (1.5–)1.6–1.8(–2) µm, cylindrical to fusoid, apex obtuse (to rounded), base never with a tail 12
11. Spores mainly *1.3–1.6 µm wide, fusoid to fusiform, apex acute (to acuminate), base often with a sometimes slightly constricted, 2–3.7 µm long tail 13

12. Spores fusoid, apex obtuse (to subacute), base often ± strongly attenuated, almost tail-like; stems of *Atropa*, temperate humid Europe ***O. rosella***, p. 908
12. Spores ± cylindrical, apex rounded to obtuse; bark of *Daphne*, stem of *Helleborus*, orosubmediterranean humid to mesomediterranean semihumid southern Europe .... ***O. paravitalbae***, p. 910

13. SBs with filiform upper part and swollen, ellipsoid to tear-shaped, 0.7–1.1 µm wide lower part; spores *(8–)9–11(–12) × 1.3–1.6(–1.7) µm, tail *0.5–0.8(–1) µm wide; herbaceous stems, petioles of deciduous trees, thermoboreal to (oro)temperate humid and mesomediterranean semihumid Europe .... ***O. ebuli***, p. 900
13. SBs filiform to subulate, 0.2–0.4 µm wide; spores *(7.8–)8.2–9.2(–9.7) × 1.2–1.5 µm, tail *0.8–1.1 µm; bark of *Rhamnus*, *Fagus*, orotemperate humid southern Europe .... ***O. somedana***, p. 904

angiosperms and on herbaceous stems. Records derive from various climatic regions: from temperate to tropical and from humid to semiarid, and the distribution is worldwide: Europe, Africa, North America, Hawaii, Asia, and Australia.

Orbilia siculispora Baral, E. Weber, Friebes & G. Marson, **sp. nov.**, MB 825634 — Pls 466–468

Etymology: named after the spores reminding a curved dagger (Latin *sicula*).
Typification: Germany, Baden-Württemberg, Tübingen, trunk of *Ulmus laevis*, 20.VI.2004, H.O. Baral (ex H.B. 7526b, M-0291766, holotype).

Latin diagnosis: *Similis* Orbiliae abutiloni *et* O. ficicolae *sed brachia conidiae latiora et parallela differt. Habitat ad corticem et lignum putridum ramorum vel truncorum siccorum* Populi *et* Ulmi *in zona temperata humida Europae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–1.3(–1.7) × 0.4–1.1 mm, (0.11–)0.14–0.2(–0.38) mm high (receptacle 0.06–0.15 mm), light to bright orange-ochraceous, not or slightly translucent, round to broadly elliptical, also irregular or strongly compressed, scattered to subgregarious, also densely gregarious in small groups; disc young strongly concave, mature slightly concave to flat, margin distinct, 0–30 µm protruding (10–50 µm including hairs), with prominent hairs forming ± distinct, whitish, teeth-like fascicles; sessile or with a more or

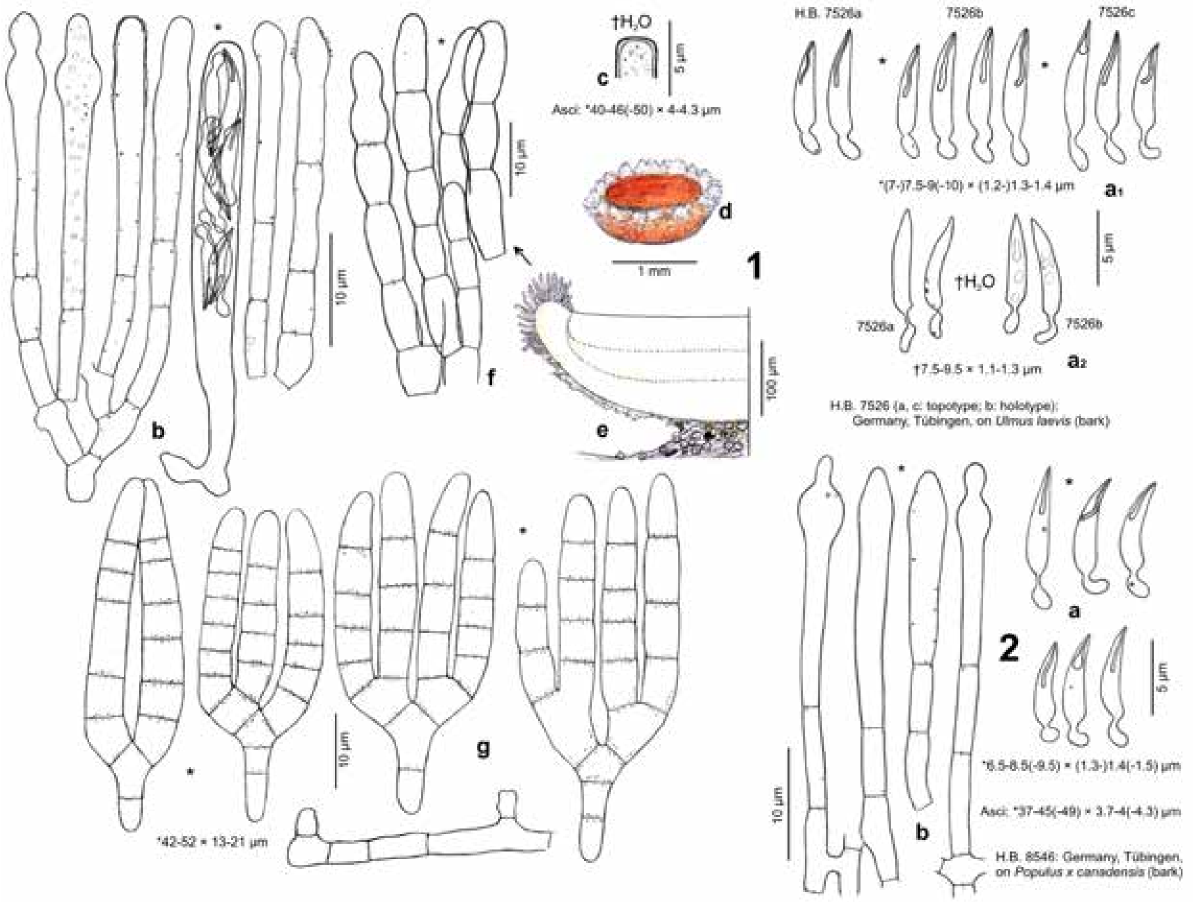


Plate 466. **1–2**: *Orbilia siculispora*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium with hairy-dentate margin; **e**. apothecium in median section; **f**. marginal hairs; **g**. conidia (from culture).

less distinct obconical stipe up to 0.25 × 0.35 mm, superficial or slightly erumpent from small alveoles of bast, also immersed in narrow clefts; dry partially to completely closed by the incurved margin and white teeth, light orange. **Asci** *(37–)40–50(–58) × 3.7–4.3 µm {3}, †35–45(–50) × 3.2–3.7 µm {1}, 8-spored, spores *2–3-seriate, 3–4(–6) spores inverted {4}, mostly strongly mixed, often 1–3 of the lower spores inverted but often also 1–2 of the upper ones, pars sporifera *18–25 µm long; **apex** (†) medium to strongly truncate (not indented, laterally scarcely inflated); **base** with short to long, ± thin, flexuous stalk, L- or T-shaped. **Ascospores** *(6.5–)7–9(–10) × (1.2–)1.3–1.4(–1.5) µm {4}, †7.5–9.5 × 1.1–1.3 µm {1}, subulate, very slightly to medium curved, apex strongly acute to acuminate, with abrupt tail of 1.7–2.6 × 0.7–1 µm (†0.6–0.8 µm wide), with mostly strong constriction, ± geniculate (reflexed and bent forward), inflated part cylindric-ellipsoid (appendage-like); **SBs** *3–4(–4.5) × 0.2–0.4 µm {3}, filiform to subulate, straight or often ± flexuous, overmature tear-shaped, 2–2.5 × 0.5–0.6 µm. **Paraphyses** apically spathulate to lageniform, lanceolate or mammiform, with beaks of *2–4 × 1.3–2.7 µm, exceptionally cylindrical or capitate, terminal cells *(15–)17–24(–26) × (2–)2.8–4 µm {2}, exceeding the dead asci by 2–8 µm, lower cells *6–10 × (1.3–)1.5–3(–3.5) µm {2}; branched only near base, hymenium pale yellowish-orange. **Medullary excipulum** pale yellowish, 10–50 µm thick, of dense, apparently non-gelatinized textura intricata with scattered inflated cells, medium sharply delimited from ectal excipulum (mainly at lower flanks) by a parallel 10–25 µm thick layer of pale orange t. porrecta. **Ectal excipulum** hyaline, with pale to light yellowish cortex, of (†) thin-walled, irregularly oriented (10–30 to 45–90°) t. globulosa-angularis-prismatica from base to mid flanks, 40–100(–250) µm thick at base, cells *8–20(–30) × (5–)7–13(–15.5) µm {3}; 20–25 µm thick at mid flanks, irregularly horizontally oriented (10–30°), at margin 20–50 µm thick, of t. prismatica(-angularis) or t.porrecta oriented at a ~10–40° angle, marginal cells forming free to scarcely agglutinated **hairs** *(15–)30–40(–45) × (2.2–)2.8–5(–5.5) µm {4}, (0–)1–4-septate, cylindrical to moniliform, thin- to firm-walled, hyaline, individual cells *(5–)7–12(–14.5) µm long, without **glassy processes**. **Anchoring hyphae** sparse to very abundant, */†(1.5–)2–3(–4) µm wide {2}, walls 0.2 µm thick {2}. **SCBs** in paraphyses and ectal excipulum absent; light golden-yellow **LBs** (carotenoids) in cells of ectal excipulum at base and flanks 0.3–2.2 µm diam. {1}; **VBs** absent {4}, or present in paraphyses as numerous, small to large, globose, medium refractive guttules {1}. **Exudate** over paraphyses absent or 0.1–0.3 µm thick, finely rough or continuous, firmly attached, very inconspicuous; over hairs and excipular cells of margin and flanks absent or forming a thin, pale to light yellow, granular-cloddy covering layer. **— ANAMORPH**: dicranidion-like (from ascospore isolate {1} and natural substrate {2}). **Conidiophores** reduced. **Conidiogenous cells** *4–6 × 3 µm. **Conidia** fork-shaped or like fingers of a hand (maniform), mostly 4-armed by dichotomous branching, also 2–3-armed, arms parallel, in one plane or sometimes somewhat contorted, total size *35–52 × 13–25 µm {2}, stipe *7–11 × 2.5–3.5 µm, (0–)1–2-septate, arms *(11–)14–38 × 3.8–5.5 µm, (2–)3–7-septate; exceptionally unbranched conidia seen.

Habitat: collected 0.3–3 m above the ground, on 15 mm thick, corticated or decorticated, still-attached or fallen dead branches or 30–100 cm thick living trunks or dead logs of *Populus alba* {1}, *P.* × *canadensis* {2}, *Ulmus laevis* {2}, on slightly to strongly decayed bark (bast) {4} or wood {2}, on outer surface of partially detaching or ± loosely adhering bark, also hidden in cracks or behind detaching periderm, not or slightly to medium greyed, with very few to many green algae. **Associated**: *Amandinea punctata* {1}, *Lecanora conizaeoides* {1}, *Nectria peziza* {1}, *Orbilia aurantiorubra* {1}, *O. carpoboloides* {1}, *O. ficicola* {1}, *Orthotrichum* sp. {1}, *Peniophora lycii* {1}, *Phaeophyscia orbicularis* {1}, *Physcia tenella* {2}, *Strossmayeria basitricha* {1}, *Xanthoria parietina* {2}, *Xanthoriicola physciae* {1}, indet. coelomycete {1}. **Desiccation tolerance**: fully viable for at least 3 months, many paraphyses and immature asci still alive after 4 months. **Altitude**:

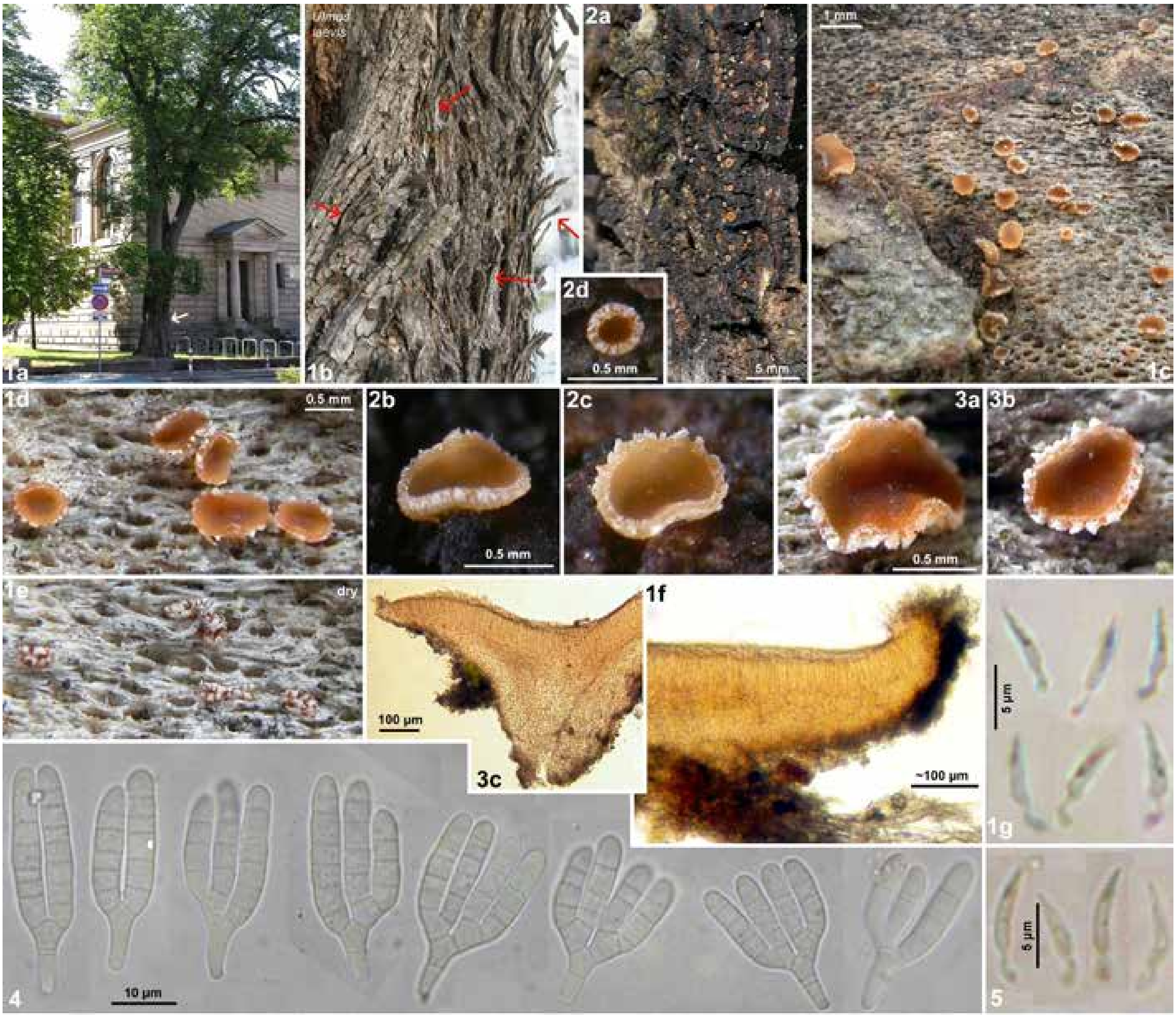


Plate 467. **1–5**: *Orbilia siculispora*. – **1a–b**. ~200 years old living *Ulmus laevis* with detaching outer layers of bark; **lc–d**, **2a–d**, **3a–b**. rehydrated apothecia; **1e**. dry apothecia; **1f**, **3c**. apothecia in median section; **1g**, **5**. ascospores; **4**. conidia (from substrate). – Living state, except for 2 spores in **5** (without SBs). — **1a–g**. H.B. 7526b (holotype): Germany, Tübingen, on *Ulmus*; **2a–d**. H.B. 8121: ibid.; **3a–c**. H.B. 7824: ibid.; **4**. H.B. 7526c: ibid.; **5**. H.B. 9119: ibid.

126–333 m a.s.l. **Geology**: Russia: Upper Devonian sediment, central Europe: alluvial deposits from Keuper etc. **Phenology**: IV–VIII, XI–XII (throughout the year, long-lived).

Taxonomic remarks. *Orbilia siculispora* is characterized by its remarkable ascospores with acute apex and knob-like basal inflation formed by a strong subbasal constriction, together with rather large apothecia with prominent thin-walled hairs in fascicles, also by dicranidion-like conidia with parallel, mainly 4 arms. However, *O. abutilonis* and *O. ficicola* more or less share the same characters of the teleomorph (see there), whereas the North American *O. subsiculispora* differs in spores with only a slight subbasal constriction and in crystalloid SCBs in the paraphyses (see below). *O. suberis* seems also closely related, but differs in non-constricted, more curved spores and yellow-ochraceous apothecia. *O. milinana* differs in consistently geniculate and hooked, hardly constricted spore bases, consistently inverse orientation of the upper spores, a tendency to capitate paraphyses, and absence of hairs.

Variation. The spores of *O. siculispora* vary between medium to very strongly constricted near the base (Pl. 466: a_1). This subbasal constriction is more prominent in dead spores, and one may easily get confused to consider the basal appendage-like inflation as a conidium. Yet, this constriction does not lead to disarticulation. The varying strength of constriction in *O. siculispora* in living spores with fully developed SBs, in comparison to spore shapes of closely related species with only slight or even absent constriction leave no doubt that this feature is a characteristic of the mature, not overmature ascospore.

Among the collections from Tübingen, those on *Populus* showed the paraphysis apices more lanceolate or mammiform (Pl. 466: 2) compared to spathulate or lageniform on *Ulmus* (Pl. 466: 1), and the apothecia were bright ochre (Pl. 468: 1) compared to ochre-orange on *Ulmus* (Pl. 467). Also in the Russian sample on *Ulmus* the apothecia were more orange (Pl. 468: 3), but the paraphysis shape was not noted. An ochre colour showed also the Slovakian sample on *Populus*, but here the paraphyses were only indistinctly lanceolate or even cylindrical. Unlike the German samples, the paraphyses were here filled with numerous conspicuous globose VB-guttules (IVV: 17.XI.2019),

Plate 468. **1–3**: *Orbilia siculispora*. – **1a**. dead, attached, corticated, 15 mm thick branch of *Populus* × *canadensis*; **1b**, **2a**. detail of xeric *Populus* branches (rehydrated), bark covered by algae, *Xanthoria* and *Peniophora*; **1c–e**, **3a–b**. rehydrated apothecia; **1f**, **2b**. apothecia in median section; **1g–h**. id., marginal ectal excipulum; **1i**. ascospores; **1j**. conidia (from substrate). – Living state. – **3**: phot. E. Popov. — **1a–j**. H.B. 8546: Germany, Tübingen, Kirchentellinsfurt, on *Populus*; **2a–b**. H.B. 8728: ibid.; **3a–b**. LE 247566: Russia (West), Nasva, on *Ulmus*.

and these guttules occurred also in an associated rose-coloured population tentatively referred here to *O. ficicola*.

Anamorph. Among the two known species of *Dicranidion* with more than two arms, the conidia of *O. siculispora* resemble those of *D. incarnatum*, a species known from branches of *Opuntia* from Galapagos Islands which deviates in 3–8 arms. The anamorph of *O. fissilis* differs in much smaller conidia with diverging arms. Similar, but larger and more slender dicranidion-like conidia with diverging arms distinguish the closely related *O. ficicola* (Pls 472: 1m; 473: 1g).

Phylogeny. A sequence was taken from apothecia of one of the samples on *Ulmus* from Tübingen (H.B. 8121), comprising SSU (V6–V9, incomplete near 3’-end), ITS (incomplete near 5’-end), and a fragment of LSU (parts of D1 and D2). The S1506 intron region was not covered. Another three sequences were taken in II.2020 from apothecia of the *Populus* sample from Bratislava (A.P. 19/36b). They comprise SSU V9, S1506 intron, ITS, and LSU D1 and partial D2, and differ from the preceding merely in 1 nt and 1 gap in ITS1 and 2 nt in ITS2.

The distance to other members of series *Abutilones* lies in the ITS region at 13.3–25 %, the lowest percentage being to *O. ficicola* (13.3–14 %), with which it forms a strongly supported clade in our analyses (Phyls 13, S15–S16), the next close being *O. ebuli* (17.5 %), and in the LSU (325 nt) at 1.5–4.5 %, the lowest again to *O. ficicola*, the next close 3.3 % to *O. aethiopica* (*O. ebuli* 4.5 %).

Ecology. *O. siculispora* was found on ± rotten bark or wood of xeric, dead or sometimes living branches and trunks of *Populus* and *Ulmus* in riparian forests in humid, cold-temperate subcontinental central Europe and hemiboreal continental eastern Europe. The two collections on elm were on *Ulmus laevis*, a typical representative of floodplain forests, which shows the highest resistance against the elm disease, but also against prolonged flooding.

One of the sites where *O. siculispora* was found in abundance was an about 160 years old living *Ulmus* tree inside the town of Tübingen close to university buildings of a similar age (Pl. 467: 1a–b). The apothecia have been collected there between 2004–2009 on detaching chips of bark on the 1 m thick trunk at a height of 1–3 m above the ground, but only on the south-oriented half of the trunk, especially on its (south-)east- but also southwest-exposed side. Mainly those chips were colonized which could easily be removed from the bark layers beneath. Lichens nearly exclusively occupied the northwestern side of the trunk. Therefore, they almost never occurred close to the *Orbilia*, which appears to prefer areas being most protected against rain falls, remaining dry for rather long periods of time. Bark pieces which superficially looked empty showed immature apothecia deeply hidden in clefts, along with abundant dicranidion-like conidia.

Specimens included. **GERMANY**: **Baden-Württemberg**, Tübingen, Neue Aula, Gmelinstraße, 333 m, trunk of *Ulmus laevis*, on bark, 20.V.2004, H.O. Baral (H.B. 7526a). – ibid., 20.VI.2004 (H.B. 7526b, M-0291766, **holotype**, anam. apoth.). – 27.VI.2004, H.O. Baral & G. Marson (H.B. 7526c, anam. substr.), – ibid., 19.VI.2005, H.O. Baral (H.B. 7824). – ibid., 1.IV.2006 (H.B. 8121; sq.: KT222452, KT222448, KT222455). – ibid., 1.VII.2009, H.O. Baral & B. Liu (H.B. 9119 ø). – ibid., 28.V.2018, H.O. Baral (H.B. 10147 ø). – 6.3 km ENE of Tübingen, 0.7 km NW of Kirchentellinsfurt, Neckar river, 305 m, branch of *Populus* × *canadensis*, on bark, 17.IV.2007, H.O. Baral (H.B. 8546, anam. substr.). – ibid., 24.XII.2007 (H.B. 8728 ø). — **SLOVAKIA**, **Bratislava**, 8.5 km WNW of Bratislava, 1.5 km SE of Devín, Dolné Koruny, 157 m, log of *Populus alba*, on wood, 17.XI.2019, A. Polhorský (A.P. 19/36b, sq.: MT274519). — **RUSSIA (West)**: **Pskov**, **Loknya**, 42.5 km NNW of Velikiye Luki, 9 km N of Nasva, N of Bashovo, 126 m, branch of *Ulmus laevis*, on wood, 17.VIII.2011, E.S. Popov (LE 247566, doc. vid.).

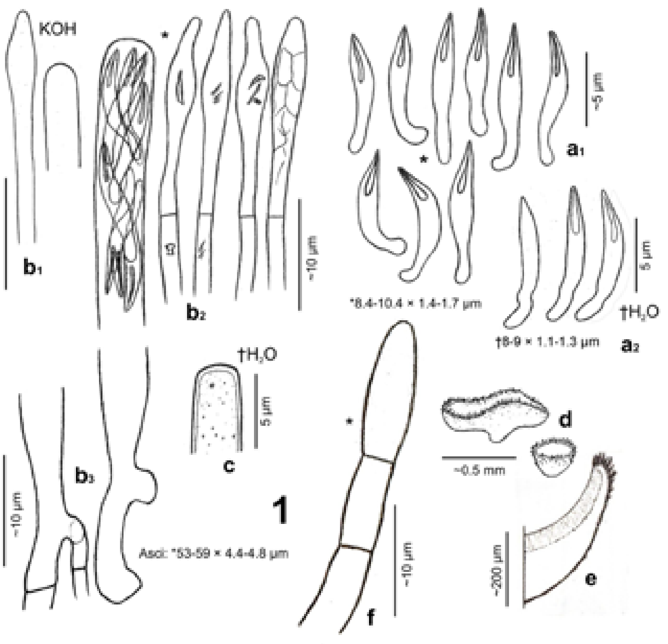
Orbilia subsiculispora G. Marson & Baral, **sp. nov.**, MB 813766 — Pl. 469

Etymology: after the similarity with *O. abutilonis*.
Typification: USA, Colorado, Cortez, branch of *Artemisia filifolia*, 31.V.1996, G. Marson (ex H.B. 6276a, M-0276590, holotype).

Latin diagnosis: *Similis* Orbiliae abutiloni *sed ascosporae basaliter minus constrictae, cellulae vivae excipuli et paraphysium corpuscula crystalloidea continentes. Habitat ad corticem putridum rami sicci* Artemisiae filifoliae *in zona supratemperata subhumida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.65 mm diam., light orange-rose, round to slightly undulating, disc strongly concave, margin crenulate to hairy; subsessile to short stipitate. **Asci** *53–69 × 4.4–4.8 µm, †45–50 × 3.5–3.8 µm, 8-spored, spores *4-seriate, 3 lower spores inverted; **apex** (†) slightly to medium truncate; **base** short-stalked, Y- to h-shaped. **Ascospores** *8.5–10.5 × 1.4–1.7 µm, †8–9 × 1.1–1.3 µm, ± fusiform, apex acute to acuminate, base medium attenuated in a thick, tail-like, often basally somewhat knob-like end, slightly to distinctly helicoid, near base partly distinctly 2 × geniculate; **SBs** ~3–4 × 0.3–0.6 µm, subulate. **Paraphyses** apically lageniform to spathulate-lanceolate, terminal cell *~18 × 2.6–2.9 µm, †2–2.7 µm wide, exceeding the dead asci by 4–8 µm. **Medullary excipulum** not examined. **Ectal excipulum** not examined; hairs 2-septate, ?30 × 4 µm, without **glassy processes**, free or slightly coherent. **Anchoring hyphae** not examined. **SCBs** in paraphyses crystalloid, filiform to plate-like. **Exudate** absent on paraphyses, present over ectal excipulum. — **ANAMORPH**: unknown.

Habitat: collected 0.1–0.6 m above the ground, corticated, 12 mm thick branch of *Artemisia filifolia*, on medium decayed bark (periderm). **Associated**: *Orbilia mesaverdiana*, *O. ocellata*, *O. plurilentiformis*. **Desiccation tolerance**: fully viable for probably at least 6 months. **Altitude**: 2290 m a.s.l. **Geology**: Upper Cretaceous sedimentary rock. **Phenology**: long-lived.



H.B. 6276a (holotype): USA, Colorado, on *Artemisia filifolia* (bark)

Plate 469. **1**: *Orbilia subsiculispora*. – **1a**. ascospores (**a**$_1$ living state, **a**$_2$ dead in H_2O); **1b**. upper part of asci and paraphyses, dead (**b**$_1$) and living state (**b**$_2$), ascus bases (**b**$_3$); **1c**. ascus apex; **1d**. apothecia with fimbriate margin (rehydrated); **1e**. apothecium in median section; **1f**. marginal hair.

Taxonomic remarks. *Orbilia subsiculispora* is very close to *O. abutilonis* and related species, from which it differs in only slightly constricted ascospores and in the presence of crystalloid SCBs in the paraphyses. It is also similar to *O. aurantiorubra* (series *Aurantiorubrae*), from which it mainly differs in lanceolate-lageniform paraphyses and a hairy apothecial margin. *O. somedana* has similar but ± straight ascospores and differs by paraphyses with capitate-clavate apices.

Ecology. *O. subsiculispora* was collected on medium rotten bark of xeric branches of *Artemisia filifolia* in the cold-temperate subhumid sagebrush desert scrub of the Colorado Plateau in the southwest of Northern America. The collection consisted of only two apothecia which were used up during this study.

Specimens included. **USA**: **Colorado**, Canyonlands, 15.5 km SSE of Cortez, Mesa Verde, 5 km NNW of Spruce Tree House, 2290 m, branch of *Artemisia filifolia*, on bark, 31.V.1996, G. Marson (ex H.B. 6276a, M-0276590, **holotype**).

Orbilia abutilonis E.K. Cash, Mycologia 30: 101 (1938) — Pls 470–471

Etymology: named after the host genus in the type collection, *Abutilon*.
Typification: Hawaii, Honolulu, branch of *Abutilon grandifolium* (as *A. molle*), 18.I.1928, C.L. Shear & N.E. Stevens (Shear & Stevens 552, BPI, holotype).
Misinterpretation: Friebes (2011: 13), = *O. ficicola*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1.3 × 0.5–1 mm, 0.09–0.12 mm high, receptacle ~0.06–0.08 mm, light ochraceous, (Cash: pale ochraceous buff to pinkish buff), slightly translucent, round to broadly elliptical, often with irregular outline, subscattered to densely gregarious in smaller or larger groups; disc slightly to medium concave, finally flat, margin distinct, 10–40 µm protruding (including hairs), distinctly crenate (denticulate) by forming whitish-yellowish teeth; broadly sessile, superficial or slightly erumpent to entirely immersed in small or large alveoles of bast; disc dry partly closed by the incurved margin, light ochraceous salmon to avellaneous (Cash). **Asci** †34–55 × 2.7–3.5 µm, 8-spored, basal 4(–6) spores inverted, often strongly mixed; **apex** (†) medium to strongly truncate (not indented, laterally scarcely inflated); **base**

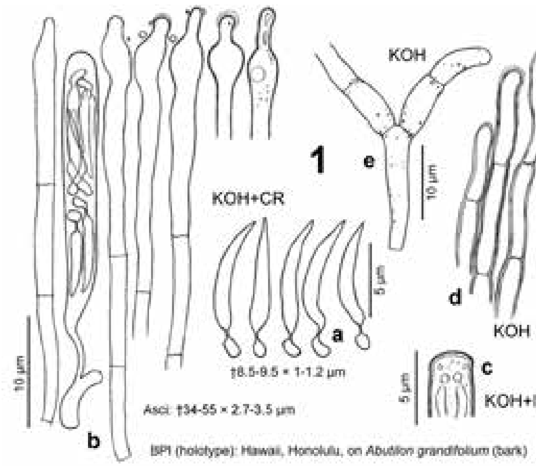


Plate 470. **1–2**: *Orbilia abutilonis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. marginal hairs; **e**. conidium from substrate.

with short to long, ± thin, flexuous stalk, L- or T-shaped. **Ascospores** †8.5–9.5 × 1–1.2 µm, subulate, very slightly to medium curved, apex strongly acute to acuminate, with abrupt tail of 1.7–2.3 × 0.7–0.8 µm, strongly constricted, straight to ± geniculate, inflated part cylindric-ellipsoid (appendage-like); **SBs** not seen. **Paraphyses** apically lanceolate or mostly lageniform to mammiform, with beaks 2–4 µm long, terminal cells †15–25 × 2–2.7(–3) µm, exceeding the dead asci by 2–4 µm, lower cells †8.5–11 × 1.3–1.6 µm; branched only near base. **Medullary excipulum** hyaline, 10–30 µm thick, of dense textura angularis-intricata, sharply delimited from ectal excipulum at flanks. **Ectal excipulum** pale yellowish, of (†) thin-walled, irregularly horizontally oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 25–30 µm thick at base, cells †10–15 × 5–9 µm; 15–20 µm thick at margin, of t. prismatica-porrecta oriented at a ~30–40° angle, marginal cells running out in **hairs** of †~20–40 × 2.5–3 µm, (1–)2-septate, cylindrical, slightly flexuous, wall 0.2–0.4 µm thick, hyaline, individual cells 10–18 µm long, without **glassy processes**, ± agglutinated by forming distinct teeth-like fascicles. **Anchoring hyphae** very abundant, †1.3–2 µm, walls 0.2 µm thick, forming a 20–60 µm thick layer of rather dense t. intricata. **SCBs** unknown. **LBs** unknown. **Exudate** over paraphyses absent or as scattered granules; over hairs and excipular cells of margin and flanks forming a thin, pale yellow, indistinctly rough covering layer by simulating a 0.5–1 µm thick hair wall. — **ANAMORPH**: dicranidion/trinacrium-like (presumed, from natural substrate). **Conidia** Y-shaped, †28 × 25 µm, stipe 13.5 × 3 µm, 0-septate, arms 15.5 × 3.5 µm, 1-septate, curved outwards.

Habitat: on 7–8 mm thick, corticated stem of *Abutilon grandifolium*, on strongly decayed bark (in alveoles of bast, periderm partly removed), also on periderm, no algae seen. **Associated**: ?*Diaporthe* sp. ?*Nectria* sp. **Desiccation tolerance**: unknown, but probably tolerant. **Altitude**: unknown (probably between 1–600 m a.s.l.). **Geology**: volcanic rock (tephrite). **Phenology**: I.

Taxonomic remarks. The Hawaiian *O. abutilonis* fits in most respects *O. ficicola* and *O. siculispora*. Especially ascospore size and shape is very much alike, although the spores of *O. abutilonis* are narrower than in *O. ficicola* when compared in the dead state, while *O. siculispora* lies between them. The ochraceous to pinkish buff original colour of the disc of *O. abutilonis* is in contrast to a more rose or orange-ochraceous disc of *O. ficicola* and *O. siculispora*. In *O. abutilonis* the anchoring hyphae formed a thick, subiculum-like layer which was also stressed by Cash, but which was often less developed in the other two species. *O. abutilonis* concurs with *O. ficicola* in hair morphology and in the presumed anamorph, whereas *O. siculispora* distinctly differs in both features.

For a long time we considered *O. abutilonis* and *O. siculispora* to belong to one species, for which reason Friebes (2011) used the name *O. abutilonis* for his Austrian collections.

Type studies. *O. abutilonis* was very misleadingly described as having uniseriate, allantoid to nearly globose spores measuring 2 × 1.5–1.7 µm. No doubt, Cash (1938) saw the spores only within the asci and there only the knob-like spore bases by overlooking the subulate upper part of the spores. The rather abundant and large apothecia looked macroscopically homogeneous so that a mixture seems to be quite improbable. Three apothecia of the holotype were examined in the present

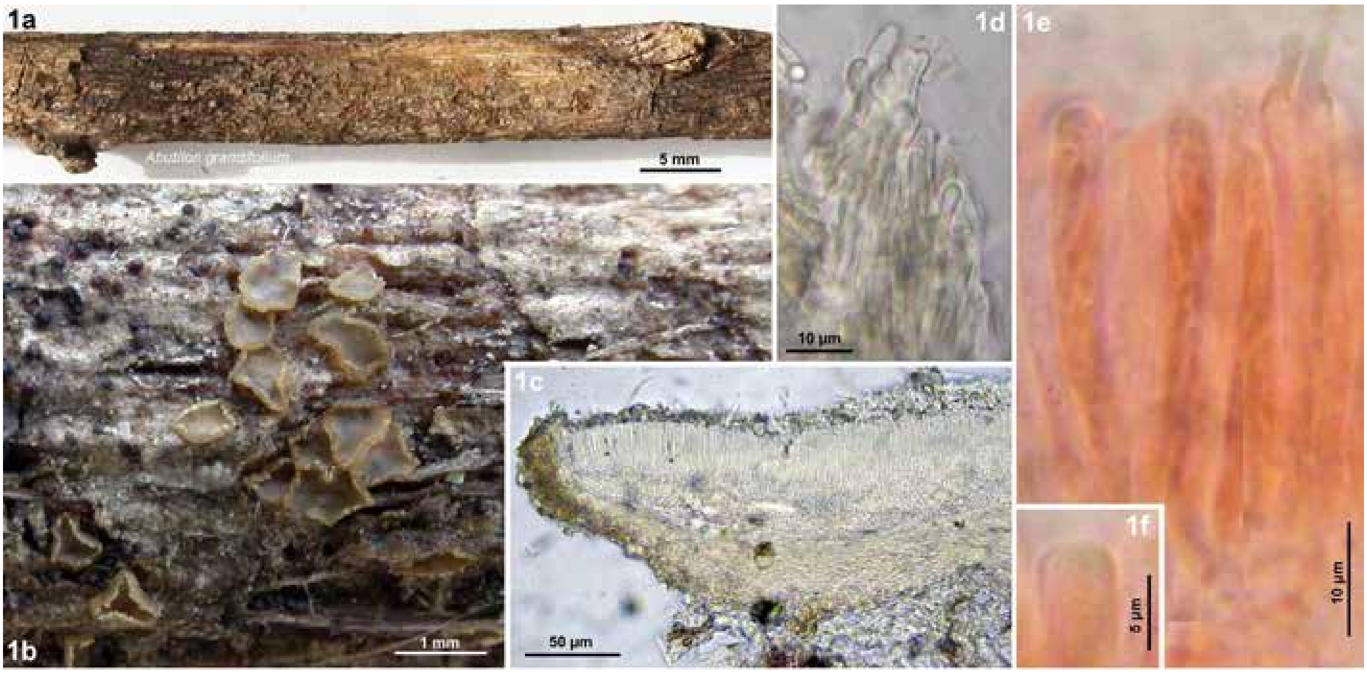


Plate 471. **1**: *Orbilia abutilonis*. – **1a**. dead, corticated branch of *Abutilon grandifolium*; **1b**. rehydrated apothecia; **1d**. apothecium in median section; **1c**. marginal hairs in squash mount; **1e**. asci and paraphyses; **1f**. ascus apex in front view. – Dead state (**1c–d** in KOH, **1e–f** in KOH+CR). —**1a–f**. BPI: Hawaii, Honolulu, on *Abutilon* (holotype).

study. Although Cash described the margin as crenulate, she did not report the hairs and their structure.

Anamorph. A single 2-armed conidium was found in an apothecium of the holotype, which closely resembles 2-armed conidia of *O. ficicola*, except for its small size (Pl. 470: 1e).

Ecology. The type collection was on bark of thin branches of *Abutilon* in the southwest exposed slopes in one of the islands of tropical semihumid (summer-dry) Hawaii. Cash (1938) did not provide ecological data apart from the substrate, and also the exact locality was not stated. *Abutilon grandifolium* is not native to Hawaii but was naturalized there, where it grows in waste areas and especially in rather dry southwest-exposed lowland regions up to 600 m a.s.l. (G. Wong pers. comm.).

Specimens included. **HAWAII**, **O'ahu**, ('N.') Honolulu, [?Kalihi valley,] branches of *Abutilon grandifolium* (as *A. molle*), on bark, 18.I.1928, C.L. Shear & N.E. Stevens (Shear & Stevens 552, BPI, **holotype**, H.B. 7600 ø, anam. substr.).

Orbilia ficicola G. Marson, Baral & E. Weber, **sp. nov.**, MB 825633 — Pl. 472–473, Map 83

Etymology: named after the host genus *Ficus* of the submediterranean collections.

Typification: France, Ardèche, Vallon-Pont-d'Arc, branch of *Ficus carica*, 12.IX.2016, G. Marson (ex G.M. 2016-09-12.1 & ex H.B. 10138a, M-0291756, holotype; sq.: MH221053 [from apothecia], MK473415 [from conidial isolate]).

Misapplied names: Friebes (2011: 13), as *O. abutilonis*.

Latin diagnosis: *Similis* Orbiliae abutiloni *sed ascosporae leniter latiores, conidia majora, 2–4-brachia. Habitat ad corticem vel lignum putridum ramorum siccorum* Fici caricae *in zona submediterranea semihumida Europae meridionalis, etiam* Populi, Tiliae, Ulmi etc. *in zona temperata humida Europae centralis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.4–1.5(–2)((–2.8)) × 0.3–1.2(–1.8)((–2.4)) mm, 0.1–0.14 mm high (receptacle 0.075–0.09 mm), pale to light pinkish-rose(-orange) {∼12}, slightly to medium translucent, round to broadly elliptical, scattered to subgregarious; disc young slightly concave, mature flat, margin distinct, (20–)50–70 µm protruding, with agglutinated hairs forming ± distinct white teeth-like fascicles; sessile or with a broad, indistinct obconical stipe, superficial; dry ± closed by the incurved margin and white teeth. **Asci** *42–48 × 3.7–4.5 µm {3}, †34–45 × (3.1–)3.5–4 µm {2}, 8-spored, spores *2–3-seriate, 3–5 spores inverted {3} (lower or upper spores, often mixed); **apex** (†) slightly to medium truncate (not indented, laterally uninflated); **base** with short to long, thin or thick, flexuous stalk, L-shaped. **Ascospores** *(7.5–)8–10(–10.5) × (1.1–)1.2–1.5(–1.6) µm {10}, †(7–)8.5–10.5(–11.5) × (1–)1.2–1.4(–1.5) µm {2}, subulate, with acute apex, straight to slightly curved, with abrupt, slight to medium inflated, often ± geniculate tail of 1.7–2.6 × 0.6–1 µm, inflated part of tail cylindric-ellipsoid (appendage-like); **SBs** *3–5.2 × 0.4–0.7 µm {5}, subulate, basally inflated, straight to slightly flexuous. **Paraphyses** apically lanceolate or mostly lageniform to mammiform, with beaks of *2–3 × 1.2–1.8 µm (†1.5–3 × 1.2–1.5 µm), also almost cylindrical, terminal cells */†13–20 × 2.2–3.5(–4) µm {3}, exceeding the dead asci by 4–7 µm, lower cells †6–11 × 1.5–1.8 µm {2}; branched only near base, hymenium pale rose-orange. **Medullary excipulum** 20–40 µm thick, pale rose, of dense textura intricata with scattered inflated cells, medium to sharply delimited from ectal excipulum by a 20–30 µm thick layer of pale to light yellow-orange t. porrecta with many inflated cells. **Ectal excipulum** hyaline, of (†) thin-walled, irregularly oriented t. angularis-prismatica from base to mid flanks, 30–50 µm thick at base, cells */†7–20(–25) × 5–13(–17.5) µm {2}; 20 µm thick at mid flanks, horizontally oriented t. angularis(-prismatica), at margin 10–15 µm thick, of t. prismatica oriented at a ∼0–10° angle, marginal cells forming agglutinated **hairs** */†(25–)30–50(–70) × 3–5.5 µm {4}, in upper part 2–3.3 {3} or 3.8–5 {1} µm wide, ∼1–2-septate, cells *(5–)7–14 µm long, cylindrical to slightly moniliform, straight to often ± flexuous, thin- to thick-walled, hyaline, without **glassy processes**, agglutinated to form 20–30 µm thick teeth of 40–80 × 40–80(–150) µm which have inwards curved lageniform paraphysis-like elements at their inward side. **Anchoring hyphae** abundant, */†1.5–3 µm wide, walls 0.2(–0.3) µm thick {T}. **SCBs** in paraphyses and ectal excipulum absent. **VBs** absent {5}, or present in paraphyses as numerous, small to large, globose, medium refractive guttules {1}. **Exudate** over paraphyses absent; over hairs and excipular cells of margin and flanks forming a thin, pale to light yellow covering layer. **— ANAMORPH**: dicranidion/trinacrium-like (from natural substrate {8}, molecular data from conidial isolate {1}). **Conidiophores** not observed. **Conidia** 2- or more often 3–4-armed by dichotomous branching, arms diverging though subparallel at the base, gradually taperings towards apex, outer arms often outwards curved, all arms apparently in one plane or somewhat contorted, total size *(45–)50–62(–70) × (37–)45–62(–90) µm when 3–4-armed, *54–60 × 15–25(–45) µm when 2-armed, stipe *15–24 × 2.5–3.5 µm, (1–)2–3-septate, arms *(24–)30–40(–55) × 3.5–4.3 µm, 3–6(–7)-septate {T}.

Habitat: collected 0–3 m above the ground, on 4–40 mm thick, ± corticated or decorticated, still-attached branches but also 25–30 cm thick trunks of *Euonymus europaeus* {1}, *Ficus carica* {6}, *Hibiscus syriacus* {1}, *Juglans regia* {2}, *Magnolia* sp. {1}, *Populus* sp. {2}, *P. alba* {1}, *Sambucus nigra* {1}, *Tilia* sp. {3}, *Ulmus laevis* {2}, on slightly to strongly decayed bark (periderm & bast) {14} or wood {6}, on outer surface or in cracks of periderm, partly close to old immersed pyrenomycete, green algae sparse to abundant. **Associated**: *Capronia pilosella* {1}, *Helminthosporium velutinum* {2}, *Hohenbuehelia cyphelliformis* {1}, *Letendraea helminthicola* {1}, *Nectria peziza* {1}, *Orbilia comma* {2}, *O. eucalypti* {1}, *O. ?fraxini* {1}, *O. pilifera* {1}, *O. siculispora* {1}, *O. vitalbae* {1}, *Patellaria atrata* {1}, *Strossmayeria basitricha* {1}, *Xanthoria parietina* {2} and other lichens. **Desiccation tolerance**: a few ectal excipular cells and some conidia still viable after 1.5 years. **Altitude**: 83–413 m a.s.l. **Geology**: alluvial deposits from Upper Jurassic, Cretaceous & Tertiary lime- & marlstone, flysch, Tertiary molasse. **Phenology**: IV, VI–VII, IX–I (throughout the year, long-lived).

Taxonomic remarks. *Orbilia ficicola* closely resembles *O. siculispora*, the Hawaiian *O. abutilonis*, and the North American *O. subsiculispora* in shape of ascospores and other elements of the teleomorph. The mostly striking difference in the fresh apothecial colour permits macroscopical distinction between *O. ficicola* (pinkish-rose) and *O. siculispora* (orange-ochraceous) which in one Slovakian sample even grew on the same branch. However, for *O. abutilonis* both colours are mentioned in the protologue, and for *O. subsiculispora* the orange-rose colour seems to be intermediate between *O. ficicola* and *O. siculispora*.

O. siculispora and *O. subsiculispora* appear to differ from *O. ficicola* and *O. abutilonis* in the marginal hairs which are in the latter two species distinctly narrower in their upper part and more flexuous and agglutinated by yellowish exudate. However, one of the two Austrian samples tentatively referred here to *O. ficicola* (from Fernitz) was described by Friebes (2011, as *O. abutilonis*) with orange- to wine-reddish apothecia (more pinkish on the photo, IVV: G.F. 20090004) and straight untapered hairs, and also the other (from Halbenrain, data on hairs unavailable) shows pinkish apothecia (Pl. 473: 4).

Two samples on *Juglans* (Serbia, IVV: 27.IX.2019; Slovakia, IVV: 25.XII.2019) fit *O. ficicola* in their rosaceous disc, spore length, and hair morphology. Based on their apothecial colour we have also tentatively considered Austrian collections on *Populus* and *Ulmus* as belonging to *O. ficicola*. The taxonomic value of disc colour is supported by DNA data

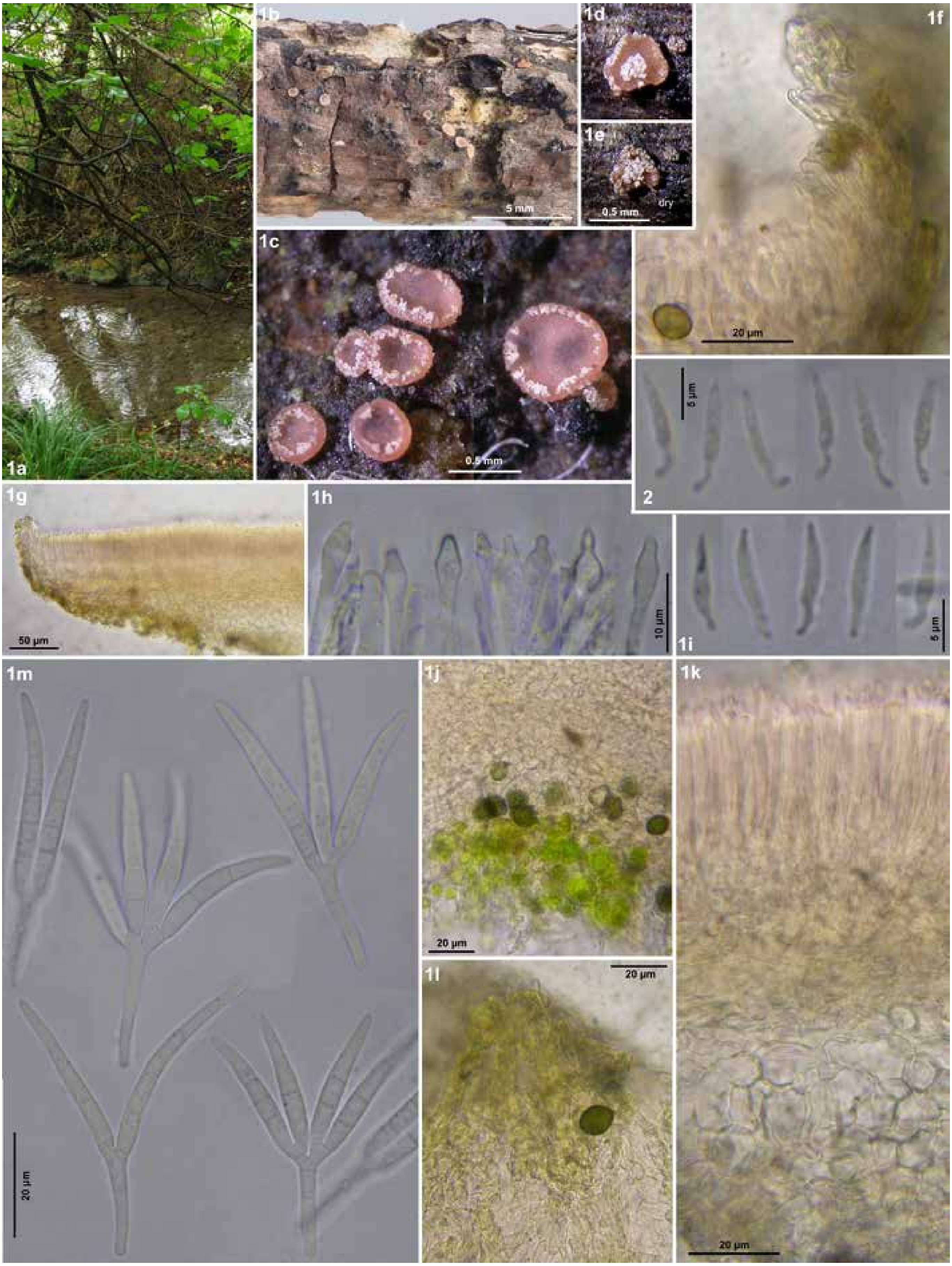


Plate 472. **1–3**: *Orbilia ficicola* (France, on *Ficus*). – **1a**. Dead attached branches of *Ficus carica* at rivulet (with *Fraxinus* & *Ulmus*); **1b**. dead, attached, corticated, 10 mm thick branch of *Ficus carica*; **1c**, **d**. rehydrated apothecia; **1e**. dry apothecia; **1g**. apothecium in median section; **1f**. id., protruding margin; **1k**. id., near base (hymenium, medullary and ectal excipulum); **1j**. id., near base, anchoring hyphae with abundant green algae and some brown alien spores; **1l**. marginal tooth of glassy processes agglutinated by yellowish exudate; **1h**. paraphysis apices; **1i**, **2**. ascospores; **1m**. conidia from substrate. – Living state, except for **1f**, **2** (in H_2O), **1g**, **k** (in KOH). — **1**. G.M. 2016-10-13.2: France, Drôme, Roussas; **2a–l**. H.B. 10138a (holotype): id., Ardèche, La Combe St. Pierre, on *Ficus*; **3**. G.M. 2016-10-12.1: id., Lagorce, on *Ficus*.

Plate 473. **1–6**: *Orbilia ficicola* (Austria). – **1a–b**, **2a**. fresh apothecia; **1d**, **3a–b**, **4a–b**. rehydrated apothecia; **1c**. marginal hairs in median section; **1f**, **5a**. paraphysis apices; **1e**, **2b**, **3c**, **5b**, **6**. ascospores; **1g**. conidia (from substrate). – Living state, except for **1c**, **1e**, **1f** right, **1e**, **5a** (in H_2O). – **2**, **3**, **4**: phot. G. Friebes, **1a–b**, **e–f**, **5**: phot. A. Gallé. — **1a–g**. 13.VI.2017: Austria, Steiermark, Feldbach, on *Tilia*; **2a–b**. G.F. 20090004: ibid., Fernitz, on *Populus*; **3a–c**. 21.IX.2011: Niederösterreich, Gänserndorf, on *Ulmus*; **4a–b**. 7.XI.2009: Steiermark, Halbenrain, on *Populus*; **5a–b**. 9.XI.2017: ibid., Feldbach, on *Tilia*; **6**. G.F. 20190001: ibid., on *Magnolia*.

from a Slovakian sample on a *Populus* branch in which both species co-occur as populations with sharply different colour (IVV: 17.XI.2019, A.P. 19/36a/b).

The observed severe differences in both conidial shape and rDNA data prompted us to distinguish *O. ficicola* from *O. siculispora*. *O. abutilonis* appears to be very close to *O. ficicola*, from which it is tentatively separated by narrower spores with a stronger subbasal constriction and perhaps by conidial shape. Since no conidia and rDNA data were available for most of the Austrian samples, their correct identity remained uncertain.

Variation. The hairs are usually somewhat flexuous and taper in their upper half (observed on *Ficus*, *Tilia*, and *Populus*), sometimes also straight and tapering only at apex of terminal cell (on *Populus*, Friebes 2011: fig. 4e). In the former case they resemble those of *O. abutilonis*, otherwise those of *O. siculispora*. Because many samples were not examined for this character, the taxonomic value of hair shape remains tentative.

In the Slovakian sample on *Populus* the paraphyses were only indistinctly lanceolate or even cylindrical and filled with numerous conspicuous globose VB-guttules (IVV: 17.XI.2019). These guttules occurred also in the associated ochre-coloured population of *O. siculispora*. The Hungarian sample was said to have rather short spores of only 6.5–8 × 1.5 µm (in KOH).

Anamorph. Dicranidion/trinacrium-like conidia were observed near apothecia in all French samples on *Ficus* and in the Austrian collections on *Tilia* and *Hibiscus* (Pls 472: 1m; 473: 1g). In their thinner, outwards curved arms they resemble the single conidium observed in *O. abutilonis*. Their strongly diverging arms sharply separate these two taxa from the anamorphs of *O. siculispora* in which the conidial arms are wider, straight and ± parallel (Pls 466: 1g; 467: 4; 468: 1j). No conidia developed in the ascospore isolate of *O. ficicola*, but a pure culture gained from conidia from the natural substrate proved to belong to the teleomorph based on molecular data gained from it.

Not included collections. Two Austrian samples from Steiermark on *Juglans* (ascospores *8–10 × 1–1.5 µm, IVV: 18.II.2017, 24.XI.2018) were not included in either description, because their orange-ochraceous discs point to *O. siculispora*.

Phylogeny. A sequence covering the almost entire rDNA derives from an ascospore isolate of the holotype of *O. ficicola* on *Ficus*. Further sequences were gained from a conidial isolate of the holotype and from apothecia of the Austrian sample on *Tilia*, three Slovakian ones on *Euonymus*, *Juglans* and *Populus*, and one from Hungary on *Sambucus*. All comprise S1506 intron, ITS, and LSU D1–D2, two Slovakian ones LSU D1–D5. The sequences of these six samples are fully identical in their overlapping part, except for 1 deviating nt in the ITS2 and one in LSU D1 of the Hungarian sample. When analysing ITS+LSU or LSU alone, *O. ficicola* clustered with *O. siculispora* (distance 15.5% in intron, 12% in ITS, 1.5% in LSU D1) and *O. ebuli* (11% in intron, 15% in ITS, 4% in LSU D1–D2) in a strongly supported clade (Phyls 13, S16). Also in the intron it clustered with medium support with *O. ebuli* in a clade (10.5% distance, S14).

Ecology. In southern Europe, *O. ficicola* was collected on rotten bark of xeric branches of *Ficus carica*, mainly in small dense mixed angiosperm woodlands with *Fraxinus*, *Ulmus* etc. along rivulets and close to roads, once also on a free-standing tree, at six different calcareous sites in the suprasub- to mesosubmediterranean semihumid lower Rhône valley in southern France. Further collections were on xeric wood and bark of twigs, branches, and trunks of *Euonymus*, *Juglans*, *Populus*, *Sambucus*, *Tilia*, and *Ulmus* in thermophilous forests of cold-temperate humid eastern Austria, southwestern Slovakia, northern Hungary, and northern Serbia. The vegetation includes floodplain forests with *Acer campestre*, *Fraxinus*, *Sambucus*, *Populus alba*, *Prunus padus* etc. along rivers (Graz and Bratislava), but also rich oak forests with *Quercus cerris*, *Sambucus nigra*, *Crataegus monogyna*, and *Pyrus pyraster* (Vértes Mt.), or *Querco-Carpinetum* with *Acer*, *Corylus*, *Fagus*, *Fraxinus ornus*, *Tilia tomentosa*, and *Staphylea pinnata* (Fruška Gora). The samples on twigs of *Magnolia* and *Hibiscus* are from a village garden near Graz.

Specimens included. **FRANCE**: **Rhône-Alpes**, **Ardèche**, 1.5 km SSE of Vallon-Pont-d'Arc, S of La Combe St.-Pierre, 90 m, branches of *Ficus carica*, on bark, 12.IX.2016, G. Marson (ex G.M. 2016-09-12.1, ex H.B. 10138a, M-0291756, **holotype**, anam. substr.; sq.: MH221053 [from apothecia], MK473415 [from conidial isolate]). – 1 km S of Vallon-Pont-d'Arc, Les Brugières, 90 m, branch of *F. carica*, on bark, 12.X.2016, G. Marson (G.M. 2016-10-12.2, anam. substr.). – 6 km S of Aubenas, S of St.-Sernin, 177 m, branch of *F. carica*, on bark, 12.X.2016, G. Marson (G.M. 2016-10-12.1, anam. substr.). – 20 km S of Aubenas, SW of Lagorce, 175 m, branch of *F. carica*, on bark, 12.X.2016, G. Marson (G.M. 2016-10-12.7, anam. substr.). – **Drôme**, 13.5 km SSE of Montélimar, 2 km NNE of Roussas, 150 m, branch of *F. carica*, on bark, 13.X.2016, G. Marson (G.M. 2016-10-13.2, anam. substr.). – 16 km S of Montélimar, ESE of Les Granges Contardes, 83 m, branch of *F. carica*, on bark, 13.X.2016, G. Marson (G.M. 2016-10-13.1, anam. substr.). — **AUSTRIA**: **Niederösterreich**, 39 km ENE of Wien, 9.5 km ENE of Gänserndorf, 1 km SE of Angern a. d. March, near March river (Slovakian border), 145 m, branch of *Ulmus laevis*, on wood, 21.IX.2011, G. Friebes (ø, doc. vid.). – **Steiermark**, 12 km SSE of Graz, 1.2 km SW of Fernitz, Mur, Kalsdorfer Au, 320 m, branch of *Populus*, on bark, 31.I.2009, G. Friebes (G.F. 20090004, doc. vid.). – 30 km ESE of Graz, 6 km WNW of Feldbach, NE of Rohr a. d. Raab, 335 m, trunk of *Tilia*, on wood, 13.VI.2017, A. Gallé (ø, anam. substr., doc. vid.). – ibid., 22.X.2017 (GJO 88305, doc. vid., sq.: MK473408). – ibid., 9.XI.2017 (ø, doc. vid.). – ibid., 305 m, twig of *Magnolia*, on bark, 21.I.2019, A. Gallé (G.F. 20190001, doc. vid.). – ibid., twigs of *Hibiscus syriacus*, on bark, 23.VI.2019, A. Gallé (anam. substr., doc. vid.). – 52 km SE of Graz, 8 km WNW of Bad Radkersburg, 4 km W of Halbenrain, SW of Unterpurkla, Donnersdorfer Au near Mur river, 218 m, trunk of *Populus*, on wood, 7.XI.2009, G. Friebes (ø, doc. vid.). – ibid., trunk of *Ulmus laevis*, on bark, 30.X.2011, G. Friebes (G.F. 20110194, non vid.). — **SLOVAKIA**, **Bratislava**, 8.5 km WNW of Bratislava, 1.5 km SE of Devín, Dolné Koruny, Danube oxbow, 157 m, log of *Populus alba*, on wood, 17.XI.2019, A. Polhorský (A.P. 19/36a, doc. vid., sq.: MT274518). – ibid., 150 m, branch of *Juglans regia*, on wood & bark, 25.XII.2019, A. Polhorský (A.P. 19/37, doc. vid., sq.: MT274520). – 10 km SE of Bratislava, 4.8 km S of Podunajské Biskupice, Topol'ové hony, 130 m, branch of *Euonymus europaeus*, on bark, 29.XII.2019, A. Polhorský (A.P. 19/38, n.v., sq.: MT274521). — **HUNGARY**: **Fejér**, 7 km NE of Mór, 4 km ESE of Pusztavám, Vértes Mt., 266 m, twig of *Sambucus nigra*, on bark, 25.XII.2019, A. Koszka (A.Ko., doc. vid., sq.: MT274522). — **SERBIA**: **Vojvodina**, Fruška Gora, 12.5 km S of Novi Sad, 6 km NNW of Irig, Iriški venac, W of WWII memorial, 415 m, branch of *Populus alba*, on bark, 12.VII.2019, D. Savić (doc. vid.). – 12 km SE of Novi Sad, 2.9 km SSE of Bukovac, Stražilovo, 215 m, wood of *Juglans regia*, 27.IX.2019, D. Savić (doc. vid.).

Map 83. Known distribution of *O. ficicola* in Europe (yellow = not included collections)

Not included. **AUSTRIA**: **Steiermark**, 3 km WNW of Gratwein, N of Stift Rein, Lechnerhof, 500 m, branch of *Juglans regia*, on wood, 24.XI.2018, G. Friebes (G.F. 20180341, doc. vid.). – 30 km ESE of Graz, 5.5 km NW of Feldbach, SW of Edelsbach, 315 m, branch of *J. regia*, on wood, 18.II.2017, A. Gallé, vid. G. Friebes (G.F. 20170002, doc. vid.).

Orbilia suberis Baral & R. Galán, **sp. nov.**,
MB 813767 — Pls 474–475

Etymology: referring to the substrate, *Quercus suber*.

Typification: Spain, Málaga, Ronda, trunk of *Quercus suber*, 26.II.2003, F. Prieto & A. González (AH 7564, holotype).

Latin diagnosis: *Apothecia rehydratata 0.8–2 mm diam., vivide lutea ad aurantio-ochracea, sessilia, margine valde fimbriato. Ascosporae *6.5–9 × 1–1.2 µm, cylindricae, apice (sub)acutae, basi rotundatae, ad basim non vel leniter et gradatim inflatae, leniter vel valde curvatae, in statu vivo corpusculum refringens filiformem vel subulatum continentes. Paraphyses ad apicem vix inflatae, spathulatae-sublanceolatae. Margo excipuli pilis longis, tenuitunicatis, 1–2-septatis, absque processis vitreis. Habitat ad corticem putridum in trunco sicco* Quercus suberis *in zona mesomediterranea semihumida Europae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** fresh or rehydrated (0.5–)0.8–1.7(–2) mm diam., 0.3–0.4 mm high (receptacle 0.13 → 0.07 mm), light to bright yellow- to orange-ochraceous, non-translucent, round, moderately gelatinous, subgregarious in small groups; disc slightly to medium concave, margin distinctly hairy-fimbriate; sessile on a broad obconical base, superficial; dry bright orange-red.

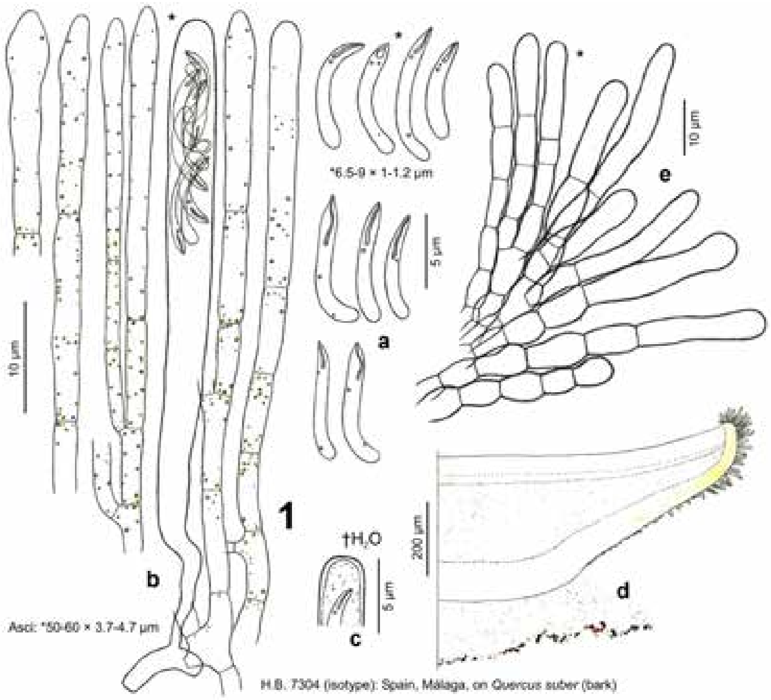


Plate 474. **1**: *Orbilia suberis*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. apothecium in median section; **e**. id., marginal ectal excipulum with hairs.

Asci *50–60 × 3.7–4.7 µm, †45–61 × 3–3.5 µm, 8-spored, spores *3–4-seriate, 3–4 lower spores inverted (very often mixed, partly also only upper spores inverted), pars sporifera *17–21 µm long; **apex** (†) medium truncate (never indented, laterally not widened); **base** with medium to very long, thin, flexuous stalk, T- to L-shaped. **Ascospores** *6.5–9 × 1–1.2 µm (~7.5–10 µm actual length), cylindrical, apex subacute to acute, base rounded, often very slightly and gradually widened, slightly to strongly curved, subhelicoid; **SBs** *1.7–3.3 × 0.2 µm in situ, filiform to narrowly subulate, straight to ± flexuous; SBs in aged spores tear-shaped, 1.3 × 0.5 µm. **Paraphyses** apically uninflated or mostly slightly (to medium) spathulate or obtusely lanceolate, terminal cells *(10–)18–28 × 2–4 µm, ± equalling the living asci, lower cells *6–11(–18.5) × 2–2.6 µm; unbranched at upper septum, hymenium pale yellow. **Medullary excipulum** hyaline, 100–200 µm thick, of very loose textura intricata without inflated cells, hyphae *1.5–2.5 µm wide, embedded in ample non-refractive gel, very sharply delimited from ectal excipulum, subhymenium 20–30 µm thick, of dense, pale yellowish-orange t. intricata. **Ectal excipulum** very pale yellowish-orange near base, of (*) thin-walled to slightly gelatinized, vertically oriented t. globulosa-angularis-prismatica from base to lower flanks, 70–100 µm thick near base, cells *7–16(–25) × 5–12 µm; 30–60 µm thick at lower flanks, 25–30 µm at mid flanks and margin, here of bright yellowish-orange t. prismatica, cells *7.5–11 × 4–6(–7) µm, oriented at a 50–80° angle to the surface, containing many small yellow LBs, marginal cortical cells running out into free, non-agglutinated **hairs** *25–65 × 5–6.3(–7) µm, 1–2-septate, cylindrical, smooth, thin-walled (wall *0.2–0.3 µm thick, at base of hair up to 0.4 µm); **glassy processes** absent. **Anchoring hyphae** very abundant, *1.5–4 µm wide, walls 0.2–0.3 µm thick, partly with inflated, ± moniliform elements *5–7 µm wide, embedded in thick non-refractive gel, forming a very loose, ~100–250 µm thick hyaline t. intricata. **SCBs** in paraphyses and ectal excipulum absent; paraphyses with quite many minute, light yellow **LBs** (carotenoids). **Exudate** over paraphyses and excipulum absent. — **ANAMORPH**: unknown (but see below).

Habitat: collected 1.75 m above the ground, on uneven exterior of 7 years old, undetached bark (cork) of a living, ~1 m thick trunk of *Quercus suber*, strongly decayed, ± greyed, without algae. **Associated**: none observed. **Desiccation tolerance**: a few excipular cells still viable after 10 months. **Altitude**: 675 m a.s.l. **Geology**: Tertiary clay, marl, lime- & sandstone. **Phenology**: II (but long-lived).

Taxonomic remarks. Macroscopically *O. suberis* is characterized by rather large, yellow-ochraceous, hairy apothecia and herein much resembles *O. pilifera*. Even the hairs are of the same type. Yet, *O. suberis* greatly differs in much narrower, strongly curved ascospores with filiform SBs. More closely related to *O. suberis* seem to be species around *O. abutilonis*, which differs in basally constricted, less curved spores. *O. suberis* further differs from these two taxa in not or hardly lageniform paraphyses.

Extraordinary in this species is the gel which forms thick sheaths over the anchoring hyphae and the hyphae of the medullary excipulum, and which is responsible for

Plate 475. **1**: *Orbilia suberis*. – **1a–e**. rehydrated apothecia; **1f**. dry apothecia (H.B. 7304, isotype); **1g–h**. fresh apothecia (AH 7564, holotype, phot. R. Galán). — **1a–h**. Spain, Málaga, on *Quercus suber*.

the gelatinous consistency of the apothecia. Due to its low refraction, the gel is quite invisible, but can be visualized by staining bright lilac in CRB.

Anamorph. A single Y-shaped, dicranidion-like conidium (*16.5 × 10.5 µm, IVV: H.B. 7304) was seen near the apothecia, which might represent the anamorph of *O. suberis*.

Ecology. The rich collection of *O. suberis* was made on rotten xeric bark still-attached to the living trunk of *Quercus suber* in a mesomediterranean semihumid mixed forest of *Quercus suber* and *Q. faginea* var. *canariensis* on a southwest-exposed slope in the Serranía de Ronda, a part of Sistema Bético, at the eastern end of Sierra de Grazalema in southern Spain. The old cork oak trees were perhaps not planted but are protected in order to extensively harvest the cork every 10 years at a height of 0.5–2.5 m above the ground. The *Orbilia* grew on the newly formed bark 7 years after the last harvest.

Specimens included. **SPAIN**: **Andalucía**, **Málaga**, Sistema Bético, Sierra de la Sanguijuela, 7 km WNW of Ronda, Puerto de la Calerilla, 675 m, trunk of *Quercus suber*, on bark, 26.II.2003, F. Prieto & A. González (AH 7564, **holotype**; H.B. 7304, **isotype**).

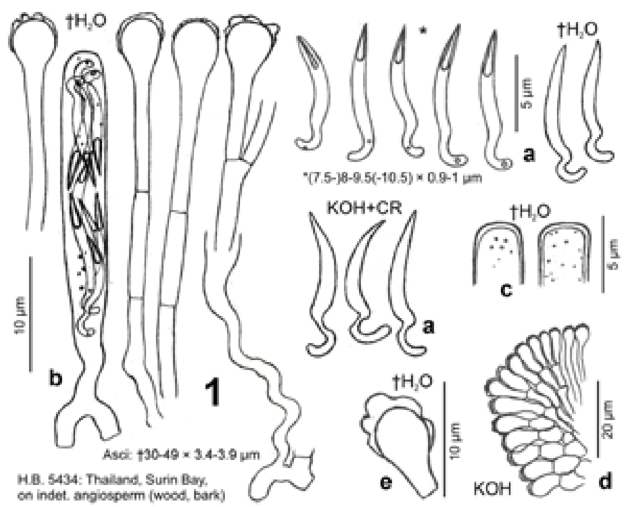


Plate 476. **1**: *Orbilia milinana*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section; **e**. cortical cell with exudate.

Orbilia milinana Bin Liu, Xing Z. Liu, W.Y. Zhuang & Baral, Fungal Diversity 22: 113 (2006) — Pls 476–477

Etymology: named after the collection site (Milin, Tibet) where the holotype was found.

Typification: China, Tibet, Zhaxiraodengxiang, wood of *Juglans regia*, 21.VII.2004, B. Liu & X.Z. Liu (HMAS 96813, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1.2 mm diam., 0.1–0.27 mm high, (very) pale yellow {2} or light cream {1} or pale to light rose-red {2}, semitranslucent, ± round, scattered; disc flat, margin indistinct, not protruding, smooth; sessile on a broad base, superficial; dry light yellow to orange-buff or rose-red. **Asci** *43–50 × 3.5–4 µm {1}, †(30–)33–45(–49) × (3–)3.4–4 µm {2}, 8-spored, spores (*/†) 4-seriate, 3–4 upper spores inverted (not or sometimes mixed) {3}, pars sporifera *19 µm long; **apex** (†) medium to strongly truncate (not indented, laterally not or scarcely widened); **base** with short to long, thin, flexuous stalk, T-, Y-, also H-shaped. **Ascospores** *(7–)7.5–9(–10.5) × 0.9–1.3 µm {6} (~8–11 µm actual length), †7.5–9.5 × 0.8–1 µm {1}, narrowly fusiform, apex gradually strongly acute († also acuminate), upper part slightly to medium curved (falcate, very slightly helicoid), lower ~1/4 of spore abruptly ± strongly reflexed and slightly to medium († more strongly) constricted by forming a short tail of 2–2.7(–3.3) × 0.7–0.8 µm which is mostly strongly bent forward to form a hook; **SBs** *(2.3–)2.5–3.5(–4) × (0.3–)0.5–0.7(–0.9) µm {3}, narrowly tear-shaped to subulate {1} or divided into a tear-shaped lower part and a short filum {T}. **Paraphyses** apically uninflated or slightly to medium clavate (to spathulate) {2}, or medium to strongly clavate-capitate {1}, terminal cells *17–26 × 2–3.3 µm {2}, †12–18 {1} × †2.5–3.1 {T} or (2.5–)3.5–4.5(–5) µm {1}, exceeding the dead asci by 3–7 µm, lower cells †7–9 × 1.2–2(–3) µm {1}, sometimes branched at upper septum. **Medullary excipulum** 15–30 µm thick, of (medium) dense, non-gelatinized textura intricata with many inflated cells, sharply or indistinctly delimited. **Ectal excipulum** of thin-walled, vertically oriented t. globulosa-angularis from base to margin, 40–100 µm thick near base, cells */†12–18 × 10–18 µm {1}; at flanks of t. angularis, cells *5–10 × 4–6 µm {1}, †5.5–13 × 4–11 µm {2}, 15–30 µm thick near margin, oriented at a 70–90° angle to the surface, marginal cortical cells *5–8 × 4–5.5 µm {1}, †6–12(–15) × 3–4.5 µm {2} (4–6 µm wide at submargin); **glassy processes** absent {4}. **Anchoring hyphae** abundant, 2–2.5(–3.2) µm wide, walls 0.2 µm thick {3}, forming a loose t. intricata. Living paraphyses without obvious inclusions {2} or containing globose **SCBs** {2} along with elongate, medium refractive **VBs** {2}. **Exudate** over paraphyses, margin and flanks rough-cloddy, (0.2–)0.5–1(–2.2) µm thick, forming isolated, firmly attached caps on each cell; at margin 0.2–1 µm thick, ± warted-cloddy. — **ANAMORPH**: unknown.

Habitat: lying on ground or 0.5–2 m above the ground, corticated, 7–15 mm thick branches or trunks of *Euphorbia canariensis* {1}, *Juglans regia* {T}, *Malus domestica* {1}, indet. angiosperm trees {2}, on medium decayed wood {3} and bark {2} (periderm), partly at splitted or broken end of branch, bark detaching; on petiole of *Arecales* {1}; ungreyed, partly covered by abundant green algae. **Associated**: ?*Opegrapha* sp. {1}, ?*Thaxteriella pezizula* {1}. **Desiccation tolerance**: basal ectal excipular cells and ascospores still viable for at least 2.5 weeks. **Altitude**: 15–2950 m a.s.l. **Geology**: China: Jurassic-Cretaceous sedimentary rock; Serbia: sericitic shale & quartzite, phyllite (near limestone); Tenerife: basaltic flow. **Phenology**: III, VII, XI (apparently throughout the year).

Taxonomic remarks. *Orbilia milinana* is characterized by very peculiar ascospores with acute apices and strongly geniculate, hooked bases (with the hook pointing forward, i. e., away from the curved dorsal side), also by the inverse orientation of the upper spores within the asci. In spore morphology the species closely resembles *O. abutilonis*, *O. ficicola*, and *O. siculispora*, which differ in less hooked spore bases and particularly in septate hairs at the margin and paraphyses with lageniform (beaked) apices.

O. lobeliae from Ethiopia might belong in the scope of *O. milinana*, judging from spore shape, especially when comparing the Chinese samples. However, its spores are distinctly narrower, and the SBs much smaller, especially shorter. Contrary to *O. milinana*, the basal spore hook points backward. Moreover, the rose-orange apothecia and the absence of VBs in the living paraphyses differ from *O. milinana* which has a yellowish-cream colour when fresh (seemingly whitish on the photo, Pl. 477: 2a).

Variation. The holotype from Tibet (Pl. 477: 2) concurs rather well with samples from Thailand (Pl. 476), Macaronesia, Puerto Rico, and Serbia (L. Quijada and D. Savić pers. comm., IVV: TFC Mic. 23222, 15.VII.2018, 29.XI.2019), also with a collection from Yunnan (Pl. 477: 3) studied by Y. Zhang and Z.F. Yu (pers. comm.), in which the paraphyses tend to have a slightly conical, spathulate apex. The sparse collection from Thailand differs in rather narrow spores and slightly shorter SBs, perhaps also in the SBs being subulate and attached without a distinct filum, moreover in more inflated paraphyses

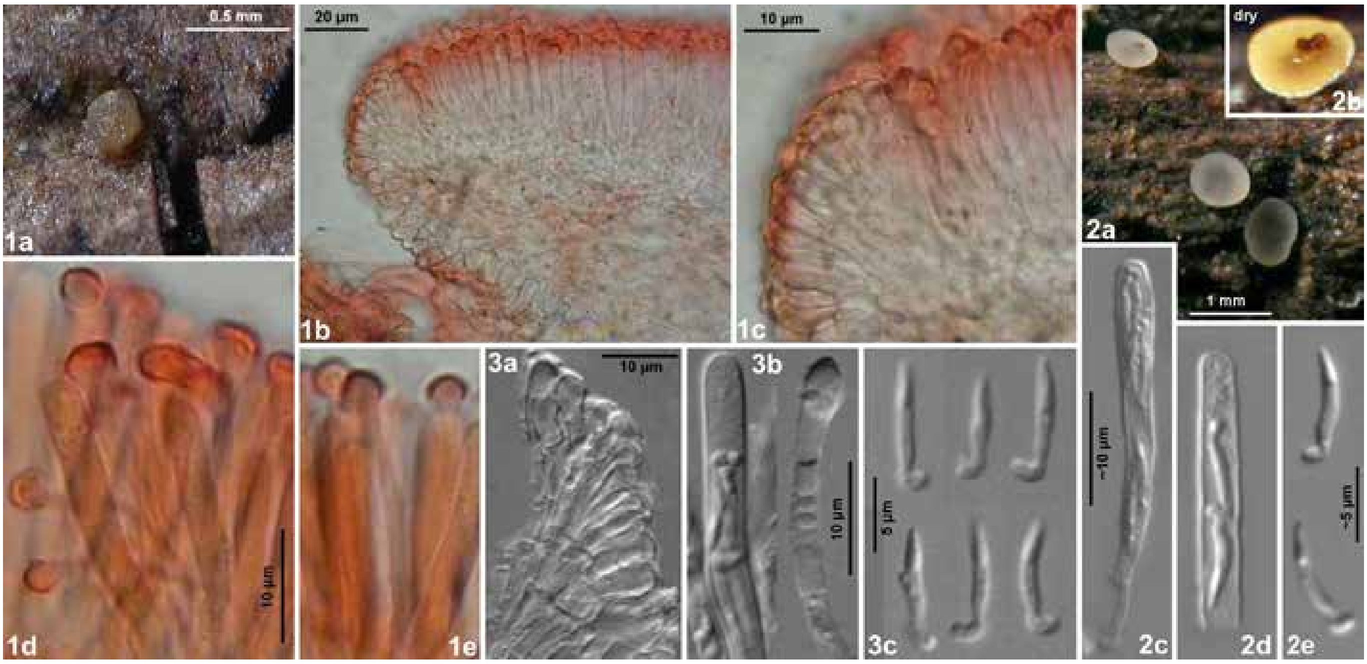


Plate 477. **1–3**: *Orbilia milinana*. – **2a**. fresh apothecia; **1a**. rehydrated apothecium; **2b**. dry apothecium (magnified), **1b**. apothecium in median section; **1c**, **3a**. id., marginal ectal excipulum; **1d–e**, **3b**. asci and paraphyses; **2e**, **3c**. ascospores. – Living state, except for **1b–e** (KOH+CR), **3a**, asci in **2c–d**. – **2a–e**: from Liu et al. (2006b, DIC), **3a–c**: phot. Z.F. Yu (DIC). — **1a–e**. H.B. 5434: Thailand, on indet. angiosperm; **2a–d**. HMAS 96813 (holotype): China, Tibet, on *Juglans* (Liu et al. 2006b); **3a–c**. Y.Z. pe-37: China, Yunnan, on indet. angiosperm.

and in smaller, more reddish apothecia, yet, short SBs and reddish apothecia were also observed in the Serbian sample. In the collections from Yunnan and Macaronesia some of the living paraphyses showed inconspicuous VBs, a feature typical of desiccation-sensitive species, but no such VBs were seen in the samples from Puerto Rico and Serbia. However, only a few living paraphyses were seen. The collection from Macaronesia fits well those from China, but in the narrower spores it concurs more with that from Thailand. The spores in the Serbian sample closely resemble those of *O. ficicola* and *O. siculispora*. An error must be mentioned for the scale bar of fig. 3 F in Liu et al. (2006a, b) which should be about 30 % longer.

Spore orientation could more or less be ascertained in five of the included samples. It remained uncertain in that from Puerto Rico, in which it is possible that the lower sp. were inverted and the upper spores not.

Not included collections. Another specimen from Yunnan (Xishan, IVV: ne4-1) differs in distinctly lanceolate paraphyses and herein strongly resembles the North American *O. subsiculispora*. However, that species has distinct marginal hairs, which are entirely absent in *O. milinana*, also the spores of *O. subsiculispora* are mostly only slightly bent at the base, and the lower spores are inversely oriented within the asci. However, in the specimen from Yunnan also some of the lower spores appear to be inverted.

A briefly studied specimen from northern Africa on wood of *Ulmus* (Maire 3055, MPU, IVV: H.B. 5602) might be conspecific. It shows the spore orientation and curved spore base of *O. milinana*, but free spores were not seen.

Phylogeny. Sequences were available for the Macaronesian sample (TFC Mic. 23222, from apothecia, S1506 intron and ITS) and the holotype from Tibet (ITS and LSU, presence of intron unclear). Although they form a strongly supported clade (Phyl. S15), the two strains surprisingly differ by 12 % in the ITS region. The ITS distance to other members of series *Abutilones* lies between 15.5–17.5 % to *O. carminorosea* and 23–24 % to *O. siculispora*. The intron shows a distance of ~ 18–24 % to other species of section *Aurantiorubrae*, and in the LSU (D1–D2) the lowest distance is 6.5 % to *O. siculispora* and *O. ficicola*, and 7.5 % to *O. carminorosea*.

Ecology. *O. milinana* s.l. was collected on rotten substrate of various angiosperms and from very different parts of the world. The holotype was from eastern China (Tibet) on wood of *Juglans regia* in an altimontane (orotemperate), cold-continental humid floodplain forest in the eastern Himalaya. The two south Chinese collections (Yunnan) on hygric branches were from montane subtropical humid (winter-dry) evergreen broad-leaved forests: one in the Xiaoheijiang Forest Park at the southern end of Hengduan Shan, a southeastern extension of Himalaya, and the other from a plateau near Kunming, east of Hengduan Shan. The sample from Thailand was on a xeric branch of a free-standing small tree close to the rocky coastline of the Phuket island, and that from Puerto Rico (Greater Antilles) on a xeric palm petiole, both with a tropical humid monsoon climate.

The European sample was from a living *Malus* tree on the trunk 2 m above the ground on dead wood of a scar where a dead branch broke down, in a supratemperate humid site on Fruška Gora in the suprasubmediterranean Vojvodina in northern Serbia. The sample from Macaronesia was on rotten xeric parts of *Euphorbia canariensis* in an inframediterranean semiarid xerophytic scrubland (cardonal, *Periploco laevigatae-Euphorbietum canariensis*). The not included northwestern African collection was from a subtropical semihumid forest close to the Mediterranean see.

Specimens included. **CHINA**: **Tibet** (Xizang), **Nyingchi**, Mainling, 56 km SW of Nyingchi, 2 km S of Zhaxiraodengxiang, N of Yaluzhangbu River, ~2950 m, on wood of *Juglans regia*, 21.VII.2004, B. Liu & X.Z. Liu (B.L. X098, HMAS 96813, **holotype**, doc. vid., DQ 656631, DQ656685). – **Yunnan**, **Pu'er**, Ning'er, 64 km N of Puér, ~25 km SE of Jinggu, Xiaoheijiang, ~1300 m, indet. branch, VII.2005, Y. Zhang & M. Qiao (Y.Z. pe-37, OT0001, YMFT, doc. vid.). — **THAILAND**: **Southern Thailand**, **Phuket**, Surin Bay, near coastline, 15 m, branch of indet. angiosperm, on bark & wood, 10.III.1996, C. Peller (H.B. 5434). — **MACARONESIA**: **Canary Islands**, **Tenerife**, La Matanza de Ajentejo, 8.5 km NE of Puerto de la Cruz, 1.1 km W of La Matanza de Acentejo, NW of Jagre, Puntillo del Sol, 95 m, on remnants of *Euphorbia canariensis*, 26.VII.2011, L. Quijada (TFC Mic. 23222, doc. vid.; sq.: KF696674). — **SERBIA**: **Vojvodina**: Fruška Gora, 18 km SW of Novi Sad, 2.7 km NNW of Bešenovački Prnjavor, Jabuka, 432 m, branch of *Malus domestica*, on wood, 29.XI.2019, D. Savić (doc. vid.). — **PUERTO RICO**: San Juan, Parque Nacional Julio Enrique Monagas, 37 m, indet. *Arecales*, on petiole, 15.VII.2018, L. Quijada (doc. vid.).

Not included. **ALGERIA**: **Algiers**, 63 km WSW of Algiers, 2 km NW of Hadjout ('Marengo'), forêt de Hadjout (Sidi Slimane), 60 m, on wood of *Ulmus campestris*, 14.I.1915, R. Maire (3055, MPU, as '*O. rubella* var.', H.B. 5602 ø). — **CHINA**: **Yunnan**, **Kunming**, ~12 km SW of Kunming, Xishan, ~1900 m, on indet. branch, S.F. Li and J.W. Guo, VII.2007 (J.W.G. ne4-1, YMFT, doc. vid.).

Orbilia lobeliae Baral, **sp. nov.**, MB 813769 — Pls 478–479

Etymology: named after the substrate of the type, *Lobelia giberroa*.

Typification: Ethiopia, Addis Ababa, Menagesha Suba, branch of *Lobelia giberroa*, 26.III.2010, U. Lindemann (ex H.B. 9318, M-0276501, holotype).

Latin diagnosis: *Differt ab* O. milinana *ascosporis ad basim abrupte et valde reflexis, corpusculis refringentibus brevioribus. Habitat ad corticem putridum siccum* Lobeliae giberroae *in zona mesotemperata humida afromontana Africae septentrio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1 mm diam., 0.12–0.15 mm high, light rose-orange, medium translucent, round, scattered or in small groups; disc slightly concave to flat, margin distinct, 5–10 µm protruding, smooth; ± broadly sessile, superficial; dry bright brick-orange. **Asci** *40–47 × 3.8–4.3 µm, †33–45(–50) × 3–3.5 µm, 8-spored, spores *4-seriate, 4–5 upper spores inverted (sometimes mixed); **apex** (†) medium to strongly truncate (not indented, laterally not or slightly inflated); **base** with medium to very long, thin, flexuous stalk, L-shaped. **Ascospores** *7–8 × 0.6–0.8 µm (~8.5–9.5 µm actual length), †7–7.5 × 0.5–0.7 µm, narrowly fusiform, apex acute to acuminate, slightly to medium curved (falcate), tail 2–2.5 × 0.6–0.7 µm, with ± strong constriction and reflexed (hook-like), ± cylindrical inflated part pointing backward; **SBs** *1.5–2 × 0.3–0.4 µm, subulate, straight. **Paraphyses** apically slightly to medium clavate-capitate, terminal cells *16–18 × (2.5–)3–4 µm, lower cells *6–12.5 × 1.5–1.8 µm; unbranched at upper septum, hymenium pale rose. **Medullary excipulum** pale rose, 50–70 µm thick, of medium dense, (†) medium to strongly gelatinized textura intricata with horizontal orientation, with many indistinctly inflated cells, medium sharply delimited. **Ectal excipulum** pale rose, of (†) thin-walled (to slightly gelatinized), vertically oriented t. globulosa-angularis from base to mid flanks, 30–40 µm thick near base, cells *10–20(–28) × 8–18 µm; 15–20 µm thick near margin, of t. prismatica oriented at a 40–60° angle to the surface, marginal cortical cells *5–10 × 3–4 µm; **glassy processes** absent. **Anchoring hyphae** abundant, †1.5–2.5 µm wide, walls 0.2 µm thick, forming a loose hyaline t. intricata 15–50 µm thick. **SCBs** in paraphyses and ectal excipulum absent; **VBs** absent. **Exudate** over paraphyses 0.3–1(–1.5) µm thick, irregularly granular-cloddy, hyaline, firmly attached, over margin and flanks 1–2 µm thick, hyaline to pale yellowish. — **ANAMORPH**: unknown.

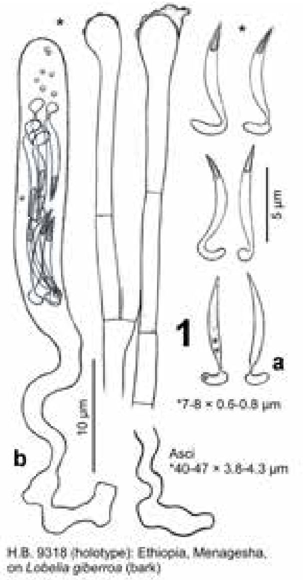


Plate 478. **1**: *Orbilia lobeliae*. – **a**. ascospores; **b**. ascus and paraphyses.

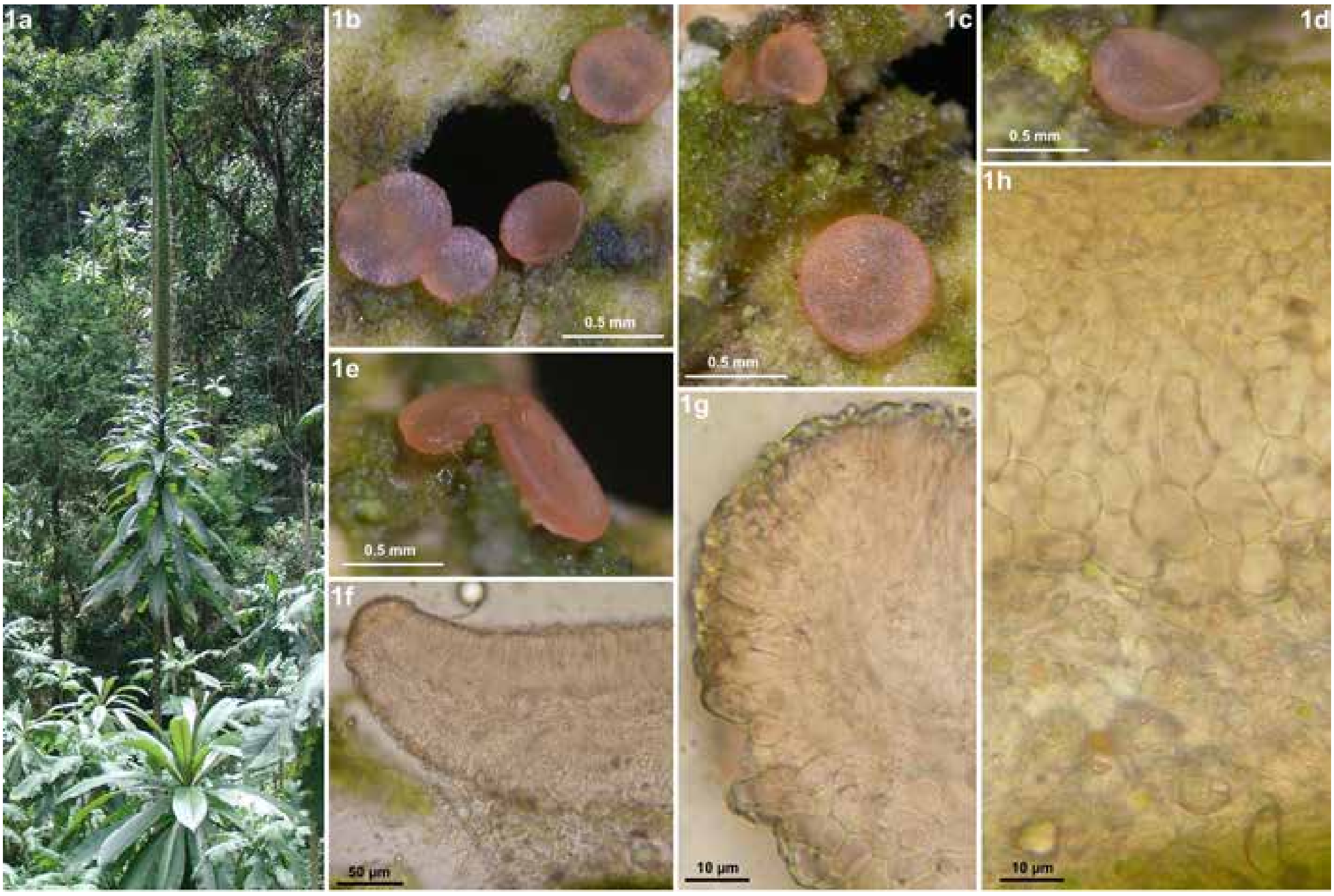


Plate 479. **1**: *Orbilia lobeliae*. – **1a**. warm-temperate afromontane forest with *Lobelia giberroa*; **1b–e**. rehydrated apothecia; **1f**. apothecium in median section; **1g**. id., marginal ectal excipulum; **1h**. id., basal excipulum and anchoring hyphae. – Living state. – **1a**: phot. U. Lindemann. — **1a–h**. H.B. 9318 (holotype): Ethiopia, Menagesha Suba, on *Lobelia*.

Habitat: on a standing, corticated, ?4 cm thick branch of *Lobelia giberroa*, on medium decayed bark (periderm), with many green algae and some black yeasts. **Associated**: *Hyalorbilia brevistipitata* (on separate branch). **Desiccation tolerance**: ± fully viable for at least 1.5 months. **Altitude**: 2520 m a.s.l. **Phenology**: III (but rather long-lived).

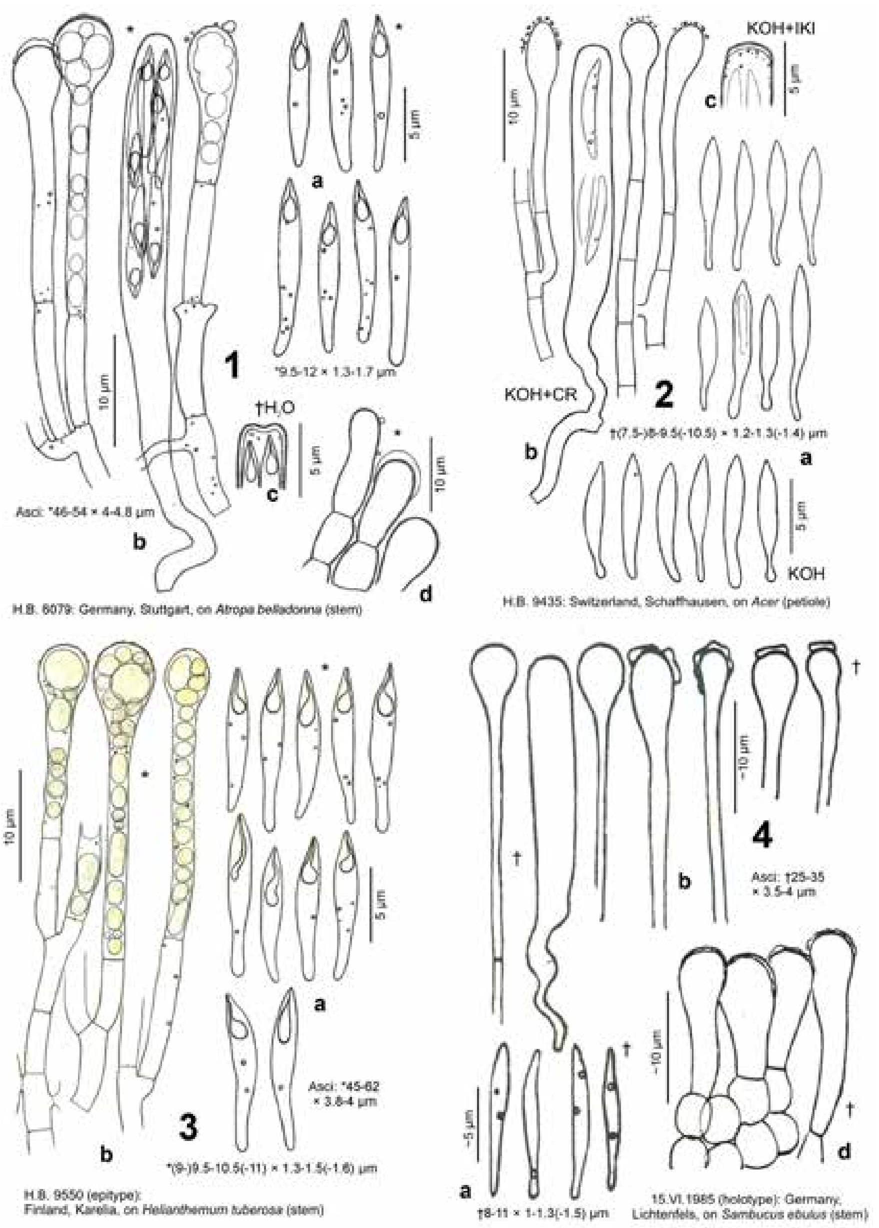
Taxonomic remarks. *Orbilia lobeliae* is easily recognized by its narrow falcate ascospores with a subbasal constriction and a sharply reflexed, ± cylindrical inflated basal end which points in backward direction, also in the upper spores being quite consistently inverted. Species with similar spores (*O. milinana*, *O. abutilonis*, *O. ficicola*, *O. siculispora*, *O. subsiculispora*) differ in the basal end being bent in a forward or ± downward direction, and in distinctly longer SBs.

Ecology. *O. lobeliae* was collected on bark of a xeric branch of *Lobelia* in a warm-temperate humid (somewhat winter-dry), evergreen, predominantly broad-leaved afromontane forest at the western slope of an old volcano in the central plateau of the Ethiopian highlands.

Specimens included. **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, southern part of Menagesha Suba State Forest, 2520 m, branch of *Lobelia giberroa*, on bark, 26.III.2010, U. Lindemann (U.L. 0310-22, **isotype**; ex H.B. 9318, M-0276501, **holotype**).

Orbilia ebuli Svrček, Česká Mykol. 41: 22 (1987) — Pls 480–481, Map 84

Etymology: after the host plant, *Sambucus ebulus*. **Typification**: Germany, Oberfranken, Serkendorf, stem of *Sambucus ebulus*, 15.VI.1985, H. Engel (holotype: illustration in Svrček 1987a: fig. 2.4). — Finland, Outokumpu, stems of *Helianthus tuberosus*, 28.V.2011, M. Pennanen (ex H.B. 9550, M-0276476, epitype, designated here, MBT202372; sq.: KT222425).



H.B. 6079: Germany, Stuttgart, on *Atropa belladonna* (stem)

H.B. 9435: Switzerland, Schaffhausen, on *Acer* (petiole)

H.B. 9550 (epitype): Finland, Karelia, on *Helianthemum tuberosa* (stem)

15.VI.1985 (holotype): Germany, Lichtenfels, on *Sambucus ebulus* (stem)

Plate 480. **1–4**: *Orbilia ebuli*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. marginal cortical cells of ectal excipulum. – **4**: from Svrček (1987a).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.5(–0.8)((–1)) mm diam., 0.09–0.2 mm high, (very) pale to light rose-cream (to rose-orange), medium to strongly translucent, ± round, scattered to ± gregarious; disc flat, margin 0–10 µm protruding, finely pubescent or mostly distinctly crenulate to subdenticulate {5}; broadly sessile, seemingly superficial but apparently partly erumpent from splits in epidermis; dry contracted or not, light cream-rose to bright orange-red. **Asci** *45–55(–62) × 3.8–4.8 µm {2}, †(31–)35–46(–52) × (3.1–)3.5–4(–4.3) µm {4}, 8-spored, spores *3–4-seriate, 4–5 lower spores inverted {2} (sometimes strongly mixed), pars sporifera *20–25 µm long; **apex** (†) slightly to strongly truncate (not or slightly to distinctly indented, laterally not widened); **base** with medium to long, thin, flexuous stalk, T- or L-shaped. **Ascospores** *(8–)9–11(–12)((–13)) × 1.3–1.6(–1.7) µm {5}, †(7.5–)8–10.5(–11.3) × (1.2–)1.3–1.5(–1.6) µm {2}, narrowly fusoid(-clavate), often with cylindrical middle part, apex (subacute to) acute (to acuminate), base slightly to strongly attenuated, often forming a tail *2–3.7 × 0.5–0.8(–1) µm, †0.4–0.5(–0.8) µm wide (sometimes with a bulbous base and subbasal constriction), straight to (very) slightly curved near base; **SBs** *2.7–4(–5.5) × 0.7–1.1 µm {4}, divided into an abruptly or gradually swollen, ellipsoid to tear-shaped lower part and a filiform upper part of equal length or slightly shorter, rarely subulate, straight or medium flexuous. **Paraphyses** apically slightly to very strongly capitate(-clavate), rarely spathulate, terminal cells *(14–)17–29 × (2.5–)3.5–5(–5.5) µm {2}, lower cells *5–14 × 1.8–2.7 µm {2}, rarely branched at upper septum. **Medullary excipulum** 20–50 µm thick, of dense textura intricata with indistinct inflated cells, sharply delimited. **Ectal excipulum** of thin-walled, indistinctly oriented t. globulosa-angularis from base to margin, 20–70 µm thick near base, cells *(7–)10–20(–25) × (6–)9–14(–17) µm {3}, †7–15 × 5–8(–13) {1}; 10–20 µm thick near margin, of. t. prismatica-porrecta oriented at a 10–40° angle to the surface, marginal cortical cells *(9–)11–14(–19) × (3.5–)4–5(–6.5) µm {2}, †6–10 × 3–4.5 µm {2}, ± thin-walled, sometimes hair-like but usually coherent to form small teeth; **glassy processes** absent {6} or sometimes present, 2–4 × 2.5–3 µm {1}. **Anchoring hyphae** abundant, */†2–3 µm wide, walls 0.2(–0.3) µm thick {2}, often forming a dense t. intricata 20–70 µm thick at the base, gelatinized or not, sometimes also with globular cells, over flanks and margin sometimes forming a 5–7 µm thick yellowish layer. **SCBs** in paraphyses and ectal excipulum absent {3}; **VBs** absent {1} or abundant in terminal cells of paraphyses {2}, low-refractive, hyaline to pale yellow, deep red-brown in IKI. **Exudate** over paraphyses, margin and flanks 0.1–0.2 µm up to 0.4–1 µm thick, rough to granular, firmly or loosely attached, on marginal cells sometimes cap-like, yellowish. — **ANAMORPH**: unknown.

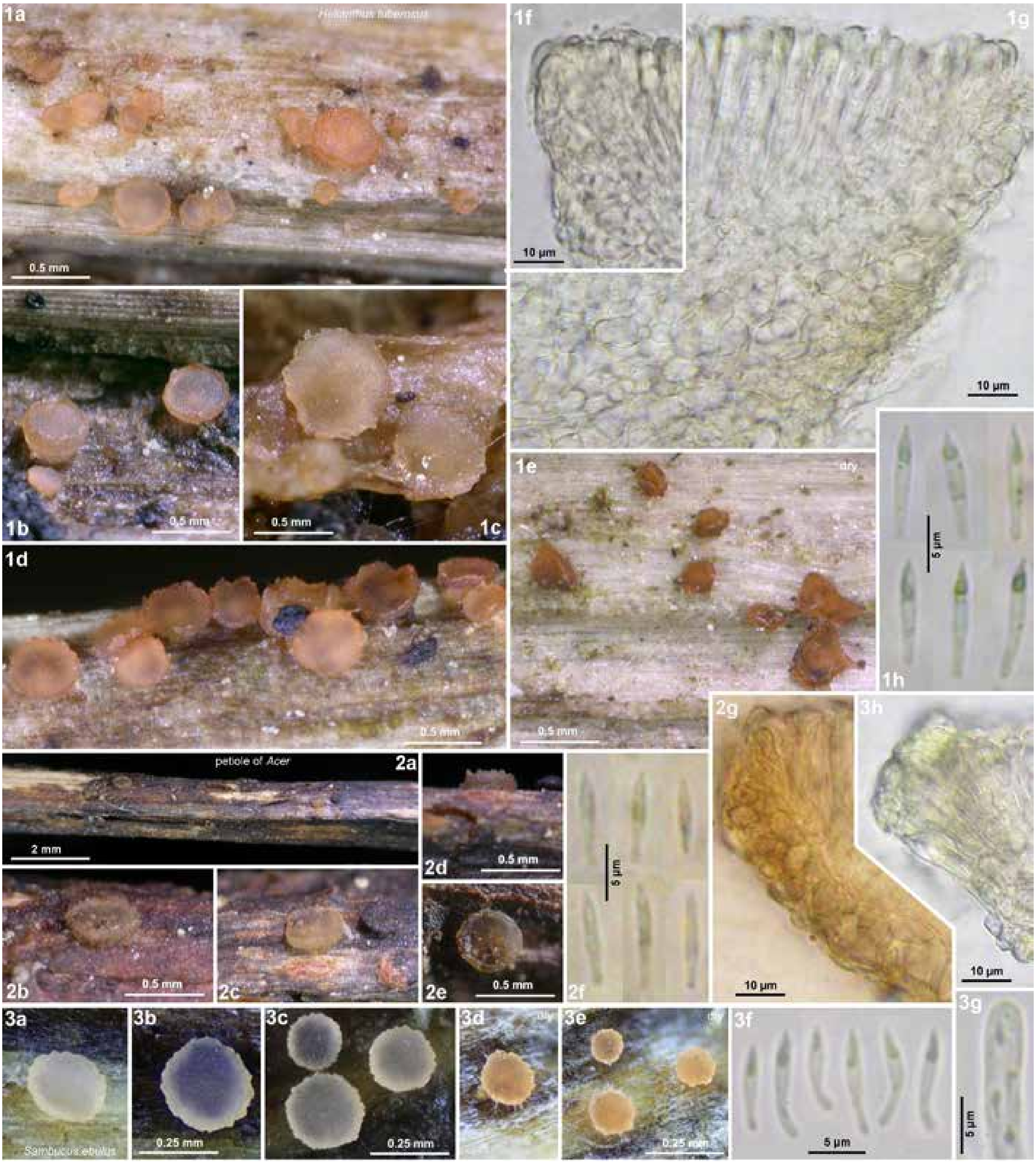


Plate 481. **1–3**: *Orbilia ebuli*. – **1a–d**, **2a–e**, **3a–c**. rehydrated apothecia (**2**: after 24 years); **1e**, **3d–e**. dry apothecia; **1f**, **2g**, **3h**. apothecia in median section (marginal region); **3g**. apex of mature ascus with spores; **1h**, **2f**, **3f**. ascospores. – Living state, except for **2f**, **3h**, ascus in **3g** (in H_2O), **2g** (in KOH). – **3a–g**: phot. S. Tello. — **1a–h**: H.B. 9550 (epitype): Finland, on *Helianthus*; **2a–g**: H.B. 9435: Switzerland, Schaffhausen, on *Acer*; **3a–h**. Spain, Jaén, on *Sambucus ebulus*.

Habitat: on previous year's stems of *Apiaceae* sp. {1}, *Atropa belladonna* {1}, *Helianthus tuberosus* {2}, *Sambucus ebulus* {3}, petiole of *Acer* sp. {1}, ungreyed, sometimes blackened, no algae. **Associated**: *Calycina drosodes* {1}, *Cyathicula ?cyathoidea* {1}, *Pirottaea* sp. {1}, *Pyrenopeziza atrata* {2}, *Trichopeziza mollissima* {1}, *Urceolella crispula* {1}. **Desiccation tolerance**: basal excipular cells and many immature asci still alive after 4 weeks, a few spores after 8 weeks. **Altitude**: 125–1630 m a.s.l. **Geology**: Muschelkalk, Middle & Upper Jurassic limestone, Cretaceous flysch, Pleistocene calcareous sand (moraine), travertine tuff; granite, granodiorite, schist, serpentinite, gabbro, basalt. **Phenology**: III–VI (but rather long-lived).

Taxonomic remarks. *Orbilia ebuli* closely resembles *O. rosella* and was once even recorded on the same substrate (*Atropa*). It differs hereof and also from *O. paravitalbae* mainly in narrower ascospores with ± acute instead of obtuse apices and partly distinct basal tails. The occasional presence of short glassy processes was observed in both species. For the similar but lignicolous *O. somedana* (p. 904) and *O. rehmii* (p. 904) see there. With its rather large, tear-shaped SBs attached by a narrow upper part, *O. ebuli* resembles species of series *Aurantiorubrae* but also section *Helicoon*.

Variation. Apothecia varied in the intensity of the rose-cream colour, also in size. On the type substrate, *Sambucus ebulus*, the specimen from Spain showed the smallest apothecia (0.13–0.31 mm diam.), whereas in the holotype from Germany they were said to be 0.4–1 mm large. The collection on *Acer* showed a tendency of the spore tails to be constricted similar as in the type on *Sambucus*, but this constriction is apparently mainly present in the dead state. In the samples on *Atropa* and *Helianthus* the asci were longer than in the other ones, while the length given in the protologue might not include the entire ascus stalk. In that on *Atropa* the SBs are ± straight (Pl. 480: 1a), whereas in those on *Helianthus* (Pls 480: 3a; 481: 1h) and *Sambucus ebulus* they are partly distinctly flexuous. Indented ascus apices were seen in the *Atropa* collection but never in those on *Acer* and *Helianthus.* Short glassy processes at the margin were only observed in the Spanish specimen (Pl. 481: 3h).

Type studies. Authentic material of *Orbilia ebuli* could not be located in Svrček's herbarium, nor in the herbarium of PRM (M. Chlebická pers. comm.). The protologue, which was based on a single collection, mentions a duplicate in Heinz Engel's private herbarium, but also there no type material could be found (H. Engel pers. comm.). In the lack of a voucher specimen, the illustration added to the protologue, from which a few details are included in the above description, must serve as holotype (Arts 8.1, 40.4 ICN). For a more precise typification we here designate a rich collection on *Helianthus* from Finland (ex H.B. 9550), studied in the living state and well corresponding to the original description (Fig. 4), as **epitype** of *Orbilia ebuli* (Pl. 480: 3). The epitype concurs morphologically also well with a recent Spanish sample on the type substrate, *Sambucus ebulus* (Pl. 481: 3).

Although a photo of a paratype collection of *O. ebuli* (Engel et al. 1987: 67, pl. 55 fig. 213) shows whitish apothecia, Engel & Hanff (1987: 67), Engel et al. (1987: 67) and Svrček (1987a) described them as rose or grey-rose when fresh, 0.4–1 mm diam., turning orange(-yellow) when dry, with a 'finely and indistinctly subdenticulate margin'. The paraphyses are described as apically oblong-clavate to subglobose-capitate, 3–5 µm wide, and the (dead) spores 8–11 × 1–1.3(–1.5) µm, inequilaterally fusiform, with both ends attenuated (but the lower part sometimes with a minute clavate inflation), partly with 1–2 small guttules (see Pl. 480: 4). Neither distinct hairs nor glassy caps are reported. Ascus size is given much shorter (25–35 × 3.5–4 µm, 'non bifurcato') than in the present observations, perhaps because the asci were broken below.

Svrček believed *O. ebuli* to be very closely related to *O. luteorubella* and to differ, e. g., in the guttulate spores, i. e., in the presence of a few small oil drops. He was unaware, however, of the characteristic spore bodies in *Orbilia*, for instance the rather long and narrow SBs in *O. luteorubella* which, contrary to *O. ebuli*, get tear-shaped only when overmature. Since no information on spore bodies of living spores is available for the original collections of *O. rosella* and *O. ebuli*, their separation remains somewhat tentative for the time being.

Not included collection. An old sparse specimen from Czechia on *Sambucus ebulus* under the name *Calloria vinosa* in M (herb. G. Niessl) was examined. It differs by rather wide, fusiform spores (†8–9.5 × 1.6–1.7 µm) with obtuse apices which would also fit *O. rosella* or a species of series *Helicoon*.

Phylogeny. A sequence taken from apothecia of the epitype of *O. ebuli* (SSU, S1506 intron, ITS, LSU) shows an ITS distance of 14% to *O. carminorosea*, 15% to *O. ficicola*, and > 18% to other species. In the LSU (D1–D2) the minimum distance is 4% to *O. ficicola* (4.5% to *O. carminorosea*), and in the intron 11% to *O. ficicola*. When analysing ITS+LSU or LSU, *O. ebuli* clustered with *O. siculispora* and *O. ficicola* in a strongly supported clade (Phyls 13, S16).

Map 84. Known distribution of *O. ebuli* in Europe (yellow = not included collection).

Ecology. *Orbilia ebuli* is only known from a few collections on herbaceous stems of different plants lying in moist or dry leaf litter, also on petioles. It was found in subcontinental, humid to rarely semihumid sites under very diverse thermotypes: in cold-temperate central and thermoboreal northern Europe but also in orosub- and mesomediterranean southern Europe, e. g. in a rather shady conifer forest rich in mosses, among garden trash (on *Helianthus*, Finland), or in a *Quercus rotundifolia*-*Q. coccifera*-*Q. faginea* shrubland on dry ground with *Rubus ulmifolius* (on *Sambucus ebulus*, Spain). Because of low-refractive VBs in the paraphyses, and the position of the substrate on the moist ground, the species probably shows an only moderate desiccation tolerance.

Specimens included. **FINLAND**: **North Karelia**, 42 km WNW of Joensuu, 0.8 km WNW of Outokumpu, Raivionmäki, 140 m, stems of *Helianthus tuberosus*, 28.V.2011, M. Pennanen (ex H.B. 9550, M-0276476, **epitype**; sq.: KT222425; **isoepitype**s in JOE and M.P. 110502). – 14 km WNW of Outokumpu, 1.5 km WSW of Rikkaranta, 125 m, stems of *H. tuberosus*, 18.V.2013, M. Pennanen (H.B. 9827). — **GERMANY**: **Bayern**, **Oberfranken**, 8.5 km SE of Lichtenfels, 1.5 km ESE of Serkendorf, Röderitz/Hoher Bühl, 530 m, stem of *Sambucus ebulus*, 15.VI.1985, H. Engel (**holotype** [illustration], doc. vid.). – **Baden-Württemberg**, Obere Gäue, 6 km W of Herrenberg, 2 km NNE of Oberjettingen, Herrenplatte, 575 m, stem of *Atropa belladonna*, 30.III.1998, A. Gminder (H.B. 6079). — **SWITZERLAND**: **Schaffhausen**, 4.5 km NE of Schaffhausen, 1.8 km NE of Herblingen, Rohrbühl, Herblinger Weiher, 500 m, petiole of *Acer*, 1.IV.1986, P. Blank (P.B. 165, H.B. 9435 ø). — **SERBIA**: **Vojvodina**, Fruška Gora, 13 km SSW of Novi Sad, 1 km E of Brankovac, 430 m, stem of *Sambucus ebulus*, 4.III.2019, D. Savić (FG-1019, doc. vid.). — **SPAIN**: **Aragón**, **Huesca**, 9 km SW of Benasque, 1.5 km WNW of Villanova, Chia Plan, 1630 m, on stem of indet. *Apiaceae*, 2.V.2016, R. Blasco (R.B. 02-05-16-918-CH, doc. vid.). – **Andalucía**, **Jaén**, Sistema Bético, 20 km S of Jaén, SW of Valdepeñas de Jaén, 913 m, on stems of *Sambucus ebulus*, 11.IV.2013, S. Tello (JA-CUSSTA 7565, H.B. 9776).

Not included. **CZECHIA**: **South Moravia**, Blansko, 12 km NNE of Brno, Adamov, ~270 m, on stem of *Sambucus ebulus*, 10.VI.1866, G. Niessl v. Mayendorf (herb. G. Niessl, M, as *Calloria vinosa*).

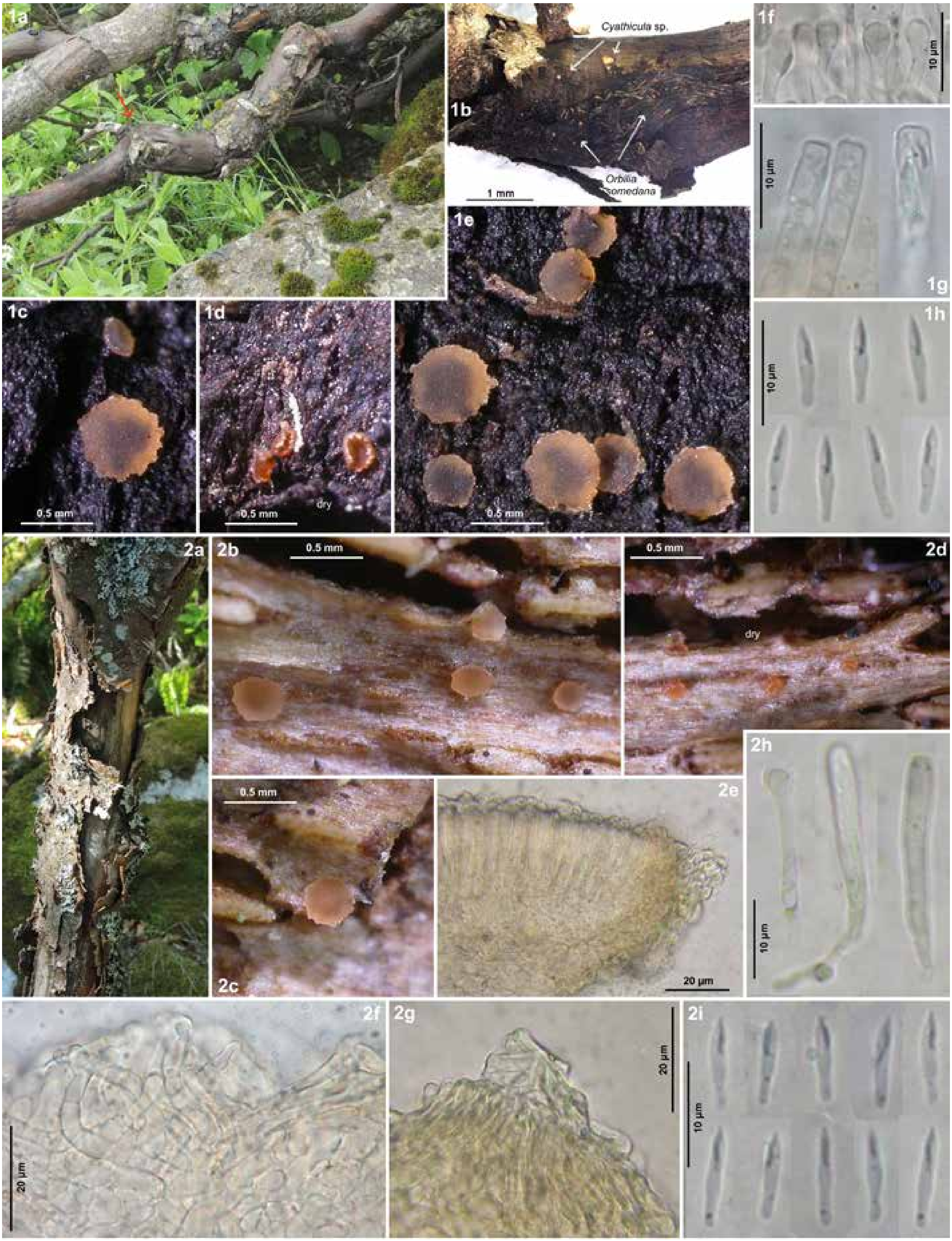


Plate 482. **1–2**: *Orbilia somedana*. – **1a**. subalpine *Erica* shrubland, dead branch of *Rhamnus alpina*; **1b**. id., with *Cyathicula* sp.; **2a**. dead trunk of *Fagus sylvatica* in beech forest; **1c**, **e**, **2b–c**. rehydrated apothecia; **1d**, **2d**. dry apothecia; **2e**. apothecium in median section; **2f–g**. margin with hairs agglutinated to teeth; **1f–g**, **2h**. asci and paraphyses; **1g**. ascus apices; **1h**, **2i**. ascospores. – Living state, except for **1g** (2 left asci), **2e**, **2h** (in H_2O). —**1a–h**. H.B. 10084e (holotype): Spain, Asturias, La Farrapona, on *Rhamnus*; **2a–i**. H.B. 10104a: id., La Peral, on *Fagus*.

Orbilia somedana Baral & E. Weber, **sp. nov.**, MB 825636 — Pl. 482

Etymology: after the geographical origin, National Park of Somiedo, Asturias.
Typification: Spain, Asturias, Pola de Somiedo, collado La Farrapona, branch of *Rhamnus alpina*, 4.VI.2017, H.O. Baral (ex H.B. 10084e, AH 52845, holotype).

Latin diagnosis: Orbiliae ebuli *similis sed corpuscula refringentia ascosporarum multo angustiores, apices paraphysium leniter inflatae. Habitat ad corticem et lignum putridum siccum* Fagi sylvaticae *et* Rhamni alpinae *in zona orotemperata humida Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.22–)0.3–0.45(–0.55) mm diam., 0.9 mm high (receptacle 0.08–0.09 mm), light to bright cream-orange, medium translucent, round, scattered to subgregarious; disc flat, margin 10 µm protruding, almost smooth to finely and irregularly crenulate; broadly sessile, seemingly superficial; dry ± strongly contracted, light to bright orange to brick-red, partly with whitish marginal tufts. **Asci** *45 × 3.5–4.2 µm {T}, †33–46 × 3–3.7 µm {2}, 8-spored, spores *~2–4-seriate, 2–4 lower or sometimes upper spores inverted {1} (sometimes mixed), pars sporifera *23 µm long; **apex** (†) strongly truncate (not indented, laterally not or hardly widened); **base** with short to long, thin to thick, ± flexuous stalk, T-, L- to Y-shaped. **Ascospores** *(7.8–)8.2–9.2(–9.7) × 1.2–1.5 µm {2}, †7.5–9.5 × 1.1–1.4 µm {2}, narrowly fusoid, apex acute, base slightly to medium attenuated, often forming a tail of *2–3.2 × (0.8–)0.9–1.1 µm {2} with sometimes a slight subbasal constriction, straight to very slightly curved near base; **SBs** *(3–)3.5–4(–4.3) × 0.2–0.3(–0.4) µm {2}, filiform to subulate, straight to often medium flexuous. **Paraphyses** apically slightly to medium capitate-clavate, terminal cells *~18–22 × 2.5–3.5 µm {T}, †11–18 × 2–3(–3.5) µm {2}, lower cells *3–13 × 2–2.7 µm {T}, †4–12 × 1.3–2 µm {2}, di- to trichotomously branched below. **Medullary excipulum** 20–25 µm thick at lower flanks, of dense textura intricata-porrecta with inflated cells, sharply delimited. **Ectal excipulum** of (†) thin-walled, indistinctly vertically oriented t. globulosa-angularis from base to margin, 20–25 µm thick at base and lower flanks, cells *6–17 × 6–13 µm {2}; 15 µm thick at mid flanks and margin, of. t. angularis-prismatica to t. porrecta oriented at a 0–20(–70)° angle to the surface, marginal cortical cells forming appressed **hairs** of *20–50 × 3–4.7 µm {1}, firm-walled (0.3–0.4 µm), 1–4-septate, ± agglutinated to form irregular, 30–50(–80) × 30–70 µm {2} large teeth; **glassy processes** absent {2}. **Anchoring hyphae** sparse, †1.7–3.3 µm wide, walls 0.2–0.3 µm thick {T}. **SCBs** in paraphyses and ectal excipulum absent {2}; **VBs** in paraphyses not observed {2}. **Exudate** over paraphyses, margin and flanks 0.1–0.2 µm thick, rough, firmly attached. **— ANAMORPH**: unknown.

Habitat: 0.3–2 m above the ground, ~5 cm thick, standing trunk of *Fagus sylvatica* {1}, 2 cm thick, horizontal branch of *Rhamnus alpina* {T}, dead, partially decorticated, on medium to strongly rotten bark (bast) {2}, on inner surface of detaching bark {1} or on outer surface (periderm removed) {T}, no algae. **Associated**: *Cyathicula* sp. {1}, *C. hysterioides* {1}, *Orbilia subtrapeziformis* {2}, *Karstenia* sp. {1}, *Parmelia sulcata* {1}, *Usnea* sp. {1}. **Desiccation tolerance**: excipular cells, a few immature asci and many spores still alive after 3 weeks. **Altitude**: 1350–1650 m a.s.l. **Geology**: Silurian-Devonian sediments: Saliencia: elution from sand and slate with limestone above, La Peral: dolomite. **Phenology**: VI (but probably long-lived).

Taxonomic remarks. The ascospores of *Orbilia somedana* closely resemble those of the caulicolous *O. ebuli*, but differ in containing much narrower SBs. They also resemble those of *O. abutilonis*, *O. ficicola*, *O. siculispora*, and especially *O. subsiculispora*, but in these four species the spores are more curved and in the former three also more constricted near the base. All of them have larger apothecia with concave disc and more protruding margin, and paraphyses with lanceolate-lageniform or mammiform apices, whereas *O. somedana* resembles *O. ebuli* in flatter apothecia and capitate paraphyses, those of *O. somedana* being apically less inflated than in *O. ebuli*.

Variation. The two included collections hardly show any deviation, except that the apothecia in the paratype are smaller and their colour slightly paler.

Ecology. *Orbilia somedana* is so far only known from two collections made at orotemperate humid sites in the Somiedo National Park in the atlantic Cantabrian Mountains of Asturias. The holotype grew on xeric bark of *Rhamnus alpina* in a subalpine shrubland with *Erica arborea* and *E. australis*, whereas the paratype was on xeric, detaching bark of *Fagus sylvatica* in a montane, rocky beech forest, in a small clearing where many fallen beech trees were lying upon each other. At both collection sites *Orbilia subtrapeziformis* grew in association.

Specimens included. **SPAIN**: **Asturias** 13.5 km ESE of Pola de Somiedo, W of collado La Farrapona, 1650 m, branch of *Rhamnus alpina*, on bark, 4.VI.2017, H.O. Baral (ex H.B. 10084e, **holotype**, AH 52845). – 6 km S of Pola de Somiedo, SSW of La Peral, 1350 m, trunk of *Fagus sylvatica*, on bark, 7.VI.2017, H.O. Baral (H.B. 10104a).

Orbilia rehmii Baral, **sp. nov.**, MB 813770 — Pls 483–484

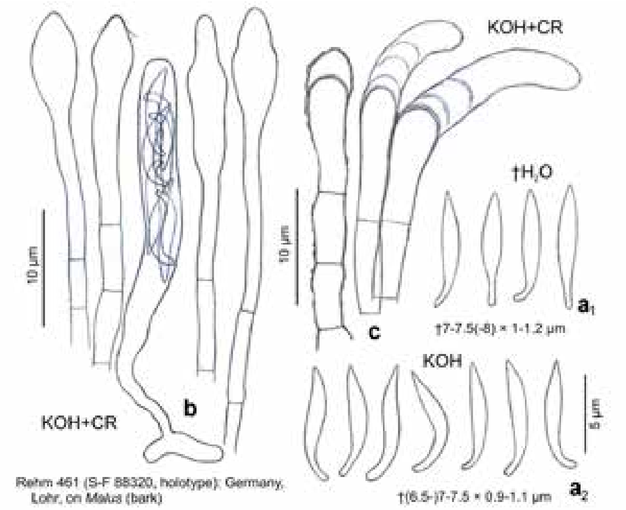
(?)= *Calloria scolicospora* f. *minor* Rehm, Ascomyceten, fasc. 10: no. 461 (1878), nom. inval., ICN Art. 38.1(a)
≡ *Calloria rubella* f. *minor* Rehm, Ber. Naturhist. Vereins Augsburg 26: 112 (1881)
≡ *Orbilia rubella* var. *minor* (Rehm) Sacc., Syll. Fung. 8: 621 (1889)

Etymology: named after the collector, H. Rehm.
Typification: Germany, Unterfranken, Lohr a. Main, bark of *Malus*, winter 1877–78, H. Rehm (ex Rehm Ascom. 461, S-F 88320, holotype).
Misapplied names: Karsten (1885: 142) & Rehm (1891: 458), as *O. rubella*; Nannfeldt (1932: 252, p.p.), as *Hyalinia rubella.*

Latin diagnosis: *Similis* Orbiliae ebuli *sed paraphysibus plerumque spathulatis, ascosporis minoribus, processis vitreis marginalibus saepe praesentibus differt.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.28–0.43 mm diam., 0.11 mm high, carneous to dark red (fide Rehm), ± round, scattered or in small groups; disc slightly concave to flat, margin 10–20 µm protruding, finely whitish crenulate; broadly sessile, superficial. **Asci** †(30–)35–53 × 3–3.5 µm, 8-spored, spores †2–3-seriate, ~3–5 spores inverted (lower or upper spores, strongly mixed); **apex** (†) medium to strongly truncate (not indented or laterally inflated); **base** with short to very long, thin, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** †(6.5–)7–7.5(–8)((–9.5)) × (0.9–)1–1.2 µm, fusiform, apex acute, base medium to mostly strongly attenuated, tail-like or with a sometimes very slightly bulbous tail of 1.2–1.5 × 0.3–0.7 µm, medium to strongly curved, especially near base, sometimes slightly helicoid, rarely straight; **SBs** not seen. **Paraphyses** apically slightly to strongly inflated, spathulate to lageniform, terminal cells *18–23(–26) × (2–)3–3.8(–4.5) µm, lower cells *4.5–8 × 1.3–2.2 µm; unbranched at upper septum, hymenium amber-yellow (fide Rehm). **Medullary excipulum** 30 µm thick, of dense textura intricata, indistinctly delimited. **Ectal excipulum** of (†) thin-walled, horizontally oriented t. angularis from base to mid flanks, 20 µm thick at base and flanks, cells †4–8 × 3–6 µm; 15–20 µm thick near margin, of a light yellow t. porrecta oriented at a 10–20° angle, partly projecting as fascicles of agglutinated hyphae, marginal cortical cells †5.5–12 × 2.5–4 µm, sometimes forming 12–30(?–60) µm long, thin-walled, 2–3-celled, ± free hair-like projections; **glassy processes** 1–15 × 3–5 µm, refractive, pale yellowish, slightly stratified. **Anchoring hyphae** sparse, †1.5–3 µm wide, walls 0.2 µm thick. **SCBs** no data available. **Exudate** over paraphyses absent, over margin and hairs forming 0.2 µm thick firmly attached granules. **— ANAMORPH**: unknown.

Habitat: on a ?standing corticated ?trunk of *Malus domestica* {1}, on inner surface of detaching bark, medium decayed, slightly greyed, algae not observed. **Associated**: ?*Nitschkiaceae*. **Desiccation tolerance**: probably tolerant. **Altitude**: ~200 m a.s.l. **Geology**: Buntsandstein. **Phenology**: winter (but presumably long-lived).



Pl. **483**. **1**: *Orbilia rehmii*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. marginal hair-like cells tipped by glassy processes.

Taxonomic remarks. *Orbilia rehmii* closely resembles *O. ebuli* and *O. somedana* in the ascospores, also in the marginal textura porrecta oriented at a low angle and running out into hair-like projections which form a crenulate margin. It differs in more curved spores and often spathulate though also clavate paraphysis apices, whilst in *O. ebuli* and *O. somedana* the spores are ± straight and the paraphyses capitate-clavate or only exceptionally spathulate (Pl. 480: 2). A more protruding margin and the partial occurrence of up to 15 µm long glassy processes, together with slightly smaller spores are further features that deviate from *O. ebuli* and *O. somedana*. The Australian *O. carminorosea* has very similar spores and paraphyses, but seems to deviate in wider marginal cortical cells running at a higher angle, larger excipular cells at lower flanks (but see below), slightly wider spores, and larger apothecia with a carmine-rose colour. *O. subsiculispora* has wider, more constricted spore tails and lacks glassy processes, and *O. rubella* (series *Rubellae*) obtuse to subacute spore apices and thick-walled hairs with longer glassy processes.

Variation. In the isotype specimen from M the spores were found to be partly longer (7–9.5 µm) than in the holotype (6.5–8 µm), also the curved base was more distinctly inflated (knob-like). No drawing or photos were made when the specimen from M was studied.

Nomenclature and type studies. Rehm's (1878 in sched.) label of Ascomyceten no. 461 bears the name *Calloria scolicospora* Rehm f. *minor* on the printed label but no diagnosis. Since this combination was not published elsewhere, it is not validly published. A handwritten description is included in the duplicate S-F 88320, suggesting that this was Rehm's personal specimen. Rehm (1881) validly published this taxon at the rank of a forma of *Calloria rubella* and Saccardo (1889) raised it to a variety of *Orbilia rubella*, whereas Karsten (1885: 142), Rehm (1891: 458), and Nannfeldt (1932: 252) listed it as a synonym of *O. rubella*. It remains unclear which collection Rehm intended under the epithet *scolicospora* (not to be confused with *Hyalinia scolecospora* G.W. Beaton), which could not be detected in later publications, so it appears that it has never been validly published and must be regarded as a nomen nudum.

Rehm's handwritten description includes a sketch of two falcate spores and a clavate paraphysis. The spores are drawn with an obtuse upper end and resemble those of *O. auricolor*. Unexplainably, Rehm (1881) cited as exsiccata for *C. rubella* f. *minor* Karsten FFE 831 instead of Ascomyc. 461. This is a misprint for FFE 834, which Karsten cited under *O. rubella* and was referred to *O. phragmotricha* in the present study, whereas FFE 831 is *Niptera graminis* in the list of FFE (S. Huhtinen & T. Pertti pers. comm.). Since Rehm's (1881) diagnosis was clearly taken from the handwritten one in Ascomyc. 461 (S-F 88320), the type of *C. rubella* f. *minor* is Rehm Ascomyc. 461.

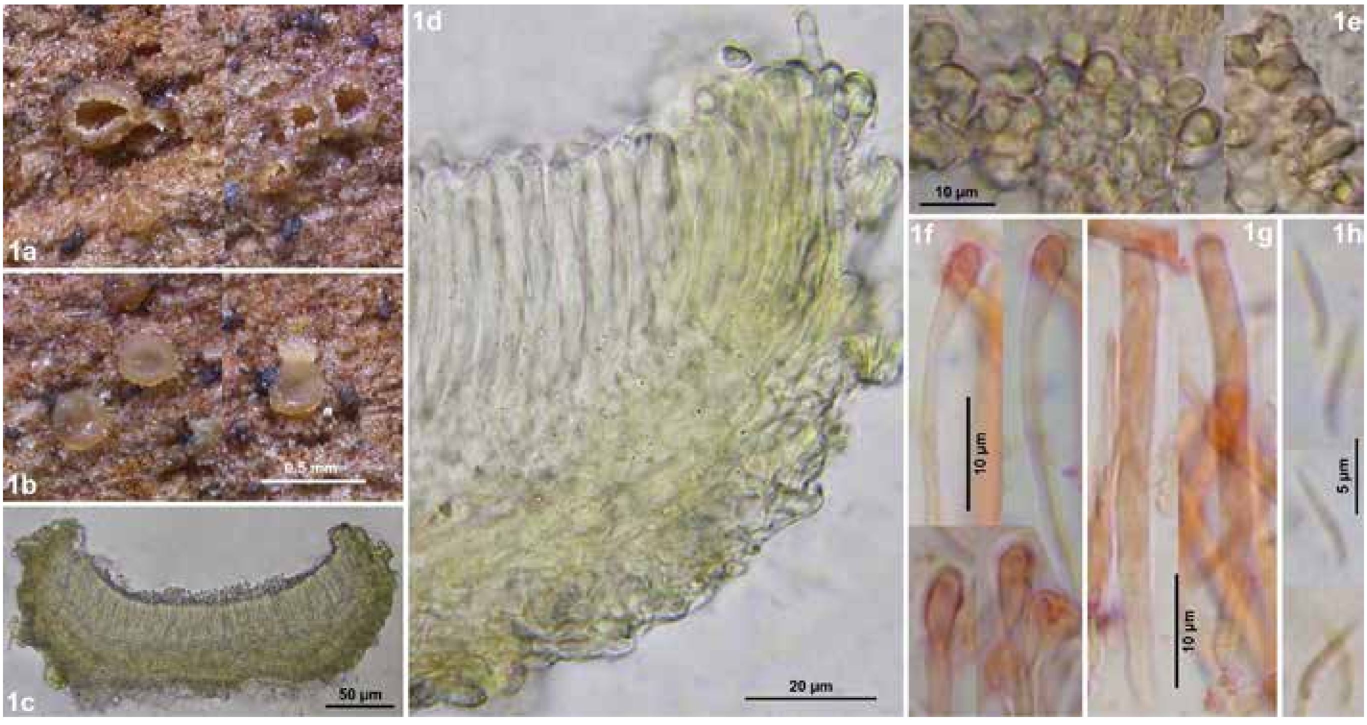


Plate 484. **1**: *Orbilia rehmii*. – **1a–b**. rehydrated apothecia; **1c**. apothecium in median section; **1d**. id., marginal region; **1e**. marginal glassy processes (squash mount); **1f**. paraphyses; **1g**. asci; **1h**. ascospores. – Dead state (**1c** in H2O, **1d** in KOH, **1e–h** in KOH+CR). — **1a–h**. S-F 88320, H.B. 9838 ø (holotype): Germany, Lohr, on *Malus*.

In his Kryptogamen-Flora, Rehm (1891) cited only Ascomyc. 461 as exsiccata, which served as the basis for his description of *O. rubella*, for which he only gave apple bark and Lohr as collection data.

Rehm's handwritten diagnosis includes asci of 30–45 × 5 µm and spores of 6–8 × 1 µm. Later, Rehm (1881) shortened these measurements to –45 × 5 µm and –8 × 1 µm, and Saccardo (1889) again changed them to 40–45 × 5 µm and 7–8 × 1 µm. Rehm's (1891) description of the same collection, now under the name *O. rubella*, gives a further variant, 30–45 × 4–5 µm and 6–12 × 1 µm, because he included also data from Karsten's description of '*O. rubella*'. The apothecia are there described as 0.2–1.5 mm diam., with a finely fimbriate margin, carneous to dark red, hymenium amber-yellow [in transmitted light], data which do not appear on the handwritten note, while his statement 'spores apically blunt, tapered and slightly curved below, intertwined within the asci' might have been taken from there. Although Nannfeldt (1932) included Rehm Ascomyc. 461 in his concept of *Hyalinia rubella*, he said that his redescription of excipular structures was solely based on the specimen from Karsten's herbarium (FFE 834).

The holotype collection of *O. rehmii* revealed ascospores very different from Rehm's description and drawing, though they concur in size. Also Rehm's (1891) remark of a large-celled ectal excipulum is in strong contrast to the present fungus. Rehm's omission of spathulate paraphyses, on the other hand, can be explained by the frequent occurrence of clavate paraphyses along with spathulate ones in the present specimen. Nevertheless, a mixed collection cannot be excluded, e. g., with a species of section *Arthrobotrys*, and the apothecial size and colour given by Rehm (1891) might partly refer to such an associated species. In any case, the here redescribed fungus differs from all other collections examined by us, therefore, it is described as a new species.

Ecology. *O. rehmii* was collected on the inner surface of detached, projecting bark of *Malus*, possibly from a standing, living trunk, at the eastern foothills of Spessart, a mountain range of acidic soil in cold-temperate humid northwestern Bayern (Germany).

Specimens included. **GERMANY**: **Bayern**, **Unterfranken**, Spessart, ~35 km NW of Würzburg, Lohr a. Main, ~200 m, bark of *Malus*, winter [1877–]1878, H. Rehm (Rehm Ascomyc. 461, as *Calloria scolicospora* f. *minor*, S-F 88320 **holotype**, H.B. 9838 ø; **isotypes** in M-0206541, M-0206542).

Orbilia carminorosea Baral, **sp. nov.**,
MB 813771 — Pls 485–486

Etymology: named according to the spectacular, comparatively large, bright carmine-rose apothecia.

Typification: Western Australia, Derby, branch of *Adansonia gregorii*, 1.XI.2007, G. Marson (ex H.B. 8777a, MEL 2389260, holotype; sq.: KT222423).

Latin diagnosis: *Apothecia rehydratata 0.6–1 mm diam., vivide carmino-rosea, sessilia, margine incrassato, albido aspero ad pulverulento. Ascosporae †6.5–8 × 1.1–1.4 µm, fusiformes, apice acutae, ad basim valde attenuatae, subcaudatae, modice vel valde curvatae. Paraphyses ad apicem non inflatae vel modice spathulatae. Margo excipuli pilis agglutinatis, septatis, subcrassitunicatis compositus, absque processis vitreis. Habitat ad lignum putridum rami sicci* Adansoniae gregorii, *in zona tropica subhumida Australiae septentrio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.5–1 mm diam., 0.17–0.22 mm high (receptacle 0.16 → 0.08 mm), (light to) bright crimson- or carmine-rose, non-translucent, ± round, scattered or in densely aggregated pairs; disc slightly concave to flat, margin thick, 10–40 µm protruding, rough to whitish pruinose, somewhat longitudinally ribbed; broadly sessile, superficial; dry bright carmine, only slightly contracted. **Asci** †30–40 × 3–3.7(–4) µm, 8-spored, spores †2–3-seriate, ~3–5 lower spores inverted (strongly mixed, sometimes upper spores inverted and lower not); **apex** (†) strongly truncate (never distinctly indented, laterally hardly inflated); **base** with short to long, thin, flexuous stalk, T-, L- or h-shaped. **Ascospores** †6.5–7.5(–8) × 1.2–1.3(–1.4) µm (~7.5–9 µm actual length), fusiform, apex acute, base strongly attenuated, tail-like, medium to mostly strongly curved near base (falcate but straight or only slightly curved in middle part); **SBs** ?2 µm long, ?elongate tear-shaped, hardly visible as a faint region in a few spores. **Paraphyses** apically uninflated or slightly to medium inflated, spathulate (to lageniform), terminal cells *(12.5–)15–22 × 2.3–3.5(–4) µm, lower cells *4–10 × 2–2.5(–3) µm; unbranched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline to pale rose, 30–60 µm thick, of medium dense textura intricata(-angularis), ± horizontally oriented, indistinctly to medium sharply delimited. **Ectal excipulum** at base hyaline to pale rose, of (†) slightly gelatinized, vertically oriented t. (prismatica-)angularis from base to mid flanks, 80–120 µm thick near base, cells *(10–)15–25(–30) × (8–)11–16(–18) µm; 50 → 30 µm thick at flanks, 20–35 µm near margin (including hair-like cell rows), submargin of t. globulosa-prismatica oriented at a 50–80° angle to the surface, upper margin of t. prismatica oriented at 20–60°, sometimes forming agglutinated, firm-walled cell rows, marginal cortical cells †5–10 × 3–5.5 µm, sometimes forming 9–14 µm long, ± free hair-like projections; **glassy processes** absent. **Anchoring hyphae** medium abundant, *2.5–3.5 µm wide, walls 0.2 µm thick, below basal excipulum forming a medium dense prismatic texture of *4–6 µm wide hyphae. **SCBs** in paraphyses and ectal excipulum absent. **Exudate** over paraphyses 0.1–0.2(–0.4) µm thick, finely rough, firmly attached to apex and subapex, at margin forming 0.3–1.5 µm thick caps on terminal cells. — **ANAMORPH**: dicranidion/trinacrium-like (presumed, from natural substrate, on apothecium). **Conidiophores** not observed. **Conidia** 3-dimensional, 4-armed by dichotomous branching, total size †26 × 16 µm, stipe †9 × 3.3 µm, non-septate, arms †8–14 × 2.7–3.2 µm, 0(–1)-septate, diverging, straight, gradually tapering towards apex {only 1 conidium seen}.

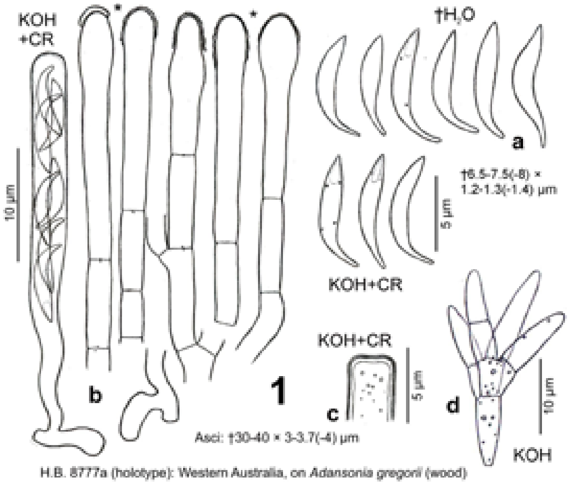


Plate 485. **1**: *Orbilia carminorosea*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. conidium.

Habitat: collected 2–3 m above the ground, decorticated, 20–25 mm thick branch of *Adansonia gregorii*, excavated by termites or ants, on 0.1–0.3 mm deep strongly decayed wood, greyed, no algae. **Associated**: *Orbilia brachychitonis*, *O. euphorbiae*. **Desiccation tolerance**: only paraphyses and excipular cells viable after 4 months. **Altitude**: 20 m a.s.l. **Geology**: Cenozoic red-brown gravel. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia carminorosea* is remarkable due to its rather large, bright carmine-rose apothecia with a whitish pruinose margin made up of distinct cell rows, and small, somewhat falcate spores with acute apex and tail-like base. Based

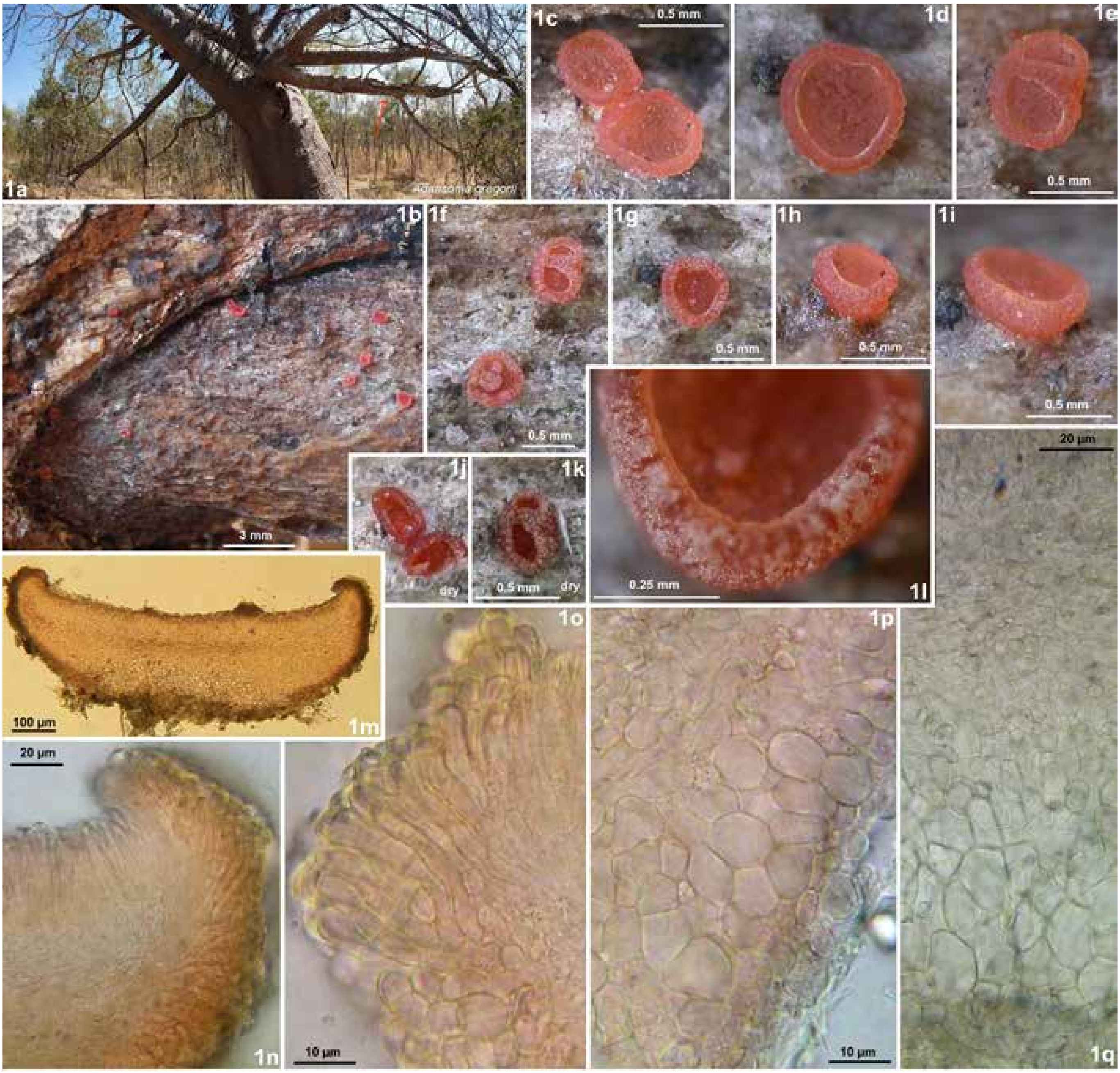


Plate 486. **1**: *Orbilia carminorosea*. – **1a**. tropical semiarid Eucalypt woodland with *Adansonia gregorii* in foreground; **1b–i**, **l**. rehydrated apothecia; **1j–k**. dry apothecia; **1m**. apothecium in median section; **1n–o**. id., ectal excipulum near margin; **1p**. id., lower flanks; **1q**. id., basal region showing ectal and medullary excipulum. – Living state. — **1a–q**. H.B. 8777a (holotype): Western Australia, Kimberley Mts., on *Adansonia*.

on its morphology, the species is difficult to place. The marginal cell rows resemble the free hairs of *O. phragmotricha* (series *Rubellae*) but are more thin-walled and always conglutinate to form a compact tissue, similar as observed in *O. fraxini*, a species assigned to series *Neodactylella* of section *Arthrobotrys*. The spathulate paraphyses with thin exudate would fit series *Rubellae* but are also similar in *O. abutilonis* and similar species. For the similar *O. rehmii* see p. 904. *O. carminorosea* resembles *O. aurantiorubra* in the acute spore apex and a strongly bent base, and an apparently elongate tear-shaped spore body. *O. aurantiorubra* differs in longer spores with thicker tail-like bases, and a marginal excipulum that lacks distinct cell rows. Mature asci were only sparsely seen in *O. carminorosea*, and all asci and spores were dead when examined 4 months after collecting.

Anamorph. A single staurosporous (4-armed) dicranidion-like conidium was seen on an apothecium (Pl. 483: 1d), showing a branching mode similar as in *O. siculispora* and *O. ficicola*.

Phylogeny. A sequence gained from apothecia of the holotype (SSU without S1506 intron, ITS, LSU) shows a minimum ITS distance of 14% to *O. ebuli* and 16% to *O. aethiopica* in (3.5–4.5% in LSU D1–D2).

Ecology. *O. carminorosea* grew on rotten wood of a xeric branch of baobab (*Adansonia gregorii*) in a tropical subhumid eucalypt open woodland (savannah, wet and dry) at the southern border of the Kimberley plateau adjacent to the Great Sandy Desert (Pilbara) in the Dampierland ecoregion of northwestern Australia.

Specimens included. **AUSTRALIA**: **Western Australia**, Dampierland, SW-border of Leopold Ranges (Kimberleys), 47 km SSW of Derby, 12 km WNW of Willare Bridge over Fitzroy River, 20 m, branch of *Adansonia gregorii*, on wood, 1.XI.2007, G. Marson (ex H.B. 8777a, MEL 2389260, **holotype**; sq.: KT222423; anam. substr.).

Orbilia rosella (Rehm) Sacc., Syll. Fung. 8: 623 (1889) — Pls 487–488

≡ *Calloria rosella* Rehm, Hedwigia 23: 56 (1884)
≡ *Laetinaevia rosella* (Rehm) Nannf. in Kanouse, Pap. Mich. Acad. Sci. 21: 100 (1936)

Etymology: named after the rose colour of the apothecia. **Typification**: Germany, Sachsen, Nossen, stems of *Atropa belladonna*, VIII.1883, K.W. Krieger (Rehm 720, M-0206546, lectotype, designated here, MBT392868). **Misinterpretation of *O. rosella***: Baral (1992, fig. 37d, as '*O.* cf. *rosella*'), = *O. caulicola*; Bommer & Rousseau (1890: 227), = ?*Calloriaceae*; Feltgen (1901: 37), on *Angelica* = *O. auricolor*, on *Knautia* = *O. flavida*.

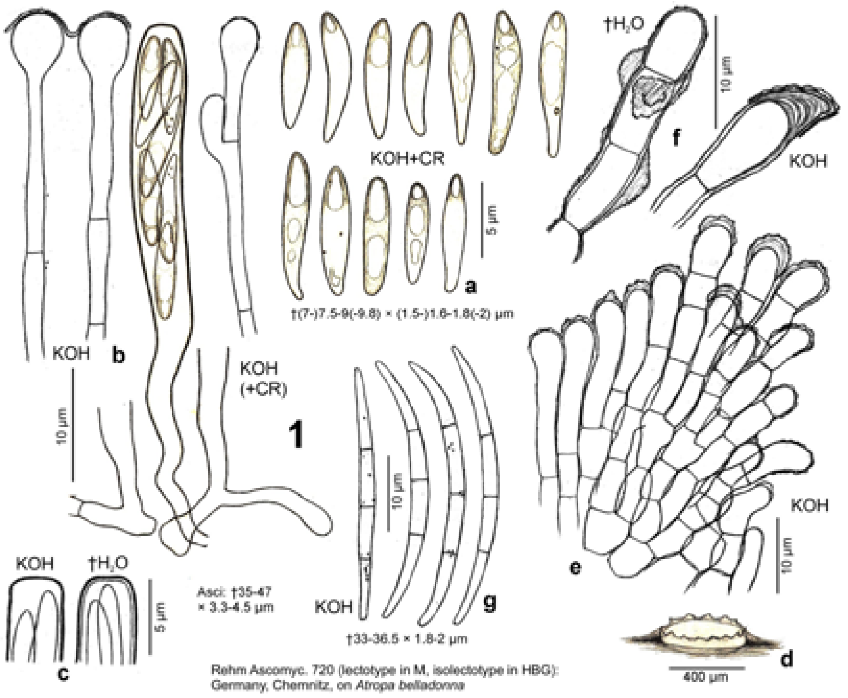


Plate 487. **1**: *Orbilia rosella* (lecto- and isolectotype). – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. apothecium with dentate margin (rehydrated); **e**. median section of marginal ectal excipulum; **f**. id., cortical cells, with or without glassy processes; **g**. conidia from natural substrate. **a–d**, **f**: M-0206546 (lectotype, H.B. 4670a); **a–b** (only SBs in spores), **g**, **e**: HBG (isolectotype H.B. 4670b).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.25–0.6 mm diam., 0.08–0.15 mm high (receptacle 0.06–0.09 mm), pale cream (Rehm: rose-red, later brownish-red), ± translucent, round to somewhat elliptical, medium gregarious; disc concave to flat, margin 10–20 µm protruding, distinctly crenulate with small teeth; broadly sessile, erumpent from slits in epidermis; dry light yellowish-ochraceous(-orange) (Rehm: rose-red), margin rolled inwards. **Asci** †(35–)40–47(–52) × (3.3–)3.7–4.5 µm {2}, 8-spored, spores †~3-seriate, 4(–5) lower spores inverted (not mixed), pars sporifera †28 µm long; **apex** (†) strongly truncate (± not indented, laterally not or scarcely widened); **base** with medium to long, thin, flexuous stalk, L- or Y- to h-shaped. **Ascospores** †(7–)7.5–9(–9.8) × (1.5–)1.6–1.8(–2) µm {T}, fusoid-clavate, apex ± obtuse (to somewhat subacute), base slightly to strongly attenuated, straight to slightly curved (entirely or near base); **SBs** †1.3–1.8 or sometimes 3–4.5 × 0.5–1.1 µm {T}, ± tear-shaped, faintly visible as a transparent region. **Paraphyses** apically (slightly to) medium to very strongly capitate-clavate, terminal cells †(10.5–)18–25 {T} × (2–)3.5–4.7 µm {2}, lower cells †~9–15 × 1.2–1.6 µm {T}, sometimes branched at upper septum. **Medullary excipulum** 10–50 µm thick, of medium loose or dense t. intricata with many inflated cells, indistinctly or sharply delimited. **Ectal excipulum** of slightly gelatinized, indistinctly oriented t. globulosa-angularis from base to margin, 30–50 µm thick near base, cells 15–24(–32) × 10–19(–23) µm {T}; 15–25 µm thick near margin, oriented at a 10–40° angle to the surface, margin with or without protruding, 2–3-celled, 15–30 µm long **hairs**, thick-walled (0.2–0.8 µm), coherent to form indistinct teeth, terminal cells †4–12 × (3–)3.5–5(–6) µm {T}, sometimes tipped by **glassy processes** up to 3–4.5 × 4–5 µm, low-refractive, stratified. **Anchoring hyphae** not examined. **SCBs** and **VBs** unknown. **Exudate** over paraphyses, margin and flanks 0.2–0.4 µm thick, rough, continuous, firmly attached. **— ANAMORPH**: unknown (but see below).

Habitat: previous year's stems of *Atropa belladonna* {3}, on outer and partly also inner surface of hollow stems, ungreyed, no algae, closely **associated** with an old subepidermal pyrenomycete. **Desiccation tolerance**: unknown (probably tolerant). **Altitude**: ~300–380 m a.s.l. **Geology**: Germany: dolerite (diabase), Czechia: mica and biotite gneiss. **Phenology**: IV, VIII (but probably rather long-lived).

Taxonomic remarks. *Orbilia rosella* is characterized by narrowly fusoid ascospores with obtuse apices and attenuated, slightly bent bases, and by apothecia with a finely denticulate margin made up of short hairs which sometimes carry small glassy caps. The species deviates from members of series *Aurantiorubrae* in its rather straight spores which more resemble those of series *Rubellae*, also in the sparse and thin exudate. For the very similar *O. ebuli* see p. 900.

O. rosella resembles *O. rectispora* and *O. cardui* in some macro- and microscopical aspects, but differs in the formation of short, septate hairs forming distinct small teeth at the margin, in wider and partly longer spores with never rounded apices and longer SBs, and in strongly capitate paraphyses, their lower cells being not much shorter than the terminal cells, finally in a reddish colour of the partly erumpent apothecia. In its fusoid to fusiform spores *O. rosella* also resembles *O. caulicola*, which differs in a smooth margin lacking septate hairs or glassy caps, and in shorter spores with shorter SBs.

O. paravitalbae (Pls 489–490) differs from *O. rosella* in distinctly longer SBs (except for *O.* cf. *paravitalbae* Pl. 489: 2) and usually wider, basally never strongly tapered spores. *O. vitalbae* (section *Habrostictis*) has similar spores (e.g., Pl. 696: 1, *O.* cf. *vitalbae*), but the apothecial margin is only minutely crenulate and lacks protruding hair-like elements. Vital characters and molecular data are required to solve the position of *O. rosella*.

Variation. A specimen from Czechia on the type substrate under the name *O. rosella* (M, herb. T. Kupka) appears to be conspecific according to its apothecia being erumpent through a slit, with ~15 µm long marginal hairs, though spores could not be seen. Also in its ascus size and paraphysis diameter it fits well the type.

A collection on *Atropa* (Bayern, Oberfranken, Lichtenfelser Forst, 4.V.1982) reported by Engel et al. (1982: 54) under the name *O. rosella* might be correctly identified, but was inadequately described. The fusoid spores measured 7–9.5(–10.8) × 1.3–1.8 µm, with obtuse ends, but one end partly acute. No SBs were seen, therefore, the upper and lower spore end cannot be recognized.

Nomenclature and type studies. Rehm (1884) described the spores of ***O. rosella*** as 'fusiform, subacute, [..], 5–6 × 1–1.5 µm' and later (Rehm 1891: 460) as '5–7 × 1–1.5 µm'. The present reexamination of one of five syntypes of Rehm Ascomyc. 720

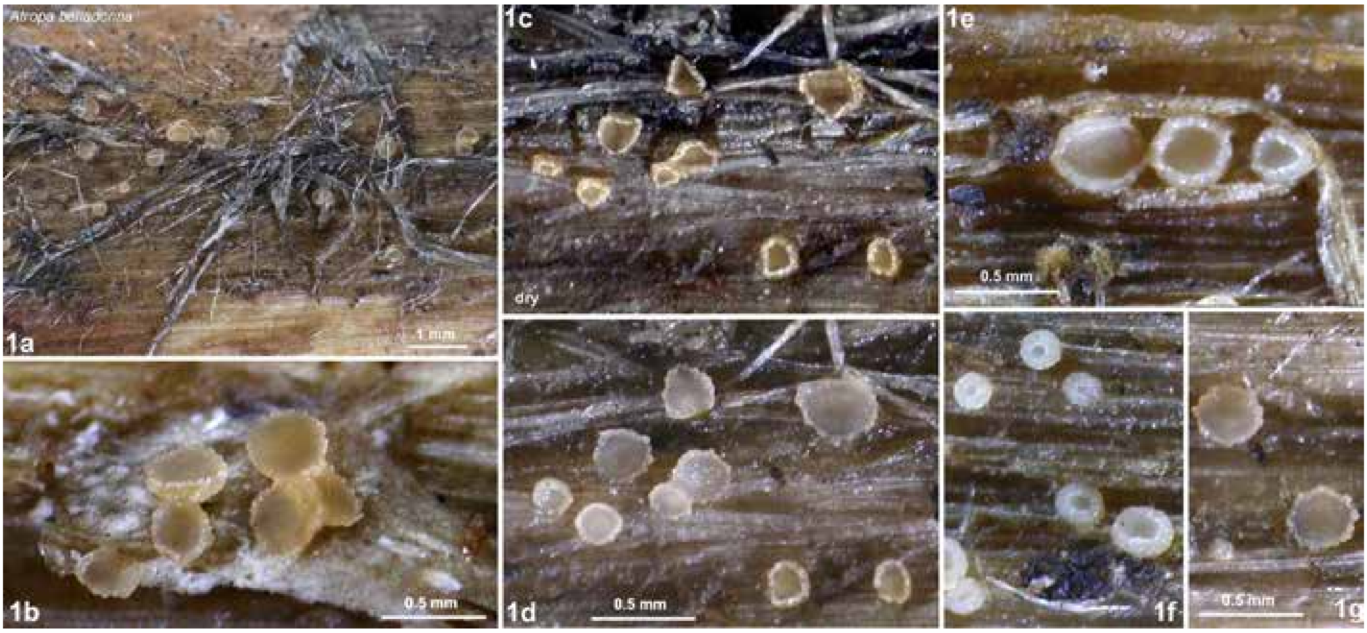


Plate 488. **1**: *Orbilia rosella*. – **1a–b**, **d–g**. rehydrated apothecia; **1c**. dry apothecia. — **1a–g**. Rehm Ascom. 720 (syntype, HBG): Germany, Nossen, on *Atropa*.

(VIII.1883, K.W. Krieger) in M and one of three syntypes in HBG revealed distinctly larger spores with more obtuse apices (Pl. 487: 1a). Rehm (1884) believed that *O. rosella* was closely related to *O. vinosa*, but later he considered a possible relationship to *O. rozei*, a helotialean species tentatively placed in synonymy of *Psilachnum rubicundum* in our list of excluded taxa (see p. 1683).

The rich type collection of *Orbilia rosella* (Germany, Sachsen, Nossen, *Atropa belladonna*, K.W. Krieger, Rehm Ascomyc. 720) was distributed as a set of exsiccata to various herbaria. A specimen with handwritten notes exists among the five syntypes in S (S-F9977, I. Olariaga pers. comm.), while syntype specimens in M and HBG did not carry handwritten notes of the protologue. On the convolutes in M and HBG, Rehm's number 720 appears not only with August 1883 as collection date, but also as 'Aug. 1883. April 1884' (M-0206548, HBG). These must be considered as topotypes, because they were collected by K.W. Krieger presumably after the manuscript was finished (the volume of Hedwigia bears the date April 1884). Three other syntypes were distributed by Rabenhorst, Fungi Eur. Exs. 3067, and the topotype by Krieger Fungi Saxon. Exs. 36.

However, we have not studied any of the specimens in S. Since specimen M-0206546 was studied in detail (Pl. 487: 1a–d, f), this is designated here as **lectotype** of *O. rosella*.

Patouillard (1886: 213, pl. 492) briefly redescribed a syntype specimen of *O. rosella*, with minute wine-rose apothecia, fusiform spores (no size stated), and apically very slightly inflated paraphyses, although Rehm reported the latter as filiform, inflated to a 5 µm wide capitate apex.

The combination *Laetinaevia rosella* (Rehm) Nannf. was published in Kanouse (1936), who reported a collection from Michigan on wet, hygric stems of *Impatiens* sp. (without microscopic data). From Kanouse's note this combination is clearly based on *Calloria rosella* Rehm (see also Seaver 1951: 161), not on *Pseudopeziza rosella* Rehm to which Hein (1976: 34) erroneously referred it. Kanouse relied on Nannfeldt (1932: 192) who listed the former under the name *Orbilia rosella* (Rehm) Sacc., besides many other taxa, as 'very probably belonging to *Laetinaevia*'.

Misapplication. Feltgen (1901: 37) reported under the name *O. rosella* two collections from Luxembourg, with ellipsoid-fusoid spores (4.5–5 × 2 µm). Reexamination of the specimen on stems of *Angelica sylvestris* revealed *O. auricolor*, and that on *Knautia arvensis O. flavida*. Also a sample on *Atropa* referred to *O. rosella* by Bommer & Rousseau (1890: 227; Belgium, Namur, Hastière, X.1890, BR) was reexamined and found to belong to an unidentified helotialean taxon with amyloid apical rings, perhaps a member of *Aivenia* (*Calloriaceae*, IVV: H.B. 8791). Not examined was a collection on *Atropa* from Bayern (Enzenauer Kopf, Bad Tölz, northern Alpine foothills), which Kirschstein (1938: 390, without microscopic data) assigned to *O. rosella* despite its golden yellow apothecia. A spore drawing in Baral (1992: fig. 37d) under the name '*O.* cf. *rosella*' represents *O. caulicola*.

A collection on *Symphytum* from Belgium reported by (Declercq & Leysen 2017), with shorter, fusiform-clavate spores of *5.5–8 × 1.5–2 µm with strongly conical apex containing several ?LBs (B. Declercq pers. comm.), requires reexamination.

Anamorph. On the substrate of the type collection we detected some slender, slightly curved phragmoconidia (†33–36.5 × 1.8–2 µm, 3-septate, Pl. 487: 1g). It is, however, not clear whether they belong to the anamorph of *O. rosella*.

Ecology. *O. rosella* is only known with certainty from the type locality in central Sachsen and a Czechian collection from the southern foothills of Erzgebirge in subcontinental, colline, cold-temperate humid central Europe. At both sites it grew on previous year's stems of *Atropa*. The species is possibly slightly desiccation-tolerant, considering the erumpent growth and rose-red colour.

Specimens included. **GERMANY**: **Sachsen**, Mittelsächsisches Lößhügelland, ~35 km NE of Chemnitz, Nossen, 'at a hill', ~300 m, stems of *Atropa belladonna*, VIII.1883, K.W. Krieger (Rehm 720, M-0206546, **lectotype**, H.B. 4670a ø; **isolectotypes** & topotypes in M-0206547, 206549, 206550, 206551, 206552, non vid.; HBG, H.B. 4670b ø; S-F9977, 9978, 88309, 88311, 88312, non vid.). – ibid., VIII.1883 & IV.1884, K.W. Krieger (herb. G. Niessl 206548, M, HBG, **isolecto-/topotype**). — **CZECHIA**: **Ústi nad Labem**, 86 km NW of Praha, 1 km N of Jirkov, Zámek Cervený Hrádek, 380 m, on stems of *Atropa belladonna*, 1912, T. Kupka (herb. T. Kupka, M).

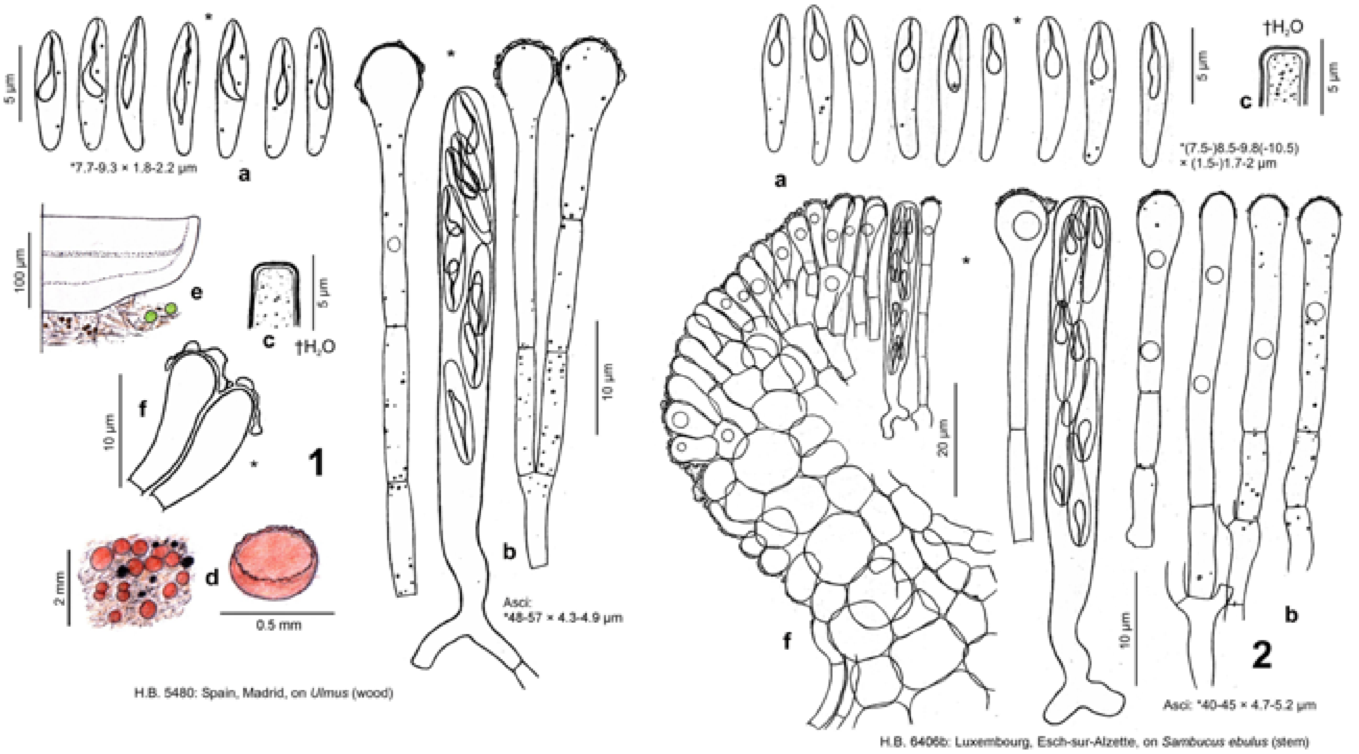


Plate 489. **1**: *Orbilia paravitalbae*; **2**: *O.* cf. *paravitalbae*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., ectal excipulum at margin and flanks.

Orbilia paravitalbae Baral, E. Weber, Priou & R. Tena, **sp. nov.**, MB 825635 — Pls 489–490

Etymology: named after the similar but distantly related *O. vitalbae*.

Typification: Spain, Murcia, Bullas, branches of *Daphne gnidium*, 10.V.2015, J.P. Priou (ex J.P.P. 15119 & ex H.B. 10081, TAAM 198539, holotype; sq.: MG372375).

Latin diagnosis: Orbiliae vitalbae *similis sed ascosporae subcylindricae vel leniter fusoideoclavatae, cellulae apicales paraphysium longiores. Habitat ad corticem et lignum putridum siccum* Daphne gnidii *et* Ulmi *vel caules* Hellebori *in zona meso- ad orosubmediterranea humida Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.5(–0.6) mm diam., 0.13–0.18 mm high (receptacle 0.1 mm), pale to bright (vinaceous-)rose to pink, ± translucent, round, very scattered to ± gregarious; disc flat, sometimes finally slightly convex, margin finely to distinctly crenulate, 0–0.5 µm protruding; sessile on a stipe-like base, superficial to slightly immersed in biofilm; dry light to deep rose or pink-red. **Asci** *48–57 {1} × 4–5 {2} µm → 5.2–5.5 µm wide, †43–50 × 3.3–3.7 µm {T}, 8-spored, spores *2-seriate, 2–5 lower spores inverted {2} (not mixed), pars sporifera *21–25 or 26–33 → 17–21 µm long; **apex** (†) strongly truncate (not indented, laterally not inflated); **base** with short to long, ± thin, flexuous stalk, L- to Y-shaped. **Ascospores** *(6.8–)7.5–9(–10) {3} × 1.5–1.7 {T} or 1.8–2(–2.2) µm {2}, †7.5–9.2 {2} × 1.4–1.6 {T} or 1.7–2 {1}, subcylindrical to slightly fusoid-clavate, apex rounded to obtuse, rarely subacute, base not or slightly attenuated, straight to slightly inequilateral; **SBs** *(3.5–)4–4.5(–5) {2} or 4.5–5.5(–6.8) {1} × 0.5–0.8(–1) µm {3}, divided into a ± abruptly swollen, tear- to stomach-shaped or ellipsoid to fusoid lower part and a filiform or continuously thickened upper part of about the length of the inflated part, narrow part slightly to strongly flexuous, wide part often oblique. **Paraphyses** apically (slightly) medium to strongly capitate(-clavate), terminal cells *16–27 {1} × (3–)4–5(–6) µm {2}, †17–25 × (3–)4–4.5(–5.5) µm {2}, lower cells *8–14 × 1.5–2.3 µm {1}, †8 × 1.2–2 µm {T}; unbranched at upper septum, hymenium pale rose. **Medullary excipulum** pale rose, 25–50 µm thick, of ± dense textura intricata with many inflated cells, medium sharply delimited. **Ectal excipulum** hyaline, towards margin pinkish, of (†) thin-walled t. globulosa-angularis from base to flanks or submargin, 30–60 µm thick near base, cells *(6–)8–14 × (4.5–)6–10 µm {2}, †8–15 × 5–8 µm {T}; 20 µm thick at margin, of t. porrecta oriented at a 20–40° angle to the surface, marginal cortical cells *13 × 3.8–4.6 µm {1}, †6–12 × 3–4 µm {T}, ± flexuous, forming ± free hair-like protrusions, or agglutinated as teeth, **glassy processes** absent. **Anchoring hyphae** medium abundant, *2.5–3.5(–4) µm wide {1}, †1.5–2.5 µm {1}, walls 0.2–0.4 µm thick {2}. **SCBs** in paraphyses and ectal excipulum globose {2}, 1.2–2.5 µm diam., or absent {1}. **Exudate** over paraphyses 0.2–1(–1.5) µm thick, granular-cloddy to continuous, firmly attached, pale yellowish; over margin and flanks 0.2–2 µm thick, cloddy to granular. **— ANAMORPH**: unknown.

Habitat: collected 0.5–2 m above the ground, ± corticated to partially decorticated, 14–15 mm thick, dead branches of *Daphne gnidium* {T}, *Ulmus* sp. {1}, medium to strongly decayed wood {1} and bark (periderm & bast) {1}, on boring dust in beetle galleries {1}; herbaceous stem of *Helleborus nitidus* {1} on the ground; slightly to strongly greyed or darkened, with a few green algae. **Associated**: *Allophylaria* sp., ?*Dothideomycetes*, *Orbilia* sp. **Desiccation tolerance**: fully viable for at least a few days. **Geology**: sandy to clayey or marly deposits from calcareous hills nearby. **Altitude**: 577–1635 m a.s.l. **Geology**: Triassic & Jurassic gypsum, sandstone & dolomite, Quaternary gravel, sand & clay. **Phenology**: II & V (but probably long-lived).

Taxonomic remarks. *Orbilia paravitalbae* is characterized by ± subcylindrical ascospores with rounded to obtuse ends containing flexuous SBs composed of a narrow filiform upper part and an inflated, ± stomach-shaped lower part, also by rose-coloured apothecia with a denticulate margin due to hair-like projections. *O. ebuli* differs in spores with acute apices and tail-like bases, also in lacking any SCBs. *O. rosella* has more fusoid-clavate spores with shorter SBs. *O. vitalbae* (section *Habrostictis*) differs in ellipsoid to fusoid-clavate spores and shorter terminal cells of paraphyses, but a sharp separation from *O. paravitalbae* based on morphology is very difficult. A mediterranean collection from Croatia referred to *O. obtusispora* (section *Habrostictis*) has similar subcylindrical spores with

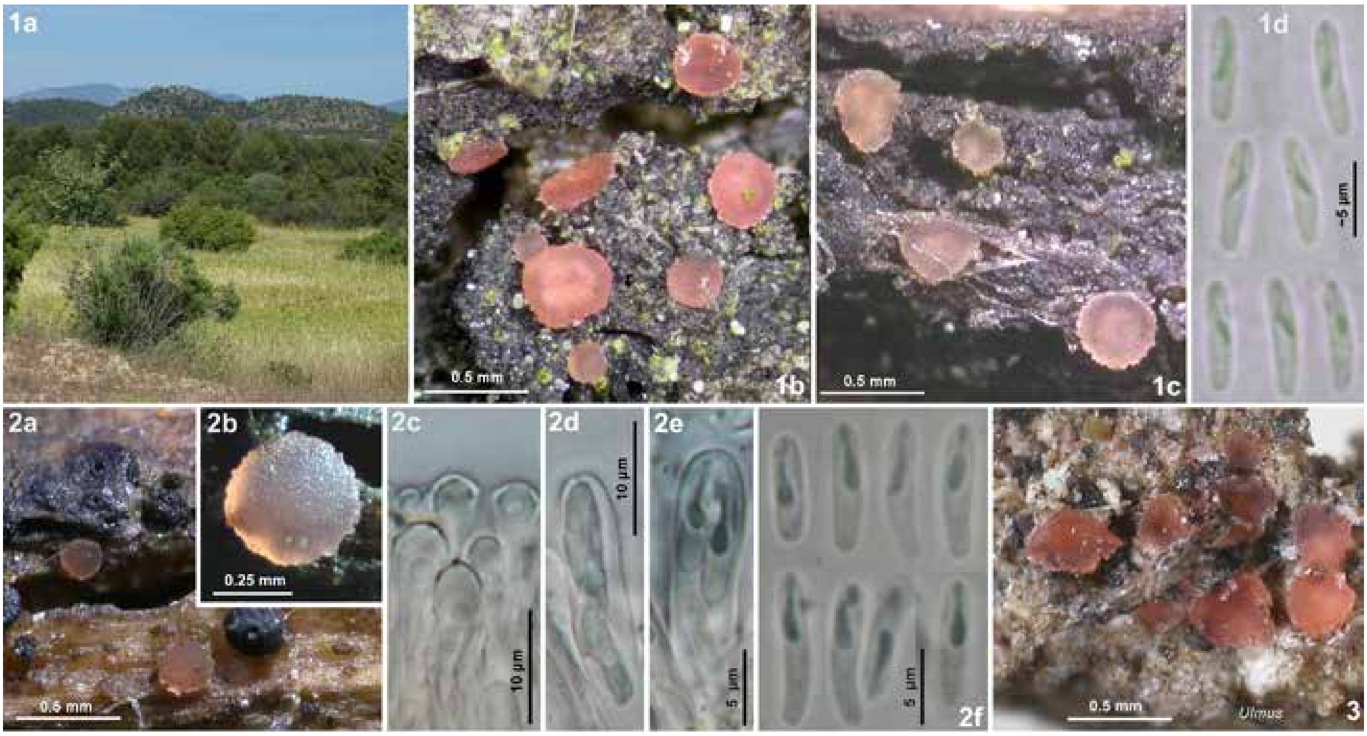


Plate 490. **1–3**: *Orbilia paravitalbae*. – **1a**. supramediterranean semihumid grassland with bushes of *Daphne gnidium* and *Juniperus phoenicea*; **1b–c**, **2a–b**, **3**. rehydrated apothecia; **2d–e**. asci with mature spores; **2c**. apices of paraphyses; **1d**, **2f**. ascospores. – Living state (**2d**: fully turgescent). – **1a–b**, **d**: phot. J.P. Priou, **2b–f**: phot. R. Tena. — **1a–d**. H.B. 10081 (holotype): Spain, Murcia, on *Daphne*; **2a–f**. H.B. 9681: Spain, Teruel, on *Helleborus*; **3**. H.B. 5480: Spain, Madrid, on *Ulmus*.

rounded to obtuse apices (e.g., Pl. 596: 3), which differ from *O. paravitalbae* in being slightly longer and in containing narrower SBs that are more gradually thickened towards their base, also in shorter terminal cells of paraphyses.

Variation. The holotype on bark of *Daphne gnidium*, Pl. 490: 1) closely resembles the other two included collections in spore and SB shape, except that the spores are distinctly narrower (*7–9 × 1.5–1.7 µm). The SBs vary between shorter and longer than half the spore length, but are never shorter in the collection on *Ulmus*, which also differs in a longer pars sporifera and in slightly more fusoid spores similar as in *O. vitalbae*.

Not included collections. A sample on herbaceous stems of *Sambucus ebulus* from Luxembourg (Pl. 489: 2) closely resembles the type of *O. paravitalbae* in shape of spores and SB which are only slightly larger, but the apothecial margin was smooth.

A collection from Tenerife mentioned in Quijada et al. (2016, fig. 8) under the name *O. vitalbae* (IVV: TFC Mic. 23937) resembles *O. paravitalbae* in spore and SB shape except for slightly shorter spores of *6.5–7.2(–8) × 1.6–2.1 µm. Because we felt unable to decide to which of the two species this collection belongs, we preferred not to include it in either description.

A collection from mediterranean Islas Baleares on bark of *Juniperus phoenicea*, studied by I. Olariaga (IVV: 6.XII.2018), deviates in shorter and wider, distinctly clavate spores (*5.7–6.4 × 2.3–2.5 µm) and shorter SBs (3 × 0.7 µm), and in prominent glassy processes. From *O. poitevinica* it differs in shorter spores and SBs, in seemingly lacking crystalloid SCBs, and in downwards curved glassy processes. Based on its deviating DNA data (see below) this represents a species of its own which is referred to as *O.* aff. *paravitalbae* here.

Phylogeny. Sequences of ITS and LSU were gained from the holotype on *Daphne* (S1506 intron absent) and from the Balearean sample on *Juniperus* (S1506 intron present). Both form a strongly supported clade in a combined ML analysis (ITS+LSU, not shown). *O.* aff. *paravitalbae* deviates from *O. paravitalbae* by 6% in ITS and 0.5% in LSU D1–D3. In comparison, *O. poitevinica* differs from both by 17% in ITS and 4.3% in LSU D1–D3.

The position of *Orbilia paravitalbae* s.l. within section *Aurantiorubrae* is problematic. A close relationship to *O. vitalbae* can be excluded based on a high distance in both gene regions. Analyses of LSU (Phyl. S16) placed *O. paravitalbae* in a weakly supported sister position to series *Piliferae*, whereas analyses of ITS (Phyls 13, S15) or SSU+ITS+LSU (Phyl. 7) left it unresolved. Because of the morphological similarity to *O. rosella* we here treat *O. paravitalbae* for the time being as a member of series *Abutilones*.

Ecology. Samples on woody plants were on attached branches, whereas that on *Helleborus* was on the underside of a stem lying on moist ground. In the holotype the apothecia grew on bast, but sometimes on wood of *Daphne* and also on old perithecia of a dothideomycete in a mesomediterranean semihumid (dry) grassland. The sample on *Ulmus* was in a mesomediterranean floodplain, and that on *Helleborus* in an orosubmediterranean *Juniperus oxycedrus* woodland. Among the not included samples, the one on *Sideritis* from Tenerife was in the south-exposed mesomediterranean semihumid *Sideritido solutae-Pinetum canariensis* on trachybasalt, that on *Juniperus* from Islas Baleares a thermomediterranean, almost semiarid, dense forest with *Pinus halepensis*, *Pistacia lentiscus* and *Juniperus phoenicea* along a ravine, and that on *Sambucus ebulus* from Luxembourg in a cold-temperate humid dwarf elder population adjacent to a small angiosperm forest.

Specimens included. **SPAIN**: **Aragón**, **Teruel**, Sierra de Javalambre, 24 km SSE of Teruel, 4 km E of Camarena de la Sierra, 1635 m, stem of *Helleborus foetidus*, 26.II.2012, R. Tena (R.T.L. 12022601, H.B. 9681). – **Murcia**, 4.3 km NW of Bullas, 3.3 km SSW of Chaparral, 577 m, branches of *Daphne gnidium*, on bark, 10.V.2015, J.P. Priou (ex J.P.P. 15119, ex H.B. 10081, TAAM 198539, **holotype**; sq.: MG372375). – **Madrid**, 32 km ENE of Madrid, 4 km ENE of Alcalá de Henares, rio Henares, 595 m, branch of *Ulmus*, on wood, 19.V.1996, H.O. Baral (H.B. 5480).

Not included. **LUXEMBOURG**: **Gutland**, **Esch-sur-Alzette**, 2.5 km W of Esch-sur-Alzette, Belval Usines, 303 m, stems of *Sambucus ebulus*, 10.VI.1999, G. Marson (H.B. 6406b). — **SPAIN**: **Islas Baleares**, **Formentera**, 3.3 km WSW of Sant Francesc, Canal de Cala Saona, 10 m, branch of *Juniperus phoenicea*, on bark, 6.XII.2018, M. Prieto & I. Olariaga (ARAN-F 11430, doc. vid., sq.: MN151401). — **MACARONESIA**: **Canary Islands**, **Tenerife**, Vilaflor, 1.3 km N of Vilaflor, Lomo Gordo, 1600 m, twigs of *Sideritis soluta*, on bark, 9.III.2013, L. & C. Quijada (TFC Mic. 23937, doc. vid.).

Orbilia aethiopica Baral & U. Lindem., **sp. nov.**,

MB 813772 — Pls 491–492

Etymology: named after the geographical origin, Ethiopia.

Typification: Ethiopia, Addis Ababa, Menagesha Suba, branch of indet. angiosperm, 22.XII.2009, U. Lindemann (ex H.B. 9246a, M-0276430, holotype; sq.: KT222424).

Latin diagnosis: *Apothecia rehydratata 0.3–0.55 mm diam., subluteo-ochracea, disco conspicue concavo, margine breviter fimbriato. Asci 8-spori. Ascosporae *4.8–6.3 × 1.8–2.5 µm, cylindrico-clavatae, apice perlate subacutae. Paraphyses ad apicem plerumque sublanceolatae, exsudato tenui. Pili marginales breves, 8–15 µm longi, aseptati, subluteo-ochracei. Habitat ad corticem putridum subsiccum arboris angiospermae in zona mesotemperata humida afromontana Africae septentrio-orientalis.*

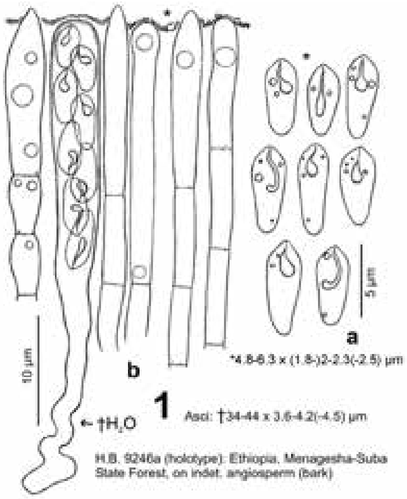


Plate 491. **1**: *Orbilia aethiopica*. – **a**. ascospores; **b**. ascus and paraphyses.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.55 mm diam., 0.14–0.19 mm high (receptacle 0.09–0.14 → 0.07–0.11 mm), pale to light yellowish-ochre, slightly translucent, round, scattered to subgregarious; disc deeply concave, margin 10–30 µm protruding, rough to warted; sessile on a narrowed base, superficial; dry with distinctly narrower aperture, bright ochre-brownish, without or with distinct

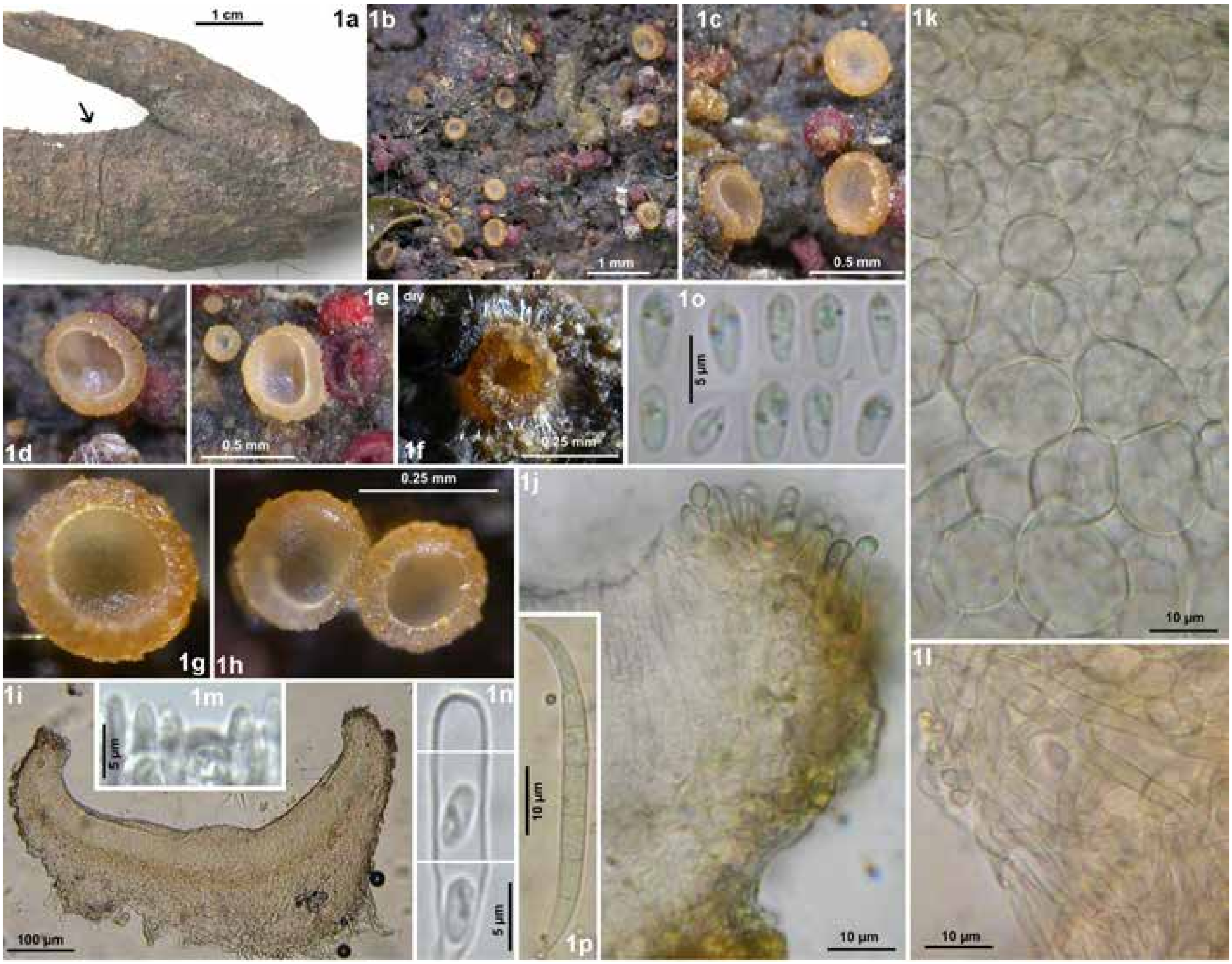


Plate 492. **1**: *Orbilia aethiopica*. – **1a**. dead, corticated, mesic branch; **1b–e**, **g–h**. rehydrated apothecia (with *Cosmospora* sp.); **1f**. dry apothecia; **1i**. apothecium in median section; **1j**. id., marginal region; **1k**. id., basal ectal excipulum; **1l**. anchoring hyphae; **1m**. paraphysis apices; **1n**. parts of basally broken ascus; **1n–o**. ascospores; **1p**. conidium (from substrate). – Living state, except for ascus in **1n** and upper cell in **1p**. – **1m–n**: phot. U. Lindemann. — **1a–p**. H.B. 9246a (holotype): Ethiopia, on indet. angiosperm.

whitish subiculum. **Asci** *4–5 µm wide, †34–44 × 3.6–4.2(–4.5) µm, 8-spored, spores †(sub)biseriate, ~3–4 lower spores inverted; **apex** (†) medium to strongly truncate (not indented, laterally not inflated); **base** with short to long, thin to thick, ± flexuous stalk, L-shaped. **Ascospores** *4.8–6.3 × (1.8–)2–2.3(–2.5) µm, cylindric-clavate, apex subacute at a wide angle (flat-conical), base very slightly to medium attenuated, straight to slightly inequilateral; **SBs** *2.2–3(–3.5) × 0.5–0.8 µm, with a usually strongly swollen, ± tear-shaped lower part and often a subulate upper part of varying length, apically narrowed to a short filum, mostly slightly to strongly flexuous. **Paraphyses** apically uninflated to slightly or medium lanceolate, terminal cells *(12–)15–20(–24) × 2–2.6(–3.7) µm, exceeding the dead asci by 0–3 µm, lower cells *(5.5–)7–9 × 1.8–2.2(–3) µm; unbranched at upper septum. **Medullary excipulum** pale cream, 30–40 µm thick, of dense, small-celled textura globulosa-intricata, somewhat horizontally oriented, sharply delimited. **Ectal excipulum** hyaline to pale yellowish, of (†) thin-walled, indistinctly oriented t. globulosa-angularis from base to margin, 80–120 µm thick near base, cells *13–20(–30) × 10–15(–16.5) µm; 10–20 µm thick at flanks and margin, cells at flanks *5–10 × 4–8 µm, at submargin and margin with protruding, non-septate **hairs** *8–15 × 3–4(–5) µm with 0.2–0.3(–0.5) µm thick smooth walls, surface yellowish-ochraceous; **glassy processes** absent. **Anchoring hyphae** abundant, *2–3(–3.5) µm wide, walls 0.2 µm thick, partly forming strands. **SCBs** in paraphyses and at flanks of ectal excipulum globose, (1–)1.5–2 µm diam. **Exudate** 0.2–0.5 µm thick, continuous to somewhat cloddy, over paraphyses ± firmly attached, subhyaline, at margin and flanks light yellowish-ochraceous. **— ANAMORPH**: unknown (but see below).

Habitat: lying on the dry ground, corticated, 18 mm thick mesic branch of unidentified angiosperm tree, on medium decayed bark (periderm), partly on old perithecia of *Cosmospora*; somewhat blackened, no algae. **Associated**: *Cosmospora* sp., *Hyalorbilia herbicola*, *Lanatonectria flocculenta*, ?*Nectriopsis* sp. **Desiccation tolerance**: excipulum and paraphyses still viable after at least 3 weeks. **Altitude**: 2520 m a.s.l. **Phenology**: XII (but rather long-lived).

Taxonomic remarks. *Orbilia aethiopica* is characterized by cupulate apothecia with short hair-like marginal projections, more or less lanceolate paraphyses, and particularly by short, cylindric-clavate ascospores with a seemingly rounded apex that is, in fact, subacute under a wide angle. The species is difficult to place based on its morphology alone. Due to the shape of the SBs, *O. aethiopica* is similar to series *Habrostictis* in which, however, the paraphyses are apically consistently inflated and often beaked. Because of similarities in the yellowish exudate, *O. aethiopica* resembles species of section *Helicoon*, such as the eastern Asian *O. hoana*. The neotropical *O. martinicensis*, assigned to series *Helicoon*, has a similar shape of spores and particularly SBs, but differs in larger, flat apothecia with glassy processes instead of short hairs at the margin. In some of its features *O. aethiopica* resembles species such as *O. cupularis* (section *Ovoideae*), *O. fraxini*, and *O. lamarcheae* (section *Arthrobotrys*), except for characters of the spores which have a very different shape and contain globose SBs.

Anamorph. Two phragmoconidia (*50 × 3.8–4.5 µm) with medium curved ends (vermispora-like) were detected on the substrate near the apothecia (Pl. 492: 1p).

Phylogeny. A sequence taken from apothecia of the holotype (SSU without S1506 intron, ITS, LSU) shows a minimum ITS distance of 16% to *O. carminorosea* (3.5% in LSU D1–D2), and 18.5% to *O. ebuli* (4.3% in LSU). In our analyses of ITS+LSU or ITS (Phyls 13, S15), *O. aethiopica* clustered strongly supported in series *Abutilones*, whereas in the LSU (S16) it clustered unresolved.

Ecology. *O. aethiopica* was detected on ± rotten periderm of a corticated mesic branch in close association with a *Cosmospora*, in a warm-temperate humid (somewhat winter-dry), evergreen, predominantly broad-leaved afromontane forest at the western slope of an old volcano in the central plateau of the Ethiopian highlands.

Specimens included. **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, southern part of Menagesha Suba State Forest, 2520 m, branch of indet. angiosperm, on bark, 22.XII.2009, U. Lindemann (ex H.B. 9246a, M-0276430, **holotype**; sq.: KT222424).

Series *Poitevinicae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Poitevinicae*** Baral, **ser. nov.**, MB 815014 – Type species: *Orbilia poitevinica* Baral

Recognized species: *O. poitevinica*.

Orbilia poitevinica Baral, **sp. nov.**, MB 813773 — Pls 493–494

Etymology: named after the site of the type collection, Marais Poitevin (W-France).
Typification: France, Charente-Maritime, Niort, branches of *Fraxinus excelsior*, 25.IV.2006, H.O. Baral & N. Van Vooren (ex H.B. 8131, M-0276566, holotype).

Latin diagnosis of series and species: *Apothecia rehydratata 0.3–1.5 mm diam., rosea, margine subtiliter vel conspicue albido-crenulato. Asci 8-spori. Ascosporae *6–9 × 2.2–3 µm, subcylindricae vel fusoideo-clavatae, in statu vivo corpusculum vermiformem, basaliter lacrimiformem, ad apicem filo minuto affixum continentes. Paraphyses ad apicem leniter capitato-clavatae. Cellulae vivae excipuli et paraphysium corpuscula crystalloidea continentes. Habitat ad corticem ramorum siccorum* Fraxini excelsioris *in zona meso ad supratemperata atlantica ad subcontinentali Europae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–1(–1.5) mm diam., 0.14–0.2 mm high, light (brick-)rose, round to

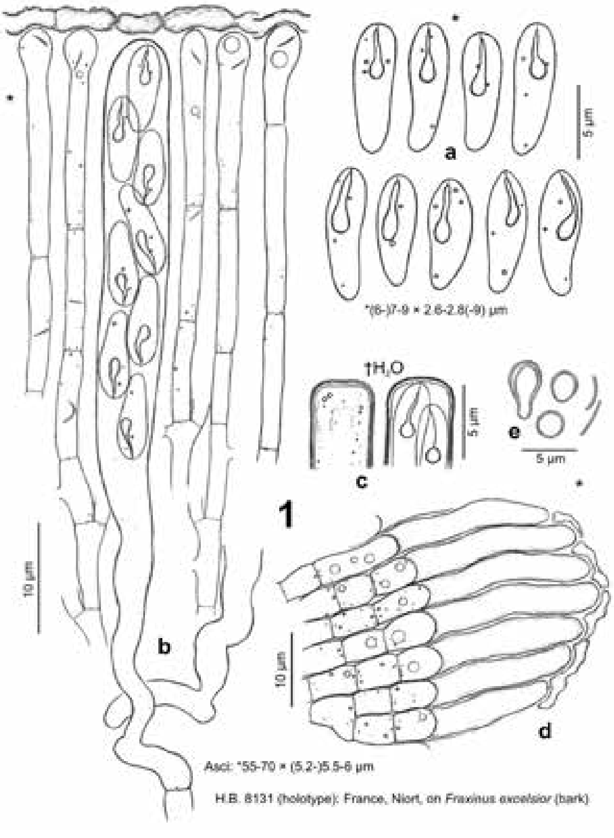


Plate 493. **1**: *Orbilia poitevinica*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. marginal ectal excipulum in median section, cortical cells with glassy processes; **e**. SCBs in cells of ectal excipulum (lower flanks).

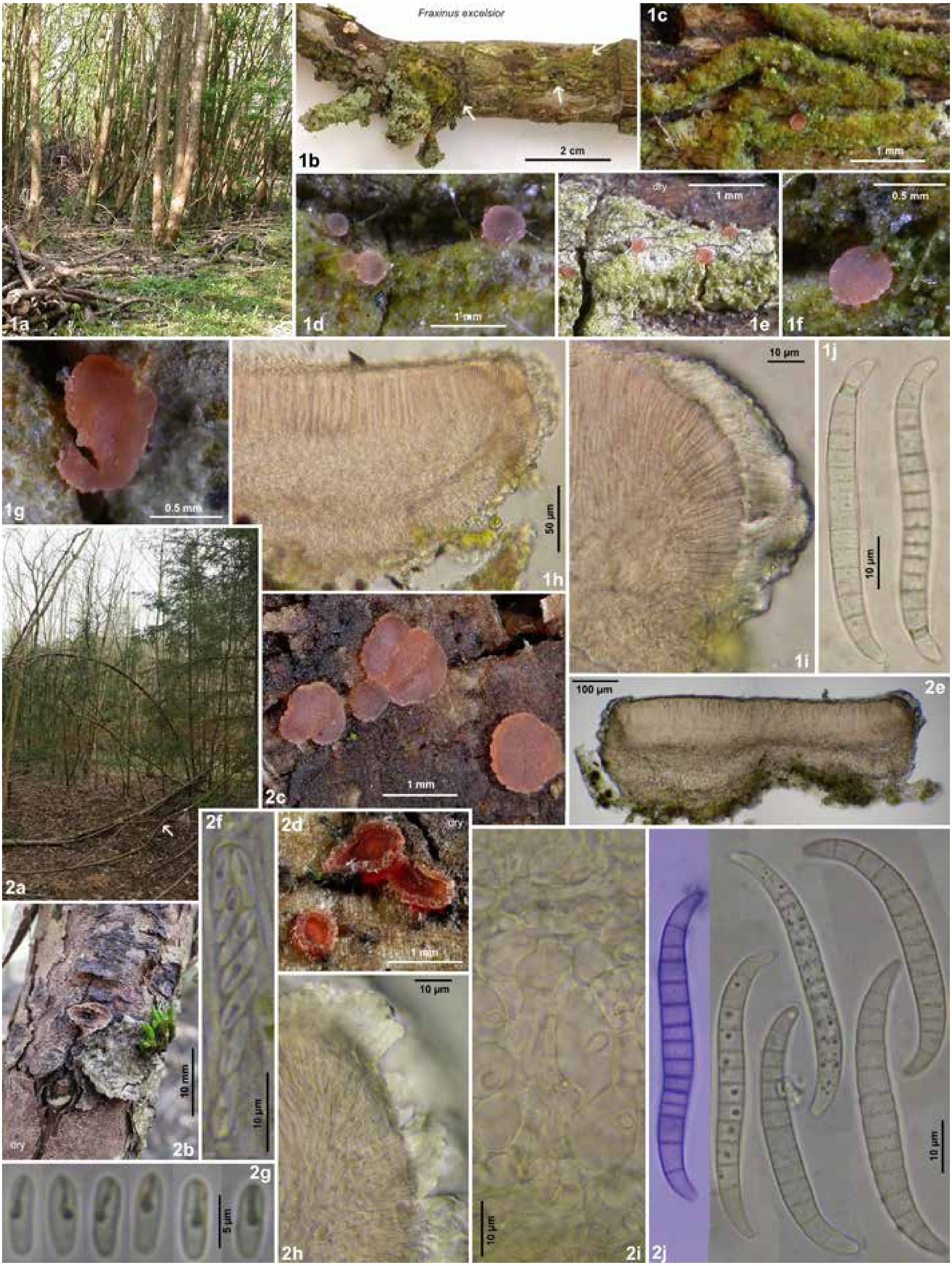


Plate 494. **1–2**: *Orbilia poitevinica*. – **1a**. swampy *Fraxinus* forest in western France; **2a**. moist depression with young ash trees in Luxembourg; **1b**. dead decorticated xeric branch of *Fraxinus* with beetle galleries; **2b**. dead corticated xeric branch in situ; **1c–d**, **f–g**, **2c**. rehydrated apothecia (**1c–f** on old boring dust, **1g**, **2c** on bark); **1e**, **2d**. dry apothecia; **1h**, **2e**. apothecia in median section; **1i**. **2h**. id., marginal ectal excipulum with glassy processes; **2i**. id., basal excipulum; **2f**. ascus with ascospores; **2g**. ascospores; **1j**, **2j**. conidia from substrate. – Living state (**2j** left in CRB), except for 2 cells in **1j**, ascus in **2f**. — **1a–j**. H.B. 8131 (holotype): France, Niort, on *Fraxinus*; **2a–j**. G.M. 2013-04-04.2: Luxembourg, on *Fraxinus*.

somewhat undulating, scattered to gregarious in small groups; disc flat to slightly convex, margin 0–10 µm protruding, finely to distinctly whitish crenulate or toothed; broadly sessile, superficial; dry light to bright rose-orange to orange-red. **Asci** *55–70 × (5.2–)5.5–6 µm {2}, †50–60 × 4.3–5.4 µm {1}, 8-spored, spores (*) biseriate, 3–5(–6) lower spores inverted {2} (rarely or sometimes mixed), pars sporifera *30–38 µm long; **apex** (†) medium to strongly truncate (not indented, laterally scarcely inflated); **base** with medium long and thick, flexuous stalk, L- to Y-shaped. **Ascospores** *(6–)7–8(–9) {2} × 2.2–2.6 {1} or 2.6–2.8(–3) µm {T}, subcylindrical to clavate or fusoid-clavate, apex rounded, more rarely obtuse, base not or slightly to medium attenuated, straight to slightly inequilateral; **SBs** *(3–)3.7–4.4(–4.7) × (0.7–)0.8–1(–1.2) µm {2}, divided into an ellipsoid to tear-shaped lower and a vermiform to subulate upper part, straight to ± flexuous; overmature with long filum and abruptly globose lower part. **Paraphyses** apically uninflated or often slightly (to medium) capitate-clavate, terminal cells *(9–)16–21(–23) × (2–)2.3–3.3 µm {T}, lower cells *(6–)9–14(–17) × (1.4–)1.6–2(–2.2) µm {T}; never branched near apex, hymenium pale rose. **Medullary excipulum** very pale rose, 50–100 µm thick, of dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** pale rose (only near margin), of thin-walled († slightly gelatinized), vertically oriented t. angularis(-prismatica) from base to mid flanks, 30–45 µm thick near base, cells *(8–)10–15(–20) × (6–)7–10(–12.5) µm {2}; 20–25(–35) µm thick near margin, of strictly parallel t. prismatica oriented at an 60–80° angle to the surface, marginal cortical cells *4–8(–12) × 2.7–4.5 µm {T}; **glassy processes** (5–)10–20(–40) × (2.5–)3–3.5(–4) µm {2}, low- to high-refractive, not or only sparsely stratified, ± straight or slightly downwards curved (those at mid flanks slightly upwards), coherent to form indistinct teeth, **hairs** absent. **Anchoring hyphae** abundant, *2–2.7(–4) µm wide, walls 0.2–0.3(–0.5) µm thick {T}, forming a 25 µm thick layer. **SCBs** in paraphyses forming thin rods, in ectal excipulum (only at lower and mid flanks) rod- or ring-shaped, 2–5.3 × 2–2.8 µm {2}, hyaline. **Exudate** over paraphyses 1.5–2.5 µm thick, cloddy-continuous, hyaline to very pale yellowish, loosely attached; over margin and flanks ~1–1.5 µm thick. — **ANAMORPH**: vermispora-like (presumed, from natural substrate {2}). **Conidiophores** not seen. **Conidia** phragmosporous, *44–58 × (4.5–)5–6(–6.5) µm, 11–15-septate {2}, slightly to strongly curved at both ends, mostly ± straight in middle part, with a few small LBs especially at the septa, sometimes also with 1–2 larger LBs in each cell (0.8–1.2 µm diam.).

Habitat: collected 1–4 m above the ground, corticated to nearly decorticated, 14–60 mm thick branches and trunks of *Fraxinus excelsior* {2}, on medium to very rotten bark (bast or over cracks in periderm) {2}, also on old boring dust of a bark beetle {1}, slightly greyed, partly blackened, sparsely to strongly covered by green algae. **Associated**: *Orbilia phragmotricha* {1}, *Orthotrichum* sp. {1}, *Peniophora* sp. {1}, *Physcia* sp. {1}, *Xanthoria parietina* {1/1}. **Desiccation tolerance**: fully viable for at least 4 weeks. **Altitude**: 4–333 m a.s.l. **Geology**: France: Holocene alluvial peaty clay adjacent to Middle & Upper Jurassic limestone, Luxembourg: Lower Jurassic sandstone. **Phenology**: IV (but rather long-lived).

Taxonomic remarks. *Orbilia poitevinica* is extraordinary within section *Aurantiorubrae* because of its rather short and wide ascospores with elongate spore bodies which resemble those of section *Habrostictis*. Judging especially from its SBs, *O. poitevinica* was first thought to belong to that section close to *O. vitalbae* or *O. trapeziformis*. However, *O. poitevinica* possesses conspicuous glassy processes that form ± distinct teeth at the margin, a character unknown in section *Habrostictis*. Similar spores are found in *O. aethiopica*, which differs, e. g., in yellowish-ochre apothecia, short marginal hairs instead of glassy processes, partly ± lanceolate paraphyses, and in lacking crystalloid SCBs.

Variation. In the holotype the apothecia were predominantly smaller [0.3–0.5(–1.3) mm] than in the specimen from Luxembourg [0.5–1(–1.5) mm], and the spores were wider [Luxembourg: *(6.5–)7–8(–9) × 2.2–2.6 µm].

Anamorph. Vermispora-like conidia were observed on the substrate near apothecia in both collections (Pl. 494: 1j, 2j). However, conidia did not develop in pure culture.

Phylogeny. A sequence gained from apothecia from the Luxembourg specimen comprises ITS and LSU (the S1506 intron is absent). Analyses of (SSU+)ITS+LSU, ITS, or LSU (Phyls 7, 13, S15–S16) placed *O. poitevinica* unresolved in the genus *Orbilia*. In Phyl. 7 *O. paravitalbae* was associated with low support with *O. poitevinica*.

In the ITS region the lowest distance was 18–19 % to *O.* cf. *paracaudata* and *O. pilifera* (series *Piliferae*) and 19 % to *O. albidorosea* and *O. albovinosa* (series *Albovinosae*), and in the LSU (D1–D2) around 2.5–3 % to *O. ovalis*, *O. albidorosea*, and *O. phragmotricha*.

Specific nucleotide positions. *O. poitevinica* concurs with series *Abutilones* at pos. 140 of the 5.8S (GGCA**C**GTCTG), by which it differs from all other series of subgenus *Habrostictis* which generally have GGCA**T**GTCTG. Similarities to series *Piliferae* can be seen in the alignment of the ITS2 region, but further characteristic nucleotides could not be found in the ITS or LSU.

Ecology. *O. poitevinica* was collected on decayed bark and bark beetle boring dust of xeric branches of *Fraxinus excelsior* in atlantic and subcontinental, warm- to cold-temperate humid western and central Europe. The type location is part of a large area of cultivated marshland with mesosubmediterranean influence (with *Fraxinus*, *Salix aurita*, *Populus* and some *Quercus pubescens*), a remnant of the former Gulf of Poitou in western France. The paratype was detected in a small moist depression with dead young ash trees surrounded by young spruce trees in a deciduous forest between airport and highway in temperate Luxembourg.

Specimens included. **FRANCE**: **Poitou-Charentes**, **Deux-Sèvres**, Poitou, 21 km W of Niort, 4 km NW of St.-Hilaire-La-Palud, Marais Poitevin, 4 m, branches of *Fraxinus excelsior*, on bark & boring dust, 25.IV.2006, H.O. Baral & N. Van Vooren (ex H.B. 8131, **holotype**, M-0276566, anam. substr.). — **LUXEMBOURG**: **Gutland**, **Luxembourg**, 4 km ENE of Luxembourg, NW of Kalchesbrück, E of Findel, 333 m, branch and trunk of *Fraxinus excelsior*, on bark, 4.IV.2013, G. Marson (G.M. 2013-04-04.2; sq.: KT380079).

Series *Piliferae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Piliferae*** Baral, **ser. nov.**, MB 815015 – Type species: *Orbilia pilifera* Baral & R. Galán

Etymology: named after the type species, *O. pilifera*.

Latin diagnosis: *Apothecia ochracea, aurantiaca vel testaceo-rubra, fimbriata vel glabra, guttulae luteae carentes, ascosporae apice rotundatae ad obtusae, raro subacutae, basaliter plerumque breviter caudata, plerumque rectae vel leniter curvatae, status anamorphicus conidiis staurosporis (typo* Trinacrium incurvum*).*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.3–1.5(–1.8) mm diam., pale to bright ochre-orange to brick-red, somewhat urceolate to flat, margin smooth to crenulate or whitish fimbriate, sessile or with a short stipe. **Asci** *(36–)40–71 × (3.5–)4–5.5(–6) µm, 8-spored, lower (1–)3–6(–7) spores inverted; **apex** (†) medium to strongly truncate, not or slightly indented and laterally inflated; **base** T-, L- to Y- or h-shaped. **Ascospores** *(5–)6–11(–12.5) × (1–)1.3–2.5(–3) µm, subcylindric- to ellipsoid- or fusoid-clavate, apex rounded to obtuse, rarely subacute, base often tail-like or with a distinct short tail, straight to slightly, sometimes medium curved or geniculate near base, **SBs** (1.2–)1.5–3(–4.2) × (0.3–)0.5–1(–1.3) µm, globose to tear-shaped or ampulliform to rod-shaped, apically untapered or narrowed to a small or wide point, rarely with a short filum, straight, sometimes medium flexuous. **Paraphyses** slightly to strongly clavate-capitate or spathulate to mammiform or lageniform at the apex, terminal cells 1– 3 × longer than lower cells. **Ectal excipulum** cells near base *(6–)8–20(–30) × (5–)7–15(–19) µm; **glassy processes** absent, rarely 5–10 µm long (*O. caudata*), **hairs** absent or ~ 10 µm up to 35–55(–80) × (3–)3.5–6.5(–8) µm, thin-walled, (2–)3–6-septate. **SCBs** absent or sometimes line- to ring-shaped, rarely globose (small); **VBs** consistently absent. **Exudate** over paraphyses and margin absent or up to 1–2(–3) µm thick, rough, cloddy or often cap-like, firmly attached. **— ANAMORPH**: trinacrium incurvum-like. **Conidiophores** short (7–20 µm). **Conidiogenous cells** monoblastic or sympodial. **Conidia** staurosporous, T-shaped (2-armed), *26–43 × 17–49 µm, the two arms curved downwards.

Habitat: on bark (exceptionally wood) of twigs and branches of angiosperms, rarely herbaceous stems, humid to semiarid, temperate to tropical, always desiccation-tolerant.

Recognized species: 7, plus 4 unnamed species ('affinis').

Taxonomic remarks. Series *Piliferae* is defined by its characteristic trinacrium-like conidia with curved arms in combination with molecular data. Although typified by *O. pilifera*, a species with prominent, septate, thin-walled hairs, the apothecia in a majority of the included species have a more or less smooth margin. In two taxa tentatively placed here (*O. caudata*, *O.* aff. *caudata*) short glassy processes occur at the margin in some specimens. As a characteristic of most of the included taxa, the spores tend to have a more or less defined, short and thick tail, also the spore apex is predominantly rounded to obtuse. Spore bodies are always visibly attached to the spore apex but vary between subglobose, tear-shaped, rod-shaped, and ampulliform. Species with elongate, apically strongly narrowed spore bodies may be confused with members of section *Habrostictis*, but also series *Ovales* (section *Lentiformes*) or series *Commatoideae.*

Series *Piliferae* is placed here in section *Aurantiorubrae* mainly because of a partial similarity of *O. pilifera* with *O. suberis* of series *Abutilones*. *O. pilifera* resembles also members of series *Albovinosae* in spore body shape, but that series is characterized by rather prominent glassy processes at the margin and by conidia with longer and thinner arms. In the marginal hairs and lageniform-mammiform paraphyses *O. pilifera* strikingly resembles *O. carpoboloides* of series *Habrostictis*. However, strong differences in the shape of SBs and conidia suggest that the two species are not closely related.

Four of the included species (*O. caudata*, *O. floridensis*, holotype collections of *O. paracaudata* and *O. farnesianae*) were first thought to belong to series *Ovales* of section *Lentiformes*, mainly because of spore bodies similar as in the type species, *O. ovalis*. On the other hand, *O.* cf. *paracaudata* and the paratype of *O. farnesianae* were first believed to belong to series *Habrostictis* (section *Habrostictis*) close to *O. mammifera*, based on partly mammiform paraphysis apices and rather long and narrow SBs. These four species share indeed some similarities, including lageniform to mammiform paraphyses in some of them, or a similar shape of ascospores and SBs, besides their characteristic trinacrium-like conidia and molecular data. *O. bannaensis* was at first tentatively affiliated in section *Helicoon* based on morphological similarities, including the unbranched conidia of its presumed anamorph.

Species delimitation. Rather strong variation was noted between populations of *O. farnesianae* (from the same site and substrate), *O. paracaudata*, and *O. caudata*, which raises the question as to whether these species are heterogeneous. The independency of *O.* aff. *farnesianae* is supported by molecular data.

Anamorph. Except for *O. bannaensis* and *O. amarilla*, quite charateristic trinacrium incurvum-like conidia with curved-down arms, resembling an anchor, were observed in all taxa of series *Piliferae*, though mostly only on the natural substrate. They were obtained in pure culture in *O. pilifera* and in two undescribed Chinese taxa here referred to as *O.* aff. *farnesianae* (Liu 2006, as *O. brasiliensis*) and *O.* aff. *bannaensis* (Guo et al. 2013, as *Orbilia* sp.). The presence of these conidia in *O. floridensis* (holotype), *O. farnesianae* (paratype), *O. caudata*, and *O.* cf. *paracaudata* and their almost exclusive appearance in one clade gave the impetus to place all these species in series *Piliferae*.

The anchor-like conidia are a main difference between series *Piliferae* and the remaining series of section *Aurantiorubrae*, in which trinacrium-like anamorphs almost never occur with certainty, except for two species of series *Albovinosae* in which the conidial arms are also curved down- or outwards but arms and stipes are more slender. Series *Piliferae* concurs with section *Habrostictis* in possessing a trinacrium-like anamorph, but in that group the two conidial arms are always straight and project upwards. Although series *Habrostictis* resembles *O. pilifera* in teleomorph characteristics, it sharply differs in vermispora-like conidia.

The observed conidia do not significantly differ among the taxa of series *Piliferae* and fit more or less *Trinacrium incurvum*, a species that was described from two isolates [Taiwan, on bark, Matsushima 1980: 75, paratype; Peru, Rio Monanti, on twig of broad-leaved tree, Matsushima 1993, holotype; see Pl. 22: d]. In the holotype the stipes are reported as 3–4-septate, whereas in the paratype they are longer and 3–6-septate. In comparison to the here reported anamorphs of series *Piliferae*, Matsushima's two strains have somewhat shorter arms with only 0–2 septa. Matsushima reported unbranched conidia in the holotype, which were also seen in B. Liu's culture of *O.* aff. *farnesianae* and a single time on the natural substrate in a collection of *O. pilifera* studied by us (H.B. 7095a). No sequence is available for Matsushima's strains, therefore, the identity of *T. incurvum* remains unclear and we refrained from adopting that name for any of our taxa.

Phylogeny. In an analysis of the LSU region by Liu et al. (2006a), *O.* aff. *farnesianae* formed with *Orbilia* sp. (both as '*O. brasiliensis*') a paraphyletic sister group to section *Helicoon*, whereas members of section *Aurantiorubrae*, represented by *O. milinana*, *O. scolecospora*, *O. bomiensis*, and *O. nemaspora*, clustered distant from those (no member of section *Habrostictis* was available).

Our molecular analysis of (SSU+)ITS+LSU or each region alone placed *O. pilifera*, *O. farnesianae*, *O.* aff. *farnesianae*, *O. amarilla*, and *O.* cf. *paracaudata* in a strongly (ITS+LSU, ITS) or medium (LSU) supported monophyletic clade distant from other taxa (Phyls 7, 13, S15–S16). Also *O. bannaensis* clustered within this clade when analysing ITS, but unresolved in the combined analysis (Phyls 13, S15), perhaps because it lacks LSU. In the S1506 intron (S14) *O. piliferae* and *O.* cf. *paracaudata* form a strongly supported (NJ analysis, not shown) or unsupported (ML, S14) clade, whereas *O.* aff. *farnesianae* clustered unresolved in section *Aurantiorubrae*. The clade indeed occupies a rather isolated position within subgenus *Habrostictis*, where it clustered in the analysis of Baral et al. (2017b) unsupported sister to section *Helicoon*.

Specific nucleotide positions. Series *Piliferae* shows in the ITS2 region a highly conservative string of 87 nt which is consistent in all five species, except for 2 variable positions: TTAAAGTTGACGTTCTGTGTGGTACTCATCCTTACCTTCCGTAGTAATTTACTTTAT*S*ACTGTTCGTT*W*GGATTTGGCACGCACCTG. Other series of section *Aurantiorubrae* are rather variable in this region. In the ITS1 no such regular pattern is observed. Pos. 295 of LSU D1 is diagnostic for series *Pilifera*, showing TCAAA**T**TG, whereas all other groups of subgenus *Habrostictis* show TCAAA**A**TG or rarely TCTAA**A**TG or TCAAA**A**CG.

At pos. 98 of the 5.8S region series *Pilferae* has CATCGA**A** except for *O. bannaensis* which has CATCGA**G**, the current motif in *Orbilia*, but CATCGA**A** also occurs in a few *Orbilia* spp. and in most basal genera.

Ecology. Probably all included species are more or less desiccation-tolerant. They grew on bark of angiosperms, rarely on wood or herbaceous stems. Records derive from warm-temperate to tropical, humid to arid regions of Europe, Macaronesia, Asia, Australia, and North America.

Key to species of series *Piliferae*

1. Inflated apex of paraphyses at least partly mammiform or lageniform (beaked); septate hairs present or absent, glassy processes always absent 2
1. Inflated apex of paraphyses capitate, never beaked; septate hairs always absent, glassy processes present or absent 7

2. Marginal excipular cells terminated by 35–55 µm long, 2–6-septate, thin-walled hairs; spores *(5–)6–8(–9.2) × (2–)2.2–2.5(–2.7) µm, with tail-like base; SBs broadly tear-shaped to subglobose; bark of *Ulmus*, cold-temperate to supramediterranean humid to semihumid, mainly western and southern Europe, also northeastern North America .... ***O*. *pilifera***, p. 918
2. Marginal excipular cells without hairs 3

3. Spores *11.5–20.5 × 2.4–3.5 µm, subcylindrical to narrowly fusoid-clavate; SBs consistently absent (living state!); wood of *Euphorbia*, subtropical (semi)arid Macaronesia .... ***O*. *asomatica*** (section *Arthrobotrys*), p. 1487
3. Spores *5.5–12.5 µm long, fusoid-clavate; SBs present in living mature spores 4

4. Spores consistently ellipsoid-fusoid, apex obtuse to subacute, base always with a short tail 5
4. Spores often cylindrical, if ellipsoid-fusoid then < *2 µm wide, apex rounded to obtuse, base attenuated, tail-like or with a short tail 6

5. Spores *(5.8–)6.4–7.3(–8) × (1.9–)2.2–2.3(–2.4) µm; SCBs ring- to S- or rod-shaped (line- to plate-like); branch of *Euphorbia*, subtropical arid Macaronesia .... ***O*. *amarilla***, p. 921
5. Spores †(7.5–)8–10 × 2.3–3 µm; data on SCBs unknown; twig of indet. angiosperm shrub, subtropical humid southern China .... ***O*. aff. *farnesianae***, p. 925

6. Spores *(5.5–)8–11(–12.5) × 1.7–2.5 µm; SBs 2–4.2 µm long; bark of *Vachellia*, subtropical arid western Australia ... ***O*. *farnesianae***, p. 923
6. Spores *6–7.5 × 1.4–1.8 µm; SBs 2–2.5 µm long; bark of woody climber, tropical semiarid western Australia.... ***O*. cf. *paracaudata***, p. 926

7. Spores *(3.7–)4.5–7.5 × 1.8–3.3 µm, ovoid, ellipsoid or fusoid, base sometimes tapered but never tail-like; conidia dicranidion-like (partly unknown) 8
7. Spores *5–8 or 7.5–12.5 × 1–2.3 µm, fusoid to subcylindrical, base partly tail-like or with distinct short tail; conidia trinacrium-like, with downwards curved arms (partly unknown) 9

8. Spores ellipsoid to ovoid, *3.7–7.5 × 2.2–3.3 µm; SBs ± ampulliform, with a rod-shaped upper part; margin without glassy processes; bark of angiosperms, Europe & North America .... see ***O*. *ovalis*** (section *Lentiformes*), p. 498
8. Spores ellipsoid-fusoid, †5–7.3 × 1.8–2.2 µm; SBs ?tear-shaped; margin with 2–5 µm long glassy processes; anamorph unknown; bark of *Cynanchum*, subtropical semiarid Pakistan .... ***O*. aff. *caudata***, p. 929

9. Spores *1.9–2.3 µm wide, with ± broad, ellipsoid-fusiform upper part; margin with or without short glassy processes 10
9. Spores *1–2 µm wide, with ± narrow, cylindric-fusoid upper part; margin without glassy processes 11

10. Spores *5–7.8 µm long; SBs tear- to rod-shaped; bark of angiosperms, herbaceous stems, (sub)tropical humid South America & eastern Asia .... ***O*. *caudata***, p. 928
10. Spores *(7–)8–9.5(–11) µm long; SBs broadly tear-shaped to globose; wood of *Euphorbia*, subtropical (semi)arid Macaronesia .... see ***O*. *pisciformis*** (series *Commatoideae*), p. 808

11. Spores *5.8–6.3 × 1.2–1.3 µm; indet. woody substrate, subtropical humid eastern Asia .... ***O*. aff. *bannaensis***, p. 932
11. Spores longer and partly wider 12

12. Spores *7–8.8 × 1–1.5 µm; asci †31–43 µm long 13
12. Spores *5.5–12.5 × 1.5–2.5 µm; asci †42–56 µm long 14

13. Spores *7–8.8 × 1.3–1.5 µm, SBs 1.2–1.8 µm long; bark of *Ficus*, tropical humid southeastern North America ... ***O*. *floridensis***, p. 927
13. Spores *7–8.5 × 1–1.3 µm, SBs 1.5–2.3 µm long; bark of *Broussonetia*, (sub)tropical humid eastern Asia .... ***O*. *bannaensis***, p. 930

14. Spores *5.8–8.5(–9.5) × (1.5–)1.6–1.8(–1.9) µm; SBs 1.5–2(–2.2) µm long; with inconspicuous crystalloid SCBs; bark of different climbers, tropical subhumid eastern & western Australia .... ***O*. *paracaudata***, p. 925
14. Spores *(5.5–)8–11(–12.5) × (1.7–)1.8–2(–2.5) µm; SBs (2–)2.3–3.2(–4.2) µm long; without crystalloid SCBs; bark of *Vachellia*, subtropical arid western Australia .... ***O*. *farnesianae***, p. 923

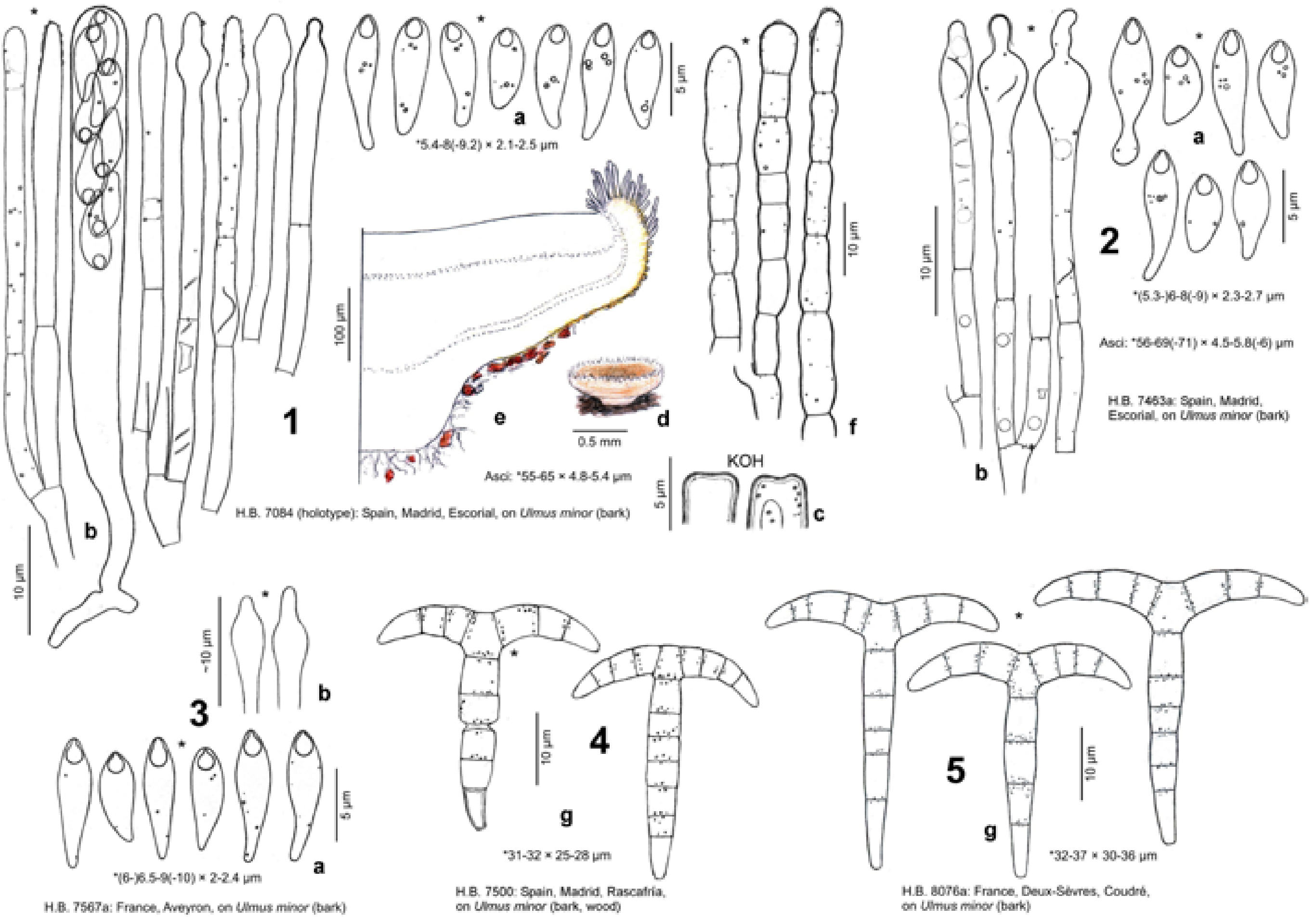


Plate 495. **1–5**: *Orbilia pilifera*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium with fimbriate margin; **e**. apothecium in median section; **f**. marginal hairs; **g**. conidia (**4** from substrate, **5** from culture).

Orbilia pilifera Baral & R. Galán, in Friebes, Joannea Bot. 9: 18 (2011) — Pls 495–497, Map 85

Etymology: referring to the hairy apothecial margin.

Typification: Spain, Madrid, Colmenarejo, trunk of *Ulmus minor*, 7.XII.2001, F. Prieto (ex H.B. 7084, M-0276554, holotype).

Misapplied name: García Alonso (2003: 228), as *O. luteorubella*.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.5–1.5(–1.8)((–2.5)) mm diam., 0.15–0.25(–0.3) mm high (receptacle 0.14–0.15 → 0.08–0.11), light to bright (yellowish-)ochre(-orange), non- to semitranslucent (hygrophan), round, soft, non-gelatinous, gregarious in small groups or often large numbers; disc slightly to strongly concave, flat only when old, margin fimbriate to crenulate by prominent, 15–60 µm protruding whitish hairs; sessile or with an obconical base or short stipe 0.1 × 0.25–0.3 mm, ± superficial, sometimes erumpent from beneath bark tissue; dry light orange-ochre. **Asci** *(52–)55–71 × 4.5–5.5(–6) µm {4}, †45–64 × 3.8–4.8 µm {3}, 8-spored, spores (*) biseriate, (1–)2–**3**–**5**–6(–7) lower spores inverted (sometimes mixed) {10}, pars sporifera *(15–)20–31(–36) µm long; **apex** (†) strongly truncate (often slightly indented, laterally sometimes slightly inflated); **base** with medium to very long, thin, flexuous stalk, T- to L-shaped. **Ascospores** *(5–)6–8(–9.2)((–10)) × ((1.8–))(2–)2.2–2.5(–2.7)((–3)) µm {7}, †(6.8–)7.3–8.5(–9) × 2–2.3 µm {1}, ellipsoid- to fusoid-(or fusiform-)clavate, exceptionally ellipsoid-fusoid or with bulbous tail, apex obtuse, sometimes subacute, base mostly strongly attenuated in a tail-like end, straight or slightly curved near base; **SBs** *(1.2–)1.4–1.8 × 1–1.3 µm {5}, broadly tear-shaped to subglobose, attached by a ± small point. **Paraphyses** apically uninflated to narrowly lanceolate or mostly slightly to very strongly spathulate or lageniform to mammiform, terminal cells *(14–)17–30(–38) × (2–)2.5–4(–5.2) µm {5}, apical beak 1–4.5 × 1.3–2 µm, exceeding the living asci by up to 2–3 µm, the dead asci by 0–5 µm, lower cells *8–17 × 1.5–2.6 µm {3}, unbranched at upper septum, hymenium pale orange. **Medullary excipulum** very pale orange, 40–130 µm thick in centre, of dense textura globulosa-angularis, partly interrupted by loose t. intricata, near base indistinctly delimited from ectal excipulum, at flanks ± sharply so by a 5–40 µm thick, pale yellow-orange layer of t. porrecta. **Ectal excipulum** hyaline to very pale yellowish-orange, near cortex light golden yellow, of thin-walled, (irregularly) vertically oriented t. angularis-prismatica from base to margin, up to 110 µm thick in stipe, 30–60 µm near base, cells *6–16(–18)((–25)) × 5–11(–14) µm {3}, 20–40 µm thick at lower flanks, cells *7–13 × 4–9 µm, 15–30 µm thick near margin, of t. prismatica-porrecta oriented at a 10–45° angle to the surface, or of t. angularis-prismatica oriented at 45–80°, cells *7–17 × 2.5–5 µm; cortical cells terminating in thin-walled, **hairs** */†35–55(–80) × (3.5–)4.5–6.5(–8) µm {6}, (2–)3–6-septate, straight or often somewhat irregularly flexuous, cylindrical to medium moniliform, wall *0.2–0.4 µm thick, †0.3–0.5(–0.7) µm, smooth, free or slightly coherent to form indistinct teeth. **Anchoring hyphae** abundant, */†(1.5–)1.8–3(–5) µm wide, walls 0.2–0.3(–0.5) µm thick {5}, forming an up to 100 µm thick, loose hyaline texture on base and lower flanks, partly as hyphal strands. **SCBs** in paraphyses forming inconspicuous rod-shaped or filiform, partly circular structures {3}, also absent {2}; similar SCBs in ectal excipulum present {1} or absent {4}; **VBs** in young paraphyses present {1}, medium refractive. **Exudate** on paraphyses forming minute warts or often absent; at margin and lower flanks ~1 µm thick, light to bright golden-orange-ochre, cloddy; dead cytoplasm light golden yellow. — **ANAMORPH**: trinacrium incurvum-like (from ascospore isolate {1} and natural substrate {9}). **Conidiophores** short. **Conidia** T-shaped, the two arms bent downwards, total size *27–37 × 22–36(–40) µm, stipe *22.5–31 × 4–4.7 µm, 4–7-septate, arms tapering, *13.5–18 × 4.2–5 µm, (2–)3–4-septate {6}.

Plate 496. **1–9**: *Orbilia pilifera*. – **1a**, **4a**. dead *Ulmus* trees in submediterranean areas, with detached bark; 3a. inner surface of bark with beetle galleries; **2**, **3a–c**, **4b**, **5a–b**, **6a–c**, **7a**. rehydrated apothecia; **6d**. dry apothecia; **5c–e**, **7b**. apothecia in median section; **9a**. hairs at margin; **5f–g**, **9c**. asci with spores (**5f–g** SBs stained in CRB); **8a**. paraphysis apices; **9b**. young paraphyses containing VBs; **8b**, **9d**. ascospores. – Living state, except for asci in **5f–g**. – **5a**: phot. M. Hairaud, **8a–b**: phot. E. Rubio, **9a–d**: phot. R. Tena. — **1**. H.B. 7567: France, Massif central, Rodez; **2**. H.B. 7500: Spain, Madrid, Rascafría; **3a–c**. H.B. 8145: France, Vienne, Ardriers; **4a–b**. H.B. 8814b: France, Deux-Sèvres, La Dame de Chambrille; **5a–g**. H.B. 8076a: ibid., Coudré; **6a–d**. H.B. 8172a: ibid., La Pommeraie; **7a–c**. H.B. 8132b: ibid., Marais Poitevin; **8a–b**. E.R.D. 5258, Spain, Pamplona; **9a–d**. Spain, Alicante; all on *Ulmus*.

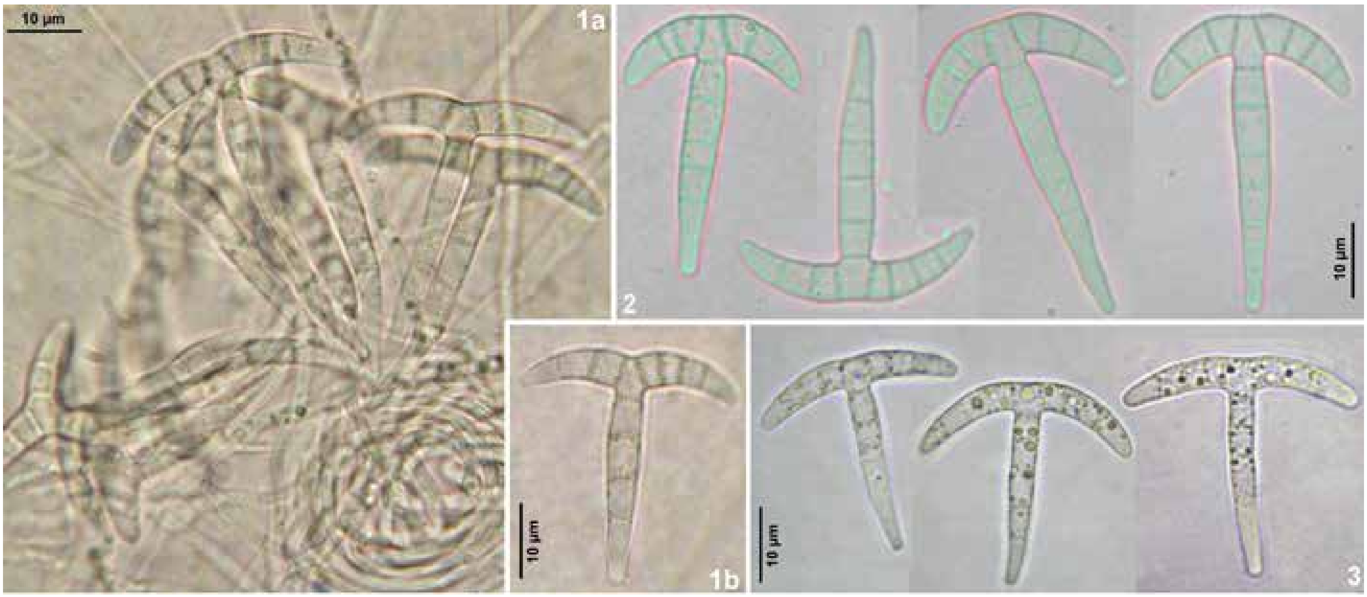


Plate 497. **1–3**: Conidia of *O. pilifera*. – **1a–b**. from pure culture (with coiled aerial hyphae); **2–3**. from natural substrate. – Living state. — **1a–b**. H.B. 8076a: France, Deux-Sèvres, Coudré; **2**. H.B. 7567: ibid., Massif central, Rodez; **3**. H.B. 8132b: ibid., Deux-Sèvres, Marais Poitevin.

Habitat: collected on the ground or more often in 0.2–2(–3.5) m above the ground, on ~3–25 cm thick trunks (or stumps), also on 12–40 mm thick branches, of ?*Populus* sp. {1}, *Ulmus* sp. {15/1}, *U. laevis* {3}, *U. minor* {12/5}, on rather large pieces of bark {36}, rarely on wood {2}, bark usually more or less detaching from standing, dead trunks, also firmly attached, sometimes fallen to ground, on inner surface, also on edges and in smaller number on outer surface (then in crevices of bark or small holes of periderm), medium to strongly decayed, regularly around and partly in old galleries of a bark beetle (*Scolytus* sp.), ungreyed, no algae, trees probably killed by the elm disease. **Associated**: *Anthostoma gastrinum* {1}, *Arthonia cinnabarina* {1}, *Ceratocystis ulmi* {1}, *Cistella chlorosticta* {2}, *Hyalorbilia juliae* {1}, *Lachnella* ?*villosa* {1}, *Lecophagus subglobosus* {2}, *Nectria cinnabarina* {1}, *N. pseudopeziza* {5}, *Opegrapha* sp. {1}, *Orbilia aurantiorubra* {5}, *O. auricolor* {1}, *O. ficicola* {1}, *O. gambelii* (on wood) {1}, *O. quaestiformis* (on wood) {1}, *O. xanthoguttulata* {2}, several crustose and foliose lichens (on exterior of bark, e.g., *Parmelia*, *Physcia*, *Xanthoria parietina*, *Lecanora*) and bryophytes (*Frullania* etc.). **Desiccation tolerance**: fully viable for at least 2.5 months, a few ascospores and many excipular cells survived for nearly 7.5 years, conidia at least 20 days. **Altitude**: 5–560 m a.s.l. (central and western Europe), 173–1135 m (southern Europe), 85–90 m (hemiboreal North America). **Geology**: Canada: Middle Ordovician sedimentary rock; Europe: Lower to Upper Jurassic clay & limestone, Cretaceous calcareous marl, Tertiary clay, partly with andesite and quartz. **Phenology**: (VIII–)X–V (long-lived).

Phenology of *O. pilifera*											
Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
4	2	8	6	6	0	0	1	0	2	2	6

Taxonomic remarks. *Orbilia pilifera* is characterized by rather large, ochraceous apothecia with prominent thin-walled, septate hairs without glassy caps, ellipsoid- to fusoid-clavate ascospores with broadly tear-shaped SBs, and a trinacrium incurvum-like anamorph.

O. pilifera resembles *O. carpoboloides* (section *Habrostictis*) which also often grows on bark of *Ulmus* and has similar lageniform-mammiform paraphyses, septate thin-walled hairs, a yellow exudate on the excipulum, and even a similar spore shape, though usually a more orange disc. *O. pilifera* sharply differs in its consistently subglobose to broadly tear-shaped SBs from the entire section *Habrostictis* which is characterized by vermiform, flexuous SBs. In the spores, *O. pilifera* also resemble some species of section *Ovoideae*. Moreover, *O. pilifera* could easily be mistaken for a *Lachnaceae* (*Helotiales*) if studied only in the dead state.

Since mycologists have rarely paid attention to spore bodies, *O. pilifera* may well have been recorded in the past under the name *O. carpoboloides* or any of its synonyms. Based on herbarium material the two species are in fact not easy to distinguish. Also the types of *O. decipiens* and *O. brasiliensis* (series *Habrostictis*) very closely approach *O. pilifera* in their persistent features, but differ in the ascospore having more tapered apices (see Pls 568–575). SB shape was hardly visible in the type of *O. brasiliensis*, therefore, the position of this taxon is somewhat uncertain. A similar uncertainty applies to some of the names mentioned as synonyms of *O. carpoboloides* (p. 1025). A taxon described under the name *O.* aff. *farnesianae* from China and Macaronesia (Pl. 501) differs from European *O. pilifera* in ± smooth apothecia and narrowly tear- to rod-shaped SBs (uncertain in the Chinese sample).

Variation. *O. pilifera* is a rather constant, easily recognizable species. Some variation concerns spore shape and size, but such diversity is generally seen within a single apothecium. The shape and size of the spore bodies was very uniform throughout the many fresh collections examined, with a large number of spores observed inside mature, living asci.

Misapplication. García Alonso (2003: 228, colour photo p.175) described *O. pilifera* under the name *O. luteorubella* on bark of 'probably *Genista patens*'. R. Tena (pers. comm.) reexamined this specimen and also a recent sample from the same locality, and confirmed identity with *O. pilifera*. The substrat turned out to be *Ulmus*.

Anamorph: With its trinacrium-like anamorph *O. pilifera* sharply differs from *O. carpoboloides* which forms phragmosporous conidia. *Trinacrium incurvum* fits quite well the present anamorph but also that of *O.* aff. *farnesianae* (Pl. 501) and several other taxa of this series.

Variation among populations of *O. pilifera* was observed in the depth of indentation between the two conidial arms above the central cell. Especially on the natural substrate this indentation was almost absent (Pl. 497: 2–3, partly in Pl. 495: 4), but also in the paratype of *T. incurvum* the indentation was partly only very slight. Conidia observed in Canadian specimens did not differ from European ones.

Phylogeny. Sequences were taken from apothecia of samples from Deux-Sèvres and Steiermark, comprising ITS, LSU D1–D2, and S1506 intron which is present in both. The two sequences differ by 4 nt in the intron, 3 nt in the ITS, and 1 nt in the LSU (that from France is incomplete in the intron and ITS1).

In the ITS region *O. pilifera* shows a distance of around 6.5–8.5 % to other members of the series, except for *O. bannaensis* which differs by 10–10.5 %. In the LSU (D1–D2) the distance is 1.5 % to *O. farnesianae* and 3 % to *O.* aff. *farnesianae*, *O. amarilla*, and *O.* cf. *paracaudata*. When analysing ITS+LSU, ITS, or LSU (Phyls 13, S15–S16), *O. pilifera* clustered unresolved in the series *Piliferae* clade.

Ecology. Judging from the available data, *O. pilifera* is a species of atlantic to subcontinental distribution, occurring in warm-temperate to mainly mesosubmediterranean (semi) humid western Europe and suprasubmediterranean to mainly supra- and mesomediterranean semihumid southern Europe, but also in cold-temperate southwestern and southern parts of Europe. It grows in riparian forests with *Fraxinus* and *Populus*, deciduous forest edges or hedge rows, or free-standing *Ulmus* trees. *O. pilifera* appears to be confined to ± rotten bark of *Ulmus* branches and trunks of usually dead trees. Collections were also made on *Ulmus* trunks in hemiboreal humid forests around Ottawa in southeastern Canada (J. Mack pers. comm.).

O. pilifera preferably inhabits large, ± rotten pieces of xeric bark detaching from standing, dead main trunks. The trees obviously die before the apothecia appear. The species usually occurs in great abundance, sometimes over a thousand of apothecia, on the inner surface of the often still-adhering bark, usually in or close to abundant galleries caused by a bark beetle (*Scolytus*), the vector agent of *Ceratocystis ulmi* which causes the elm disease. *O. pilifera* was also often found on corticated branches and in two collections on decorticated wood (Austria & Spain).

Specimens included. **AUSTRIA**: **Steiermark**, 8 km WNW of Bad Radkersburg, 4 km W of Halbenrain, SW of Unterpurkla, Donnersdorfer Au, 218 m, branch of *Ulmus laevis*, on bark, 24.I.2009, G. Friebes (G.F. 20090005, doc. vid.). – ibid., on wood, 12.XII.2009, G. Friebes (G.F. 20090146, doc. vid.). – ibid., trunk of *U. laevis*, on bark, 30.X.2011, G. Friebes (G.F. 20110193, non vid.; sq.: MK473413). — **FRANCE**: **Poitou-Charentes**, **Deux-Sèvres**, Poitou, 14 km WSW of Niort, 1.2 km NNE of Amuré, Marais Poitevin, Port Goron, 5 m, trunk of *Ulmus*, on bark, 15.IV.2008, J.P. Priou (ø). – 4.5 km NW of Chizé, 1.3 km SSE of Villiers-en-Bois, Forêt de Chizé, RBI-area, clearing, 72 m, branch of *Ulmus*, on bark, 27.IV.2011, P. Perz (P.P., doc. vid.). – 13.5 km N of Melle, 2 km SW of La Mothe-St.-Héray, La Dame de Chambrille, 103 m, branch of *Ulmus*, on bark, 17.IV.2008, H.O. Baral (H.B. 8814b). – 13 km ESE of Melle, Coudré, 158 m, trunk of *U.* (?)*minor*, on bark, 25.II.2006, B. Coué (M.H. 040206, J.P.P. 26051, H.B. 8076a, anam. cult., anam. substr.). – ibid., 25.X.2006, B. Coué (ø, non vid.). – trunk of *U.* (?)*minor*, on bark, 25.IV.2006, B. Coué (H.B. 8132b, anam. substr.). – 16 km ESE of Melle, 2 km ENE of Clussais-la-Pommeraie, E of Clussais, 130 m, trunk of *Ulmus*, on bark, 6.V.2006, B. Coué (H.B. 8172a, anam. substr.). – ibid., 5.XI.2006, B. Coué (H.B. 8362a; sq.: KY463697, KT222364). – 18.5 km ESE of Melle, 2 km N of Mairé l'Evescault, 135 m, trunk of *Ulmus*, on bark, 1.V.2006, B. Coué (H.B. 8170b). – 14 km SSE of Niort, Poivendre de Marigny, Impasse des Marronniers, 48 m, trunk of *U.* (?)*minor*, on bark, 28.XII.2011, M. Hairaud (M.H. 151211 ø, doc. vid.). – **Vienne**, 7 km NNE of Ruffec, 1.7 km SSE of Voulème, SE of La Boutrie, 115 m, trunk of *Ulmus*, on bark, 1.V.2006, B. Coué (ø, non vid.). – 6,5 km NW of Adriers, 1 km S of Nérignac, 0.3 km E of Les Aimardières (farm), 160 m, trunk of *Ulmus*, on bark, 19.III.2006, B. Coué (H.B. 8145). – **Charentes**, 18 km SE of Cognac, E of Bouteville, Bourg, 85 m, trunk of *Ulmus*, on bark, 5.III.2007, R. Lagarde, vid. P. Tanchaud (ø, doc. vid.). – **Midi-Pyrénées**, **Aveyron**, Massif central, 8 km ENE of Rodez, 0.5 km ENE of Canabols, 560 m, trunk of *U. minor*, on bark, 25.VIII.2004, G. Marson (H.B. 7567a, anam. substr.). — **SPAIN**: **Navarra**, 11 km NE of Pamplona, SSE of Sarasibar, NW of Idoi, 520 m, branch of *U. minor*, on bark, 1.III.2011, F. Julien, vid. E. Rubio (E.R.D. 5258, doc. vid.). – ibid., S of Idoi, Agra river bank, 490 m, branch of *Ulmus*, on bark, 2.XI.2016, F.J. Balda (anam. substr., doc. vid.). – **Castilla y León**, **Valladolid**, 20 km N of Tordesillas, San Pelayo, 773 m, trunk of *Ulmus*, on bark, 29.IV.2012, J.P. Priou (J.P.P. 12099, doc. vid.). – **Segovia**, 51 km NE of Segovia, ~1.5 km ENE of Sepúlveda, ~E of Santa Cruz, 920 m, trunk of *U. minor*, on bark, 23.II.2004, A. González, F. Prieto & G. Sastre (AH 7589, non vid.). – **Madrid**, 42 km NW of Madrid, 7 km NW of Collado Villalba, 1.3 km SE of Guadarrama, Guadarrama river, 935 m, on bark of *U. minor*, 15.V.2004, F. Prieto (AH 7645, non vid.). – 7.5 km S of Collado Villalba, 0.5 km W of Colmenarejo, Arroyo Peraleda, 850 m, trunk of *U. minor*, on bark, 7.XII.2001, F. Prieto (AH 7404, **isotype**; ex H.B. 7084, M-0276554, **holotype**). – ibid., 29.XII.2001, F. Prieto (AH 7408, non vid.). – ibid., 24.I.2002, F. Prieto (AH 7420, H.B. 7095a, anam. substr.). – ibid., 15.XII.2003, F. Prieto (AH 7585, H.B. 7463a). – 1 km SW of Colmenarejo, W of Fuente del Conejo, 832 m, trunk of *U. minor*, on bark, 20.I.2004, F. Prieto, A. González & G. Sastre (AH 7584, H.B. 7463b). – 14 km SW of Collado Villalba, 6 km SSE of San Lorenzo del Escorial, SW of Peralejo, 923 m, on bark of *U. minor*, 13.V.2004, F. Prieto & I. Otero (AH 7644, non vid.). – Sierra de Guadarrama, 20 km ESE of Segovia, 1 km S of Rascafría, 1135 m, trunk of *U. minor*, on bark & wood, 5.III.2004, A. González, F. Prieto & G. Sastre (AH 7590, H.B. 7500, anam. substr.). – 36 km NW of Madrid, 1.5 km W of Collado Villalba, 886, branch of *U. minor*, on bark, 16.III.2004, F. Prieto (AH 7591, non vid.). – **Extremadura**, **Cáceres**, 9 km SW of Guadalupe, N of Cañamero, bridge over Ruecas river, 620 m, stump of ?*Ulmus*, on bark, 6.III.1995, M. Lizárraga & R. Galán (AH 6953). – **Com. Valenciana**, **Alicante**, 43 km NNW of Alicante, 1 km SW of Banyeres de Mariola, Molí de l'Ombría, 705 m, branch of *Ulmus*, on bark, 20.III.2004, F. García Alonso, vid. R. Tena (F.G.A. 042607, as *O. luteorubella*, ?*Genista patens*, doc. vid.). – ibid., 17.III.2011, F. García Alonso (ø, doc. vid.). – **Cataluña**, **Barcelona**, 19 km NW of Barcelona, 5.5 km SSE of Terrassa, S of Les Fonts, 173 m, trunks of *U. minor*, on bark, 22.I.2015, J. Bometón (J.B. 594/15, doc. vid.). — **CANADA**: **Ontario**, 18.5 km ENE of Ottawa, 1 km SW of Notting Hill, Portobello Park, 90 m, trunk of *Ulmus*, on bark, 6.XII.2015, J. Mack (ø, anam. substr., doc. vid.). – ibid., 12.XII.2015 (doc. vid.). – 19 km ENE of Ottawa, Notting Hill, Lalande Park, 90 m, trunk of *Ulmus*, on bark, 6.IV.2014, J. Mack (anam. substr., doc. vid.). – 21 km ENE of Ottawa, 5 km N of Notting Hill, Meadow Lane Road, 85 m, trunk of *Ulmus*, on bark, V.2015, J. Mack (ø, anam. substr., non vid.).

Map 85. Known distribution of *O. pilifera* in Europe

Orbilia amarilla Quijada & H.O. Baral, Fungal Planet 853, in Crous et al., Persoonia 41: 238–417 (2018) — Pl. 498

Etymology: named after the orange apothecial colour, which coincides with the locality name Llanos de Amarilla.

Typification: Macaronesia, Tenerife, Montaña Amarilla, branch of *Euphorbia canariensis*, 16.XII.2012, L. Quijada & R. Castro (TFC Mic. 23767, holotype; sq.: MH221071).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.5–)0.8–1.8 mm in diam, up to 0.2 mm high (receptacle 0.17 mm), bright orange-yellow to vivid orange, non-translucent, round to slightly undulating, scattered to subgregarious; disc slightly concave to slightly convex, margin smooth, 0–8 µm protruding; broadly sessile, superficial. **Asci** *(49.5–)53–58(–61) × 4.5–5.5 µm, †(36.5–)39–46(–52) × 3.4–4.3 µm, cylindric-clavate, 8-spored, spores (obliquely) *2-seriate,

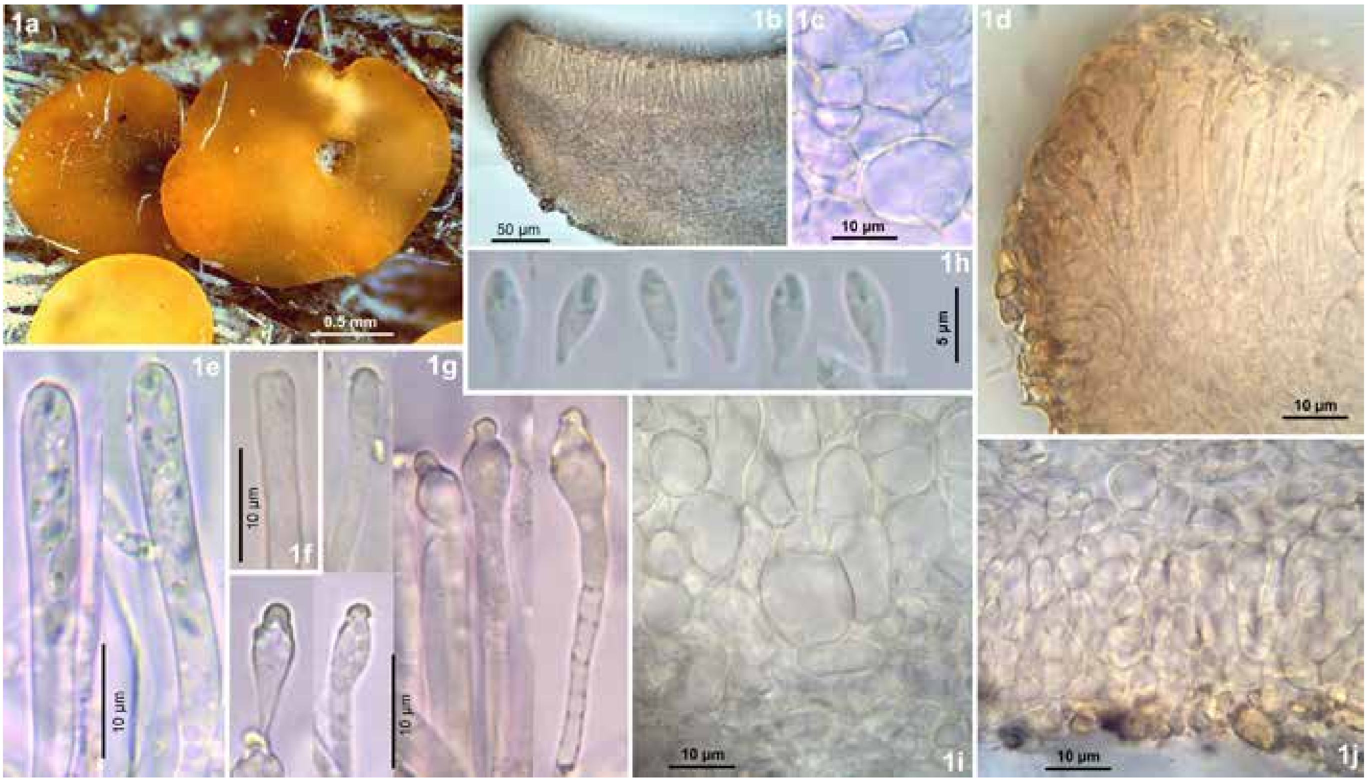


Plate 498. **1**: *Orbilia amarilla*. – **1a**. rehydrated apothecia; **1b**. apothecium in median section; **1d**. id., marginal ectal excipulum; **1i**. id., basal ectal excipulum, with anchoring hyphae; **1j**. id., at lower flanks **1c**. ring-shaped crystalloid SCBs in cells of ectal excipulum (flanks); **1e**. asci; **1f**. ascus apex (immature, dead state); **1g**. upper part of paraphyses; **1h**. ascospores. – Living state, except for **1f**. **— 1a–j**. phot. L. Quijada (p.p. from Quijada & Baral 2018), TFC Mic. 23767: Tenerife, on *Euphorbia*.

2–4(–6) lower spores inverted (usually mixed), pars sporifera *20–26 µm long; **apex** (†) strongly truncate (slightly indented, laterally hardly inflated); **base** with medium to long, thin, flexuous stalk, L- to Y-shaped. **Ascospores** *(5.8–)6.4–7.3(–8) × (1.9–)2–2.2(–2.4) µm, †4.3–6.8 × 1.6–2 µm, fusoid to fusiform-clavate, straight, apex obtuse to subacute, base with a straight to slightly curved tail of *0.7–1.8 × 0.5–0.9 µm, sometimes slightly to distinctly bulbous at base; **SBs** *1.7–2.1 × 0.6–0.8(–1) µm, plug- to rod-shaped with a slightly bulbous base, straight to slightly, rarely medium bent, apically slightly widened and broadly attached at spore apex, often obliquely oriented. **Paraphyses** apically slightly to very strongly spathulate to mammiform, terminal cell *(10–)14–19(–22) × 2.5–4.5 µm, apical beak 1.3–1.7 × 1.7–2.2 µm (including exudate), exceeding the living asci by up to 3–7 µm, lower cells *(9–)10–13.3(–14.7) × 1.5–2.3(–3) µm, unbranched at upper septum, hymenium pale orange. **Medullary excipulum** very pale orange, 120 µm thick in centre, of loose to dense textura intricata(-globulosa), at flanks sharply delimited from ectal excipulum (partly by an indistinct ~5–10 µm thick layer of t. porrecta). **Ectal excipulum** from base to mid flanks of thin-walled, t. globosa, at flanks and margin light yellow-orange, 50 µm thick at base, cells *(8–)11–20(–23) × (7–)10–15(–17) µm, 25–35 µm thick at flanks, of vertically oriented t. globulosa-angularis-prismatica, cells *3.5–8.5 × 3.5–7 µm, at margin of 17 µm thick t. prismatica-globulosa oriented at 80°, marginal cortical cells *4–9 × 3–5 µm. **Anchoring hyphae** 2.5–5 µm wide, thin-walled, forming a rather dense t. inricata-globulosa. **VBs** often abundant in terminal cells of paraphyses, ± globose, medium refractive, hyaline. **SCBs** line- or ring-shaped, in lower cells of paraphyses and in ectal excipulum at lower flanks. **Exudate** over paraphyses 0.5–1 µm thick, cloddy to cap-like, individually firmly attached on beak and also sublaterally (beak seemingly thick-walled), pale yellow, at margin and flanks 1–1.5 µm thick, yellow-brownish. **— ANAMORPH**: unknown.

Habitat: on superficially decayed, greyed wood of detached, branch of *Euphorbia canariensis* lying on the ground. **Associated**: *Orbilia asomatica*, *O. beltraniae*, *O. pisciformis*. **Desiccation tolerance**: examined a few days after collecting in dry state, but certainly highly tolerant. **Altitude**: 35 m a.s.l. **Geology**: volcanic basaltic flow. **Phenology**: XII (but long-lived).

Taxonomic remarks. *Orbilia amarilla* was only studied by L. Quijada (pers. comm.). It resembles *O. farnesianae*, from which it differs in shorter, fusoid-clavate, consistently tailed ascospores, also in having line- to ring-shaped crystalloid SCBs. From *O.* aff. *farnesianae*, which is only known in the dead state, it differs in distinctly smaller spores with shorter tails. In spore and SCB shape *O. amarilla* resembles *O. pisciformis* (series *Commatoideae*), which occurs in the same habitat, and in spore and SB shape it resembles *O. caudata*. These two species sharply differ, however, in having capitate paraphyses and partly glassy processes. *O. pilifera* and *O. pisciformis* differ in having tear-shaped, narrowly attached SBs.

Phylogeny. A sequence of *O. amarilla* comprising SSU, ITS, and LSU (S1506 intron absent) was taken from apothecia of the holotype. The species shows an ITS distance of 7–7.2 % to *O. farnesianae* and *O.* aff. *farnesianae* (1.3–1.5 % in LSU D1–D2) and 7.5 % to *O. pilifera* (3 % in LSU). When analysing ITS+LSU (Phyl. 13) it formed with them a strongly supported clade, while in the LSU (S16) only *O. amarilla* and *O.* aff. *farnesianae* form a supported clade.

Ecology. *O. amarilla* was collected on rotten wood of a detached, xeric branch of *Euphorbia canariensis* in an inframediterranean hyperarid *Ceropegio fuscae-Euphorbietum balsamiferae* xerophytic scrubland in the south of Tenerife.

Included specimen. **MACARONESIA**: **Canary Islands**, **Tenerife**, San Miguel de Abona, 4 km SSW of Las Chafiras, 1.5 km NE of Costa del Silencio, NNE of Montaña Amarilla, 35 m, branch of *Euphorbia canariensis*, on wood, 16.XII.2012, L. Quijada & R. Castro (TFC Mic. 23767, **holotype**; sq.: MH221071).

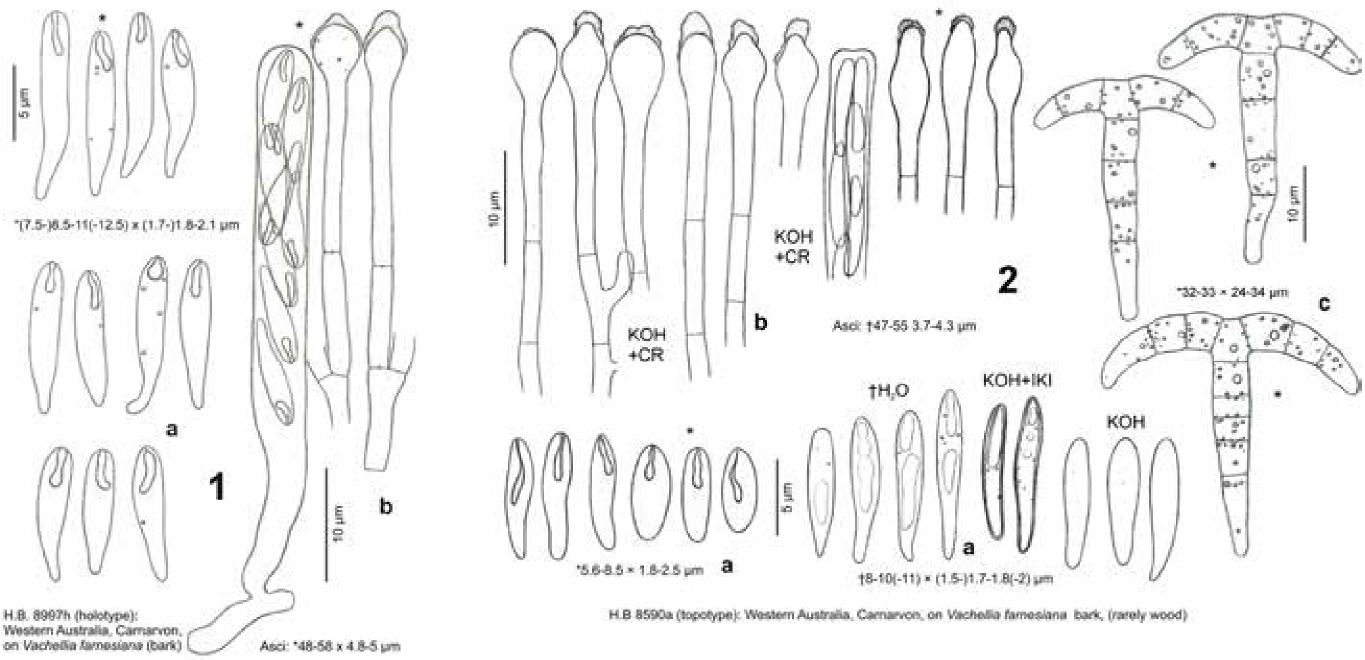


Plate 499. **1–2**: *Orbilia farnesianae*. – **a**. ascospores; **b**. asci and paraphyses; **c**. conidia (from substrate).

Orbilia farnesianae Baral, **sp. nov.**, MB 813774 **— Pl. 499–500**

Etymology: named after the host species, *Vachellia farnesiana*.

Typification: Western Australia, Minilya Roadhouse, branch of *Vachellia farnesiana*, 6.XI.2007, G. Marson (ex H.B. 8997h, MEL 2389271, holotype; sq.: KT222421).

Latin diagnosis: Orbiliae paracaudatae *similis sed ascosporae et corpuscula refringentia majores, corpuscula crystalloidea paraphysium et excipuli carentes. Habitat ad corticem putridum siccum* Vachelliae farnesianae *in zona subtropica arida Australiae septentrio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.3–)0.45–1(–1.3) mm diam., 0.11–0.17 mm high (receptacle 0.08–0.12 mm), light to bright, partly dirty orange-ochraceous (brick-red), ± translucent, round to elongate, partly rather irregular, scattered to gregarious in small groups; disc flat, margin thin or thick, 0–12 µm protruding, finely rough; broadly sessile, superficial or immersed in cracks. **Asci** *48–58 × 4.8–5 µm {T}, †40–55 × (3.7–)4–4.5(–5) µm {2}, 8-spored, spores (*) 2–3-seriate, 4–5 lower spores inverted (not mixed), pars sporifera *26–33 µm long; **apex** (†) strongly truncate (slightly indented, laterally slightly inflated), hemispherical in side view, thin-walled; **base** with short to medium long, ± thin, flexuous stalk, L-shaped. **Ascospores** *(5.5–)8–11(–12.5) × (1.7–)1.8–2(–2.5) µm {2}, †(7–)8–10(–11) × (1.4–)1.6–1.8(–2) µm {2}, cylindric- to fusoid-clavate, rarely ellipsoid, apex rounded to obtuse, base medium to strongly attenuated (often tail-like or rarely with a basally slightly bulbous tail), straight to slightly (rarely medium) curved at base; **SBs** *(2–)2.3–3.2(–4.2) × (0.4–)0.5–0.6(–0.8) µm {2}, ± rod-shaped or sometimes dumbbell-shaped or subulate, apically untapered or narrowed to a point, sometimes with a short filum, straight to medium flexuous, overmature tear-shaped, 1.5–1.8 × 1–1.2 µm. **Paraphyses** apically medium to strongly clavate to spathulate or lageniform, terminal cells *19–21 × 3–4 µm {T}, †15–21 × (2.5–)3.5–4.5(–5.5) µm {1}, lower cells *9–11 × 1.8–2.5 µm {T}, †7.5–10 × 1.5–1.8 µm {1}; rarely branched near upper septum. **Medullary excipulum** 20–50 µm thick, of ± loose or dense textura intricata, with many inflated cells, horizontally oriented, sharply delimited. **Ectal excipulum** very pale rose, of (†) thin-walled, vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks, 30–110 µm thick near base, cells *15–25(–30) × 10–18 µm {T}, †8–15 × 6–10 µm {1}; 20–25 µm thick at margin, of t. prismatica(-porrecta) oriented at a 30–90° angle to the surface, marginal cortical cells partly bent upwards to an angle of 10–20°, *8–12 × 4–5 µm {T}, †8–12 × 2.5–4 µm {2}; **glassy processes** absent {2}. **Anchoring hyphae** sparse to abundant, †2–3.5(–5) µm wide, walls 0.2 µm thick {2}, sometimes forming a 10–20 µm thick layer up to mid flanks. **SCBs** in paraphyses and ectal excipulum absent {T}. **Exudate** over paraphyses (0.3–)0.7–1.8 µm thick, hyaline to pale yellow-orange, forming individual, firmly attached caps, over margin and flanks 1–2(–3) µm thick, rough-cloddy. **— ANAMORPH**: trinacrium incurvum-like (presumed, from natural substrate {2}). **Conidiophores** not observed. **Conidia** T-shaped, the two arms ± bent downwards, *32–39 × 23–30(–34) µm, stipe *27–34 × 4.3–6.3 µm, 4–5(–6)-septate, arms *(10–)12–17 × 4.2–6.8 µm, 2–3-septate, distinctly bent downwards {2}.

Habitat: on corticated to partially decorticated, 4–15 mm thick branches of *Vachellia farnesiana* {2}, on 0.1–0.2 mm deep medium to very decayed, easily detaching bark (on bast or over splits in periderm) {2}, rarely on wood {1}, strongly greyed, no algae, often close to a black immersed ?pyrenomycete. **Associated**: *Hysterobrevium mori* {1}, *Orbilia corculispora* {2}, *O.* ?*myriella* {1}, *O. octocercocarpi* {1}, *O. pleioaustraliensis* {1}, *Patellaria* '*andina*' {1}, ?*Stictis* sp. {2}. **Desiccation tolerance**: ectal excipulum, some mature asci and paraphyses, and many spores viable after 20 months. **Altitude**: 13 m a.s.l. **Geology**: Cenozoic regolith (light brown soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia farnesianae* differs from *O. paracaudata* in wider ascospores and slightly longer SBs, also in the absence of crystalloid SCBs. From *O. mammifera* (section *Habrostictis*) the species differs in spores with obtuse to rounded apices and wider SBs, also in the paraphysis apices mostly lacking abrupt beaks. *O. farnesianae* also resembles *O. acaciae* and *O. dixiensis* (section *Habrostictis*), but also *O. rosella* (series *Abutilones*); from all these it differs in a clear tendency to spathulate paraphyses, also in larger apothecia.

Variation. When the topotype was still alive, it was only sketchily drawn, and much later it was restudied in more detail in the dead state. Only here, the paraphyses were sometimes found to be provided with a beak at the apex. The topotype further deviates from the holotype in somewhat larger apothecia, slightly wider paraphysis apices, and smaller basal excipular cells, but these features are quite variable. The spores of the topotype varied strongly in length and shape, and only some of them closely resemble those of

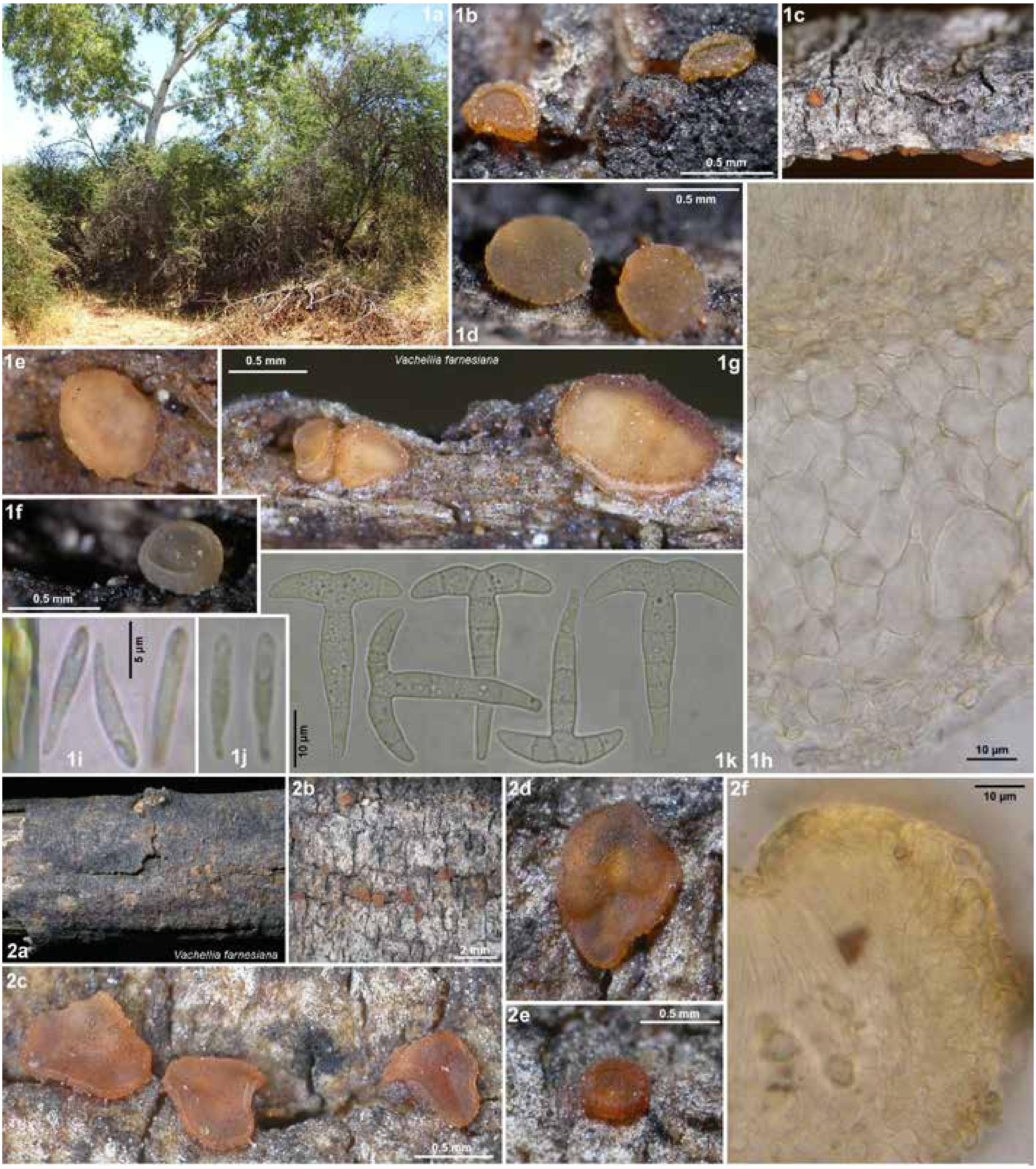


Plate 500. **1–2**: *Orbilia farnesianae*. – **1a**. subtropical arid acacia shrubland with *Eucalyptus* tree and *Vachellia* shrubs; **2a**. dead, corticated branch of *Vachellia*; **1b–g**, **2b–e**. rehydrated apothecia; **1h**. ectal excipulum in median section at flanks; **2d**. id., at margin; **1i–j**. ascospores; **1k**. conidia from substrate. – Living state, except for **1j** and **2f** (in KOH). — **1a–k**. H.B. 8997h (holotype): Western Australia, Carnarvon, Barrabiddy Creek, on *Vachellia farnesiana*; **2a–d**. H.B. 8590a: ibid., on *Vachellia farnesiana*.

the holotype. Also the SBs had a more consistent shape in the holotype. The observed rather short and wide ellipsoid spores are possibly abnormal, since such spores were no more seen during reexamination of the topotype.

Anamorph. The staurosporous trinacrium incurvum-like conidia were observed on the natural substrate near the apothecia in both collections (Pls 499: 2c; 500: 1k).

Phylogeny. A sequence comprising SSU, ITS, LSU (S1506 intron absent) was taken from apothecia of the holotype. In the ITS region it shows a distance of 4 % to *O.* aff. *farnesianae*, 7 % to *O. amarilla* and *O.* cf. *paracaudata*, and 9 % to *O. pilifera* and while in the LSU (D1–D2) the distance is 1.5 % to all of them.

Ecology. The two rather rich collections of *O. farnesianae* were on rotten xeric bark (rarely wood) of *Vachellia farnesiana* in a subtropical arid acacia shrubland 50 km from the coastline of western Australia. The first collection (topotype) was rather abundant. When revisiting the type locality 6 years later, only 1 branch of the very same shrub was found to carry apothecia referable to this species.

Specimens included. **AUSTRALIA**: **Western Australia**, Carnarvon, 117 km NNE of Carnarvon, 7 km SSE of Minilya Roadhouse, Barrabiddy Creek, 13 m, branches of *Vachellia farnesiana*, on bark & wood, 6.XII.2001, G. Marson (H.B. 8590a, anam. substr.). – ibid., branch of *Vachellia farnesiana*, on bark, 6.XI.2007, G. Marson (ex H.B. 8997h, MEL 2389271, **holotype**, anam. substr., sq.: KT222421).

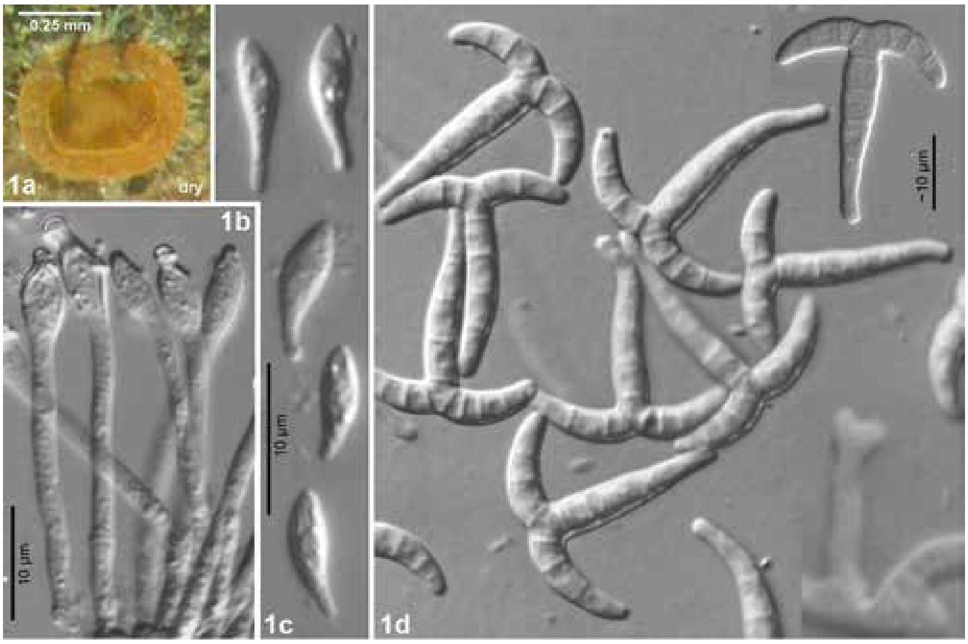


Plate 501. **1**: *Orbilia* aff. *farnesianae*. – **1a**. dry apothecium; **1b**. paraphyses; **1c**. ascospores; **1d**. conidia in pure culture. – Living state, except for **1b–c**. **— 1a–d**. from Liu (2006, fig. 17), HMAS 139700: China, Hunan, on indet. angiosperm.

Orbilia aff. *farnesianae* — Pl. 501

Misapplied name: Liu (2006: 59), Liu et al. (2006a), as *O. brasiliensis.*

Description: — **TELEOMORPH**: **Apothecia** 0.5–0.8 mm diam., round, orange to orange-red, translucent, scattered, sessile, margin ± smooth; dry with thick, protruding margin. **Asci** †38–49 × 3.5–5 µm, 8-spored, lower spores inverted; **apex** (†) truncate, hemispherical in side view, stalked, base h-shaped. **Ascospores** †(7.5–)8–10 × 2.3–3 µm, fusiform-clavate, apex subacute, base with a distinct, partly slightly constricted tail of 1.7–3 × 0.9–1.1 µm, straight to slightly curved; **SBs** ?broadly tear-shaped, †~1.5–2.3 × 0.8–1.2 µm. **Paraphyses** apically spathulate to mammiform, with a distinct beak, ~5–10 µm longer than asci, terminal cell †23–26 × 2.5–4 µm. **Ectal excipulum** of t. globulosa-angularis, at base 35–80 µm thick, at margin without any hairs or glassy processes. **— ANAMORPH**: trinacrium incurvum-like (from ascospore isolate). **Colonies** white to pale pink. **Conidiophores** branched or unbranched, 7–20 × 2.5–3 µm, conidia arising singly or sympodially. **Conidia** T-shaped, the two arms bent downwards, *26–31 × 22–31 µm {1}, stipe *22–26 × 4–5.5 µm, 4(–5)-septate, arms *7–15 × 3.5–5 µm, 2–4-septate; rarely unbranched conidia seen.

Habitat: on a xeric twig of an unidentified broad-leaved shrub. **Associated**: none observed. **Desiccation tolerance**: probably tolerant. **Altitude**: 600 m a.s.l. **Phenology**: IV (but presumably long-lived).

Taxonomic remarks. This species was studied by B. Liu (2006) and tentatively identified by him as *O. brasiliensis* (series *Habrostictis*, see also p. 1040), but it fits in series *Piliferae* because of its anamorph and molecular data. The apothecial margin is completely smooth similar as in *O. farnesianae* and *O. paracaudata*, from which it differs in broader, fusiform ascospores with subacute apices. Also from European *O. pilifera* it deviates in slightly larger spores with more subacute apices, besides the absence of hairs. The apothecia were studied in the dead state only, therefore, the SBs are hardly recognizable as broad, tear-shaped regions.

Anamorph. The trinacrium incurvum-like conidia obtained in pure culture match very well those of *O. pilifera*. Liu and Liu et al. (l.c.) referred to it as *Trinacrium incurvum*, but the identity of this anamorph remains unsettled (see also under *O. pilifera*, p. 920).

Phylogeny. A sequence of *O.* aff. *farnesianae* comprising S1506 intron, ITS, and LSU taken from pure culture by B. Liu shows an ITS distance of 4% to *O. farnesianae* as the closest match (1.5% in LSU), but 7% to *O. amarilla* and *O.* cf. *paracaudata* (1.3% and 2.2% in LSU D1–D2, respectively) and 9% to *O. pilifera* (3% in LSU). When analysing ITS+LSU or LSU (Phyls 13, S16), *O.* aff. *farnesianae* clustered with *O. amarilla* in a strongly supported clade, while in the intron region it clustered unresolved in section *Aurantiorubrae* (S14).

Another specimen identified by B. Liu as *O. brasiliensis* or *O. decipiens* (B.L. 4099, HMAS 139701), collected in the same area at the same day, clustered in analyses of ITS and LSU by Liu et al. (2006a) with high distance in a clade with the present taxon. However, the available members of section *Aurantiorubrae* were rather few in this study, and in our analyses it clustered distantly near *O. comma* (series *Commatoideae*, see p. 815).

Ecology. *O.* aff. *farnesianae* is from a subtropical humid, somewhat winter-dry mountainous area in southeastern China.

Included specimen. **CHINA**: **Hunan**, **Chenzhou**, 88 km S of Chenzhou, ~5 km ESE of Dashi Ling, Mangshan, 600 m, on unidentified angiosperm shrub, 7.IV.2002, W.Y. Zhuang, Y.H. Zhang & B. Liu (B.L. 4090, HMAS 139700, doc. vid., anam. cult.; sq.: DQ656643, DQ656688 [intron not uploaded]).

Orbilia paracaudata Baral & G. Marson, **sp**. **nov**., MB 813775 — Pls 502–503

Etymology: named after the similarity with *Orbilia caudata*.

Typification: Australia, Queensland, Mingela, branches of indet. climber, 17.X.1998, G. Marson (ex H.B. 6280d, BRI AQ799180, holotype).

Latin diagnosis: Orbiliae caudatae *similis sed ascosporae angustiores, subcylindricae, exsudatum crassius. Habitat ad corticem putridum rami sicci angiospermae volubilis in zona tropica subhumida Australiae septentrio-orientalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.4–1.1 mm diam., 0.14–0.18 mm high (receptacle 0.12 mm), scarcely translucent, round to often somewhat undulating to lobate, light orange, subgregarious; disc slightly concave to flat, margin distinctly raised, 10 µm protruding, finely rough; with an indistinct broad stipe, nearly superficial but emerging from cracks in periderm; dry ± deep (apricot-) orange. **Asci** *50–53 × 4–4.4 µm, †42–56 × 3.8–4.5 µm, 8-spored, spores (†) biseriate, 3–6 lower spores inverted, pars sporifera *30–34 µm long; **apex** (†) strongly truncate (slightly indented, laterally ± inflated); **base** with short to long, thin, flexuous stalk, L-shaped. **Ascospores** *5.8–8.5(–9.5) × (1.5–)1.6–1.8(–1.9) µm, narrowly ellipsoid to subcylindric, base with a distinct, thick, 1–3 µm long tail, also narrowly clavate with tail-like base, apex rounded to obtuse, slightly to medium curved near base; **SBs** *1.5–2(–2.2) × 0.5–0.7 µm, rod-shaped, partly slightly inflated

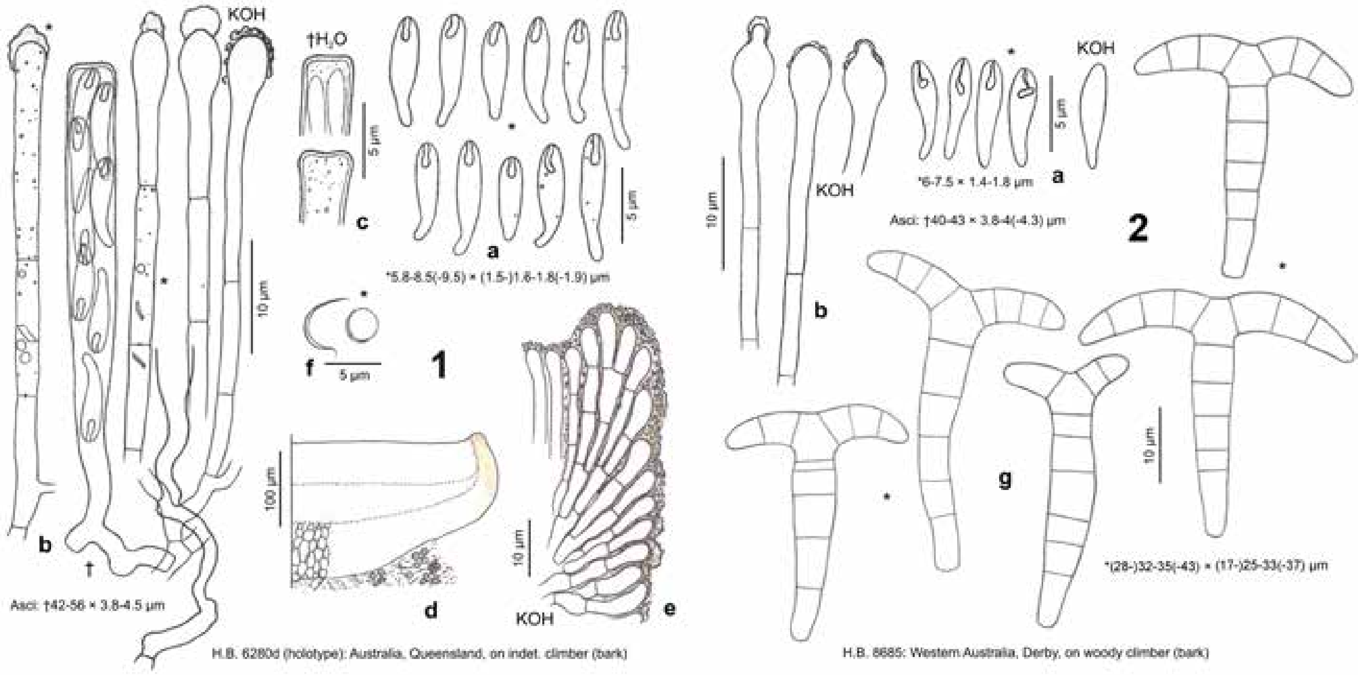


Plate 502. **1**: *Orbilia paracaudata*; **2**. *O.* cf. *paracaudata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. id., marginal ectal excipulum; **f**. crystalloid SCBs in cells of ectal excipulum at lower flanks; **g**. conidia from substrate.

at base (narrowly pyriform), apically untapered or narrowed to a ± wide point, straight to sometimes medium geniculate. **Paraphyses** apically slightly to medium clavate-spathulate, terminal cell *14–23 × 2.5–4 µm, lower cells *6–12 × 1.5–2.3 µm; hymenium pale yellowish. **Medullary excipulum** subhyaline (lower part pale orange), 30–50 µm thick, of dense textura angularis-intricata, horizontally oriented, sharply delimited. **Ectal excipulum** subhyaline, light orange near margin, of thin-walled, vertically oriented t. angularis(-prismatica) from base to mid flanks, 60–80 µm thick near base, cells *10–30 × 9–19 µm; 15–20 µm thick near margin, oriented at a 30–50° angle to the surface, marginal cortical cells †7–10 × 3–4(–5) µm; **glassy processes** absent. **Anchoring hyphae** abundant, *2–4 µm wide, walls 0.2–0.3 µm thick. **SCBs** in paraphyses and ectal excipulum forming thin rods or rings, also small globose SCBs in paraphyses. **Exudate** over paraphyses 1–3 µm thick, mostly forming firmly attached individual caps, pale yellowish-chlorinaceous; over margin and flanks 1–3 µm thick, granular, light orange-yellow. — **ANAMORPH**: trinacrium incurvum-like (presumed, from natural substrate). **Conidiophores** not seen. **Conidia** T-shaped, the two arms somewhat bent downwards, total size †25 × 21 µm, stipe †21 × 5 µm, 4-septate, arms †8–12 × 4 µm, 2-septate.

Habitat: collected 0.5–3 m above the ground, corticated to nearly decorticated, 9–13 mm thick branch of indet. climber, on medium to strongly decayed bark (periderm and bast), partly on clefts over old ?pyrenomycete, greyed, with green algae. **Associated**: *Corticiaceae*, *Hyalorbilia ?erythrostigma*, *Hysteropatella ?prostii*, *Orbilia mammifera*, *O. neocomma*, *O. scandens*, *O. subfabacearum*, *Rhytidhysteron ?rufulum*, some lichens. **Desiccation tolerance**: ectal excipulum still viable after 2 months, also some paraphyses and mature asci. **Altitude**: 286 m a.s.l. **Geology**: granite. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia paracaudata* differs from *O. caudata* in the ascospores being narrower and more cylindrical instead of ellipsoid, in thick glassy caps of exudate on the paraphyses, and in a distinctly protruding apothecial margin. For the similar *O. farnesianae* see p. 923. *O.* aff. *farnesianae* differs in mammiform paraphysis apices and fusoid spores. *O. paracaudata* resembles also some members of series *Commatoideae*, e.g., *O. comma*, which features the same type of crystalloid SCBs, or *O. mali* of series *Regales*, but the SBs in these series have an inflated, broadly tear-shaped lower part or appear almost globose, while their attachment is very narrow. The unrelated *O. subclavuliformis* (section *Hemiorbilia*) has similar but much larger spores and strongly deviates in hemispherical, thick-walled ascus apices.

Not included collection. The western Australian specimen (Pl. 502: 2) was only sketchily documented. Merely the spores were studied in the living state, therefore the presence of crystalloid SCBs is unknown. The paraphyses are sometimes provided with a beak at the apex (mammiform), and are covered by a thinner exudate compared to the holotype. The spores are slightly smaller than in the holotype and more fusoid-clavate, and the SBs with a thinner, narrowly attached upper part.

Anamorph. The observed conidia of *O. paracaudata* (Pl. 503: 1j) are similar to those of other members of series *Piliferae*. The conidia of the western Australian specimen (Pl. 502: 2g) have a (3–)4–5(–6)-septate stipe of *23–29(–32) × 5–6 µm, and consistently downwards curved, (1–)2–4-septate arms of *(7–)10–16 × 4.8–5.2 µm.

Phylogeny. A sequence comprising SSU, S1506 intron, ITS, and LSU, taken from apothecia of *O.* cf. *paracaudata* from western Australia, shows an ITS distance of 7% to *O. farnesianae* and *O.* aff. *farnesianae* (1.5% and 2.2% in the LSU D1–D2, respectively). In the intron the distance is generally above 20%.

Ecology. The type collection of *O. paracaudata* was made on ± rotten bark of dead, hanging, xeric branches of an unidentified climber in a tropical subhumid (winter-dry, savannah climate) eucalypt open woodland in a dry riverbed in northeastern Australia east of Great Dividing Range, ca. 75 km from the coastline. The not included *O.* cf. *paracaudata* was on xeric bark of a different unidentified climber on Devonian sedimentary rock in a tropical savannah-like eucalypt woodland in the broad riverbed of the Windjana Gorge 140 km from the coastline in northwestern Australia, flanked on the plateau by acacia shrubland and tussock grassland.

Plate 503. **1**: *Orbilia paracaudata*; **2**: *O.* cf. *paracaudata*. – **2a**. tropical semiarid acacia shrubland at slope above gorge; **1a–b**, **2b**. dead, xeric branch of indet. climber (dry, **1a** with apothecia); **1c–i**, **2c–g**. rehydrated apothecia; **1j**. conidium from substrate. – Living state, except for **1j** (in H_2O). — **1a–j**. H.B. 6280d (holotype): Australia, Queensland, Mingela, on indet. climber; **2a–g**. H.B. 8685: Western Australia, Derby, Windjana Gorge, on indet. climber.

Specimens included. **AUSTRALIA**: **Queensland**, Einasleigh Uplands, 75 km SSW of Townsville, 2 km WSW of Mingela, 286 m, branches of indet. climber, on bark, 17.X.1998, G. Marson (ex H.B. 6280d, BRI AQ799180, **holotype**, anam. substr.).

Not included. **Western Australia**, Dampierland, 140 km E of Derby, 108 km NW of Fitzroy Crossing, Windjana Gorge, 115 m, branch of indet. climber, on bark (partly on *Diatrypaceae*), 2.XII.2001, G. Marson (H.B. 8685; sq.: KT222422).

Orbilia floridensis Baral, **sp. nov.**, MB 813776 — Pl. 504–505

Etymology: named after the geographical origin (Florida, USA).

Typification: USA, Florida, Homestead, branch of *Ficus*, ~12.IX.1998, L. Ferron (ex H.B. 6241b, M-0276483, holotype**)**.

Latin diagnosis: Orbiliae paracaudatae *similis sed ascosporae angustiores, asci minores. Habitat ad corticem putridum siccum* Fici ?benjamini *in zona tropica humida Americae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3 mm diam., 0.15 mm thick, pale yellowish-rose-cream, round, scattered; disc slightly concave, margin distinct, 10–20 µm protruding, smooth; sessile, superficial. **Asci** *~3.6–4.2 µm wide, †33–35 × 3.3–3.8 µm, 8-spored, lower spores inverted; **apex** (†) medium to strongly truncate (sometimes slightly indented, laterally not inflated), hemispherical in side view, thin-walled; **base** with long, flexuous stalk. **Ascospores** *7–8.8 × 1.3–1.5 µm, narrowly cylindric- to fusoid-clavate, apex rounded to obtuse, base medium attenuated, with or without a thick tail, slightly to medium curved near base; **SBs** *1.2–1.8 × (0.3–)0.4–0.6 µm, tear-shaped to ampulliform or rod-shaped, apically untapered or narrowed to a point, ± straight. **Paraphyses** apically slightly clavate-capitate to spathulate, terminal cells †15–21 × 2–2.5 µm, lower cells †3–8 × 1.3–1.6 µm; unbranched at upper septum, hymenium pale yellowish.

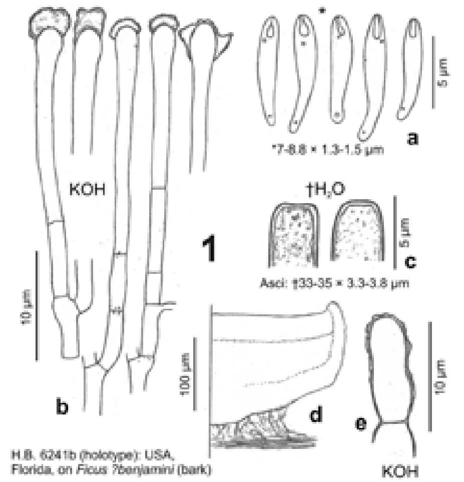


Plate 504. **1**: *Orbilia floridensis*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apices; **d**. apothecium in median section; **e**. hair-like cortical cell (lower flanks).

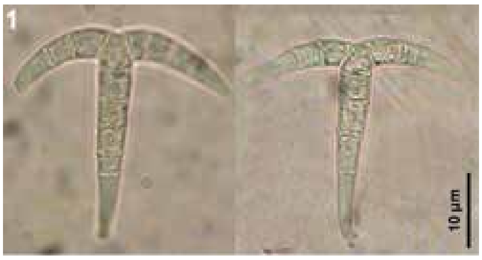


Plate 505. **1**: *Orbilia floridensis*. – Conidia from substrate (dead state). — **1**. H.B. 6241b (holotype): USA, Florida, on *Ficus*.

Medullary excipulum hyaline, 60 µm thick, medium sharply delimited. **Ectal excipulum** hyaline, of vertically oriented textura angularis from base to margin, 30 µm thick near base, cells *8–12 × 6–8 µm; 20 µm thick at flanks, 10 µm near margin, oriented at a 70–80° angle to the surface, cortical cells from lower flanks up to margin †9–11 × 3–4(–4.5) µm, sometimes ± free (hair-like); **glassy processes** absent. **Anchoring hyphae** abundant, *2–3 µm wide, walls 0.2–0.25 µm thick, forming a dense, 40 µm thick textura intricata-porrecta. **SCBs** in ectal excipulum not seen. **Exudate** over paraphyses 0.7–2 µm thick, pale golden yellow, cap-like, firmly attached on each paraphysis, over margin and flanks 0.2–0.4 µm, rough. **— ANAMORPH**: trinacrium incurvum-like (presumed, from natural substrate). **Conidiophores** not seen. **Conidia** T-shaped, the two arms bent downwards, total size †28–30 × 28–30 µm, stipe 23–25 × 4 µm, 4–5-septate, arms 12–14 × 3.5–3.8 µm, 3–4-septate.

Habitat: collected on hanging, mainly decorticated, 9 mm thick branch of *Ficus ?benjamini*, on strongly decayed bark (periderm). **Associated**: *Nectria* sp., *Orbilia neocomma*. **Desiccation tolerance**: after 2 weeks many immature asci still alive. **Altitude**: 1 m a.s.l. **Geology**: Quaternary sedimentary deposits. **Phenology**: IX (but probably long-lived).

Taxonomic remarks. *Orbilia floridensis* differs from the Australian *O. paracaudata* in distinctly narrower spores and smaller asci, also in smaller apothecia. Therefore, it is regarded to be a different species. For the differences to *O. bannaensis* see p. 831.

Anamorph. The trinacrium incurvum-like conidia (Pl. 505) found on the substrate are quite similar as in other species of this series.

Ecology. The collection was made on bark of a xeric branch of *Ficus* in the tropical humid, monsoon-influenced (winterdry) Everglades of Florida.

Specimens included. **USA**: **Florida**, southern part, 55 km SW of Miami, 12 km SW of Homestead, Everglades, ahead of entrance to national park, 1 m, branch of *Ficus ?benjamini*, on bark, ~12.IX.1998, L. Ferron (H.B. 6241b, M-0276483, **holotype**, anam. substr.).

Orbilia caudata Starbäck, Bih. K. Sven. Vetenskapsakad. Handl. 25: 8, pl. 1 figs 45–47 (1899) — Pls 506–507

Etymology: named after the ascospores provided with a tail.

Typification: Brazil, Rio Grande do Sul, near Cachoeira do Sul, branch of indet. angiosperm, 21.I.1893, G.A. Malme (Brasil. Regnell., I. Exped. Fungi No. 164, S-F41422, holotype).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.8(–1) mm diam., 0.08–0.14 mm high (receptacle 0.08–0.1 mm), pale to light cream-yellowish-orange to orange-red (Starbäck: brickred-orange), ± translucent, round to slightly undulating when large, scattered or usually (sub)gregarious; disc slightly concave to slightly convex, margin distinct, thin, slightly raised, 0–5 µm protruding, smooth or sometimes finely crenulate; broadly sessile but only centrally attached, superficial; in dry state a subiculum visible as white strands around some apothecia. **Asci** †32–44 {2} or 45–53 {T} × 3.5–4.2 µm {3}, 8-spored, spores †(sub)biseriate, (2–)3–6(–7) lower spores inverted {3} (sometimes mixed); **apex** (†) (medium to) strongly truncate (sometimes slightly indented and laterally inflated); **base** with short or mostly medium to very long, thin, flexuous stalk, Y- to L-shaped. **Ascospores** *5–7.8 × 1.9–2.3 µm {2}, †(4.5–)5–6.5(–7.5) × (1.7–)1.8–2(–2.2) µm {3}, ellipsoid-fusoid with a distinct tail, sometimes fusoid-clavate with a tail-like base, apex obtuse, tail *1–1.5 × 0.4–0.8 µm {1}, †1–2.3 × 0.4–0.6(–0.7) µm {2}, rarely with a slight basal inflation, straight or slightly (to medium) curved at base; **SBs** *(1–)1.4–1.8(–2) × 0.5–0.7(–0.9) µm {2}, rod-shaped to ± pyriform or tear-shaped to ampulliform, rarely ellipsoid, apically narrowed to a wide or narrow point, straight. **Paraphyses** apically medium to strongly capitate(-clavate), terminal cell †12–21 × 2.5–4.5 µm {3}, lower cells †4.3–9.5(–11) × (1.2–)1.4–1.8(–2.5) µm {3}; unbranched at upper septum. **Medullary excipulum** 20–30 µm thick, of dense textura intricata(-prismatica) with some or many inflated cells, medium to sharply delimited from ectal excipulum by a layer of t. porrecta. **Ectal excipulum** of thin-walled, ± vertically oriented t. globulosa-angularis(-prismatica) from base to mid flanks or margin, 15–60 µm thick near base, cells †(6–)7–13(–17) × 5–10 µm {2} or †10–24 × 9.5–16 µm {T}; 15–40 µm thick at flanks, 15–20 µm near margin, of t. prismatica(-angularis) oriented at a 50–90° angle to the surface, marginal cortical cells †4.5–10 × (2.5–)3.5–4.5(–5) µm {3}; **glassy processes** absent {2} or 6–10 × 2.5–3 µm {1}, low-refractive, stratified, outwards curved. **Anchoring hyphae** medium to very abundant, †1.5–2.5(–3) µm wide, walls 0.2(–0.3) µm thick {3}, sometimes forming a 10–20 µm thick t. porrecta at base and lower flanks, agglutinated by gel. **SCBs**: no data available. **Exudate** granular(-cloddy), over paraphyses 0.2–0.5(–1) µm thick, firmly attached, pale chlorinaceous-yellowish; over margin and flanks 0.2–1(–1.3) µm thick. **— ANAMORPH**: trinacrium incurvum-like (presumed, from natural substrate {1}). **Conidiophores** not seen. **Conidia** T-shaped, the two arms somewhat bent downwards, total size †38–42 × 40–49 µm, stipe †32–35 × 5–5.5 µm, 6-septate, arms tapering, †16–25 × 4.2–5 µm, 4–5-septate {1}.

Habitat: on moist ground or hanging in 1.5 m above the ground, corticated, 4–12 mm thick twigs and branches of indet. angiosperm trees {2}, on strongly decayed bark {2} (periderm {T} or bast {1}), on herbaceous, 2–3 mm thick stems of indet. climber {1}, on medium decayed epidermis or often on epidermis-free areas {1}, slightly greyed, no algae observed. **Associated**: ?*Peroneutypa scoparia* {1}, old black ?pyrenomycete. **Desiccation tolerance**: not tested, a few spores still alive after 8 months {Taiwan}. **Altitude**: ~100–1890 m a.s.l. **Phenology**: V–VI (N-hemisphere, but possibly long-lived).

Taxonomic remarks. *Orbilia caudata* is characterized by ellipsoid-fusoid ascospores provided with a short, ± distinct tail, and by rod-shaped to somewhat ampulliform SBs. For the similar *O. ovalis* (section *Lentiformes*), *O. mali* (series *Regales*), and *O. paracaudata* see there. *O. pisciformis* from Macaronesia (series *Commatoideae*, Pls 419–420) and a not included collection from Pakistan (Pl. 506: 4) have similar ascospores and possess short glassy processes at the margin. *O. pisciformis* closely resembles *O. caudata* in the distinct spore tails, but differs in much longer spores.

Variation. The collection from Taiwan (Pl. 506: 1) differs from the other two specimens in slightly longer spores and SBs. The holotype from Brazil (Pl. 506: 2) deviates from the two Asian collections in distinctly longer asci, a thicker ectal excipulum, and larger basal excipular cells. The Chinese collection (Pl. 506: 3) was presented in Zhang et al. (2009b). It differs from the other two in rather small and thin apothecia, and particularly in the presence of short glassy processes which are responsible for the crenulate margin. For the time being, all these differences are thought to lie within the scope of variation of *O. caudata*.

Type studies. The rather detailed original description by Starbäck (1899), repeated by Saccardo & Sydow (1902:

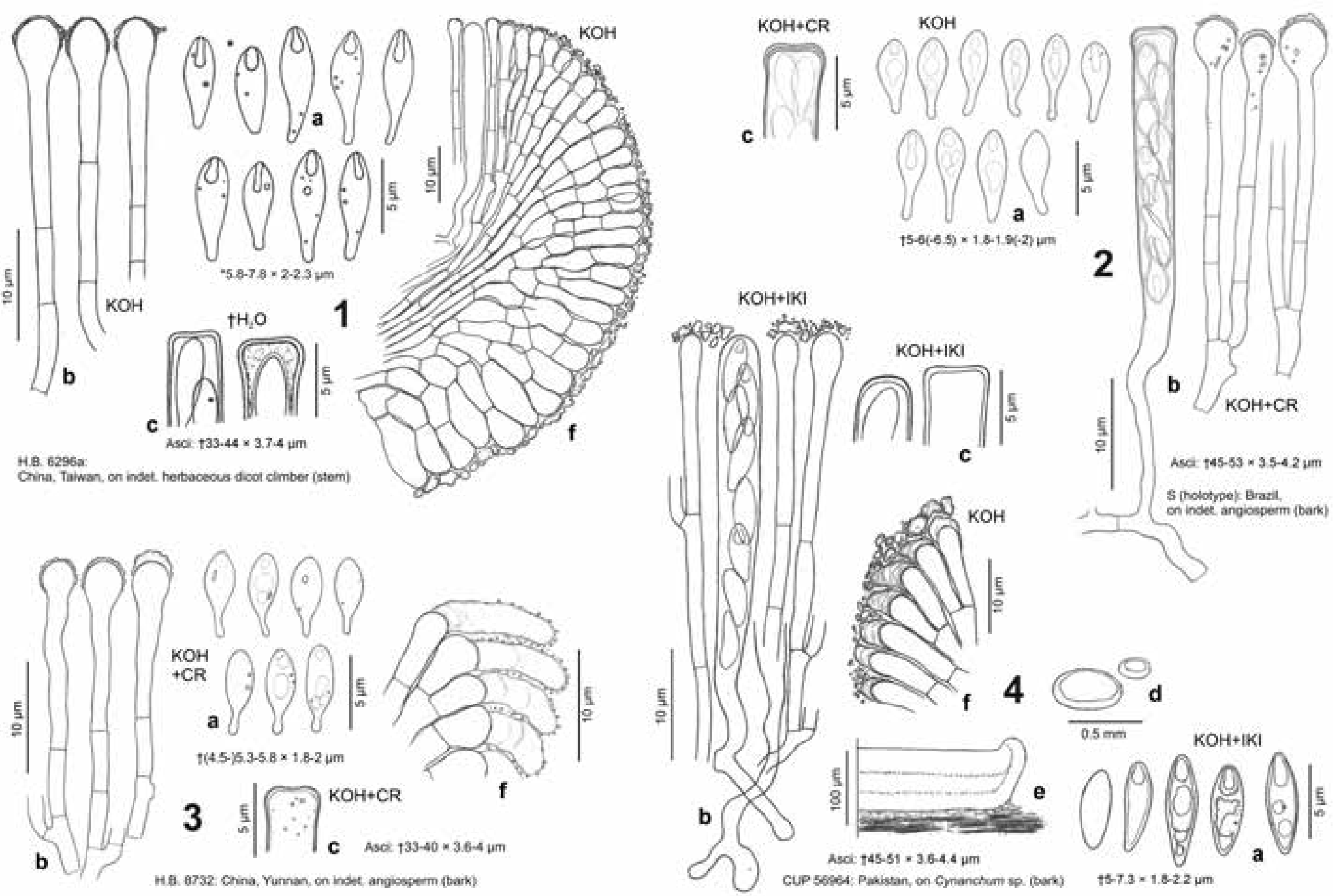


Plate 506. **1–3**: *Orbilia caudata*; **4**. *O.* aff. *caudata*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apices; **d**. rehydrated apothecia; **e**. apothecium in median section; **f**. id., ectal excipulum at margin and mid flanks.

768) and Rick (1932), fits well the microscopic features here evaluated from the well-preserved holotype in S. Two details in the protologue should be correct: the ascus tips are reported as very faintly amyloid, and all spores within the asci are depicted as pointing with their tails towards the ascus base. Starbäck gave the spore size as 5–6.5 × 1.5–2 µm, and described the tails as filiform, 0.5–1 µm wide, curved, acute (but he figured straight tails). The paraphyses are reported as abruptly inflated to a 4.5–6 µm wide, globose to obconical apex. Based on a similar spore shape, Starbäck compared *O. caudata* with *O. occulta*.

Not included collections. A sparse, partly immature sample from Ethiopia on stems of *Solanecio gigas* (IVV: H.B. 9240b) differs mainly in curved (comma-shaped) spore tails. It was only studied in the dead state and possibly represents an undescribed species. Vermispora-like conidia were observed on the substrate. Whether it is related to *O. caudata* or perhaps to *O. comma* remains uncertain. A collection from Northern Thailand on ?herbaceous stem referred by Ekanayaka et al. (2018) to *O. caudata* shows a very variable spore shape which only partly resembles the holotype, or the collection from China with which it was compared by the authors. The spores are given much longer and also partly narrower (*/†7–9 × 1.4–2 µm) than here described for *O. caudata*. The yellow-orange apothecia are up to 1 mm diam. according to the scale (0.2–0.7 mm in description). In the collection from Pakistan (Pl. 506: 4) the fusoid spores are consistently without tails. The spore body region suggests a relationship to series *Ovales*, but the elongate spores exclude *O. ovalis* and better fit the specimen from Taiwan (Pl. 506: 1).

Anamorph. The T-shaped trinacrium-like conidia found on the substrate of H.B. 6296a resemble those of *Trinacrium incurvum*, but have longer arms similar as in the other species of the series (Pl. 507: 2d).

Phylogeny. Sequences were only available for the not included sample from Thailand, comprising ITS and LSU. It falls in series *Regales* and here to *O. brachychitonis* with an 8.5 % ITS distance (1.2 % in LSU D1–D2), with which it forms a supported clade (Phyls 13, S16). Also a motif in the LSU (pos. 239–245, TT**TC**A**AT**) supports placement in this series (Tab. 68). This result suggests that it is probably not conspecific with the present concept of *O. caudata*.

Ecology. *O. caudata* was collected on rotten bark of hygric and xeric twigs and branches of unidentified angiosperm trees, also on herbaceous stems of a climber. The holotype locality is a subtropical humid lowland rainforest area at the Rio Grande river in southern Brazil, and the other two are in a subtropical humid (winterdry) monsoon rainforest in the Yunnan-Guizhou high plateau of southern China, and in a similar but tropical lowland rainforest at the southernmost end of Taiwan. In the Taiwan collection the substrate was hanging in 1.5 m above the ground. The apothecia of this population probably show some tolerance to drying, though growing under a rather high atmospheric humidity. The not included sample on *Cynanchum* is from a subtropical semiarid lowland floodplain of the Indus river, that on *Solanecio* from a warm-temperate humid, evergreen afromontane forest in the Ethiopian highlands, and that on indet. ?herbaceous plant in tropical humid (wet and dry) lowland of northern Thailand.

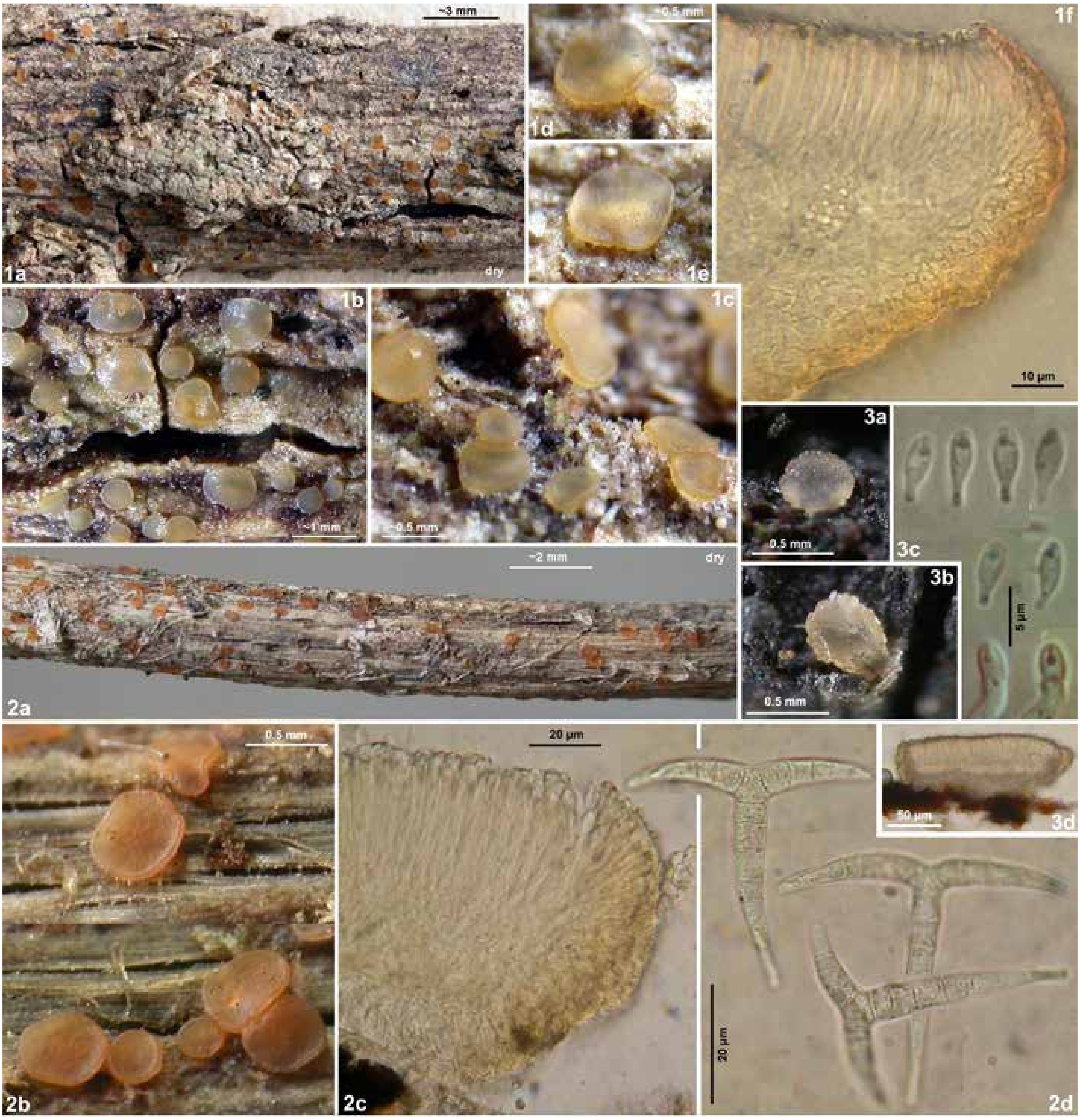


Plate 507. **1–3**: *Orbilia caudata*. – **1a**, **2a**. corticated, ?hygric branch and xeric herbaceous stem of angiosperms with dry apothecia; **1b–e**, **2b**, **3a–b**. rehydrated apothecia; **3d**. apothecium in median section; **1f**, **2c**. id., marginal region; **3c**. ascospores; **2d**. conidia from substrate. – Dead state (**2c–d** in water; **1f**, **2c** in KOH), except for **3c**. – **3c**: from Zhang et al. (2009b). — **1a–f**. S-F41422 (holotype): Brazil, Rio Grande do Sul, on indet. woody angiosperm; **2a–d**. H.B. 6296a: China, Taiwan, on indet. herbaceous dicot climber; **3a–d**. YMFT 033: China, Yunnan, on indet. woody angiosperm.

Specimens included. **BRAZIL**: **Rio Grande do Sul**, 200 km WNW of Porto Alegre, ~55 km NNW of Cachoeira do Sul, Colônia Santo Ângelo (now Agudo), ~100 m, branch of indet. angiosperm, on bark, 21.I.1893, G.A. Malme (Brasil. Regnell., I. Exped. Fungi No. 164, S-F41422, **holotype**, H.B. 7681,ø). — **CHINA**: **Yunnan**, **Yuxi**, Yimen, Central Highlands, 75 km SW of Kunming, 53 km NW of Yuxi, Longkou Forest Park, 1890 m, twig of indet. angiosperm, on bark, 27.VI.2006, Z.F. Yu (YMFT 033, H.B. 8732). – **Taiwan**, **Pingtung**, 70 km SSE of Pingtung, 9 km ESE of Hengchun, Kenting Botanical Garden, 300 m, stem of indet. herbaceous dicot climber, 25.V.1998, F. Oberwinkler & C.J. Chen (F.O. 47270, H.B. 6296a, anam. substr.).

Not included. **PAKISTAN**: **Punjab**, Indus River Plain, Lahore, ~220 m, ?woody stem of *Cynanchum*, on bark, 3.I.1954, collector unknown [?S. Ahmad] (Fungi of West Pakistan 9012, CUP-056964, as *Orbilia* sp., H.B. 5862 ø). — **ETHIOPIA**: **Oromia**, 22 km WSW of Addis Ababa, 10 km NW of Sebeta, southern part of Menagesha Suba State Forest, 2520 m, stem of *Solanecio gigas*, 22.XII.2009, U. Lindemann (U.L. 1209-7 ø, H.B. 9240b). — **THAILAND**: **Northern Thailand**, **Chiang Rai**, 16 km NNE of Chiang Rai, Mae Fah Luang University, 460 m, stem of herbaceous plant (?, as 'wood'), 18.III.2015, A.H. Ekanayaka (dh018, MFLU 16-0580; sq.: MG599271, MG599274).

Orbilia bannaensis Ying Zhang, Z.F. Yu & K.Q. Zhang in Zhang et al., Cryptog. Mycol. 27(4): 290 (2006) — Pls 508–509

Etymology: named after the geographical origin (Xishuangbanna County, Yunnan Province).

Typification: China, Yunnan, Menglunzhen, branch of *Broussonetia*, 20.VII.2004, Z.F. Yu (Z.F.Y. xsbn-1, OT003, YMFT, holotype; sq.: DQ512888).

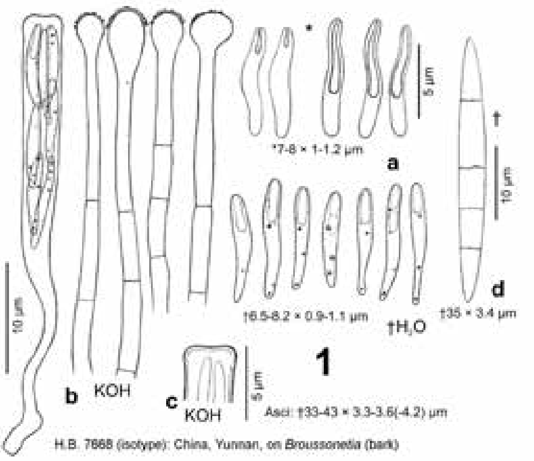


Plate 508. **1**: *Orbilia bannaensis* (from holotype). – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apex; **d**. conidium (from substrate).

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.6 mm diam., 0.15–0.16 mm thick, light orange(-rose), medium translucent, round or slightly undulating, often gregarious; disc flat (to slightly convex), margin thick, hardly protruding, smooth; sessile on a ± broad base, superficial. **Asci** *~36–46 × 4.5–5 µm, †31–43 × 3.3–4.5 µm, 8-spored, spores *3–4-seriate, ~4 lower spores inverted (?somewhat mixed); **apex** (†) truncate (sometimes slightly indented and laterally inflated); **base** with short to long, thin or thick, flexuous stalk, L- to Y-shaped. **Ascospores** *7–8.5 × 1–1.3 µm, †6.5–8.2 × 0.9–1.1 µm, narrowly subcylindrical to mostly cylindric-clavate (to fusoid-clavate), apex rounded to obtuse, base slightly to medium attenuated, with or without a tail, slightly inequilateral to ± distinctly curved (helicoid); **SBs** *1.5–2.3 × 0.5–0.8 µm, ellipsoid or tear- to rod-shaped, apically narrowed to small point attached to the wider spore end [or *5–5.3 × 0.6–0.7 µm, subulate, flexuous, attached to the narrower end]. **Paraphyses** apically slightly to strongly clavate-capitate, terminal cells †(11–)15–18 × 2.5–4(–4.3) µm, lower cells †5–9 × 1.3–1.7 µm, unbranched at upper septum. **Medullary excipulum** 15–40 µm thick, of dense textura intricata with some slightly inflated cells, medium sharply delimited. **Ectal excipulum** of (†) thin-walled to slightly gelatinized, indistinctly oriented t. globulosa-angularis from base to margin, 50–60 µm thick near base, cells †10–15 × 8–12 µm diam.; 15–20 µm thick near margin, oriented at a 45–70° angle to the surface, marginal cortical cells †8–10 × 4–5 µm; **glassy processes** absent. **Anchoring hyphae** abundant, †1.7–2.5(–3) µm wide, wall 0.1–0.2 µm thick. **SCBs** and **VBs**: no data available. **Exudate** over paraphyses 0.2–0.3 µm thick, over margin 0.2–0.5 µm, granular to continuous, light yellowish-orange. — **ANAMORPH**: unknown (but see below).

Habitat: on a pile of logs near a house, medium decayed bark of *Broussonetia* sp., on outer surface of detached periderm, greyed, without algae. **Associated**: none observed. **Desiccation tolerance**: unknown, but some spores still viable after 6 months. **Altitude**: 1400 m a.s.l. **Geology**: Jurassic sedimentary rock. **Phenology**: VII.

Taxonomic remarks. *Orbilia bannaensis* shows some similarities with series *Helicoon*. Because of its rather short SBs it resembles especially *O. yuanensis*, a species that differs in somewhat shorter and wider, more straight spores and in more whitish to yellow-cream apothecia. The contents of the dead paraphyses and cortical excipular cells in *O. bannaensis* show a light yellow-orange colour, therefore, the living cells might have contained hyaline or yellowish VBs similar as in *O. yuanensis*. However, our phylogenetic analysis showed that *O. bannaensis* is excluded from section *Helicoon* (see below).

Also *O. rectispora*, *O. cardui* and some further taxa of section *Arthrobotrys* have very similar spores but deviate in more globose SBs and are obviously not closely related. Zhang et al. (2006) compared with *O. bannaensis* another member of section *Arthrobotrys*, *O. quercus*, which differs in shorter spores and more roundish SBs, and whitish to pale yellowish apothecia. However, this species clustered very distantly in their phylogenetic tree. Also *O. ellipsospora* has very similar though distinctly smaller spores (4.5–7 × 1–1.2 µm). Like *O. quercus*, this species forms a dactylellina-like anamorph in pure culture. *O. kingsiana* was compared by Zhang et al. 2006 (as '*O. regalis* aff.') with *O. bannaensis*, but differs in spores with more curved bases and more globose SBs. It is affiliated here in series *Regales* although it lacks glassy processes.

Within series *Piliferae O. floridensis* is morphologically close to *O. bannaensis*. It has similar but somewhat wider spores with similar SBs, but differs in cap-like exudate over the paraphyses.

Variation. When a part of the type collection of *O. bannaensis* was studied in Jan. 2005, a few spores were still viable and contained mainly very long SBs (Pl. 508: 1a, above), also the spores were more distinctly curved (helicoid), and they were tapered above rather than below. Another apothecium was examined more than 3 years later: the dead spores were less curved and had ± tapered bases, and the region of the SBs was much shorter (1a, below). This better corresponds to the photos of living spores in the protologue, though the SBs were here still longer (2.2–3.3 µm) than in the protologue (1.5–2 µm). Spore size was given in the protologue as *7.5–9.5 × 1.5–1.8 µm. However, from the scale on the photo plate a spore size of *7.5–8.5 × 1.1–1.3 µm can be evaluated which is obviously more correct. Also the SBs are a bit narrower (~0.8 µm as a maximum) than indicated in the protologue (0.5–1 µm).

Although the observations by Zhang et al. (2006) are said to be based on living elements (asci, paraphyses, ascospores) in a tap water mount of a fresh specimen, a majority of their figures

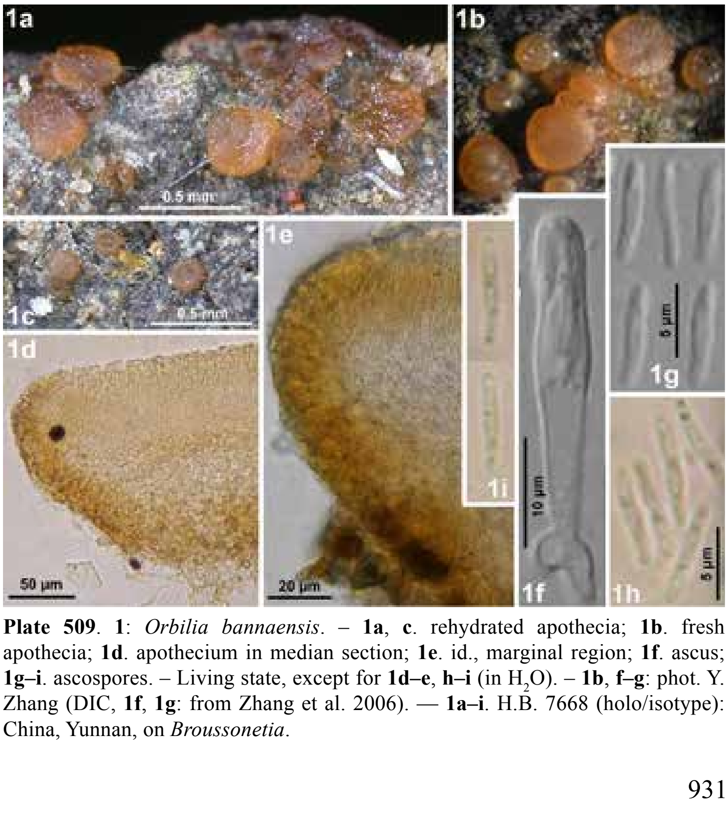


Plate 509. **1**: *Orbilia bannaensis*. – **1a**, **c**. rehydrated apothecia; **1b**. fresh apothecia; **1d**. apothecium in median section; **1e**. id., marginal region; **1f**. ascus; **1g–i**. ascospores. – Living state, except for **1d–e**, **h–i** (in H_2O). – **1b**, **f–g**: phot. Y. Zhang (DIC, **1f**, **1g**: from Zhang et al. 2006). — **1a–i**. H.B. 7668 (holo/isotype): China, Yunnan, on *Broussonetia*.

refer to dead cells, except for the spores (Pl. 509: 1g) and one of the asci (1f).

Not included collections. An unidentified species of *Orbilia*, here referred to as *O.* aff. *bannaensis*, was reported by Guo et al. (2013) from three localities in China. Regrettably, the authors described only its anamorph (see below). According to an unpublished plate of the teleomorph (see IVV), it differs from *O. bannaensis* in apically less inflated paraphyses and in shorter ascospores (*5.8–6.3 × 1.2–1.3 µm) without a tail-like base; the broadly cylindrical spore bodies measure 1.2–1.5 × 0.7–0.8 µm (both evaluated from scale).

A collection from Guizhou examined and cultured by M. Mo (pers. comm.) resembles *O. bannaensis* because of similar ascospores and conidia, but appears to belong near *O. rosea* (Pl. 533).

Anamorph. Zhang et al. (2006) did not obtain a culture of *O. bannaensis*. A single 4-septate conidium was found by us close to the apothecia in the isotype (Pl. 508: 1d), which resembles the dactylella-like conidia of *O.* cf. *rosea* obtained by M. Mo in pure culture (Pl. 533: 1e–f). In a Chinese collection of *O. rosea* from Henan a similar anamorph developed in pure culture, but its conidia are shorter and appear to represent microconidia of *O. rosea* (see Pl. 532).

Guo et al. (2013) reported under the name *Trinacrium incurvum* an anamorph (IVV: jhs-40) gained from an ascospore isolate of one of the three collections which we here identify as *O.* aff. *bannaensis*. The anamorph was believed by the authors to be the first record of a *Trinacrium* within China. Its conidia have about the same size and shape as those of *O.* aff. *farnesianae* in Liu (2006, as *O. brasiliensis*). No sequence was available of this isolate (J.W. Guo pers. comm.). Guo et al.'s observation raises the questions whether *O. bannaensis* might also possess a trinacrium incurvum-like anamorph.

Phylogeny. A sequence of the ITS region was gained from apothecia of *O. bannaensis* by Zhang et al. (2006). The S1506 intron is absent. In their phylogenetic analysis the species clustered with *O. sinensis* (as *O. luteorubella* and *O. vinosa*) in a clade. However, members of section *Aurantiorubrae* were not available for comparison at that time. In our analysis of ITS (Phyl. S15) it clustered in the strongly supported clade of series *Piliferae*, whereas a relation to section *Helicoon* was not confirmed. The distance in the entire ITS region is 8–12% to other members of series *Piliferae*, the lowest to *O.* cf. *paracaudata*, but ~20–22% to those of section *Helicoon*. The alignment of the ITS1 and ITS2 region actually shows great divergences between section *Helicoon* and *O. bannaensis*. Regrettably, Guo's isolates of *O.* aff. *bannaensis* were not investigated by molecular methods.

Ecology. *O. bannaensis* was found on rotten periderm of a semihygric log of *Broussonetia* (*Moraceae*) in a subtropical (almost tropical) humid (winter-dry, monsoon-influenced) rainforest in southernmost China. The three samples of *O.* aff. *bannaensis* Guo et al. (2013) originate from similar but subtropical forests in eastern and southern China.

Specimens included. **CHINA**: **Yunnan**, **Xishuangbanna**, 25 km SE of Menglunzhen, NE of Mengyuan, Mengyuan Rainforest, 1400 m, branch of *Broussonetia*, on bark, 20.VII.2004, Z.F. Yu (Z.F.Y. xsbn-1, OT003, YMFT, **holotype**; H.B. 7668, **isotype**; sq.: DQ512888).

Not included. **CHINA**: **Anhui**, Jiuhuashan, substrate not stated, 29.IX.2009, J.W. Guo (jhs-40, anam. cult.). – Further collections from **Jiangsu**, Nanjing, Zijinshan and **Yunnan**, Yuxi, Xinhua Forest Park (J.W. Guo pers. comm., not clear for teleomorph which collection is figured).

Series *Albovinosae*

Orbilia subgenus ***Habrostictis*** section ***Aurantiorubrae*** series ***Albovinosae*** Baral, **ser. nov.**, MB 815016 – Type species: *Orbilia albovinosa* Baral & G. Marson

Etymology: named after the type species, *O. albovinosa*.

Latin diagnosis: *Apothecia rosacea (ad aurantiaca), fimbriata vel dentata, corpuscula crystalloidea saepe praesentia, guttulae luteae carentes, cellulae marginales processis vitreis generaliter perlongis praeditae, ascosporae fusoideae vel fusiformes, raro subcylindricae, apice subacutae ad acutae, raro obtusae ad rotundatae, corpusculum lacrimiformem, raro globosum continentes, ad basim leniter ad valde attenuatae vel longe caudatae, rectae vel leniter curvatae, status anamorphicus conidiis staurosporis* (*typo* Trinacrium/Dicranidion *vel* Dwayaangam).

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.6(–1) mm diam., pale to bright rose(-orange), margin pubescent or with prominent white hairs or teeth, sessile or with an ill-defined stipe. **Asci** *34–60(–70) × (4–)5–7(–7.5) µm, 8–32-spored, lower 0–5(–6) spores inverted when 8-spored, about 8 or 16 spores inverted when 16-/32-spored; **apex** (†) slightly to mostly medium to strongly truncate, thin-walled, not or sometimes distinctly indented and laterally inflated; **base** T-, L-, Y- or h- but never H-shaped. **Ascospores** *(4–)5–22(–25) × (1–)1.2–2.9(–3.3) µm, ellipsoid-fusoid to fusiform(-clavate), rarely subcylindrical, apex subacute to acute, rarely obtuse to rounded, base slightly to strongly attenuated, partly tail-like or with an abrupt, long, basally partly inflated tail, straight or slightly (rarely medium) curved in lower part; **SBs** 0.6–3.5 × (0.4–)0.6–1.5(–2) µm, broadly (rarely narrowly) tear-shaped to ampulliform, rarely globose, apically narrowed to a ± small point. **Paraphyses** not or slightly to medium inflated at the apex, spathulate-lageniform, also clavate(-capitate) or uninflated, terminal cells 1–2(–3)× longer than lower cells. **Ectal excipulum** cells near base *(6–)8–20(–27) × (4–)7–15(–20) µm; **glassy processes** 1–7 µm up to 100–250 µm long, **hairs** absent. **SCBs** globose, often mixed with crystalloid ones; **VBs** consistently absent. **Exudate** ± absent or 0.2–3 µm thick, continuous-cloddy to granular, ± firmly or loosely attached, hyaline to pale yellowish. **— ANAMORPH**: trinacrium/dicranidion- or dwayaangam- like. **Conidiophores** not observed. **Conidia** staurosporous, either Y- to T-shaped (2-armed), *35–74 × 39–73 µm, the two arms slightly to strongly curved out- or downwards, or dwayaangam-like (4-armed), *40–60 × 13–46 µm, arms straight or curved.

Habitat: on wood and bark of angiosperms, temperate to subtropical, humid to semiarid, on bark (exceptionally wood).

Recognized species: 8, plus 1 with a provisional name and 3 unnamed species ('affinis').

Taxonomic remarks. Series *Albovinosae* appears to form a rather natural group, being characterized by ± straight ascospores and often long glassy processes at the margin which are ± free or form prominent white hairy teeth. The rather large spores are mostly fusoid to fusiform and have ± acute apices which contain rather large, mostly broadly tear-shaped SBs. The asci are predominantly 8-spored, but in some taxa 16-spored, an exceptional feature within section *Aurantiorubrae*. The somewhat marginal species *O. gemma* deviates from the remaining of this series in 32-spored asci containing small, subcylindrical spores with rounded to obtuse apices with small, almost globose SBs.

O. pseudoaristata and *O. pseudoflagellispora* may easily be confused with *O. aristata* and *O. flagellispora* of section *Hemiorbilia*. However, their truncate, thin-walled ascus apices forbid placement in that series. Despite this fundamental difference, the spores closely resemble each other, and also the texture of the marginal excipulum carrying glassy processes is very much alike. Even the anamorph in *O. pseudoaristata* and the tendency that only very few basal spores are inverted within the asci coincides in both groups. *O. subalbovinosa* forms a transition in spore shape between *O. albovinosa* and *O. pseudoaristata*, and thus supports, along with molecular data, placement of these tailed-spored species in series *Albovinosae*. *O. pilifera* resembles series *Albovinosae* in its large, broadly tear-shaped SBs, but the marginal hairs are septate and without a solid part.

Species delimitation. Considerable variation is observed among the studied collections treated under *O. pubescens*, *O. albovinosa*, and *O. albidorosea*, e.g., in spore size or length of glassy processes, which questions the homogeneity of these taxa. Also the limits between *O. pubescens* and *O. albidorosea* are not fully clear.

Anamorph. Conidia were only observed in three of the nine accepted species. Accordingly, series *Albovinosae* is characterized by a staurosporous anamorph with either trinacrium/dicranidion-like conidia with down- or outwards-curved arms (*O. albovinosa*, *O. pseudoaristata*), or dwayaangam-like conidia with straight (*O. albidorosea*) or curved arms (exceptionally in *O. albovinosa*). With its trinacrium-like conidia series *Albovinosae* resembles the anamorph of series *Piliferae*, while sharply differing from the vermispora-like anamorph typical of the remaining series of section *Aurantiorubrae*.

Phylogeny. Sequences were available for six species of series *Albovinosae* (SSU+ITS+LSU: *O. albidorosea*, *O. albovinosa*, *O. navicularis*, ITS+LSU: *O. pleioalbidorosea*, *O. pseudoaristata*, *O gemma*). In combined analyses, *O. albidorosea* and *O. albovinosa* form a strongly supported clade in Baral et al. (2017b), in which also *O. navicularis* and *O. pleioalbidorosea* clustered and to which *O. pseudoaristata* formed with low support a sister clade (Phyls 7, 13). The morphologically somewhat different *O gemma* formed an unsupported sister clade to the core of series *Albovinosae* (Phyl. 13). The same tree topology was obtained when analysing ITS (Phyl. S15),

Key to species of series *Albovinosae*

1. Margin without glassy processes; apothecia ochre-orange .... ***O. pilifera*** (series *Piliferae*), p. 918
1. Margin with short to long glassy processes (sometimes at the tip of hairs); apothecia orange to rose, rarely with ochraceous tint 2

2. Asci 32-spored; spores *(4–)5–6(–8) × 1–1.3 µm, subcylindrical with rounded to obtuse apex, SBs globose; bark of *Lamarchea*, subtropical semiarid western Australia .... ***O. gemma***, p. 934
2. Asci 8–16-spored; spores longer or wider, fusoid with acute to subacute apex, SBs tear-shaped 3

3. Asci 8-spored 4
3. Asci 16-spored; spores *8.5–15 µm long 11

4. Spores †7–8 × 3–3.3 µm, fusiform-subclavate, without tail; glassy processes 30–70 µm long, curved inwards; bark of *Dodonaea*, subtropical semiarid western Australia .... ***O.* aff. *pubescens***, p. 938
4. Spores max. *3 µm wide 5

5. Spores *2.3–3 µm wide 6
5. Spores *1.2–2.4 µm wide 8

6. Spores fusoid, without distinct tail, *(8.5–)9–12(–13) × (2.3–)2.5–3 µm; bark of *Pistacia*, supramediterranean semihumid southern Europe .... ***O. navicularis***, p. 936
6. Spores divided into an ellipsoid-fusoid head and a ± abrupt, much thinner tail of at least about the same length, *14–25 µm long 7

7. Spores *13–19(–26.5) × 2.3–2.8(–3) µm, tail medium thick (0.5–1 µm), not or hardly inflated at base; SBs 2–3 × 1.2–1.5 µm; bark or wood of mainly *Salix* & *Cornus*, cold-temperate humid to mesomediterranean semihumid Europe, subtropical humid eastern Australia .... ***O. pseudoaristata***, p. 947
7. Spores *20–25 × 2.7–2.9 µm, with a very thin (0.2–0.4 µm) tail with distinctly bulbous base; SBs 2.8–3.5 × 1.4–2 µm; bark of *Lamarchea* & *Melaleuca*, subtropical semihumid to semiarid western Australia .... ***O. pseudoflagellispora***, p. 951

8. Spores *11–14 × 1.3–1.8 µm, base attenuated in a thick tail; SBs 0.5–0.8 µm wide; with crystalloid SCBs in paraphyses and excipulum; bark of ?*Eucalyptus*, subtropical semihumid western Australia .... ***O. subalbovinosa***, p. 946
8. Spores *7–19 × 1.5–2.4 µm; SBs 1–1.5 µm wide 9

9. Spores *16–19 × 2–2.4 µm, with long-cylindrical middle part; SCBs globose; paraphyses spathulate; glassy processes 25–80(–140) µm long; bark of *Lonicera*, mesosub- to mesomediterranean semihumid Europe & northern Africa.......... ***O. albovinosa***, p. 945
The included mesosubmediterranean collection on wood of *Ficus* has only 1–7 µm long glassy processes and non-spathulate paraphyses covered by distinct exudate. A similar sample on *Euphorbia* from Montenegro deviates by much shorter spores of *12–16 × 1.9–2.3 µm.
9. Spores 7–11 µm long, fusoid, only sometimes with short-cylindrical middle part 10

10. Spores *(5.5–)6–10(–11) × (1.3–)1.4–1.8(–2) µm; excipular cells and/or paraphyses with crystalloid SCBs; paraphyses with ± spathulate apex; glassy processes up to 100 µm long, forming distinct teeth; apothecial disc rose; wood & bark of *Acacia*, *Eucalyptus*, *Jacksonia*, (sub) tropical subhumid to semiarid western & eastern Australia, (sub)mediterranean semihumid southern Europe .... ***O. albidorosea***, p. 939
10. Spores *8.5–11 × 2–2.2 µm; excipular cells apparently without crystalloid SCBs; paraphyses lageniform with long apical beak; glassy processes up to 35 µm long, not forming distinct teeth; apothecial disc orange; wood of *Ribes*, bark of *Acer*, boreal to cold-temperate humid North America .... ***O. pubescens***, p. 936
A collection from semiarid Australia on bark of *Lamarchea* differs in †2.2–2.4 µm wide spores and in hairs with a basal lumen terminated by 3–15 µm long glassy processes (p. 939).

11. Spores *2–2.8 µm wide; bark of *Amelanchier*, *Pistacia* etc., supra(sub)mediterranean (semi)humid southern Europe ***O. pleioalbidorosea***, p. 943
A similar collection was on *Amelanchier* in cold-temperate semiarid western North America.
11. Spores *3–3.5 µm wide; branch of *Pinus ponderosa*, cold-temperate humid western North America .... ***O.* aff. *pleioalbidorosea***, p. 943

but here the core clade received strong support. When analysing LSU (Phyl. S15), series *Albovinosae* is paraphyletic by forming three unresolved clades: one contains *O. albidorosea*, *O. pleioalbidorosea*, and *O. navicularis*, another *O. albovinosa* and *O. pseudoaristata*, and a third *O. gemma*.

Series *Albovinosae* clustered weakly supported sister to the core clade of series *Aurantiorubrae* (Phyl. 13), or unresolved among members of section *Aurantiorubrae* and *Habrostictis* in Baral et al. (2017b). In our combined analysis of the entire genus *Orbilia* (Phyl. 7), however, the marginal *O. gemma* clustered weakly supported with series *Vibrioides* (section *Hemiorbilia*).

Specific nucleotide positions. Two nucleotides in the LSU D2 domain characterize series *Albovinosae* s.str. within sections *Aurantiorubrae* and *Helicoon*: at pos. 527 (G**A**GAA vs. G**G**GAA or A**G**GAA) and at pos. 559 (AGC**T** vs. AGC**C**). However, the two motifs of series *Albovinosae* are also highly diagnostic of the *Serpentinae-Habrostictis* clade of section *Habrostictis* and were otherwise only seen in *O. octocorculispora* and *O. microsoma*. *O. gemma* shows the more frequent versions A**G**GAA + AGC**C** that occur in this combination only in series *Regales* and *Xanthoguttulatae*.

Ecology. Probably all included species are more or less desiccation-tolerant. They grew on bark of angiosperms, rarely on wood or herbaceous stems. Records derive from temperate humid to subtropical semihumid (mediterranean) Europe and northern Africa, subtropical semiarid to tropical humid Australia, and cold-temperate semiarid to boreal humid North America.

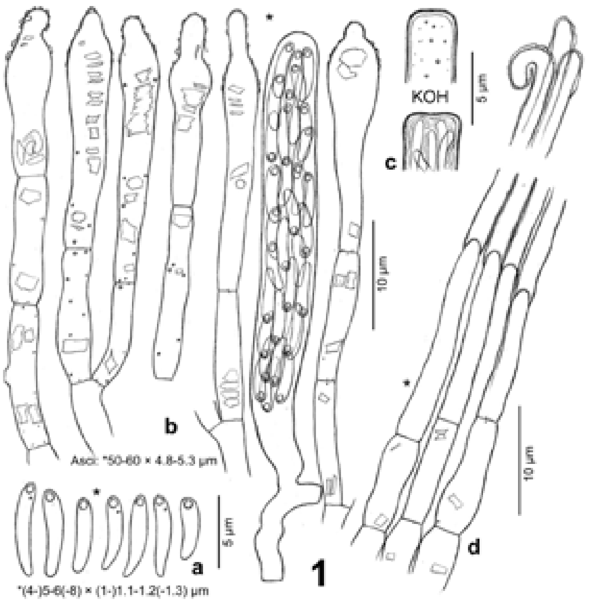
Orbilia gemma Baral & G. Marson, **sp. nov.**, MB 813777 — Pls 510–511

Etymology: resembling a gem (jewel).

Typification: Western Australia, Toolonga, twig and trunk of *Lamarchea hakeifolia*, 8.XI.2007, G. Marson (ex H.B. 9020a, MEL 2389273, holotype; sq.: KT222350).

Latin diagnosis: *Apothecia rehydratata 0.3–0.7 mm diam., vivide rosea, sessilia, margine exigue albido-dentata. Asci 32-spori. Ascosporae *4–8 × 1–1.3 µm, subcylindricae, basi partim leniter attenuatae, rectae vel saepe leniter curvatae, corpusculum refringens globosum vel late lacrimiforme, ad apicem cuspide brevissime affixum continentes. Paraphyses ad apicem distincte mammi- vel lageniformes, exsudato tenui tectae. Excipulum marginale processis vitreis perlongis hyalinis agglutinatis praeditum. Cellulae excipuli marginalis et paraphysium in statu vivo corpuscula crystalloidea continentes. Habitat ad corticem profusum putridum siccum rami et trunci vivi* Lamarcheae hakeifoliae *in zona subtropica semiarida Australiae occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.6(–0.7) mm diam. (0.35–0.8 mm incl. teeth), 0.11–0.16 mm high, light to bright rose-pink, indistinctly translucent, ± round, scattered; disc flat, margin 0–10 µm protruding (excl. teeth), with prominent, straight white teeth 100–250 × 40–100 µm; broadly sessile, superficial; dry ± completely closed by the teeth. **Asci** *50–60 × 4.8–5.3 µm, †49–59 × 4.3–4.7 µm, 32-spored (26–30 spores counted), spores *5–6-seriate, lower spores inverted (strongly mixed), pars sporifera *34–38 µm long; **apex** (†) strongly truncate (not or slightly indented and laterally inflated); **base** with short to long, thick or thin, flexuous stalk, T-, L- or h-shaped. **Ascospores** *(4–)5–6(–8) × (1–)1.1–1.2(–1.3) µm, subcylindrical, apex rounded to obtuse, base not or slightly attenuated, straight to often slightly curved; **SBs** *0.6–0.8 × 0.4–0.6 µm, globose to broadly tear-shaped, apically narrowly attached. **Paraphyses** apically slightly or medium (rarely strongly) inflated, spathulate or mostly lageniform to mammiform, terminal cells *(12–)16–27 × 2.7–4.5 µm, beaks 2–6 × 1,6–2 µm, exceeding the dead or immature asci by 4–8 µm, lower cells *11–13(–18) × 1.8–3(–3.5) µm; never branched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline, 20–40 µm thick, of dense textura intricata with many inflated cells, sharply delimited from ectal excipulum by a 5–10 µm thick layer of t. porrecta. **Ectal excipulum** hyaline to pale rose, of (†) thin-walled, irregularly vertically oriented t. angularis-globulosa(-prismatica) from base to mid flanks, 40–60 µm thick near base, cells *10–16(–19) × 6–10(–11.5) µm; 20–25 µm thick at flanks, 15–25 µm near margin, of t. prismatica oriented at a 40–70° angle to the surface, outer layer of t. porrecta oriented at 10–40°, marginal cortical cells *8–19 × 2–2.8 µm; **glassy processes** 100–250 × (1.8–)2.5–3(–4) µm, high-refractive, not stratified, ± straight, coherent to form distinct teeth, terminally sometimes strongly hooked (outwards, also inwards). **Anchoring hyphae** ± sparse, †2–2.5(–3.5) µm wide, walls 0.2(–0.3) µm thick. **SCBs** in paraphyses and entire ectal excipulum crystalloid, 2–4.5 × 1.5–3 µm in excipulum, hyaline. **Exudate** over paraphyses 0.l–0.4 µm thick, granular, hyaline, firmly attached, over glassy processes 0.3–1 µm thick. — **ANAMORPH**: unknown.



H.B. 9020a (holotype): Western Australia, Yalgoo, on *Lamarchea hakeifolia* (bark)

Plate 510. **1**: *Orbilia gemma*. – **a**. ascospores; **b**. ascus and paraphyses (containing crystalloid SCBs); **c**. ascus apices; **d**. marginal ectal excipulum in median section, cortical cells terminated by long glassy processes.

Habitat: collected 0.5–1.5 m above the ground, 3–5 mm thick dead twig or 10–18 cm thick living trunk of *Lamarchea hakeifolia*, on outer but sometimes also inner surface of paper-like, hanging bark being almost entirely detached, strongly decayed and greyed, no algae. **Associated**: *Capronia* spp. {2}, *Claussenomyces* sp., *Hyalorbilia pleioerythrostigma*, *Orbilia austroobtusispora*, *O. kingsiana*, *O. lamarcheae*, *O. myriolilacina*, *O. pseudoflagellispora*, *O.* ?*pubescens*, *Ostropales*, *Symbiotaphrina desertorum*, ?*Xerotrema* sp. **Desiccation tolerance**: fully viable for at least 17 months. **Altitude**: 190 m a.s.l. **Geology**: Cretaceous sedimentary rock (red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia gemma* is readily recognized by its apothecia with a pure rose-pink hymenium and very long, straight, white teeth which easily break off at their base, and microscopically by 32-spored asci, lageniform paraphyses, and small cylindrical ascospores with globose SBs.

With its rose colour, glassy processes, and spathulate-lageniform paraphyses containing crystalloid SCBs, *O. gemma* resembles members of series *Albovinosae*, except for its ascospores which are in the other species larger and apically consistently ± acute, containing larger, tear-shaped SBs. Species of series *Regales* concur with *O. gemma* in their lageniform paraphyses, glassy processes, and shape of spores and SBs. However, crystalloid SCBs as well as asci with more than 8 spores are so far unknown in that series.

In spore morphology *O. gemma* also resembles four species

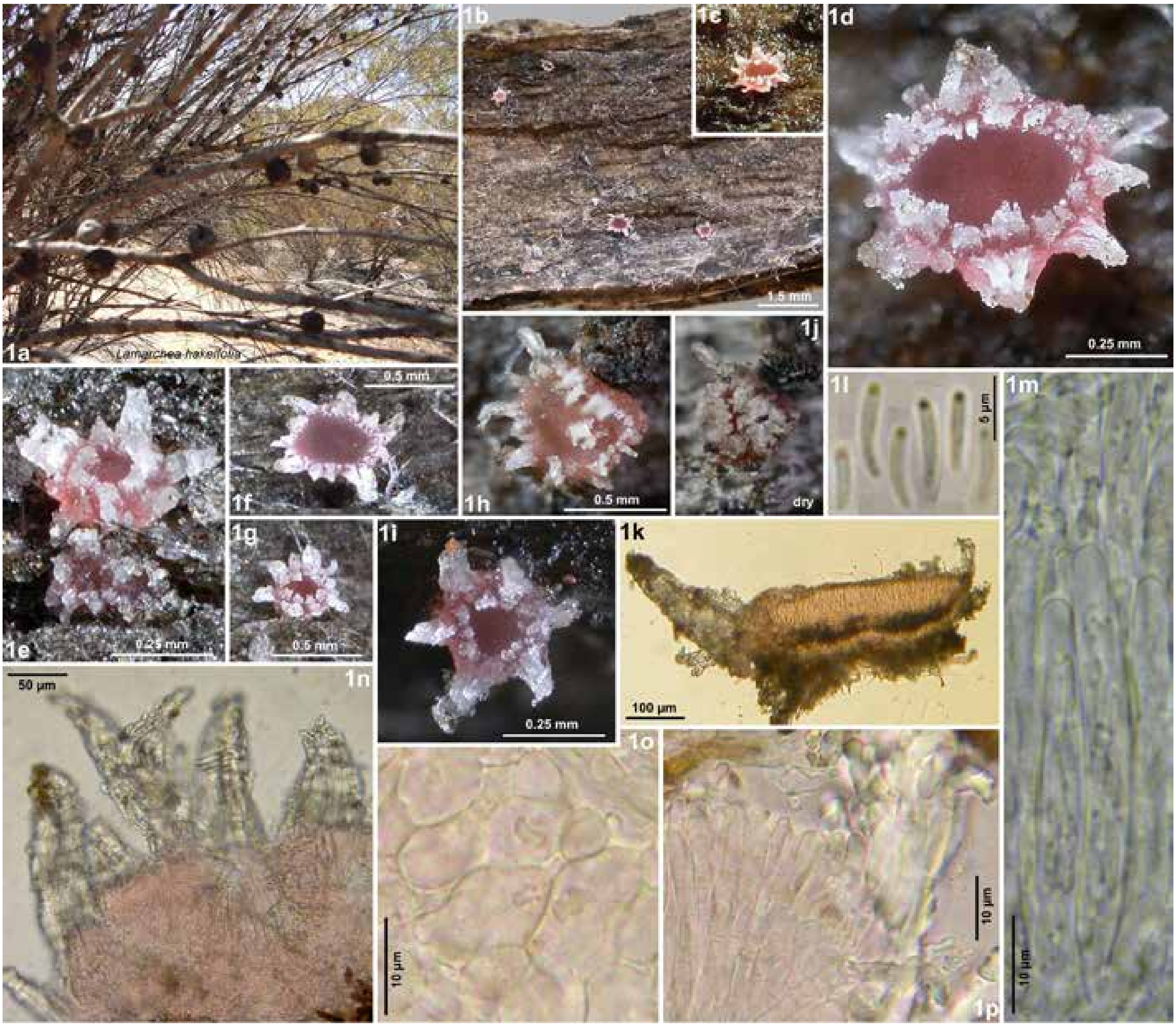


Plate 511. **1**: *Orbilia gemma*. – **1a**. semiarid acacia shrubland with *Lamarchea hakeifolia* in foreground; **1b**. xeric bark of *Lamarchea* detached from living trunk; **1b–i**. rehydrated apothecia; **1j**. dry apothecium; **1k**. apothecium in median section; **1p**. id., marginal ectal excipulum with glassy processes; **1n**. dentate margin of glassy processes in squash mount; **1o**. crystalloid SCBs in ectal excipular cells at lower flanks; **1m**. mature asci (and paraphyses); **1l**. ascospores. – Living state. — **1a–p**. H.B. 9020a (holotype): Western Australia, Yalgoo.

of series *Microsomates* (section *Orbilia*), which differ in orange apothecia: *O. mirabilis* and *O. myriopseudoregalis* further deviate in outwards curved teeth, the former also in much larger, more curved spores; *O. multinanosoma* and *O. myrionanosoma* differ in spores with smaller, more rod-shaped SBs, also in predominantly non-lageniform paraphyses and in short or even absent teeth. In ascospore morphology *O. gemma* further resembles species of section *Orbilia*, such as *O. pleioaustrocylindrica* and *O. multiaustrocylindrica*, or the rose-lilaceous *O. myriolilacina* of section *Ovoideae*. Yet, none of these have spathulate-lageniform paraphyses, glassy processes, or crystalloid SCBs.

Phylogeny. A sequence from apothecia of the holotype comprises SSU (S1506 intron absent), ITS, and LSU. *O. gemma* formed an unsupported clade with an environmental sequence from arctic Canada (Northwest Territories, Banks Island, ~50 m, arctic soil, 103_NA8_P31_K7, KC965955), with very high distance (20% in ITS, 4.7% in LSU D1–D2). The clade clustered unsupported sister to the remaining members of series *Albovinosae* when analysing ITS (S15) or ITS+LSU (Phyl. 13), to which *O. gemma* shows a similarly high ITS distance of 17–20.5%, the lowest to *O. pseudoaristata*. Also when comparing only the 5.8S region, *O. pseudoaristata* was the closest species. In our combined analysis of the entire genus *Orbilia* (Phyl. 7), however, *O. gemma* clustered weakly supported with series *Vibrioides* of section *Hemiorbilia*, a rather unexpected placement from a morphological point of view. This placement is supported by a rare deviation at pos. 70 of LSU (CAAC**C**GGGA) which *O. gemma* shares with some members of section *Hemiorbilia*, including series *Vibrioides*, and which so far does not occur in any other section of *Orbiliomycetes* (see under section *Hemiorbilia*, p. 544).

Ecology. *O. gemma* was found on strongly detaching xeric bark of a twig and a living trunk of *Lamarchea hakeifolia* (*Myrtaceae*) in a subtropical semiarid acacia open shrubland with *Callitris* and *Lamarchea* in the Yalgoo ecoregion of western Australia (see also under the associated *O. lamarcheae*, p. 1486, Pl. 929: 1k–l).

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, twig & trunk of *Lamarchea hakeifolia*, on bark, 8.XI.2007, G. Marson (ex H.B. 9020a, MEL 2389273, **holotype**; **isotype** MEL 2389275B; sq.: KT222350, MH221052).

Orbilia navicularis S. Tello, Baral & E. Weber, **sp. nov.**, MB 825637 — Pls 512–513

Etymology: referring to the naviculate (boat-shaped) ascospores.

Typification: Spain, Andalucía, Jaén, Sierra de Ventisqueros, El Parrizoso, branch of *Pistacia terebinthus*, 18.IV.2017, S. Tello (ex S.T. 18041702 & ex H.B. 10113a, AH 52847, holotype; sq.: MK473416).

Latin diagnosis: *Similis* Orbiliae pubescenti *sed apothecia margine denticulata, processis vitreis agglutinatis, deorsum curvatis, ascosporae latiores. Habitat ad corticem leniter putridum rami sicci* Pistaciae terebinthi *in supramediterranea semihumida Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.5–)0.7–1.3 mm diam., 0.13–0.23 mm high (receptacle 0.1–0.13 mm), pale to bright (ochraceous-)orange-rose, round, undulating when large, scattered to gregarious in small groups; disc ± concave, margin and exterior densely covered by crystal-like tufts of white hairs, 36–100 µm projecting including hairs; sessile on a broad or narrow, conical base. **Asci** *45–55 × 5.7–6.5 µm, †40–46 × 5.2–5.7 µm, 8-spored, spores (*/†) 2-seriate, ((1–))(2–)4(–6) lower spores inverted (sometimes mixed, rarely upper spore inverted), pars sporifera *30–36 µm long; **apex** (†) medium to strongly truncate (not or very slightly indented and/or laterally inflated); **base** with short stalk, L- to Y-shaped. **Ascospores** *(8.5–)9–12(–13) × (2.3–)2.5–3((–3.2)) µm, †8–9.5 × 1.8–2.5 µm, fusiform-naviculate, apex subacute, medium to strongly attenuated towards straight to sometimes slightly curved base; **SBs** *2.7–3.3 × 1.3–1.6 µm, with inflated, globose basal part and 0.8–0.9 µm wide, cylindric-subulate upper part. **Paraphyses** apically not or slightly inflated, cylindrical to sublageniform, terminal cells *13–22 × 2–3 µm, †1.3–2.3 µm wide, 3–6 µm longer than dead asci, lower cells *(3–)7–9.5 × 1.8–2.5 µm; unbranched at upper septum. **Medullary excipulum** 20–60 µm thick, of dense, small-celled textura angularis with some inflated catenate cells. **Ectal excipulum** of vertically oriented t. globulosa-angularis from base to margin, 50–140 µm thick at base, cells *(6–)8–20(–27) × (5–)7–15(–20) µm, (†) slightly gelatinized, 25–40 µm thick at lower flanks, 15–25(–35) µm at mid flanks and margin, externally covered by a layer of t. porrecta passing into ~50–100 µm long **hairs** composed of a 2–3-celled, 35–45 µm long, thin-walled basal part (terminal cell *13–25 × 3.3–4 µm) tipped by **glassy processes** (8–)20–55(–70) × 3–3.5(–4.5) µm, high-refractive, appearing stratified only in KOH, curved outwards, agglutinated to form teeth-like tufts. **Anchoring hyphae** abundant, */†1.5–3 µm wide, walls 0.2–0.5 µm thick, forming a very dense t. intricata 10–60 µm thick. **SCBs** in paraphyses absent or present, faintly refractive, hyaline, globose, 1.5–2 µm diam., also rhomboid (crystalloid); none seen in ectal excipulum. **Exudate** on paraphyses and hairs sparse, finely granular, firmly attached. **— ANAMORPH**: unknown.

Habitat: collected 1.8 m above the ground, corticated, 16–20 mm thick branch of *Pistacia terebinthus*, on little to medium decayed bark (outer surface of bast or on periderm amidst lichens), algae not observed. **Associated**: *Lecanora* sp., *Lecidella elaeochroma*, *Melanohalea exasperata*, *Orbilia xanthoguttulata*, *Physcia* sp. etc. **Desiccation tolerance**: many mature asci, paraphyses, and excipular cells viable after 2.5 months. **Altitude**: 1130 m a.s.l. **Geology**: Tertiary calcareous sandstone and breccia with red matrix below dolomite (close to Jurassic and Cretaceous sediments). **Phenology**: IV (but long-lived).

Taxonomic remarks. *Orbilia navicularis* resembles the Australian *O. albidorosea*, from which it differs in an orange hymenium, glassy processes being curved outwards, sublageniform paraphyses, and distinctly wider and slightly longer ascospores. The mediterranean *O. albovinosa* differs in much longer spores. *O. navicularis* is doubtfully distinct from the American *O. pubescens* nom. prov. on *Ribes* (Pl. 514: 1), from which it differs in glassy processes being curved outwards and agglutinated to form teeth, and distinctly wider ascospores. Another American collection, which was also from the Southern Rocky Mountains but ~90 km away and on *Acer* (Pls 514: 2; 515: 1), was only studied in the dead state; it even concurs with *O. navicularis* in spore size (when compared in the dead state) and in having outwards curved glassy processes being agglutinated to form teeth.

Phylogeny. A sequence from apothecia gained from the holotype comprises SSU (without S1506 intron), ITS, and LSU. In our combined analysis (Phyl. 13) it clustered strongly supported with *O. albidorosea* and particularly *O. pleioalbidorosea*, to which it shows a 7% and 2.5% ITS distance (2.5% and 0.5% in LSU D1–D2), respectively, whereas to *O. albovinosa* the distance is 11% (4.5% in LSU).

Ecology. *O. navicularis* grew amidst a large number of lichen species on slightly to moderately rotten bark (bast and periderm) of a xeric branch of *Pistacia terebinthus*, residing in a row of trees and shrubs across a dry pasture land grazed by goat and sheep. The nearby vegetation is a supramediterranean semihumid, north-exposed open woodland with *Quercus rotundifolia*, *Q. faginea*, *Crataegus monogyna*, *Acer monspessulanum*, and *Juniperus oxycedrus*.

Specimens included. **SPAIN**: **Andalucía**, **Jaén**, Sierra de Ventisqueros, 7 km ENE of Valdepeñas de Jaén, 1.9 km S of El Parrizoso, 1130 m, branch of *Pistacia terebinthus*, on bark, 18.IV.2017, S. Tello (ex S.T. 18041702, ex H.B. 10113a, AH 52847, **holotype**; sq.: MK473416).

Orbilia pubescens Baral & G. Marson, **nom. prov.**, MB 813779 — Pls 514–515

Etymology: referring to the hairy apothecia.

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.45 mm diam., 0.13 mm high, bright orange-red, round to broadly elliptical, scattered; disc flat, margin pubescent with whitish hairs, 80 µm projecting including hairs; subsessile. **Asci** *40 × 5–5.6 µm, †33–40 × 4.2–4.6 µm, 8-spored, spores (†) ~3-seriate, 3–5 lower spores inverted; **apex** (†) medium to strongly truncate (not indented, laterally not widened); **base** with short stalk, bifurcate. **Ascospores** *8.5–11 × 2–2.2 µm, fusiform to fusiform-clavate, apex subacute to acute, towards base medium to strongly attenuated, here straight to slightly curved; **SBs** *2–3 × 1.1–1.4 µm, tear-shaped. **Paraphyses** apically slightly to medium inflated, sublageniform, terminal cells *12–22 × 2.5–3.5 µm, †1.7–2.8 µm wide, lower cells *(3–)6–10 × 1.5–2.3 µm; unbranched at upper septum. **Medullary excipulum** 30 µm thick, not further examined. **Ectal excipulum** of vertically oriented textura angularis from base to margin, 40–60 µm thick near base, cells *10–20 × 10–14 µm, (†) slightly gelatinized, 30–40 µm thick at lower flanks, 20 µm at mid flanks and margin, oriented at 40–80°, externally covered by a layer of t. porrecta passing into 35–55 µm long **hairs** composed of a 1–2-celled basal part (terminal cell *21–24 × 3.5–4.5 µm) tipped by **glassy processes** 10–35 × 3–5 µm, high-refractive, appearing stratified only in KOH, curved inwards, not agglutinated. **Anchoring hyphae** abundant, */†2–3 µm wide, walls 0.2–0.3 µm thick, forming a very dense t. intricata up to 100 µm thick. **SCBs** in paraphyses globose. **Exudate** on paraphyses and hairs very sparse, finely granular, firmly attached. **— ANAMORPH**: unknown.

Habitat: collected 0.1–0.8 m above the ground, decorticated, 12 mm thick branch of *Ribes cereum*, on slightly decayed wood, ungreyed, algae not observed. **Associated**: *Durella* sp., *Hysteropatella* sp., *Melaspilea ermergens*, *Orbilia delphinus*, *O. lentiformis*, *O. maeandrina*, *Ostropales*, *Patellaria* sp. **Desiccation tolerance**: a few mature asci still viable after 7.5 months. **Altitude**: 2615 m a.s.l. **Geology**: granite & gneiss. **Phenology**: VI (but long-lived).

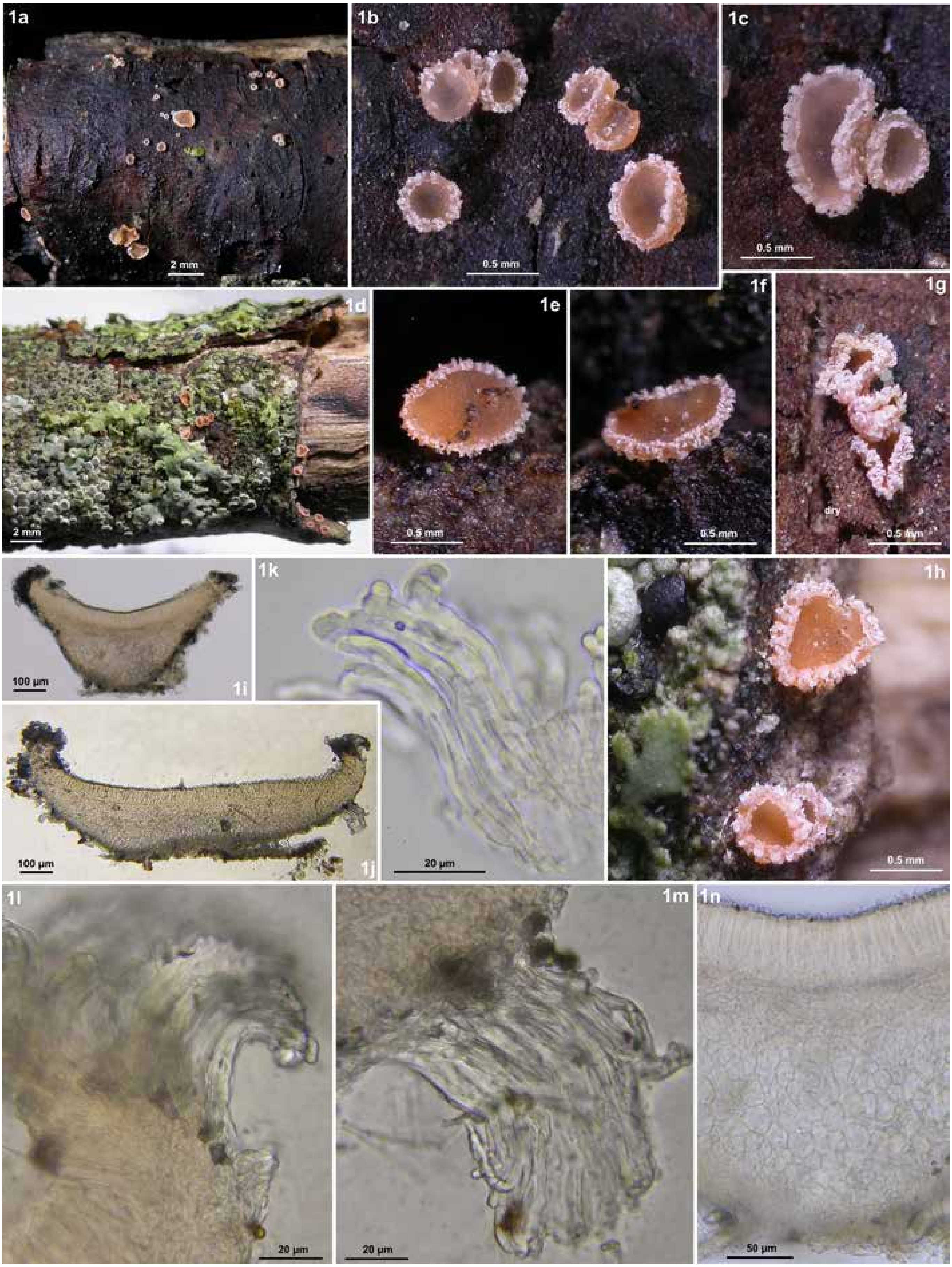


Plate 512. **1**: *Orbilia navicularis*. – **1a–f**, **h**. rehydrated apothecia; **1g**. dry apothecia; **1i–j**. apothecia in median section; **1n**. id., central part; **1k–m**. id., agglutinated glassy processes at margin and flanks. – Living state. – **1i**, **n**: phot. S. Tello. — **1a–n**. H.B. 10113a: Spain, Andalucía, Jaén, on *Pistacia*.

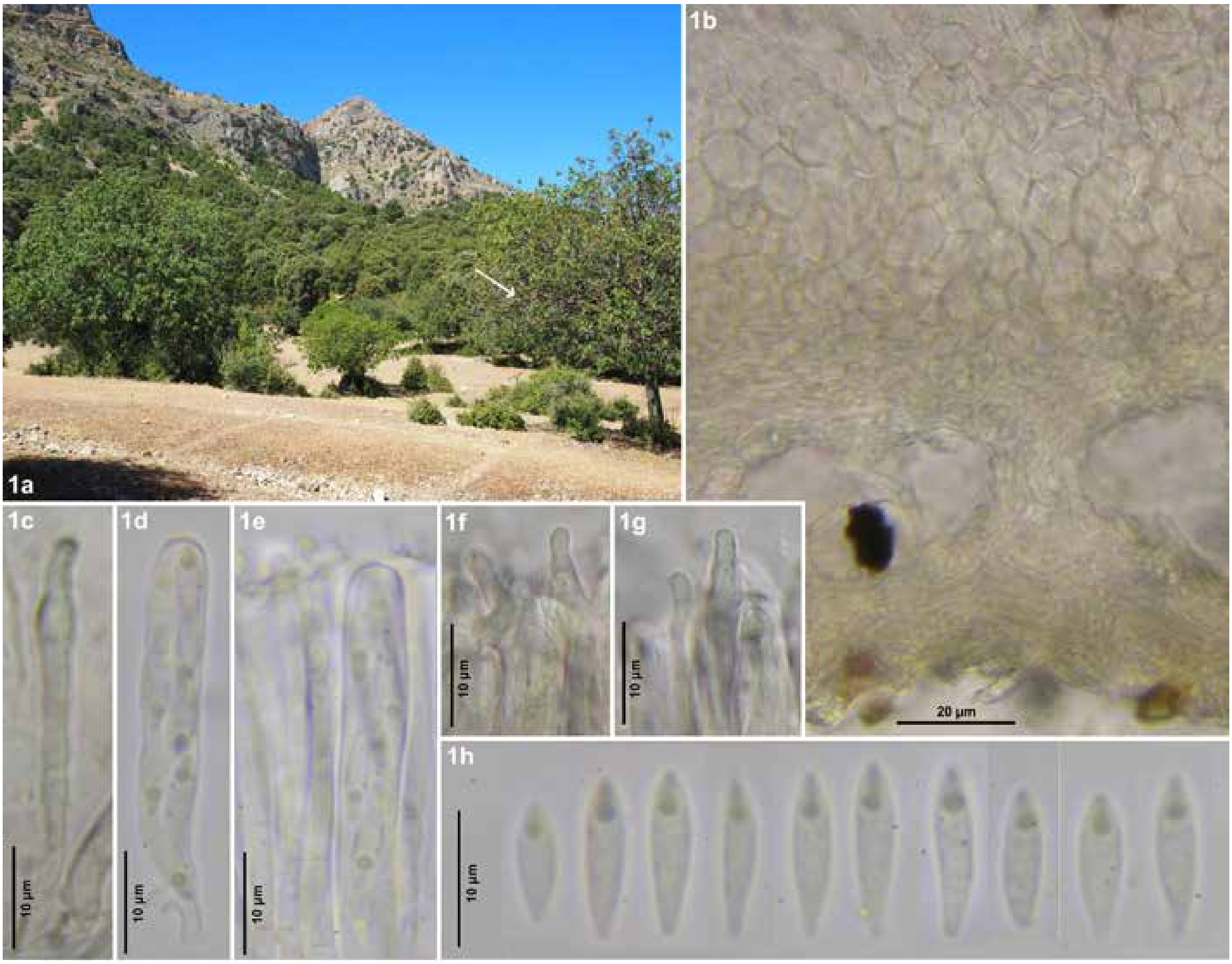
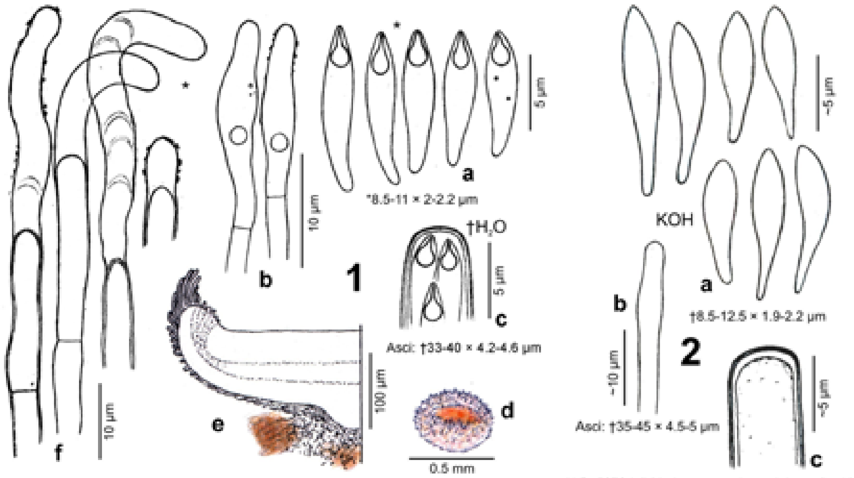


Plate 513. **1**: *Orbilia navicularis*. – **1a**. dry pasture land with *Pistacia terebinthus* tree in front of *Quercus rotundifolia* woodland; **1b**. basal ectal excipulum with abundant anchoring hyphae, in median section; **1c–g**. asci and paraphyses; **1h**. ascospores. – Living state, except for ascus in **1d**. – **1a**, **d–e**, **h**: phot. S. Tello. — **1a–g**. H.B. 10113a: Spain, Andalucía, Jaén, on *Pistacia*.

Taxonomic remarks. *Orbilia pubescens* differs from *O. navicularis* in narrower ascospores and in glassy processes being curved inwards and not agglutinated to form teeth. *O. albidorosea* differs from *O. pubescens* in an (orange-)rose to rose hymenium, longer glassy processes which are agglutinated to form teeth, spathulate-lanceolate paraphyses, and slightly narrower ascospores, and in the presence of crystalloid SCBs (but their absence in *O. pubescens* could not be assessed with certainty).

The collection of *O. pubescens* nom. prov. consists of a single apothecium, of which only a fragment and a slide remained.



H.B. 5705g (holotype): USA, Colorado, Shawnee, on *Ribes cereum* (wood)

H.B. 5672d: ibid., Lyons, on *Acer glabrum* (bark)

Plate 514. **1**: *Orbilia pubescens* nom. prov.; **2**: *O.* cf. *pubescens*. – **a**. ascospores; **b**. paraphysis apices; **c**. ascus apices; **d**. apothecium with fimbriate margin; **e**. apothecium in median section; **f**. marginal cortical cells with glassy processes.

Not included collections. A sparse sample on bark of *Acer glabrum* (Pls 514: 2; 515: 1) was only studied in the dead state and differs in more clavate, basally more strongly attenuated spores (†8.5–12.5 × 1.9–2.2 µm) and in somewhat shorter glassy processes (18–27 µm) which are curved outwards and more agglutinated to form teeth.

Two bark-inhabiting Australian records resemble *O. pubescens* and *O. navicularis* in various respects, but seem to belong to two different species. Both are merely known from a single unpreserved apothecium and were only briefly studied, mainly in the dead state. The two were collected at a single site though on different hosts. One (on trunk bark of *Dodonaea*, Pl. 515: 2) differs from the above in distinctly shorter and wider spores (†7–8 × 3–3.3 µm). The 30–70 µm long

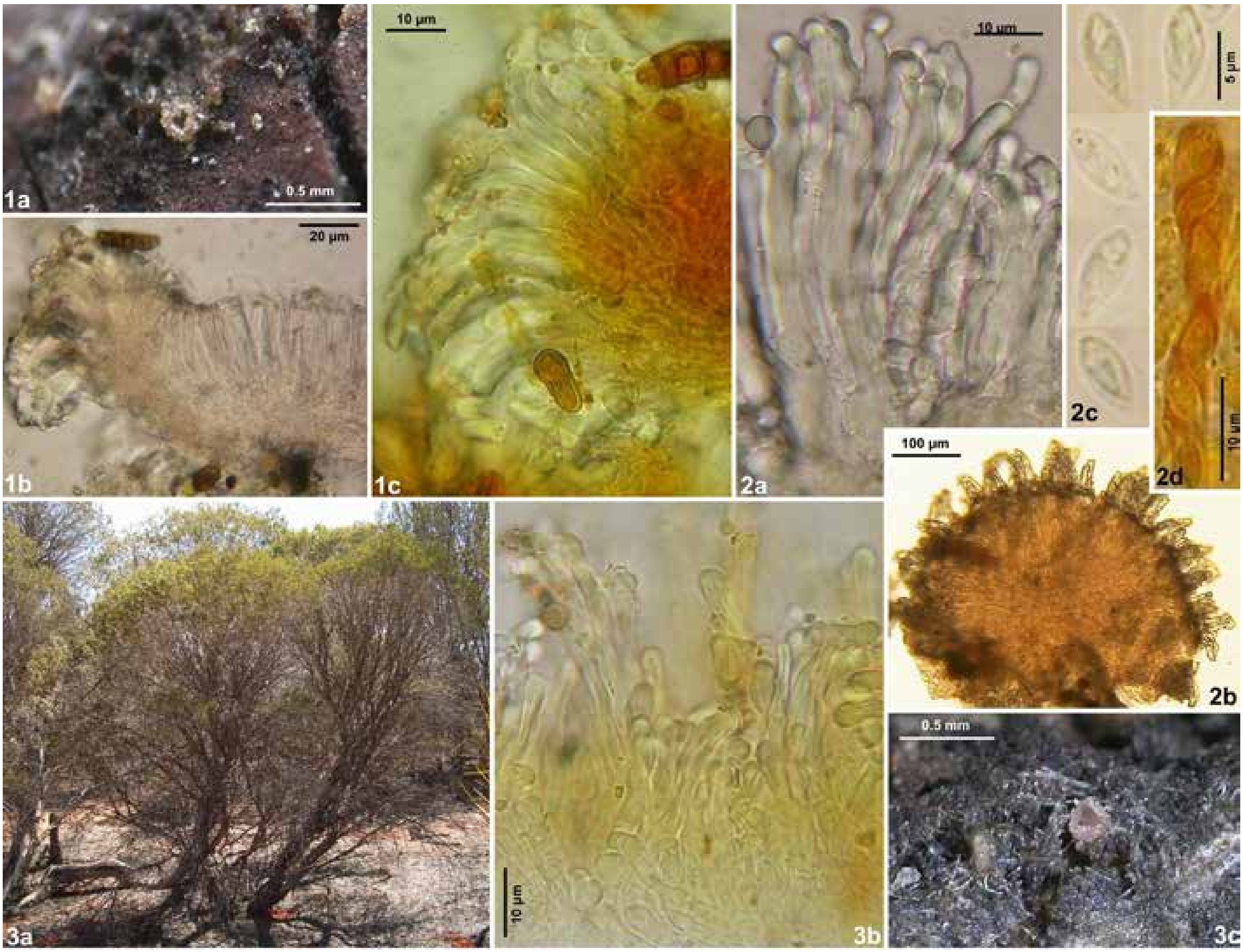


Plate 515. **1**: *Orbilia* cf. *pubescens*; **2–3**: *O.* aff. *pubescens*. – **3a**. *Lamarchea hakeifolia* in semiarid acacia shrubland; **1a**, **3c**. rehydrated apothecia; **1b**. apothecium in median section; **1c**. id., marginal ectal excipulum; **2a**. long glassy processes; **3b**: hairs with thin glassy caps; **2b**. apothecium in top view; **2c**. ascospores; **2d**. mature ascus. – Dead state (in water, **2d** in IKI, **1c**, **3b** in KOH+IKI). — **1a–c**. H.B. 5672d: USA, Colorado, on *Acer*; **2a–c**. H.B. 8838c: Western Australia, Nerren Nerren, on *Dodonaea*; **3a–c**. H.B. 9020n: ibid., on *Lamarchea*.

glassy processes are curved inwards. The other grew on bark of a *Lamarchea hakeifolia* twig (Pl. 515: 3), with spores †8–9 × 2.2–2.4 µm and ~35–65 µm long hairs which have thickened lateral walls and a lumen almost up to the apex, being terminated by 3–15 µm long glassy processes. The spores appear to have a short tail, but were not seen outside the asci.

Ecology. *O. pubescens* was found on slightly rotten wood of a xeric branch of *Ribes cereum* (wax currant) in a boreal humid Engelmann spruce forest of the Southern Rocky Mountains in western North America. The not included collection on bark of *Acer glabrum* (Rocky Mountain maple) was made in a similar region and forest but at lower altitude in a cold-temperate humid Douglas fir forest. The two samples from western Australia derive from a subtropical semiarid acacia open shrubland in the Yalgoo ecoregion.

Specimens included. **USA**: **Colorado**, Southern Rocky Mountains, 65 km SW of Denver, 7.5 km WNW of Shawnee, Santa Maria, north slope of mountain, 2615 m, branch of *Ribes cereum*, on wood, 14.VI.1996, G. Marson (ex H.B. 5705g, **holotype**, M-0276572).

Not included. **USA**: **Colorado**, Southern Rocky Mountains, ~26 km NNW of Boulder, ~6 km WNW of Lyons, ~1885 m, branch of *Acer glabrum*, on bark, 13.VI.1996, G. Marson (H.B. 5672d). — **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, trunk of *Dodonaea viscosa* subsp. *angustissima*, on bark, 8.XI.2007, G. Marson (H.B. 8838c ø). – ibid., twig of *Lamarchea hakeifolia*, on bark, 8.XI.2007, G. Marson (H.B. 9020n ø).

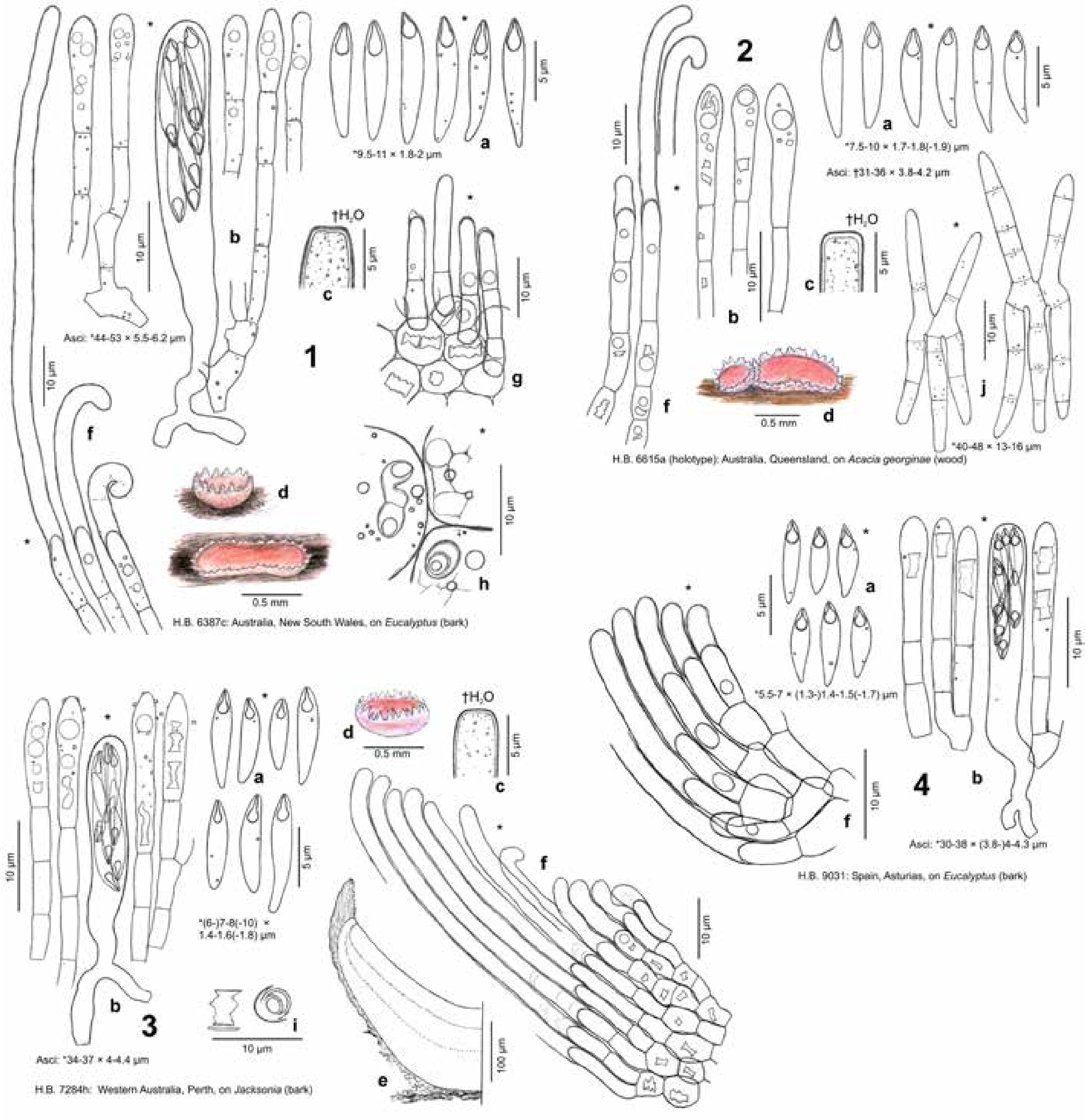
Orbilia albidorosea Baral & G. Marson, **sp. nov.**, MB 813780 — Pls 516–517, Map 86

Etymology: referring to the rose apothecia with white marginal teeth.

Typification: Australia, Queensland, Karoon Station, branches of *Acacia georginae*, 16.X.1998, G. Marson (ex H.B. 6615a, BRI AQ799188, holotype; ex-type culture: CBS 140818; sq.: KT215254, MH878188).

Latin diagnosis: *Apothecia rehydratata 0.2–1 mm diam., rosea, sessilia, margine longe albido-denticulato. Asci 8-spori. Ascosporae *5.5–11 × 1.3–2 µm, fusoideae vel fusiformes, (sub)acutae, basi leniter vel valde attenuatae, rectae vel leniter curvatae, in statu vivo corpusculum refringens lacrimiformem continentes. Paraphyses ad apicem subtiliter vel modice inflatae, spathulatae ad obtuse lanceolatae. Margo excipuli processis vitreis longis agglutinatis praedito. Cellulae vivae excipuli et paraphysium corpuscula globosa et crystalloidea continentes. Habitat ad corticem putridum, etiam lignum, ramorum siccorum* Acaciae, Eucalypti *et* Jacksoniae *in zona tropica ad submediterranea semiarida ad semi- vel subhumida Australiae occidentalis et orientalis et Europae meridionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.4–0.8(–1) mm diam., 0.1–0.14 mm high (receptacle 0.06–0.1 → 0.04–0.07 mm), whitish to very pale rose-lilaceous or usually pale to bright rose-pink or (orange-)rose, round, elliptical when growing in crevices, scattered to gregarious; disc flat, margin with prominent whitish teeth 30–150 × 20–130 µm; sessile, superficial or suberumpent; dry ± completely closed by the marginal teeth (hysteriform). **Asci** *30–38 × (3.8–)4–4.4 {2} or *44–53 × 5.5–6.2 µm {1}, †26–36 × 3.4–4.2 µm {3}, 8-spored, spores *3–4-seriate, 3–5(–6) lower spores inverted {4} (sometimes mixed), pars sporifera *13.5–19 {2} or *17–26 {1}



H.B. 6387c: Australia, New South Wales, on *Eucalyptus* (bark)

H.B. 6615a (holotype): Australia, Queensland, on *Acacia georginae* (wood)

H.B. 9031: Spain, Asturias, on *Eucalyptus* (bark)

H.B. 7284h: Western Australia, Perth, on *Jacksonia* (bark)

Plate 516. **1–4**: *Orbilia albidorosea*. – **a**. ascospores; **b**. asci and paraphyses (with crystalloid SCBs); **c**. ascus apices; **d**. apothecia with dentate margin; **e**. apothecium in median section; **f**. id., marginal ectal excipulum, hair-like cortical cells with long glassy processes; **g**. ectal excipulum at mid flanks in surface view, with crystalloid SCBs, short hairs without glassy processes; **h–i**. crystalloid SCBs in ectal excipular cells near base and lower flanks; **j**. conidia from culture.

µm long; **apex** (†) medium to strongly truncate (not or sometimes slightly indented, laterally not or scarcely widened); **base** with short to medium long, ± thick, flexuous stalk, L-, Y- to h-shaped. **Ascospores** *(5.5–)6–10(–11) × (1.3–)1.4–1.8(–2) µm {6}, †7–8 × 1.5–1.7 µm {1}, fusoid to fusiform, sometimes fusoid- to fusiform-clavate, apex subacute to acute, rarely obtuse or acuminate, not or sometimes slightly to strongly attenuated towards base (partly tail-like), here straight or slightly curved; **SBs** *(1.5–)1.8–2.5(–3) × (0.7–)0.9–1.2(–1.4) µm {4}, tear-shaped, sometimes pear-shaped to ampulliform. **Paraphyses** apically (uninflated to) very slightly or medium spathulate to obtusely lanceolate, terminal cells *(9–)12–18 × (2–)2.3–3.2 µm {4}, protruding *1–5 µm beyond asci (†5–7 µm), lower cells *4–9.5 × 1.6–2.3 µm {4}; unbranched at upper septum. **Medullary excipulum** 30–45 µm thick, of ± dense textura intricata-globulosa with many inflated cells, (medium) sharply delimited only at flanks. **Ectal excipulum** pale rose-pink, of (†) not or slightly gelatinized, vertically oriented t. (globulosa-) angularis(-prismatica) from base to margin, 30–70 µm thick near base, cells *10–25 × 8–17 µm {3}; 15–30 µm thick at lower flanks, 10–20 µm at mid flanks and margin, inner layer of t. prismatica-angularis oriented at a 40–70° angle, cells of *5–9 × 6–9 µm, cortical layer of t. porrecta oriented at 10–50°, partly as free, 2–3-celled **hairs** 18–45 µm long, terminal cells longest, *7–20 × 2.5–3.5 µm {4}; hairs at margin tipped by **glassy processes** 30–100 × (2.3–)2.7–3.5(–5) µm {5} (at upper margin only 3–20 long), high-refractive, not stratified or sometimes near insertion or overall, terminally slightly to strongly curved inwards {5}, sometimes outer processes outwards curved, agglutinated to form teeth, at flanks absent or 40–60 µm long. **Anchoring hyphae** abundant, */†1.7–3.5 µm wide, walls 0.2–0.5(–1) µm thick {4}. **SCBs** in paraphyses and hair bases globose to ellipsoid {4} and crystalloid {4}; in angular excipular cells from base to margin absent {1} or crystalloid {4}, (sub)hyaline, 3–5 × 2–3.5 µm. **Exudate** absent or scattered, finely granular, on hairs absent. — **ANAMORPH**: dwayaangam-like (from ascospore isolate {1}). **Conidiophores** not observed. **Conidia** with a central stipe and 4 straight or only slightly diverging arms, two arms pointing upwards, 2 downwards, total size *40–48 × 13–16 µm, stipe *19–**20** × 3–3.5 µm, 3-septate, arms *15–23 × 2.5–3.5 µm, 1–4-septate, not or slightly tapering {1}.

Habitat: collected 0.5–5 m above the ground, corticated or decorticated, 8–25 mm thick branches or ~20 cm thick logs of *Acacia* sp. {1}, *A. georginae* {1}, *Eucalyptus* sp. {2}, *E. camaldulensis* {1}, *E. globulus* {1}, *Jacksonia* sp. {1}, on 0.1–1 mm deep medium to strongly decayed inner and outer surface of bark (bast) {6}, rarely wood {1}, slightly to strongly greyed, green algae absent or sparse to abundant. **Associated**: *Calycellina* sp. {1}, *Claussenomyces* sp. {1}, *Durella* sp. {1}, *D.* aff. *connivens* {1}, *Gloniopsis praelonga* {1}, *Orbilia acaciae* {1}, *O. arachnopus* {1}, *O. australiensis* {1}, *O. austroocculta* {1}, *O. austroregalis* {1}, *O. curvativitalbae* {1}, *O. eucalypti* {2}, *O. gambelii* {1}, *O. kingsiana* {1}, *O. macrotrapeziformis* {1}, *O. microserpens* {1}, *O. multinanosoma* {1}, *O. myriofusiclava* {1}, *O. myrioobliqua* {1}, *O. nothovinosa* {1}, *O. pleiocrescens* {1}, *Psiloglonium lineare* {1}. **Desiccation tolerance**: fully viable for at least 7.5 months, some mature asci still alive after 14.5 months, many immature asci after 20 months. **Altitude**: 37–514 m a.s.l. **Geology**: Spain: Triassic & Tertiary dolomite, sandstone & gypsum; granite & granodiorite, migmatite & gneiss; Australia: Jurassic & Cretaceous sedimentary rock, Cenozoic regolith; granulite with granitic gneiss. **Phenology**: probably all year round (long-lived).

Taxonomic remarks. *Orbilia albidorosea* is characterized by apothecia with a rosaceous-pinkish hymenium and prominent white marginal teeth composed of long glassy processes, also by rather small, fusoid ascospores, spathulate-lanceolate paraphyses, and the presence of crystalloid SCBs. In all four Australian specimens and that from Asturias the glassy processes attained a maximum length of ~100 µm, while in the other Spanish ones they ranged more at a maximum of 60 µm. The European *O. pleioalbidorosea* differs in 16-spored asci, the mediterranean *O. albovinosa* in much longer spores, absence of crystalloid SCBs, and a different anamorph. For the similar North American *O. pubescens* see p. 936.

Variation. The two collections from eastern Australia (Pl. 516: 1–2) deviate from most of the others in larger asci and spores (ascus size and spore width do not overlap when compared in the living state), but in the sample from Cataluña the spores had an intermediate size (*6.2–8.5 × 1.5–2 µm, IVV: 24.X.2015). The collection in Pl. 516: 1 deviates also in the absence of crystalloid SCBs in the paraphyses though present in the excipular cells. The other features of all these specimens are so similar that we consider them to belong in the scope of a single species. The specimen from Asturias had whitish to very pale rosaceous-lilaceous apothecia apparently due to growing on the moist ground (Pl. 517: 4a), but the other two from Spain had light to bright rose apothecia and were also at rather moist places and partly hidden behind bark. In that from Asturias crystalloid SCBs were only found in the paraphyses, but in that from Cataluña also throughout the ectal excipulum.

Anamorph. The conidia of *O. albidorosea* resemble *Dwayaangam yakuensis* but have distinctly longer arms and stipes, both with more septa. The lower arms are close and parallel to the stipe in their proximal part, which is only exceptionally the case in *D. yakuensis*, e.g., in the Australian strain (Matsushima 1989). However, only very few conidia developed in our culture when flooded by water, and only two could be documented.

Phylogeny. A sequence taken from the ex-type culture comprises SSU, S1506 intron, ITS, and LSU. The entire ITS region shows a distance of 12.5 % to *O. albovinosa* and 15 % to *O. pseudoaristata*. In the LSU D1–D2 the closest species is *O. poitevinica* (series *Poitevinicae*, 2.5 %) which, however, shows a 16.5 % ITS distance, while the LSU distance to *O. pseudoaristata* is 3.5 % and to *O. albovinosa* 4.5 %. *O. albidorosea* formed with *O. pleioalbidorosea* and *O. navicularis* a strongly supported clade in analyses of ITS+LSU or ITS (Phyl. 13, S15). When analysing the intron, *O. albidorosea* clustered unsupported sister to the rest of the section (Phyl. S14), to which it shows a distance of ~ 17–22 %.

Ecology. *O. albidorosea* was found on ± strongly rotten bark (rarely wood) of xeric branches of trees and shrubs of different *Fabales* in a tropical semiarid eucalypt open woodland in northeastern Australia (west of Great Dividing Range), in a subtropical subhumid eucalypt woodland with *Acacia* and *Callitris glaucophylla* in southeastern Australia (west of Great Dividing Range), and in a subtropical semihumid banksia-eucalypt woodlands with *Macrozamia* in southwestern Australia (Darling Range). The three collections from southwestern Europe were on ± hygric bark of *Eucalyptus* logs in mesosub- to mesomediterranean semihumid eucalypt plantations in northern, western, and eastern Spain.

Specimens included. **AUSTRALIA**: **Western Australia**, Jarrah Forest, 25 km NNE of Bindoon, 12 km ESE of Wannamal, 272 m, branch of *Acacia*, on bark, 4.IX.2006, G. Marson (H.B. 8582d). – Swan Coastal Plain, 30 km NE of Perth, 4 km N of Upper Swan, W of Walyunga, 37 m, branch of *Jacksonia*, on bark, 23.XI.2001, G. Marson (H.B. 7284h). – **Queensland**, Desert Uplands, 57 km E of Hughenden, 3 km WSW of Karoon Station, 437 m, branches of *Acacia georginae*, on wood, 16.X.1998, G. Marson (ex H.B. 6615a, BRI AQ799188, **holotype**, anam. cult., CBS 140818; sq.: KT215254, MH878188). – **New South Wales**, Brigalow Belt South, 16 km S of Coonabarabran, Mendooran Rd, 514 m, branches of *Eucalyptus*, on bark, 25.X.1998, G. Marson (H.B. 6387c). — **SPAIN**: **Asturias**, 6 km SE of Avilés, SE of Núñez, 200 m, log of *E. globulus*, on bark, 14.III.2009, A. Suárez (E.R.D. 4716, H.B. 9031). – **Extremadura**, **Cáceres**, 9.3 km SE of Jarandilla de la Vera, 8.5 km NNE of Talayuela, Cuestas de Torresca, 363 m, bark of *E. camaldulensis*, 28.II.2016, E. Rubio (E.R.D. 6658, doc. vid.). – **Cataluña**, **Girona**, 10 km SW of Girona, 2 km NNW of Sant Dalmai, 180 m, log of *Eucalyptus*, on bark, 24.X.2015, M.À. Pérez-de-Gregorio & J. Carbó, vid. J. Bometón (J.B. 621/15, doc. vid.).

Map 86. Known distribution of *O. albidorosea* in Australia.

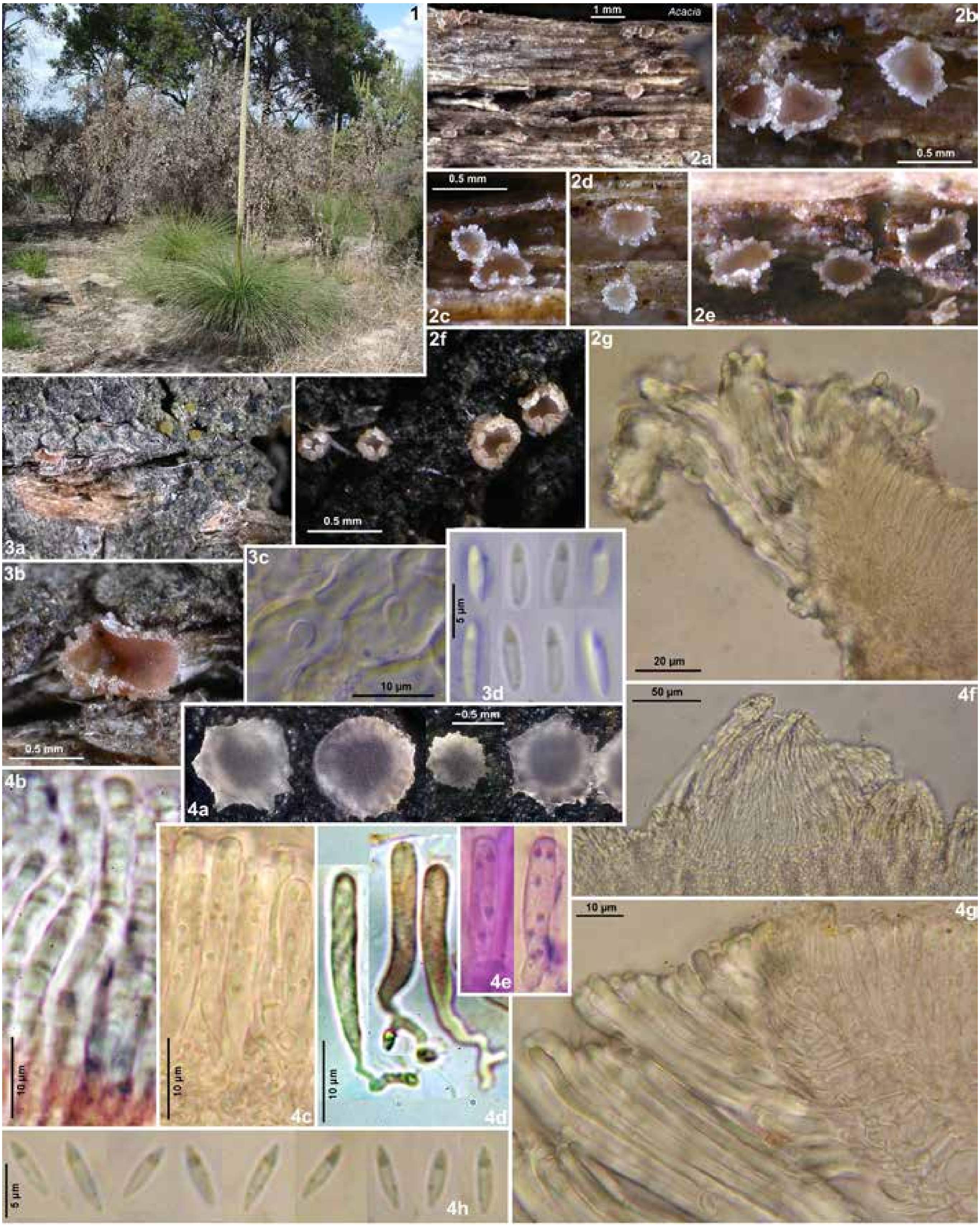


Plate 517. **1–4**: *Orbilia albidorosea*. – **1**. semihumid banksia-eucalypt open woodland with *Xanthorrhoea*; **2a–f**, **3a–b**. rehydrated apothecia; **4a**. fresh apothecia; **2g**, **4g**. marginal ectal excipulum in median section, with agglutinated glassy processes; **4f**. marginal tooth in top view, composed of glassy processes; **4b**. stratified glassy processes; **3c**. SCBs in cells of ectal excipulum; **4c–e**. asci with spores (SBs stained); **3d**, **4h** ascospores. – Living state, except for **4b**, **d** (in CR), asci in **4e** (in CRB). – **4a–b**, **d**: phot. E. Rubio. — **1**. H.B. 7284h: Western Australia, Swan Valley, on *Jacksonia*; **2a–g**. H.B. 6615a (holotype): Australia, Queensland, on *Acacia*; **3a–d**. H.B. 8582d: Western Australia, Bindoon, on *Acacia*; **4a–h**. H.B. 9031: Spain, Asturias, on *Eucalyptus*.

Orbilia pleioalbidorosea Baral, **sp. nov.**, MB 813781 — Pls 518–519

Etymology: similar to *O. albidorosea*, but with 16-spored asci.

Typification: Spain, Teruel, Guadalaviar, branch of *Amelanchier ovalis*, 26.IX.1999, G. Marson (ex H.B. 6486a, M-0276556, holotype).

Latin diagnosis: *Differt ab* O. albidorosea *ascis 16-sporis, ascosporis magis fusiformibus, processis vitreis excipuli marginalis brevioribus. Habitat ad corticem putridum rami sicci* Amelanchieris *et* Pistaciae *in zona supra(sub) mediterranea humida ad semihumida Europae meridionalis.*

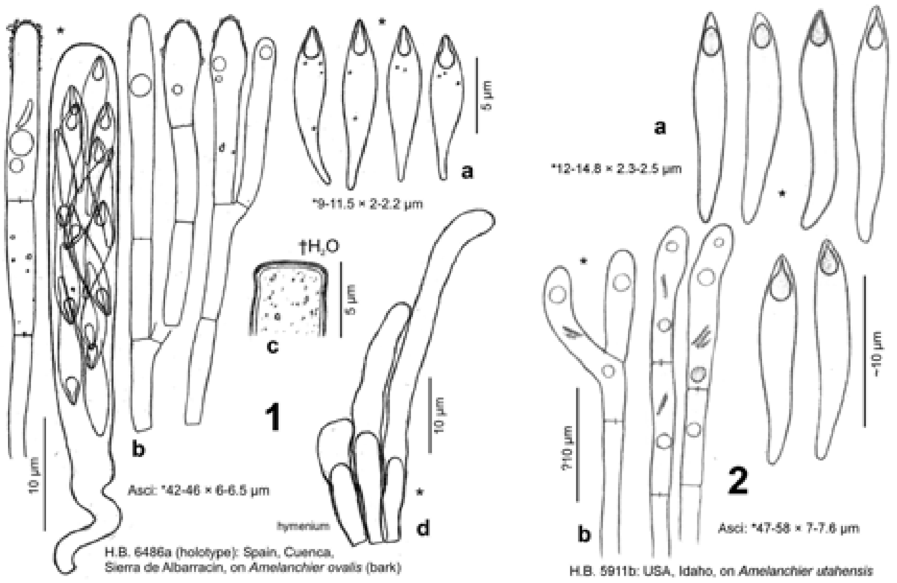


Plate 518. **1**: *Orbilia pleioalbidorosea*; **2**: *O.* cf. *pleioalbidorosea*. – **a**. ascospores; **b**. ascus and paraphyses (with globose and crystalloid SCBs); **c**. ascus apex; **d**. marginal cortical cells with glassy processes, in median section.

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.2–)0.3–0.7(–0.85) mm diam., 0.1–0.17 mm high, ± round, solitary or gregarious in small groups; disc medium concave to flat, bright orange-rose(-ochraceous), margin with prominent, whitish, hairy teeth; broadly sessile, superficial. **Asci** *42–46 × 6–6.5 µm {T} or *45–69 × 7–7.5 µm {2}, †39–45 × 5–5.5 {T} or †41–58 × 4.7–6.5 µm {2}, 16-spored, spores *~4-seriate, lower ~8 spores inverted (± mixed), pars sporifera *34 {T} or *43 {1} µm long; **apex** (†) strongly truncate (not indented, laterally not or slightly widened); **base** with short, ± thick, flexuous, L- to Y- or h-shaped stalk. **Ascospores** *9–11.5 × 2–2.2 µm {T} or *(8.5–)10–13(–14.5) × (2–)2.2–2.6(–2.8) µm {2}, †8–10 × 1.8–2 µm {T} or †9–12 × 1.8–2.2 µm {1}, fusiform, apex acute, base strongly attenuated (often tail-like), straight to slightly curved near base; **SBs** 1.9–2.6 × 1–1.3(–1.5) {T} or 2.7–3.2 × 1–1.4 → 2.5 × 1.4–1.6 µm {2}, tear-shaped (to ampulliform). **Paraphyses** apically uninflated to slightly or medium obtusely lanceolate to spathulate or lageniform, terminal cells *(9.5–)13–20(–22) × (1.8–)2.3–3.3(–3.7) µm {3}, lower cells *8–13 × 1.8–2.5 µm {2}; rarely branched at upper septum. **Medullary excipulum** 20–70 µm thick, of dense textura intricata-angularis, indistinctly delimited. **Ectal excipulum** pale rose, of thin-walled, irregularly oriented small-celled t. angularis from base to mid flanks; 30–40 µm thick at base, cells *9–22 × 6–13 µm {1}; ~15 µm thick at margin, of t. porrecta oriented at a ~20–30° angle to the surface, marginal cortical cells */†10–16 × 2–4 µm (at submargin 4–5 µm wide) {2}; **glassy processes** at margin 20–50 × 3–4 µm {2}, high-refractive, stratified or not, outwards curved, loosely agglutinated to form teeth, from lower flanks to submargin forming glassy caps 3–6 × 3.5–5 µm {T} or also up to 50 µm long glassy processes {1}. **Anchoring hyphae** sparse, †2–3 µm wide, walls 0.2 µm thick {T}. **SCBs** in paraphyses globose, rarely with rod-shaped SCBs {2}; in excipulum forming large, thin, rod- to ring-shaped structures {2}. **Exudate** over paraphyses thin, granular, firmly attached. **— ANAMORPH**: unknown.

Habitat: collected 0.3–0.8 m above the ground, corticated to partially decorticated, 10–30 mm thick branches of *Amelanchier ovalis* {T}, *Pistacia terebinthus* {1}, *Rosa sicula* {1}, on medium to strongly decayed bark {2}, on periderm or bast (periderm rolled aside), bark partially detaching, also on inner surface of bark or at edge, strongly greyed or blackened when exposed, with some or many green algae. **Associated**: *Lecidea ?leprarioides* {1}, *Melanohalea exasperata* {1}, *Orbilia ovalis* {1}, *O. xanthoguttulata* {1}, *Physcia stellaris* {1}. **Desiccation tolerance**: fully tolerant for at least 2.5 months. **Altitude**: 1130–1818 m a.s.l. **Geology**: Jurassic dolomite and Cretaceous marly limestone & clay. **Phenology**: III, IX–X (but long-lived).

Taxonomic remarks. *Orbilia pleioalbidorosea* differs from *O. albidorosea* in 16-spored asci, ascospores with or without a short tail-like base, and outwards curved glassy processes.

Variation. The collections on *Pistacia* (Pl. 519: 3) and *Rosa* (Pl. 519: 2) deviate from the holotype in larger, especially longer asci, spores, and SBs, nevertheless we consider them as conspecific. The paraphyses in the *Pistacia* sample were apically almost uninflated, while in that on *Rosa* they were spathulate as in the holotype, though distinctly wider.

Not included collections. Two very sparse, unpreserved North American collections are not included in the description of *O. pleioalbidorosea*. That from Idaho on *Amelanchier utahensis* (Pl. 518: 2) differs from the holotype in distinctly longer spores but falls in the scope of the two paratypes. Another from Arizona on *Pinus ponderosa* differs in much wider spores (*8.5–11.5 × 3–3.5 µm) with wider SBs (1.8–2.4 × 1.3–1.6 µm) and probably belongs to a separate species. Only a few microphotos of the hymenium exist (IVV: 17.VI.2003). Whether the apothecia possessed glassy processes was not documented in both.

Phylogeny. A sequence from one of the Andalusian strains comprises ITS (without S1506 intron) and LSU (D1–D2). In our combined analysis (Phyl. 13) it clustered strongly supported with *O. navicularis* (distance in ITS 2.5%, LSU 0.5%), and *O. albidorosea* sister to them (distance in ITS 6.5%, LSU 2.6%).

Ecology. *O. pleioalbidorosea* occurred on rotten bark of xeric branches of angiosperm shrubs in mountainous calcareous sites of different regions of Spain. The holotype of *O. pleioalbidorosea*, which consisted of only three apothecia, was collected on *Amelanchier ovalis* in a suprasubmediterranean semihumid, south-exposed pine-juniper woodland in the Sierra de Albarracín in eastern Spain. The two paratypes derive from the supramediterranean (semi)humid Sierra Sur de Jáen in southern Spain, that on *Pistacia* from a *Quercus rotundifolia-Q. faginea* open forest with *Juniperus oxycedrus* and *Crataegus monogyna*, and that on *Rosa* from a shrubland with *Amelanchier ovalis*, *Berberis hispanica*, *Crataegus monogyna*, *Prunus mahaleb*, *Rhamnus saxatilis*, *Sorbus aria* etc.

The two not included collections from western North America were on *Amelanchier* from Idaho in a cold-temperate subhumid sagebrush desert scrub at the foot of the Middle Rocky Mountains bordering the Great Basin, and on *Pinus* from Arizona in a cold-temperate humid ponderosa pine forest in the Mogollon Rim.

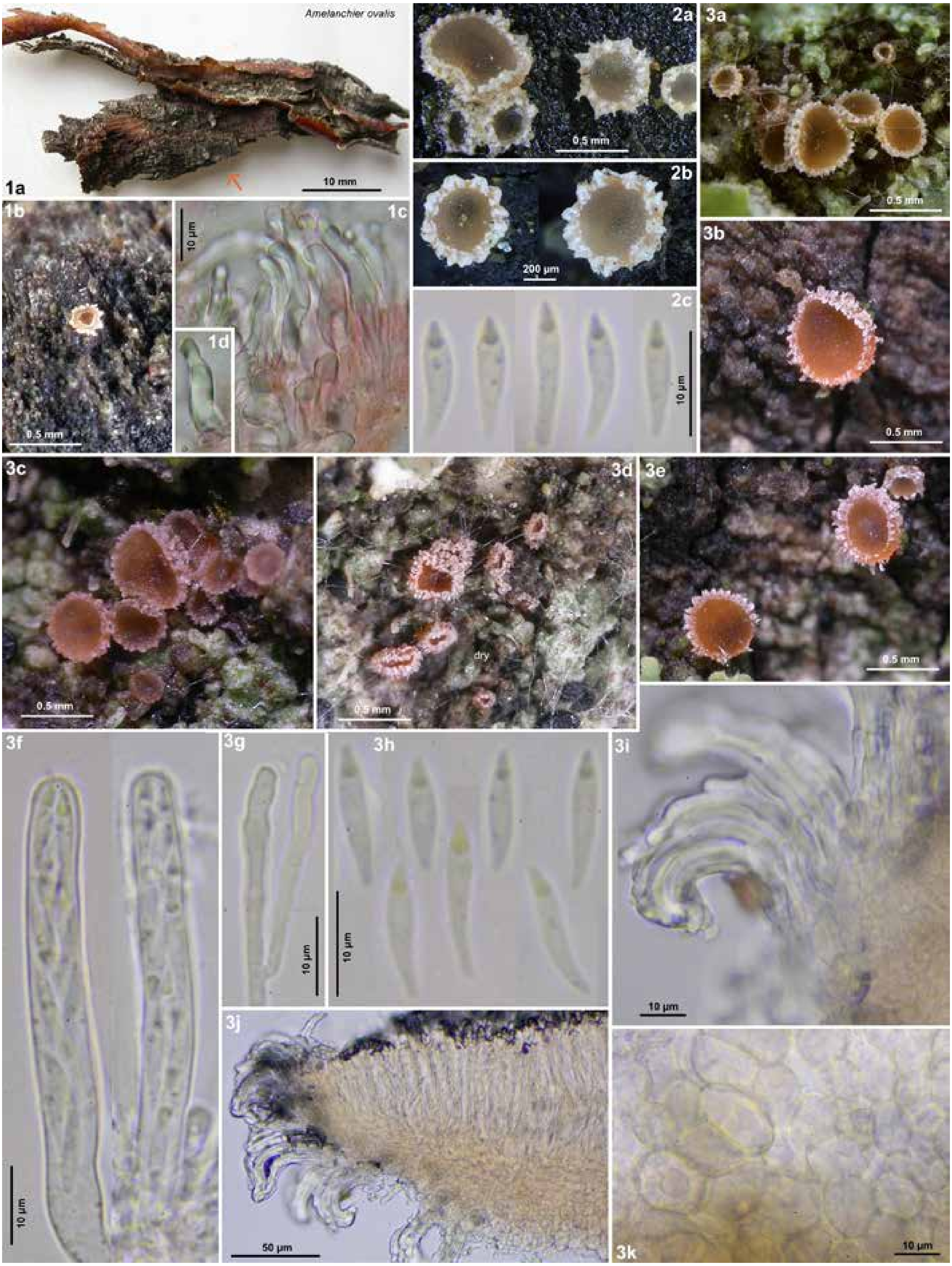


Plate 519. **1–3**: *Orbilia pleioalbidorosea*. – **1a**. xeric bark of a corticated branch of *Amelanchier ovalis*; **1b**, **2a–b**, **3a–c**, **e**. rehydrated apothecia; **3d**. dry apothecia; **3j**. apothecium in median section; **1c–d**, **3i**. marginal glassy processes; **3k**. indistinct crystalloid SCBs in cells of ectal excipulum at lower flanks; **3f–g**. asci and paraphyses; **2c**, **3h**. ascospores. – Living state, except for **1c–d** (in KOH+CR), right ascus in **3f** (in H_2O). – **2a–c**, **3a**, **f–k**: phot. S. Tello. — **1a–d**. H.B. 6486a (holotype): Spain, Cuenca, Sierra de Albarracín, on *Amelanchier*; **2a–c**. S.T. 01101702: Andalucía, Sierra de la Pandera, on *Rosa*; **3a–k**. S.T. 05031721: id., Sierra Sur de Jáen, on *Pistacia*.

Specimens included. **SPAIN**: **Castilla-La Mancha**, **Cuenca**, Sierra de Albarracín, 43 km NE of Cuenca, 8 km SW of Guadalaviar, S of Mt. Mogorrit, E of Peñu la Varga, 1600 m, branch of *Amelanchier ovalis*, on bark, 26.IX.1999, G. Marson (ex H.B. 6486a, M-0276556, **holotype**). – **Andalucía**, **Jaén**, Sierra Sur de Jáen, 21 km SSE of Jaén, 9.5 km E of Valdepeñas de Jaén, El Moralejo, 1218 m, branch of *Pistacia terebinthus*, on bark, 5.III.2017, S. Tello (S.T. 05031721, H.B. 10080a; sq.: MK493146). – Sierra de La Pandera, 15.5 km S of Jaén, 3 km W of El Parrizoso, Pico de la Pandera, 1818 m, branch of *Rosa sicula*, on bark, 1.X.2017, S. Tello (S.T. 01101702, doc. vid.).

Not included. **USA**: **Idaho**, Great Basin, Malad City, ~1435 m, branch of *Amelanchier utahensis*, 3.VI.1996, G. Marson (H.B. 5911b ø). – **Arizona**, Mogollon Rim, 16 km NW of Flagstaff, San Francisco Peaks, 6 km WSW of Humphreys Peak, 2550 m, branch of *Pinus ponderosa*, 17.VI.2003, G. Marson (ø).

Orbilia albovinosa Baral, **sp. nov.**, MB 813782 — Pl. 520

≡ *Hyaloscypha albovinosa* Maire in sched., nom. inval., ICN Art. 30.6

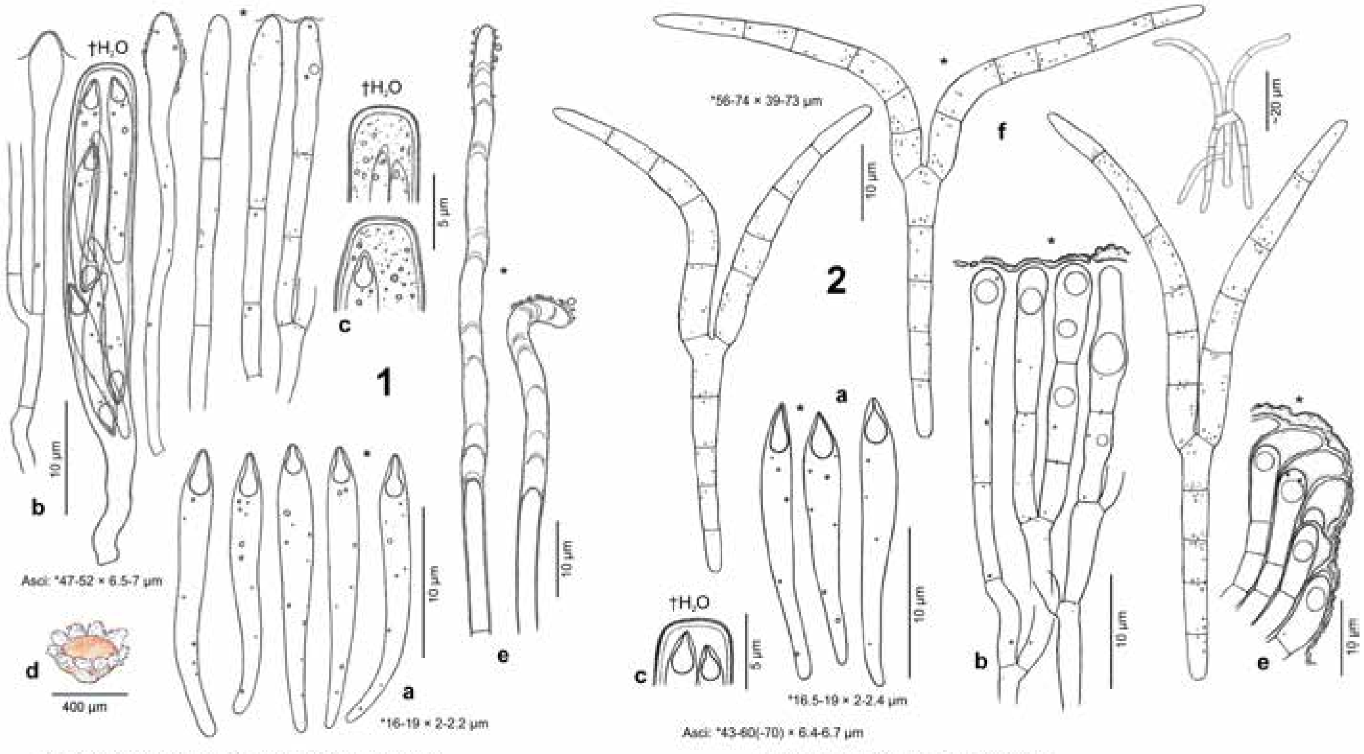
Etymology: referring to the colour of the apothecia with a reddish disc and whitish marginal teeth.

Typification: Croatia, Korčula island, branch of *Lonicera* (?)*implexa*, 4.VI.2000, H.O. Baral (ex H.B. 6683, M-0276431, holotype).

Latin diagnosis: *Differt ab* O. albidorosea *ascosporis multo longioribus*, *cellulis vivis excipuli et paraphysium corpusculis crystalloideis carentibus. Habitat ad corticem putridum ramorum siccorum* Lonicerae *et in lignum* Fici *in zona (sub) mediterranea semihumida Europae meridionalis et Africae septentrionalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.3–0.6(–0.8) mm diam. (incl. teeth), 0.9–1.1 mm high, pale to light (orange-) rose, semitranslucent, round, scattered or in small groups; disc flat, margin thin and smooth {1} or with prominent whitish, rounded, hairy teeth {2}; sessile to substipitate, superficial. **Asci** *(43–)47–60(–70) × 6.4–7 µm {2}, †(38–)43–55 × 5–6(–6.5) µm {3}, 8-spored, spores *4-seriate, 3–5 lower spores inverted {2}; **apex** (†) (slightly to) medium to strongly truncate (not or slightly indented, laterally not widened); **base** with short to medium long stalk, simple or L- to h-shaped. **Ascospores** *16–19 × 2–2.4 µm {2}, †~13–18.5 × 1.5–2 µm {1}, narrowly fusiform(-clavate) with a short to long cylindrical middle part, apex subacute to acute, base gradually attenuated in a thick tail-like end, ± straight but slightly to medium curved or geniculate near base; **SBs** (2–)2.5–3(–3.5) × 1.1–1.4 µm {2}, tear-shaped (to ampulliform). **Paraphyses** apically uninflated to slightly or medium spathulate to obtusely lanceolate {2}, or cylindrical to very slightly capitate {1}, terminal cells *8.5–18 × (1.8–)2.5–3.3 µm {2}, †2–3(–3.5) µm wide {1}, lower cells *(4.5–)6.5–10(–15) × 1.5–2.6 µm {2}; unbranched at upper septum. **Medullary excipulum** hyaline, 20–25 µm thick, rather sharply delimited. **Ectal excipulum** very pale rose, of thin-walled, irregularly oriented textura angularis(-prismatica) from base to mid flanks, 25 µm thick near base, cells *6–11 × 4–9 µm {1}; 20 µm thick near margin, of t. prismatica-porrecta oriented at a 20–30° angle to the surface (inner layer at 45°), marginal cortical cells *8–20 × 2.7–4 µm {3}; **glassy processes** 1–7 {1} or 20–80 µm {2} × (2.5–)3–4(–5) µm, medium to high-refractive, stratified, straight, some apically hooked, when long loosely coherent to form large teeth. **SCBs** in paraphyses absent or mostly present, globose. **Exudate** over paraphyses absent {2} or 0.3–2 µm thick {1}, continuous-cloddy, loosely attached; over margin and flanks sparse to abundant, granular to cloddy. **Anchoring hyphae** medium abundant, *2–3 µm wide, walls 0.2–0.5 µm thick {1}. — **ANAMORPH**: dicranidion/trinacrium-, rarely dwayaangam-like (from ascospore isolate {1}). **Conidiophores** not observed. **Conidia** Y- to T-shaped with the two arms slightly to strongly curved outwards, total size *56–74 × 39–73 µm, stipe *28–33 × 3–4 µm, 4-septate, arms slightly tapering, *33–47 × 3.5–4 µm (in situ, actual length ~38–50 µm), 5–7-septate {1}; rarely 4-armed conidia seen (dwayaangam-like).

Habitat: collected 1–3 m above the ground, corticated, 8–40 mm thick branches of *Ficus carica* {1}, *Lonicera etrusca* {1}, *L.* (?)*implexa* {T}, partly still-living (*L. implexa*), on medium to strongly decayed wood {1} or loosely attached bark (periderm) {T}, strongly greyed or not, no green algae. **Associated**: ?*Nectria* sp. {1}, *Orbilia caulicola* {1}, *O. cylindrosoma* {1}, *O. flavida* {1}, *O. pleiolentiformis* {1}, *O. ungulata* {1}, *O. vitalbae* {1}, *Patellaria atrata* {1}, *Peroneutypa* ?*scoparia* {1}, *Trichopeziza* ?*perrotioides* (immature) {1}. **Desiccation tolerance**: fully viable for at least 3 weeks. **Altitude**: 120–1000 m a.s.l. **Geology**: Croatia: Cretaceous limestone, France: Miocene calcareous sandstone (molasse). **Phenology**: I, VI, X (probably long-lived and throughout the year).



H.B. 6683 (holotype): Croatia, Korčula, on *Lonicera implexa* (bark)

H.B. 7231f: France, Drôme, on *Ficus carica* (wood)

Plate 520. **1–2**: *Orbilia albovinosa*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. rehydrated apothecium with hairy-dentate margin; **e**. marginal ectal excipulum (**2e** in median section), cortical cells with glassy processes; **f**. conidia from culture.

Taxonomic remarks. Typical *O. albovinosa* (on *Lonicera*) is macroscopically characterized by apothecia with a rose hymenium and prominent white teeth at the margin which are composed of long glassy processes, while a sample on *Ficus* had a smooth margin. The species differs from *O. albidorosea* in much longer ascospores, also in lacking crystalloid SCBs. For the similar Australian *O. subalbovinosa* see p. 946. A North American collection differs in 16-spored asci and the presence of crystalloid SCBs (see below).

Variation. *O. albovinosa* was available for study only from very sparse material. The collection on wood of *Ficus* deviates from those on bark of *Lonicera* in having only very short glassy processes, also in a much thicker exudate and in non-spathulate paraphyses. Together with the deviating substrate it possibly represents a different species. It is included in the description since the other features closely concur with the two specimens on *Lonicera*.

Not included collection. A sample on *Euphorbia* from Montenegro (IVV: 21.VI.2019) is not included because of its much shorter spores (*12–16 × 1.9–2.3 µm), but it concurs with that on *Ficus* in the short glassy processes (5–15 × 2.5–3 µm), thick exudate, and non-spathulate paraphyses

Nomenclature and type studies. The north-African specimen of *O. albovinosa*, which bears R. Maire's handwritten diagnosis, was labelled '*Hyaloscypha albo-vinosa* n. sp.' by him. It appears to fit very well the specimen from Croatia. Duplicates of it do not appear to have been distributed in other herbaria. Since the name could not be traced in Maire's publications, his epithet is apparently an invalid herbarium name that appears only in this single specimen. His drawing (Fig. 170: a) shows living paraphyses which he described as apically slightly inflated [narrowly clavate to somewhat (obtusely) lanceolate], with mostly 1 guttule [SCB] below their inflated upper part, and the partly hooked glassy processes with a distinct stratification. Asci ('40–55 × 5.5–6.5 µm, 4–8-spored') and spores ('14–15 × 2 µm') were drawn by him in the dead state, therefore, no SBs are reported. During his monograph of *Hyaloscypha* and a study on glassy-haired taxa of *Hyaloscyphaceae*, Huhtinen (1987a: 281) examined also Maire's specimen, which he considered at that time to belong to *Hyalopeziza*. Huhtinen's unpublished drawing (IVV: H.B. 6707) shows glassy processes 20–80 µm long. In the present study, Maire's collection was only examined from a permanent slide kindly sent by S. Huhtinen.

Anamorph. The peculiar conidia of *O. albovinosa* show similarities to species of both *Dicranidion* and *Trinacrium*. Among the described species, *Trinacrium gracile* comes closest but has much smaller conidia with straight arms. Rarely 4-armed, dwayaangam-like conidia were observed. Révay & Gönczöl (2010: fig. 19–20) illustrated conidia as 'unknown sp. 8' from rainwater on living *Vaccinium myrtillus* in Sweden which are very similar to the 2-armed ones observed in *O. albovinosa*.

Phylogeny. A sequence taken from the ex-type culture (SSU without S1506 intron, ITS, LSU) shows in the entire ITS region a distance of 12.5% to *O. albidorosea* and 16% to *O. pseudoaristata*. The lowest distance in the LSU D1–D2 is 3.5% to *O. pseudoaristata* and 4.5% to *O. albidorosea*. *O. albovinosa* formed in the analysis of LSU a weakly supported clade with *O. pseudoaristata* (Phyl. S16), whereas in the combined analysis it clustered closer to the clade with *O. albidorosea* (Phyl. 13).

Ecology. *O. albovinosa* was found on medium rotten bark of xeric branches of *Lonicera*, but also on xeric wood of *Ficus*, in mesosub- to mesomediterranean semihumid southern Europe and northern Africa. The holotype locality is a shady maquis with *Quercus ilex* and *Arbutus unedo* around a cave in the Dinaric karst. Also the not included sample from Montenegro was from a mesosubmediterranean area.

Specimens included. **ALGERIA**: **Algiers**, Atlas Mts., ~60 km SSW of Algiers, Ben-Chicao, ~1000 m, branch of *Lonicera etrusca*, 3.I.1920, collector unknown (MPU C04768, R. Maire, Champ. de l'Afrique du Nord 6775, as *Hyaloscypha albovinosa*, H.B. 6707 ø). — **CROATIA**: **Dubrovnik-Neretva**, **Korčula**, 11.5 km W of Korčula, 2 km W of Račišće, Samograd cave, 120 m, branch of *Lonicera* (?)*implexa*, on bark, 4.VI.2000, H.O. Baral (ex H.B. 6683, M-0276431, **holotype**). — **FRANCE**: **Rhône-Alpes**, **Drôme**, Préalpes du Dauphiné, 1 km N of Nyons, W of Col du Pontias, S of Forêt Domaniale de Vaux, 415 m, branch of *Ficus carica*, on wood, 11.X.2002, G. Marson (H.B. 7231f, anam. cult., CBS 140882; sq.: KT215255).

Not included. **MONTENEGRO**: 1.5 km NW of Herceg Novi, SW of Trebesinj, 185 m, stem of *Euphorbia*, 21.VI.2019, D. Savić (FG-1090, doc. vid.).

Orbilia subalbovinosa Baral & G. Marson, **sp. nov.**, MB 813783 — Pls 521–522

Etymology: named after the similarity to *O. albovinosa*.
Typification: Western Australia, Nornalup, branches of *Eucalyptus*, 15.XII.2001, G. Marson (ex H.B. 7202, MEL 2389221, holotype).

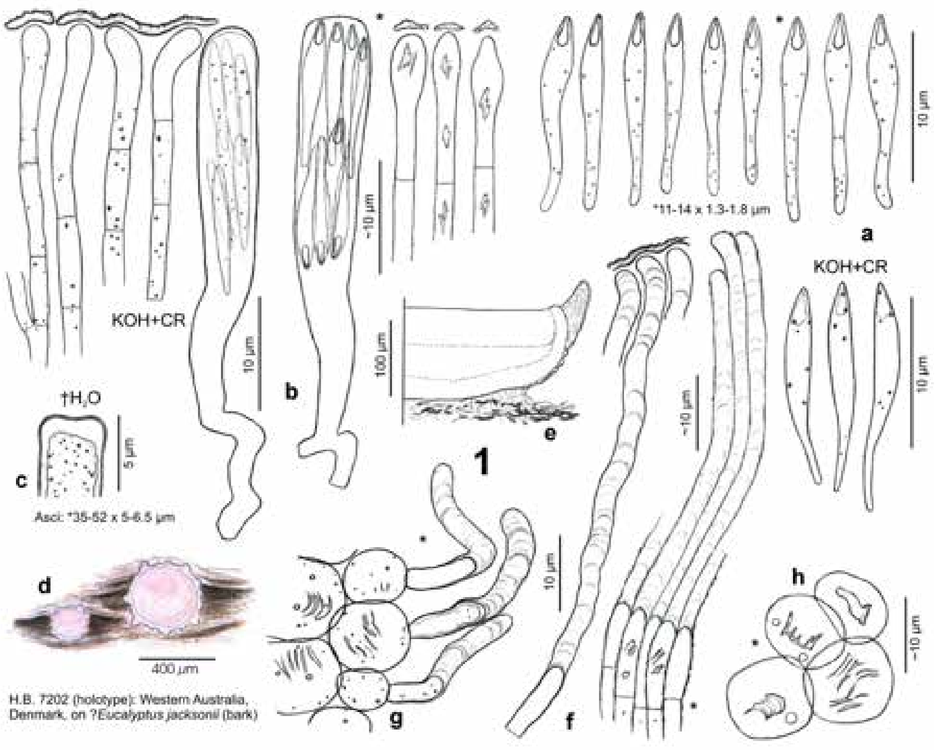


Plate 521. **1**: *Orbilia subalbovinosa*. – **a**. ascospores; **b**. asci and paraphyses; **c**. ascus apex; **d**. apothecia with dentate margin (rehydrated); **e**. apothecium in median section; **f**. id., marginal cortical cells tipped by long glassy processes; **g**. id., at mid flanks, hairs here not agglutinated; **g–h**. ectal excipular cells with crystalloid SCBs.

Latin diagnosis: *Differt ab* O. albovinosa *ascosporis et corpusculis refringentibus multo angustioribus, hymenio exsudato distincte tecto. Habitat ad corticem putridum ramorum siccorum* Eucalypti *in zona subtropica semihumida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.15–0.4 mm diam., 0.08–0.12 mm high, (very) pale rose, translucent, round, very scattered; disc flat, margin distinct, with prominent whitish teeth protruding 45 µm beyond disc; broadly sessile, superficial to slightly erumpent; dry disc half closed by the incurved teeth. **Asci** *35–52 × 5–6.5 µm, †38–46 × 4.7–5.3 µm, 8-spored, spores *4-seriate, 3 lower spores inverted; **apex** (†) strongly truncate (distinctly indented, laterally slightly widened); **base** with short to medium long, thick, flexuous stalk, L- to h-shaped. **Ascospores** *11–14 × 1.3–1.8 µm, †13–15 × 1.6–1.7 µm, narrowly fusiform-clavate, apex acute, base always attenuated in a distinct *0.5–1 µm thick tail, straight to slightly curved in lower part; **SBs** *1.8–2.5 × 0.5–0.8 µm, narrowly tear-shaped. **Paraphyses** apically uninflated to medium clavate, sometimes spathulate-lanceolate, terminal cells *~9.5–17 × 2.8–3.5, †8.5–17 × 1.5–2.5 µm, not exceeding the living or dead asci, lower cells †6–8.5 × 1.5–2 µm; unbranched at upper septum. **Medullary excipulum** 20–50 µm thick, of medium dense textura intricata with many inflated cells, sharply delimited. **Ectal excipulum** of thin-walled († slightly gelatinized) t. globulosa-angularis-prismatica from base to submargin, 20–30 µm thick near base, cells *8–27 × 7–12 µm, guttulate; 15 µm thick near margin, of t. prismatica-porrecta oriented at a 50–70° angle to the surface, marginal cortical cells †7–9 × 2.5–3.5 µm; **glassy processes** 10–70 × 2.5–4 µm, high-refractive, strongly stratified in KOH, inwards curved, coherent to form distinct teeth. **Anchoring hyphae** medium abundant, †1.5–2.7 µm wide, walls 0.2–0.3(–0.4) µm thick. **SCBs** in paraphyses and ectal excipulum crystalloid, in excipulum also small globose SCBs. **Exudate** over paraphyses 0.3–2 µm thick, rough-continuous, hyaline, loosely attached; over margin and flanks 1–2 µm thick, cloddy-continuous. **ANAMORPH**: unknown.

Habitat: collected 1–2 m above the ground, 7–8(–?20) mm thick corticated branches of *Eucalyptus* sp., on bark (periderm & bast), partly on detached bark (on both sides), medium decayed, medium greyed, no algae. **Associated**: *Peniophora* sp., *Sclerococcum* sp. **Desiccation tolerance**: fully viable for at least a few months, after 9 months only ectal excipulum and a few immature asci still alive. **Altitude**: 60 m a.s.l. **Geology**: granulite with granitic gneiss. **Phenology**: long-lived.

Taxonomic remarks. *Orbilia subalbovinosa* resembles *O. albovinosa* and *O. pseudoaristata* in the ascospores and the rose-coloured apothecia with large whitish marginal teeth. It differs in narrower spores and SBs, paraphyses being covered by a distinct exudate, and the presence of crystalloid SCBs (but the *Ficus* collection included in *O. albovinosa* also shows a distinct exudate). *O. albidorosea* differs in much shorter spores and a very sparse exudate.

Ecology. *O. subalbovinosa* was collected on medium decayed bark of xeric branches of *Eucalyptus* sp. in a subtropical semihumid eucalypt (karri-tingle) open forest in a hilly sandy area in the Warren ecoregion of southwestern Australia. The identity of the host genus is not fully certain. It was thought to be *Eucalyptus jacksonii* (Red Tingle), but the wood anatomy of that species shows the largest vessel diameters in the genus in contrast to the present substrate which has very small vessels.

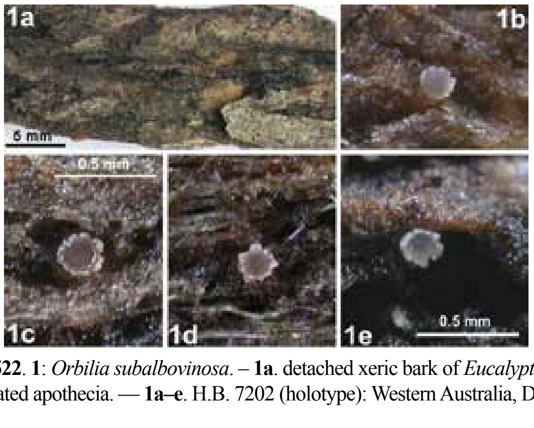


Plate 522. **1**: *Orbilia subalbovinosa*. – **1a**. detached xeric bark of *Eucalyptus*; **1b–e**. rehydrated apothecia. — **1a–e**. H.B. 7202 (holotype): Western Australia, Denmark.

Specimens included. **AUSTRALIA**: **Western Australia**, Warren, 40 km W of Denmark, 8.5 km E of Nornalup, SE of Valley of the Giants, 60 m, branches of *Eucalyptus*, on bark, 15.XII.2001, G. Marson (ex H.B. 7202, MEL 2389221, **holotype**).

Orbilia pseudoaristata Baral & G. Marson, **sp. nov.**, MB 813784 — Pls 523–525, Map 87

Etymology: referring to the similarity in spore shape with *Orbilia aristata* and *O. clavuliaristata.*

Typification: Germany, Baden-Württemberg, Tübingen, branch of *Salix alba*, 19.III.2003, H.O. Baral (ex H.B. 7313, M-0276570, holotype).

Latin diagnosis: *Differt ab* O. albovinosa *ascosporis abrupte caudatis*, *ab* O. subalbovinosa *ascosporis latioribus*, *cellulis vivis excipuli et paraphysium corpusculis crystalloideis carentibus*, *ab* O. aristata *et* O. clavuliaristata *ascis in statu emortuo truncatis*, *tenuitunicatis. Habitat ad corticem putridum ramorum siccorum* Salicis *et* Corni *etc. in zona temperata ad subtropica humida ad semihumida Europae et Australiae.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated (0.15–)0.2–0.6(–0.9) mm diam. (excl. teeth), 0.09–0.2 mm high (receptacle 0.08–0.12 mm), pale to light rose to greyish rose(-orange), semitranslucent, round, scattered to subgregarious; disc slightly to medium concave, margin with prominent whitish hairy teeth 40–100 × 40–100 µm, protruding 30–60 µm beyond disc; sessile or with an ill-defined stipe 0.04–0.05 × 0.15–0.17 mm, superficial, somewhat immersed in detritus; dry nearly closed, disc light to bright rose-red. **Asci** *(38–)42–60(–70) × 6–6.7 µm {4} → 6–7.5 µm, †(37–)40–50(–57) × (4.8–)5–5.7(–6) µm {3}, 8-spored, spores (*) biseriate, 0–4(–5) lower spores inverted {8} (not mixed), pars sporifera *28–40 → 17–23 µm long; **apex** (†) (slightly to) medium (to strongly) truncate (not indented, laterally not widened) {5}; **base** with short to very long, thin, flexuous stalk, T-, L-, Y- or h-shaped. **Ascospores** *(13–)14–18(–19)(–24.7) × (2.3–)2.4–2.7(–2.8) µm {6} or 16.7–24.5 × 2.2–3 µm {2}, †13–16(–18.7) × 2.3–2.8 µm {1} or 25–26.5 × 2.3–2.5 µm {1}, with fusiform head and medium sharply differentiated tail of about equal length or slightly longer, apex subacute to acute, tail base not or sometimes very slightly inflated, *0.5–1 µm wide, tail straight to slightly (rarely medium) curved; **SBs** *(2–)2.3–3 {7} × (1.1–)1.2–1.4(–1.5) {6} or 1.6–2 µm {1}, broadly tear-shaped to pyriform. **Paraphyses** apically uninflated to very slightly clavate(-capitate) or subspathulate, terminal cells *(7–)9–15(–19) × 2–2.5(–3) µm {4}, †10–15 × 1.5–2.3 µm {1}, sometimes ± flexuous, protruding 5–10 µm beyond dead asci, lower cells *(5–)7–11(–14) × 1.5–2.5(–3) µm {5}; rarely branched at upper septum. **Medullary excipulum** hyaline to pale rose, 20–70 µm thick, of dense textura intricata with many inflated cells, indistinctly to sharply delimited. **Ectal excipulum** hyaline to pale rose, of (†) thin-walled, vertically oriented t. globulosa-angularis-prismatica from base to mid flanks or submargin, 25–80 µm thick near base, cells *(6–)8–16(–22) × (5–)7–10(–13) µm {3}, †7–10 × 5–9 µm {1}; 20 µm thick at flanks, 15–30 µm near margin, oriented at a 45–80° angle to the surface, externally or at upper margin of t. prismatica-porrecta oriented at (10–)30–45°, cortical cells bearing ± free, 17–30 µm long, 3–4-celled hairs with terminal cells *5–15 × 3–4 µm {2}, †7–10 × 2.8–3 µm {1}; tipped by **glassy processes** (13–)20–70(–120) × (2.5–)3–4(–5) µm {5}, low- to high-refractive, ± stratified only in KOH, very strongly outwards curved, coherent to form distinct hairy teeth (sometimes also in centre of disc with fascicles of proliferating glassy processes). **Anchoring hyphae** abundant, */†1.5–3 µm wide, walls 0.2–0.4(–0.5) µm thick {4}. **SCBs** globose, in paraphyses 0.8–1.3 µm diam.; in ectal excipulum (at flanks and margin) 1.2–2.8 µm, rarely with very low-refractive, very pale reddish, angular SCBs 2–3 µm diam. {H.B. 8456b}. **Exudate** over

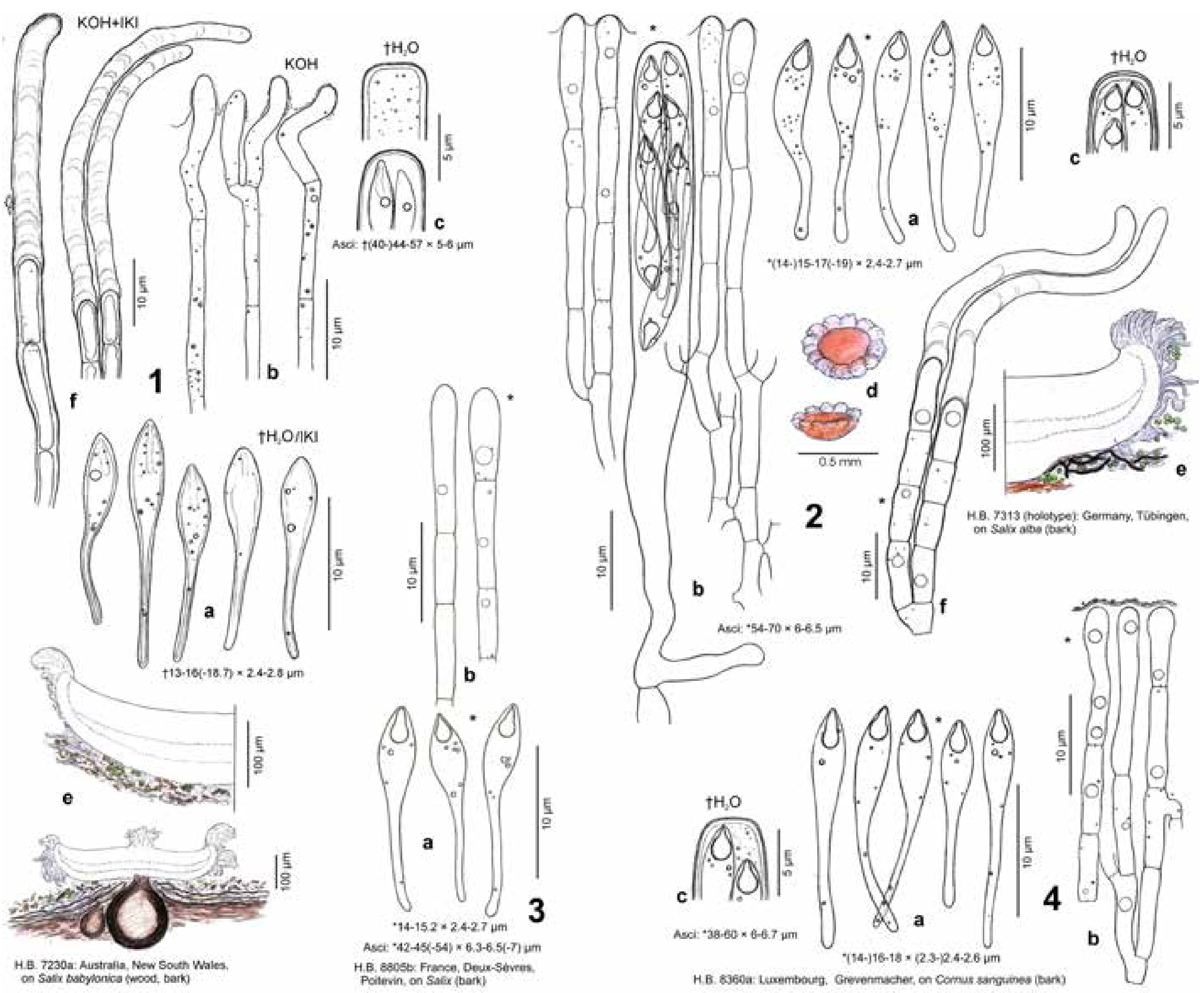


Plate 523. **1–4**: *Orbilia pseudoaristata*. – **a**. ascospores; **b**. ascus and paraphyses; **c**. ascus apices; **d**. apothecia with hairy-dentate margin; **e**. apothecia in median section (**1**: on old pyrenomycete); **f**. id., marginal hair-like cells with long glassy processes.

paraphyses and hairs absent or 0.2 µm thick, sparse, minutely granular. **— ANAMORPH**: trinacrium-like (presumed, from natural substrate {3}). **Conidiophores** not seen. **Conidia** T-shaped with the two arms curved downwards, total size *35–46 × 39–52 µm, stipe *28–38 × 2.7–3 µm, 5–6-septate, arms slightly tapering, *17–31 × 2.7–3.5 µm in situ (actual length ~24–32 µm), 4–6(–7)-septate {2}.

Habitat: collected 1–3 m above the ground, ± corticated, 6–40 mm thick branches or > 10 cm thick trunks of *Cornus* sp. {1}, *C. sanguinea* {5}, *Fraxinus excelsior* {1}, *Malus domestica* {1}, *Pistacia lentiscus* {1}, *Prunus padus* {1}, *Salix* sp. {1}, *S. alba* {1}, *S. babylonica* {1}, *Sorbus aucuparia* {1}, *Ulmus glabra* {1}, ?*U. minor* {1}, on medium to strongly decayed bark {12} (bast {6} and periderm {2}) or wood {4}, stem of *Rubus ?armeniacus* {1}, partly beneath periderm rolling aside, also on small cracks in periderm or on peeling bark, sometimes directly over ostioles of an old pyrenomycete, entire bark partially detaching, some apothecia on inner surface of bark, somewhat greyed, mostly covered by many green algae. **Associated**: *Caloplaca ?cerinella* {1}, *Craterocolla cerasi* {1}, *Cryptodiaporthe rostellata* {1}, *Dacrymyces* sp. {1}, *Eutypa* sp. {1}, *Flagelloscypha* sp. {1}, *Gloniella* sp. {1}, *Hyalorbilia fusispora* {1}, *Karstenia rhopaloides* {2}, *Lasiosphaeria* sp. {1}, *Lophiostoma* sp. {1}, *Octospora affinis* {1}, *Orbilia aristata* {2}, *O. aurantiorubra* {1}, *O. clavuliformis* {1}, *O. eucalypti* {1}, *O. ?hesperidea* {1}, *O. xanthoguttulata* {1}, *Orthotrichum ?affinis* {1}, *Parmelia sulcata* {1}, *Patellaria atrata* {2}, *Peniophora lycii* {1}, *Physcia tenella* {3}, *Pyrenopeziza rubi* {1}, *Sclerencoelia fraxinicola* {1}, ?*Synaptospora* sp. {1}, *Thyronectria aurigera* {1}, *Unguiculariopsis* sp. {2}, *Xanthoria parietina* {3}. **Desiccation tolerance**: fully viable for at least 3 months, many cells of paraphyses and excipulum, but also a few spores and immature asci still alive after 15 months. **Altitude**: 3–430 m a.s.l. (temperate Europe), 740 m (southern Europe), 537 m (Australia). **Geology**: Silurian shale, lime- & sandstone, Devonian & Lower Carboniferous greywacke & shale, Buntsandstein, Keuper (Lettenkohle), Lower & Upper Jurassic & Cretaceous shale, sand- & limestone, Pleistocene loess, peat, Holocene alluvial deposits; Australia: Cenozoic regolith (sand). **Phenology**: II–VII, XII (N-hemisphere, probably throughout the year, long-lived).

Taxonomic remarks. *Orbilia pseudoaristata* is characterized by ascospores with very distinct, long tails. Together with the rather long glassy hairs forming whitish teeth at the margin, the species can easily be confused with members of section *Hemiorbilia*, such as *O. aristata*, *O. clavuliformis*, or *O. clavuliaristata*. However, these species differ in asci with a thick-walled, hemispherical apex when viewed in the dead state, partly also in narrower SBs. *O. subalbovinosa* differs in narrower spores and in the presence of crystalloid SCBs, *O. albovinosa* in lacking distinct spore tails.

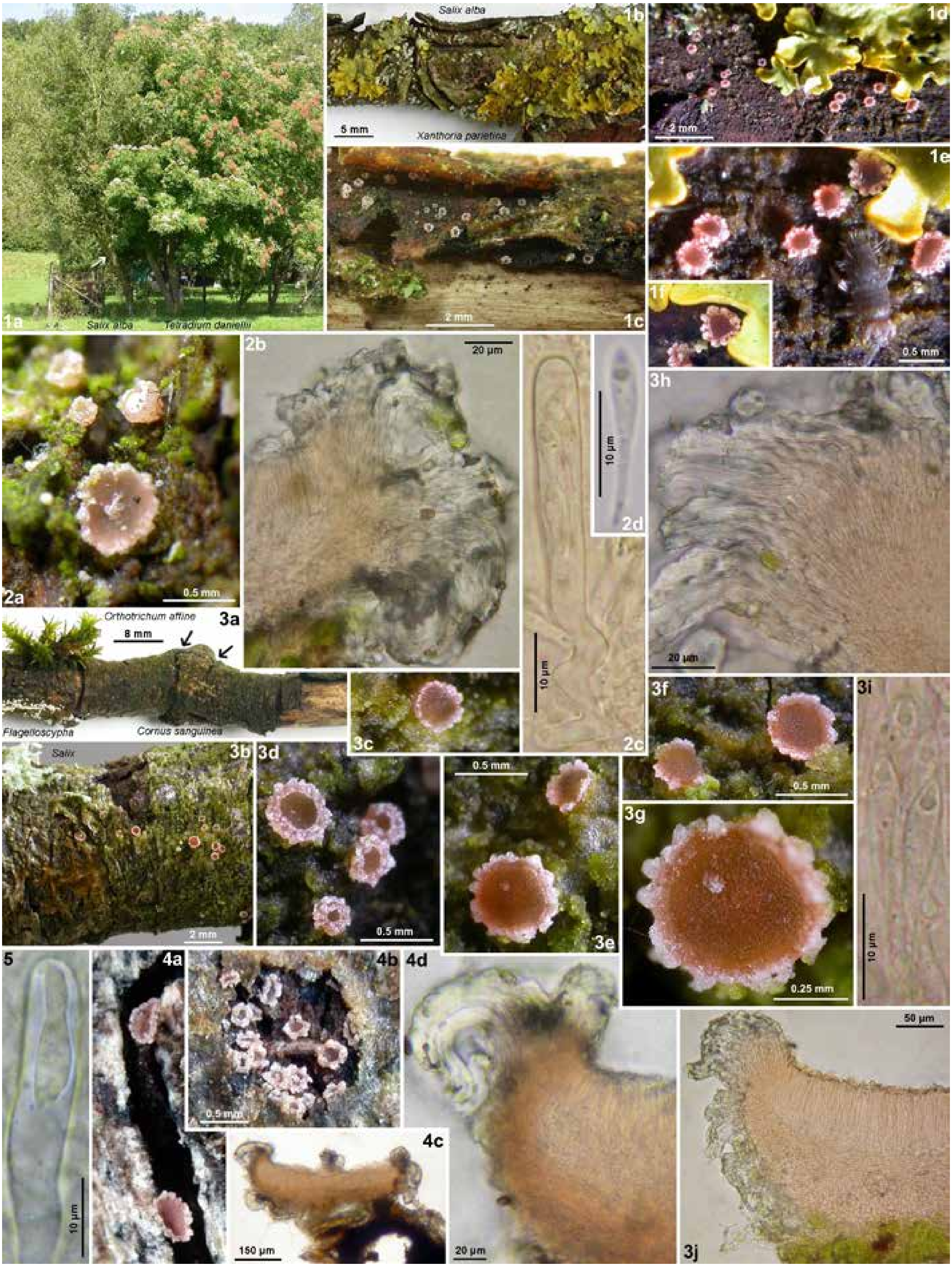


Plate 524. **1–5**: *Orbilia pseudoaristata*. – **1a**. garden estate near Neckar river, with *Salix* and *Tetradium*; **1b**, **3a**. dead xeric corticated branches; **1c–f**, **2a**, **3b–g**, **4a–b**. rehydrated apothecia; **3j**, **4c–d**. apothecia in median section; **2b**, **3h**. id., marginal region with glassy processes; **2c–d**, **3i**, **5**. asci and ascospores. – Living state (**5**: fully turgescent), except for **3l** (living spores in a dead ascus), **4c–d** (in H_2O). — **1a–f**. H.B. 7313 (holotype): Germany, Tübingen, on *Salix*; **2a–d**. H.B. 8360a: Luxembourg, Grevenmacher, on *Cornus*; **3a–j**. H.B. 8456b: ibid., on *Cornus*; **4a–d**. H.B. 7230a: Australia, New South Wales, on *Salix*; **5**. 9.V.2010, Luxembourg, Grevenmacher, on *Cornus*.

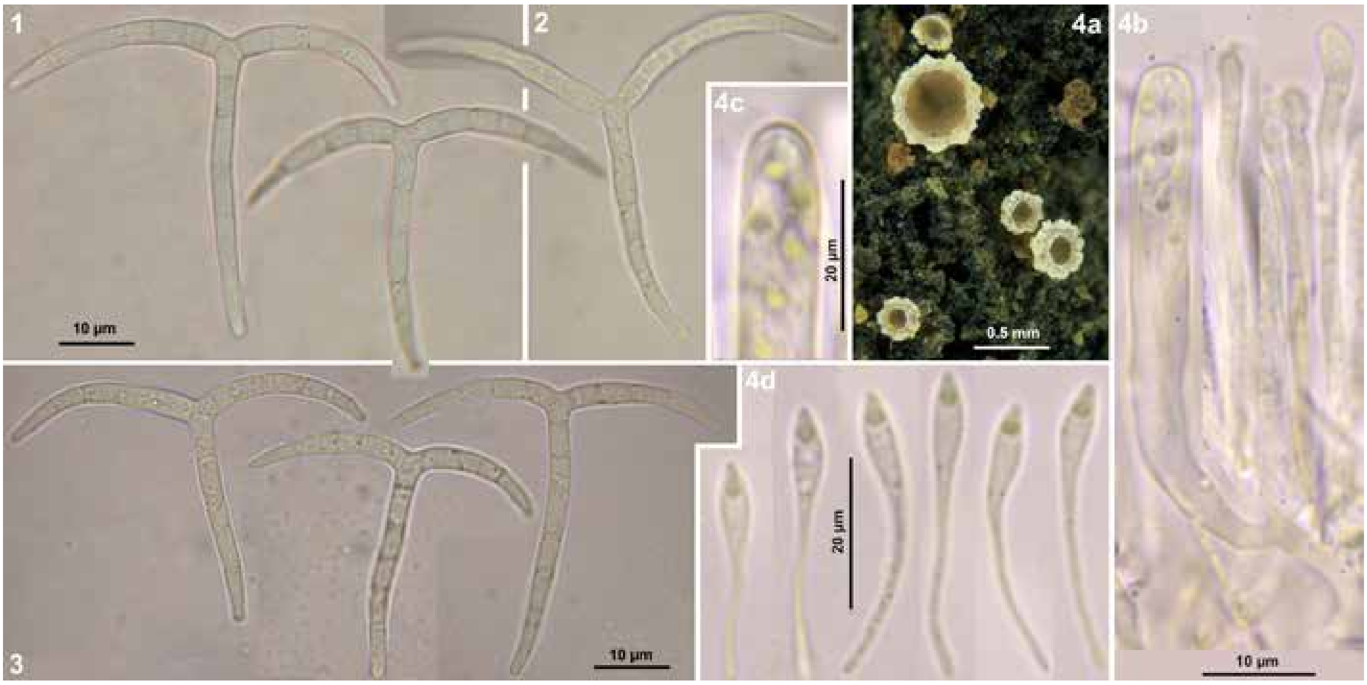


Plate 525. **1–4**: *Orbilia pseudoaristata*. – **1–3**. conidia from substrate (living state), **4a**. apothecia, 4b. ascus and paraphyses, **4c**. ascus apex, **4d**. ascospores. – Living state, except for ascus in **4c**. – **4a–d**: phot. S. Tello. — **1**. H.B. 8360a: Luxembourg, Wasserbillig, on *Cornus*; **2**. 9.XI.2006: ibid., Differdange, on *Cornus*; **3**. H.B. 8436a: ibid., Dudelange, on *Rubus*; **4**. 5.IV.2014: Spain, Andalucía, on *Pistacia*.

Variation. Within Europe, *O. pseudoaristata* varies only slightly in spore size and shape. However, two recent samples (on *Pistacia* from Spain, Pl. 525: 4; on *Malus* from Austria, IVV: 3.II.2019) have distinctly longer spores compared to the other records due to much longer tails, and the latter also extraordinarily broad SBs (1.6–2 µm). The rich Australian collection was examined only 4 years after being harvested, therefore, the drawing shows only dead elements (Pl. 523: 1). Judging from its persistent characters, it concurs in most respects with the typical European samples. Yet, the very faintly perceptible SBs might differ, looking more filiform (perhaps 3–4 × 0.5 µm) rather than tear-shaped, and the paraphyses are apically flexuous, a feature also seen in the Spanish sample (Pl. 525: 4b). For the time being all these specimens are considered to be conspecific with the typical European samples.

Anamorph. Although *O. pseudoaristata* is phylogenetically distant from series *Hemiorbilia*, its conidia resemble those of *Trinacrium subtile*, a type of anamorph found in several taxa of series *Hemiorbilia*, except that they differ in downwards curved arms.

Phylogeny. Sequences were taken from two samples from Luxembourg, comprising ITS and LSU D1–D3 (G.M. 2013-06-25.2, ascospore isolate; G.M. 2014-12-07.1, from apothecia). Both are without S1506 intron and the latter includes a short part of SSU (V9). Only 1 nt near the 5'-end of ITS1 differs between them. An environmental sequence obtained by Menkis et al. (2016) from elm bark beetles in Gotland (Sweden) comprises 5.8S+ITS2 and differs by 1 nt in the ITS2 and 1 nt in the 5.8S, the latter being a rare deviation.

O. pseudoaristata shows in the entire ITS region a distance of 15% to *O. albidorosea* and 16% to *O. albovinosa*. In the LSU D1–D2 the distance is 3.5% to both but also to *O. jugulospora* and *Orbilia* sp. B.L. 4099 (as *O. decipiens*).

When analysing LSU (Phyl. S16), *O. pseudoaristata* clustered weakly supported with *O. albovinosa*, whereas in the combined analysis (Phyl. 13) sister to the majority of series *Albovinosae*.

Ecology. *O. pseudoaristata* was collected on ± rotten bark of xeric branches of *Salix* and *Cornus* and other angiosperms at ± thermophilous sites, often in floodplains, in atlantic to subcontinental cold- to warm-temperate humid western and central Europe, but also in mesomediterranean semihumid southern Europe. The environmental sample from cold-temperate humid southern Sweden (Gotland) was isolated from elm bark beetles, and the fungus probably originated from *Ulmus* bark. A single collection was made in a subtropical humid eucalypt woodland with *Casuarina cunninghamiana* in the Great Dividing Range of southeastern Australia.

Specimens included. **SWEDEN**: **Gotland**, 12.5 km S of Visby, 1.8 km NNE of Hogräns kyrka, 45 m, from trapped adults of *Scolytus multistriatus* (pheromone trap, probably emerging from *Ulmus minor*), VII–VIII.2013 (Menkis et al. 2016, clone 2170_622, mol. extr.; sq.: KP891509). — **FRANCE**: **Centre**, **Indre-et-Loire**, 3 km SW of Bourgueil, 1 km NE of Le Plessis, 28 m, branch of *Ulmus glabra*, on wood, 10.V.2010, J.P. Priou (J.P.P 10092, doc. vid.). – **Poitou-**

Map 87. Known distribution of *O. pseudoaristata* in Europe.

Charentes, **Deux-Sèvres**, Poitou, 12.5 km WSW of Niort, 1 km ENE of Le Vanneau-Irleau, Marais Poitevin, 3 m, branch of *Salix*, on bark, 15.IV.2008, J.A. Camy (H.B. 8805b ø). — **LUXEMBOURG**: **Gutland**, **Luxembourg**, 3.5 km S of Luxembourg, S of Howald, Drosbach, 288 m, branch of *Cornus sanguinea*, on wood, 3.XII.2011, G. Marson (anam. substr.). – 5 km S of Luxembourg, 1.8 km WSW of Hesperange, Fennerholz, 295 m, on twig of *C. sanguinea*, 25.VI.2013, G. Marson (G.M. 2013-06-25.2; sq.: KT380078). – **Grevenmacher**, Valée de Moselle, 6 km NE of Grevenmacher, 1.3 km NW of Wasserbillig, N of Wollefsmillen, Neieberg, 195 m, branch of *C. sanguinea*, on bark, 17.III.2007, G. Marson (H.B. 8456b). – ibid., 1.5 km N of Wasserbillig, N of Langsur, S-exposed slope at Sauer River, 150 m, branch of *C. sanguinea*, on bark, 15.VII.2006, G. Marson (H.B. 8360a, anam. substr.). – ibid., NE of Langsur, 210 m, branch of *C. sanguinea*, on bark & wood, 7.XII.2014, G. Marson (G.M. 2014-12-07.1; sq.: MH221037). – 4 km NE of Grevenmacher, 1.1 km N of Mertert, Rauschelsgruef, 195 m, branch of *Cornus*, on bark, 9.V.2010, G. Marson (ø). – **Esch-sur-Alzette**, Terres rouges, 2 km N of Dudelange, 1.5 km SSW of Bettembourg, near Hela Baumarkt, 285 m, stem of *Rubus* (?)*armeniacus*, on bark, 7.II.2007, G. Marson (H.B. 8436a ø, anam. substr.). — **GERMANY**: **Baden-Württemberg**, 9.5 km E of Heidelberg, NNE of Neckargemünd, Kleingemünd, twig of *Sorbus aucuparia*, on bark, 12.V.2013, M. Bemmann (ø). – 5.3 km ENE of Tübingen, 1.4 km SE of Pfrondorf, Neckar river, 312 m, branch of *Salix alba*, on bark, 19.III.2003, H.O. Baral (ex H.B. 7313, M-0276570, **holotype**). — **AUSTRIA**: **Steiermark**, 22 km NNW of Graz, 3 km SSW of Frohnleiten, S of Burg Rabenstein, 430 m, branch of *Malus domestica*, on bark, 3.II.2019, G. Friebes (G.F. 20190013). — **CZECHIA**, **Olomouc**, 3.3 km NNE of Olomouc, 1 km NE of Černovír, Černovírske slatiniste, 220 m, trunk of *Fraxinus excelsior*, on bark, 19.XII.2019, V. Halasů (V.H. 1208, doc. vid.). – ibid., branch of *Prunus padus*, on bark (immature, doc. vid.). — **SPAIN**: **Andalucía**, **Jaén**, 22 km SSW of Jaén, 4.7 km S of Fuensanta de Martos, 4 km SE of Vadohornillo, 740 m, branch of *Pistacia lentiscus*, on bark, 5.IV.2014, S. Tello (JA-CUSSTA 7932, doc. vid.). — **AUSTRALIA**: **New South Wales**, South Western Slopes, 183 km NW of Sydney, 20 km SE of Mudgee, 537 m, branches of *Salix babylonica*, on bark & wood, 25.X.1998, G. Marson (H.B. 7230a).

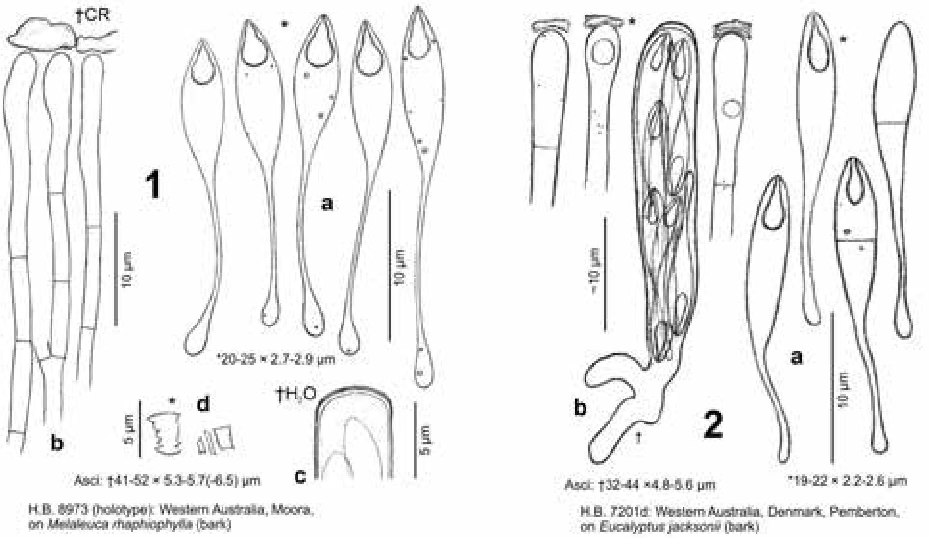


Plate 526. **1**: *Orbilia pseudoflagellispora*; **2**: *O.* cf. *pseudoflagellispora*. – **a**. ascospores; **b**. paraphyses; **c**. ascus apex; **d**. SCBs in cells of basal ectal excipulum.

Orbilia pseudoflagellispora Baral & G. Marson, **sp. nov.**, MB 813785 — Pls 526–527

Etymology: named after the similarity of the ascospores with *O. flagellispora*. **Typification**: Western Australia, Moora, trunks of *Melaleuca rhaphiophylla*, 11.XI.2007, G. Marson (ex H.B. 8973, MEL 2389268, holotype).

Latin diagnosis: *Differt ab* O. flagellispora *ascis in statu emortuo truncatis, tenuitunicatis, corpusculis refringentibus ascosporarum latioribus. Habitat ad corticem putridum siccum in trunco vivo* Melaleucae *et* Lamarcheae *in zona subtropica semihumida ad semiarida Australiae meridio-occidentalis.*

Description: — **TELEOMORPH**: **Apothecia** rehydrated 0.2–0.4 mm diam., 0.1–0.16 mm high, round, very scattered; disc flat, pale to light pure or dirty (brick-)rose to rose-orange, medium translucent; margin distinct, 0–15 µm protruding (incl. teeth), finely crenulate to denticulate, whitish to pale rose; broadly sessile or with a narrowed stipe-like base, superficial but often in cracks of periderm; dry with thick protruding margin, disc bright brick-red. **Asci** †(35–)38–50(–54) × 5.3–6(–6.5) µm {2}, 8-spored, spores (†) biseriate, 0–1 lower spores inverted {2} (not mixed); **apex** (†) medium to strongly truncate (not indented, laterally not or hardly inflated) {2}; **base** with or without short, slightly flexuous stalk, L-, Y- or h-shaped. **Ascospores** *20–25 × 2.7–2.9 µm {1}, †19.5–25 × 2.4–2.8 µm {2}, with fusiform 8–11 µm long head and sharply differentiated narrow tail */†10–14 × 0.2–0.4 µm, apex subacute to acute, tail always with a bulbous base */†0.8–1.4 µm wide {2}, straight to slightly curved in the tail region; **SBs** *2.8–3.5 × 1.4–1.8(–2) µm {T}, tear- to pear-shaped. **Paraphyses** apically uninflated to indistinctly clavate-spathulate, terminal cells †12–18 × 1.6–2.5 µm {T}, lower cells †7.5–9 × 1.2–1.8 µm {T}; never branched at upper septum, hymenium pale rose. **Medullary excipulum** hyaline to pale rose, 20–30 µm thick, of dense textura intricata with many inflated cells, ± sharply delimited. **Ectal excipulum** hyaline, of (†) thin-walled t. globulosa-angularis from base to mid flanks, 40–60 µm thick near base, cells */†9–18 × 8–14(–17) µm {T}; 20–25 µm thick near margin, inner part of t. prismatica-angularis oriented at a 30–50° angle to the surface, outer part of t. porrecta oriented at 10–30°, marginal cortical cells †8–15 × 2–3(–3.5) µm {2}; **glassy processes** 10–30 × 2.5–4 µm {2}, medium refractive, faintly stratified, ± straight or outwards curved, at upper margin also curved inwards, coherent to form ± distinct teeth. **Anchoring hyphae** abundant, */†1.8–3 µm wide, walls 0.2 µm thick {T}, forming a loose hyaline t. intricata 20–30 µm thick. **SCBs** in paraphyses unknown, in ectal excipulum (from base to margin) crystalloid, 2–4 × 1–2 µm {T}, hyaline, at margin mixed with globose ones. **Exudate** over paraphyses and marginal teeth 1–3 µm thick, cloddy, pale yellowish, loosely attached. **— ANAMORPH**: unknown.

Habitat: collected 0.2–2 m above the ground, corticated, ~8–16 cm thick living trunks of *Lamarchea hakeifolia* {1}, *Melaleuca rhaphiophylla* {1}, on medium to strongly decayed, paper-like bark {2}, on outer but apparently also inner surface, slightly to medium greyed, with a few to rather many green algae. **Associated**: *Capronia* sp. {2}, *Claussenomyces* sp. {1}, *Hyalorbilia pleioerythrostigma* {1}, *Orbilia austroobtusispora* {1}, *O. gemma* {1}, *O. kingsiana* {1}, *O. lamarcheae* {1}, *O. myriolilacina* {1}, *O. ?pubescens* {1}, *Ostropales* {1}, *Symbiotaphrina desertorum* {1}, ?*Xerotrema* sp. {1}. **Desiccation tolerance**: ectal and medullary excipular cells, some ascospores, exceptionally also some submature asci still viable after 13 months. **Altitude**: 83–190 m a.s.l. **Geology**: Cretaceous sedimentary rock (whitish or red-brown sandy soil). **Phenology**: long-lived.

Taxonomic remarks. *Orbilia pseudoflagellispora* is readily recognized by its rather long ascospores with fusiform heads and long thin tails with a striking bulbous basal inflation. Apart from their wide SBs, the spores strongly resemble those of *O. flagellispora* (section *Hemiorbilia*) known from Europe and North America. However, *O. pseudoflagellispora* is believed to belong to series *Albovinosae* because of its truncate thin-walled ascus apices (dead state) and the similarity to *O. pseudoaristata*.

Not included collection. A very sparse, unpreserved sample from *Eucalyptus jacksonii* bark (Pl. 526: 2) differs in slightly narrower spores (*19–22 × 2.2–2.6 µm) which were frequently 1-septate, though apparently because of overmaturity. Whether the ascus apex was devoid of an apical thickening was not verified.

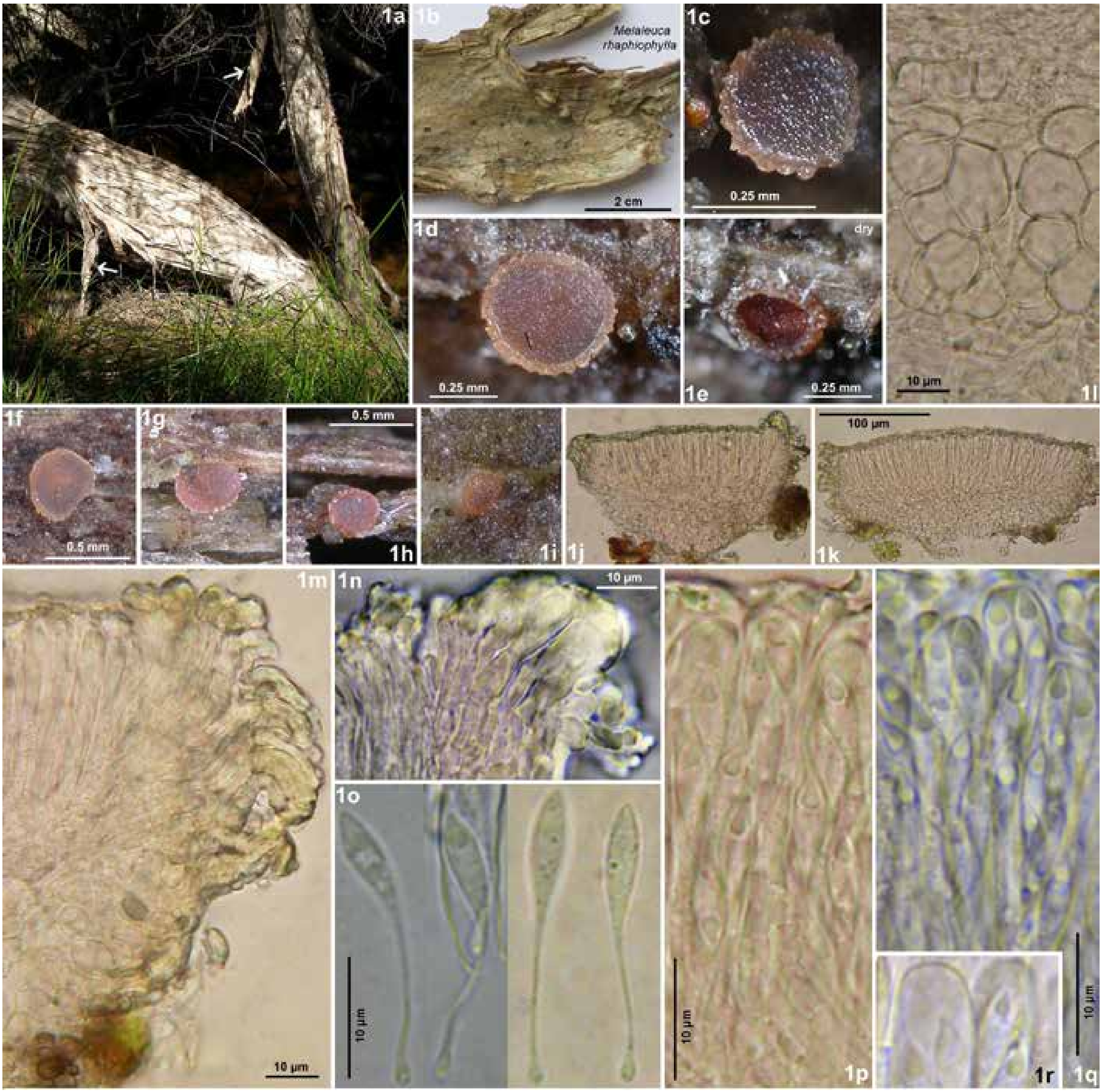


Plate 527. **1**: *Orbilia pseudoflagellispora*. – **1a**. semihumid banksia-eucalypt woodland, living trunk of *Melaleuca rhaphiophylla* at rivulet; **1b**. detaching xeric bark; **1c–d**, **f–i**. rehydrated apothecia; **1e**. dry apothecium; **1j–k**. apothecia in median section; **1m**. id., marginal ectal excipulum; **1n**. id., marginal cortical cells with glassy processes; **1l**. id., basal ectal excipulum; **1o**. ascospores; **1p–r**. upper part of asci, ascospores. – Living state, except for **1o** (3 dead spores, in H_2O), asci in **1p–r**. — **1a–r**. H.B. 8973 (holotype): Western Australia, Moora, on *Melaleuca*.

Ecology. *O. pseudoflagellispora* was found on rotten, xeric, detaching bark of living trunks of two different *Myrtaceae* in subtropical (south)western Australia. The paratype was from a semiarid acacia open shrubland with *Callitris* and *Lamarchea* in the Yalgoo ecoregion, the holotype from a semihumid banksia-eucalypt woodland with *Melaleuca*, *Eremaea* and *Adenanthos* in a marshy area very close to a rivulet in the Swan Coastal Plain. The not included collection was on detached fallen bark of *Eucalyptus* in a subtropical semihumid eucalypt (karri-tingle) open forest on granite in the coastal area south of Darling Range.

Specimens included. **AUSTRALIA**: **Western Australia**, Yalgoo, 187 km N of Geraldton, W of Toolonga, Nerren Nerren, 190 m, twig & trunk of *Lamarchea hakeifolia*, on bark, 8.XI.2007, G. Marson (H.B. 9020m ø). – Swan Coastal Plain, 55 km SSW of Moora, 30 km NNE of Gin Gin, Moore River, 83 m, trunks of *Melaleuca rhaphiophylla*, on bark, 11.XI.2007, G. Marson (ex H.B. 8973, MEL 2389268, **holotype**).

Not included. **AUSTRALIA**: **Western Australia**, Warren, 30 km SE of Pemberton, 14 km ENE of Northcliffe, 195 m, branch of *Eucalyptus jacksonii*, on bark, 16.XII.2001, G. Marson (H.B. 7201d ø).

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