

Flora of Lichenicolous Fungi

Volume 1 · Basidiomycota

Paul Diederich · Ana M. Millanes · Mats Wedin · James D. Lawrey



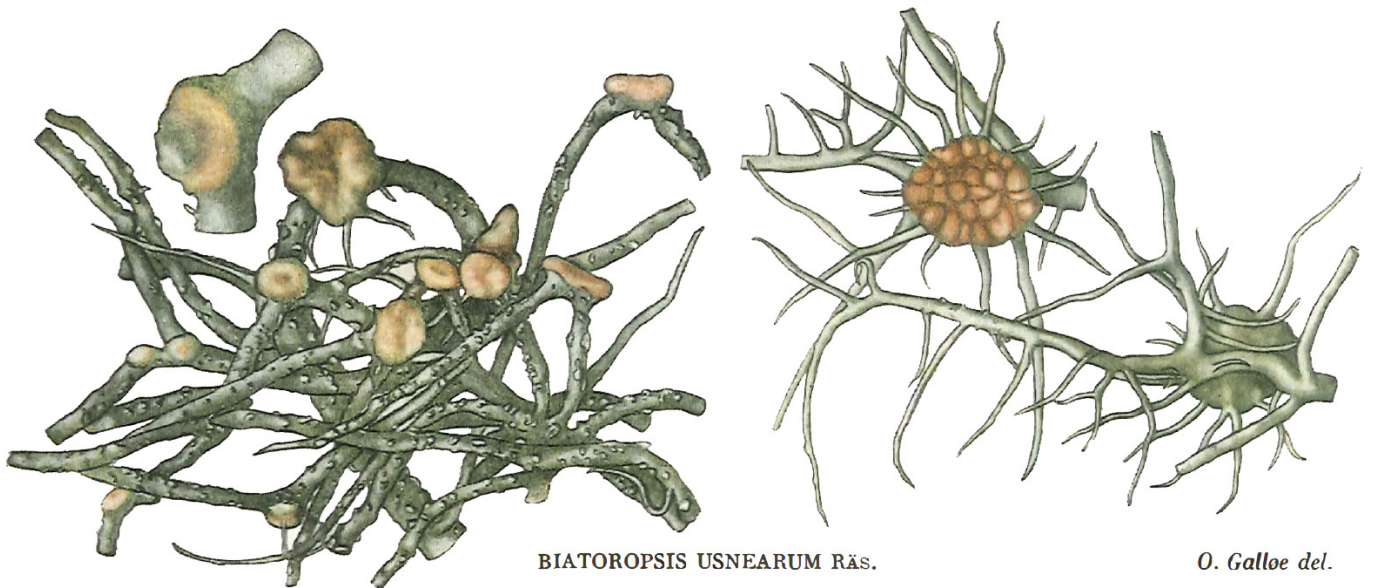
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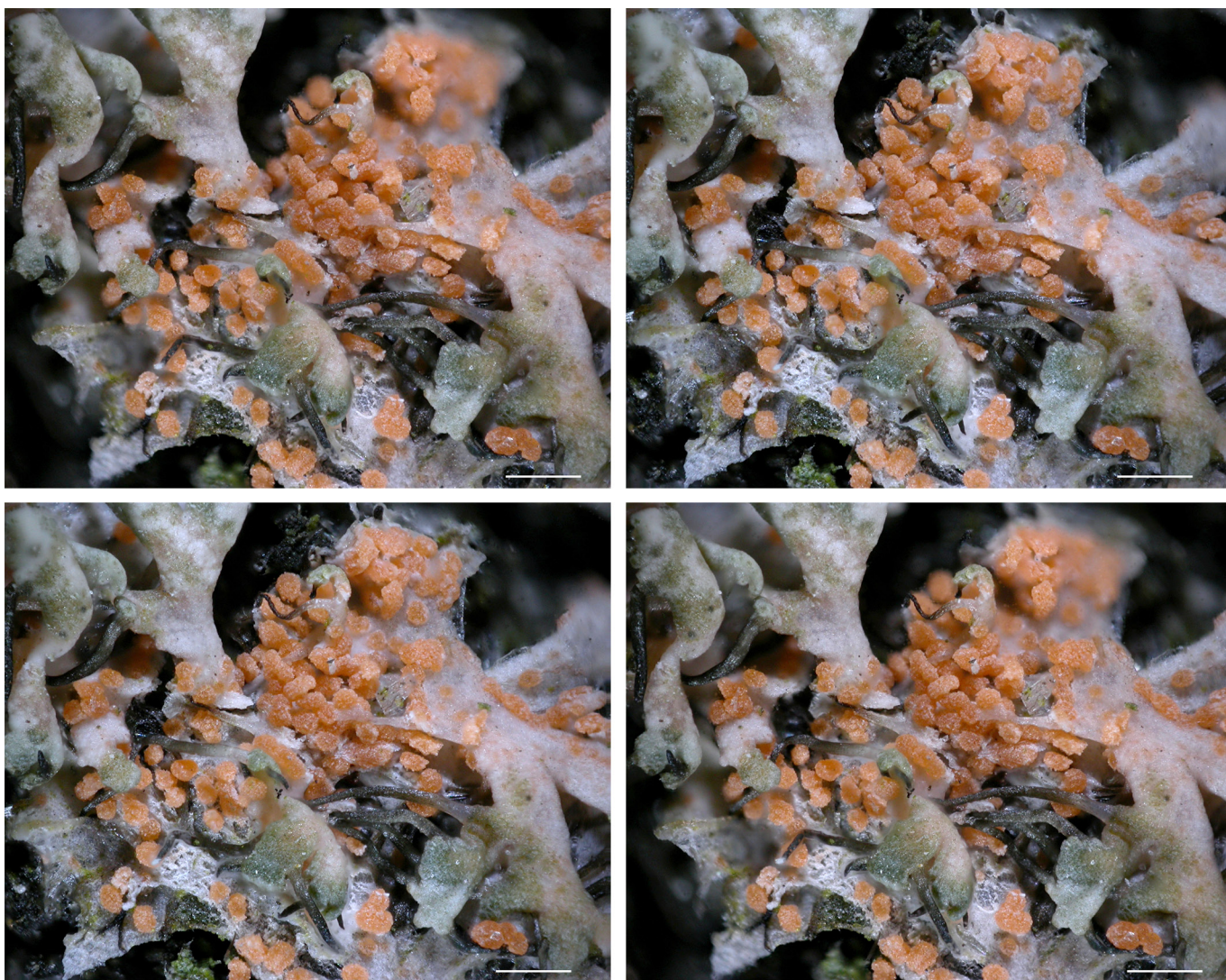
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National Museum of Natural History

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3D-photography of *Erythricium aurantiacum*, a basidiomycete of the family *Corticaceae* with bright orange 'bulbils' parasitizing the thallus of the lichen *Physcia adscendens*. *Erythricium aurantiacum* is one amongst c. 200 currently known lichenicolous basidiomycetes. Upper pair: crossed eyes viewing; lower pair: parallel eyes viewing; vertical pairs: KMQ viewer. Photos: Guy Marson. Scale bars: 500 μ m.

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Abstract

This first volume of a worldwide Flora of Lichenicolous Fungi deals with the *Basidiomycota*. A total of 197 species are accepted, described, illustrated and keyed out, and 13 additional species are shortly introduced but not formally described. They belong to the *Agaricomycetes* (4 species in 2 genera of *Agaricales*, 2 – 1 *Atheliales*, 1 – 1 *Boletales*, 11 – 8 *Cantharellales*, 12 – 5 *Corticiales*) and the *Tremellomycetes* (8 – 1 *Filobasidiales*, 129 – 3 *Tremellales*) in the *Agaricomycotina*, and to the *Agaricostilbomycetes* (18 – 1 *Agaricostilbales*), *Cystobasidiomycetes* (9 – 1 *Cyphobasidiales*) and *Microbotryomycetes* (1 – 1 *Kriegeriaceae*) in the *Pucciniomycotina*, while 2 species incertae sedis are provisionally treated in ‘*Syzygospora*’. The species of *Agaricomycetes* belong to the informal group of homobasidiomycetes and are mainly generalists, while the species of *Tremellomycetes*, *Agaricostilbomycetes*, *Cystobasidiomycetes*, *Microbotryomycetes* and ‘*Syzygospora*’ belong to the heterobasidiomycetes and are all host-specific. Three new genera, 74 new species, 1 new subspecies, and 3 new combinations are introduced. Phylogenetic trees are given for each taxonomic group, some being obtained from previous papers, while most are based on new phylogenetic results, based on hundreds of new DNA sequences obtained during the preparation of this volume. The former *Biatoropsis usnearum*, *Syzygospora physciacearum*, *Tremella parmeliarum* and *T. pertusariae* are regarded as species complexes, including many newly described species, while some other species complexes, especially *Cyphobasidium hypotrachynicola*, *C. usneicola*, *Tremella caloplacae*, *T. lobariacearum* and *T. ramalinae* need further studies. Six new species of *Biatoropsis* or *Tremella* have basidia producing conidia instead of basidiospores, one new *Tremella* species has deciduous epibasidia acting as diaspores, and four new asexual taxa of *Tremella* have a layer of conidiogenous cells producing clamped conidia. Six types of host-specific galls resembling *Tremella* basidiomata, but probably induced by bacteria, are briefly described and included in the host-based key.

Taxonomic and nomenclatural novelties

Agaricomycetes – Cantharellales

- Parmeliicida* Diederich, F. Berger, Etayo & Lawrey, gen. nov.
Parmeliicida pandemica Diederich, F. Berger, Etayo & Lawrey, sp. nov.

Tremellomycetes – Filobasidiales

- Zyzygomyces* Diederich, Millanes & Wedin, gen. nov.
Zyzygomyces aipoliae Diederich, Millanes, F. Berger & Ertz, sp. nov.
Zyzygomyces bachmannii (Diederich & M. S. Christ.) Diederich, Millanes & Wedin, comb. nov.
Zyzygomyces bunodophori Diederich, Etayo & Palice, sp. nov.
Zyzygomyces leucodermiae Diederich, Millanes, Ertz, Etayo & Flakus, sp. nov.
Zyzygomyces mobergei Diederich & Millanes, sp. nov.
Zyzygomyces physciacearum (Diederich) Diederich, Millanes & Wedin, comb. nov.
Zyzygomyces physconiae Diederich, Millanes, P. Pinault & Brackel, sp. nov.
Zyzygomyces polyblastidii Diederich, Flakus, Etayo & Rodr. Flakus, sp. nov.

Tremellomycetes – Tremellales

- Biatoropsis angulatae* Diederich & Millanes, sp. nov.
Biatoropsis antarcticae Diederich, Etayo & Millanes, sp. nov.
Biatoropsis hirtae Diederich & Millanes, sp. nov.
Biatoropsis macaronesica Diederich & Millanes, sp. nov.
Biatoropsis nigrescens Diederich, Millanes & F. Berger, sp. nov.
Biatoropsis rubicundae Diederich & Millanes, sp. nov.
Tremella abrothalli Diederich & Goward, sp. nov.
Tremella acarosporae Diederich & Hollinger, sp. nov.
Tremella alectoriae Diederich & Holien, sp. nov.
Tremella aptrootii Diederich & Common, sp. nov.
Tremella aspicilliae Diederich, Coppins & A. Fletcher, sp. nov.
Tremella brodoae (P. Pinault & Cl. Roux) Diederich, Millanes & Hafellner, comb. nov.
Tremella cervina Diederich & Millanes, sp. nov.
Tremella cetraculeata Diederich, Millanes & Hollinger, sp. nov.
Tremella cetrariae Diederich, Millanes, F. Berger & Zamora, sp. nov.
Tremella confluens Pippola, Diederich & Goward, sp. nov.
Tremella conidioparmotrema Diederich, Etayo & Millanes, sp. nov.

Tremella conidiopunctelia Diederich, Millanes, Lendemer, D. P. Waters & Giavarini, sp. nov.
Tremella conidiopunctelia subsp. *parmelinellae* Diederich, Millanes, Common & Lawrey, subsp. nov.
Tremella coniocarpi Diederich & Common, sp. nov.
Tremella emmanueliae Diederich & Aptroot, sp. nov.
Tremella ertzii Diederich, sp. nov.
Tremella flakusii Diederich, Millanes, Rodr. Flakus & Aptroot, sp. nov.
Tremella flavoparmeliae Diederich, Hodkinson & Millanes, sp. nov.
Tremella graphidicola Diederich & Common, sp. nov.
Tremella herpothalli Diederich, Flakus, Rodr. Flakus, Etayo & Palice, sp. nov.
Tremella lecidellae Diederich & Brackel, sp. nov.
Tremella leprae Diederich & W. R. Buck, sp. nov.
Tremella leprariae Diederich, sp. nov.
Tremella leucodermiae Diederich, Etayo, Flakus & Millanes, sp. nov.
Tremella nephromopsisidis Diederich, sp. nov.
Tremella occultixanthoriae Diederich, Geyselings & Millanes, sp. nov.
Tremella octosporae Diederich & Sérus., sp. nov.
Tremella pacificae Diederich & van den Boom, sp. nov.
Tremella parmogardneri Diederich, Etayo & Millanes, sp. nov.
Tremella parmohypotropi Diederich, Gockman & Millanes, sp. nov.
Tremella parmoperforati Diederich & Millanes, sp. nov.
Tremella pertuceracea, Diederich, Flakus & Rodr. Flakus, sp. nov.
Tremella pertusae Diederich, Millanes, Brackel & Etayo, sp. nov.
Tremella pertusariicola Diederich, Flakus, Etayo & Rodr. Flakus, sp. nov.
Tremella pertutexanae Diederich, Millanes & Common, sp. nov.
Tremella pertuthalamiae Diederich & Millanes, sp. nov.
Tremella pinaultii Diederich & Millanes, sp. nov.
Tremella pisutiellae Diederich & W. R. Buck, sp. nov.
Tremella placynthiellae Diederich & W. R. Buck, sp. nov.
Tremella pseudocyphellariae Diederich, Millanes & Ertz, sp. nov.
Tremella puncteliae Diederich, Etayo & Millanes, sp. nov.
Tremella puncteliotegens Diederich, Etayo & Millanes, sp. nov.
Tremella purpurascens Diederich, Common & Millanes, sp. nov.
Tremella pyrenaica Diederich, Poumarat, Daval & Millanes, sp. nov.
Tremella ramboldiae Diederich & W. R. Buck, sp. nov.
Tremella rhabdodisci Diederich, Thor, Ertz & Millanes, sp. nov.
Tremella robusta Diederich, Ertz, van den Boom & Millanes, sp. nov.
Tremella sarcographae Diederich & Aptroot, sp. nov.
Tremella strigulae Diederich, sp. nov.
Tremella synarthoniae Diederich & Common, sp. nov.
Tremella teloschistis Diederich, Gockman, Walden & Millanes, sp. nov.
Tremella tornabeae Diederich, Etayo, Pérez-Ortega & Millanes, sp. nov.
Tremella xanthomendozae Diederich, C. A. Morse & Brinker, sp. nov.
Tremella zamorae Diederich & Millanes, sp. nov.

Cystobasidiomycetes

Cyphobasidium buelliicola Diederich & W. R. Buck, sp. nov.
Cyphobasidium crocodiicola Diederich & W. R. Buck, sp. nov.
Cyphobasidium enterographicola Diederich, Ertz & Millanes, sp. nov.
Cyphobasidium hypotrachynicola Diederich, Flakus, Etayo & Rodr. Flakus, sp. nov.
Cyphobasidium lecaniicola Diederich, Ertz & Millanes, sp. nov.
Cyphobasidium puncteliicola Diederich & Millanes, sp. nov.
Cyphobasidium ramalinicola P. Pinault & Diederich, sp. nov.

Microbotryomycetes

Kriegeriopsis Etayo, Diederich, Millanes & Wedin, gen. nov.
Kriegeriopsis livingstonensis Etayo, Diederich, Millanes & Wedin, sp. nov.

Species incertae sedis

Syzygospora septata Diederich & Etayo, sp. nov.

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Preface

Lichenicolous fungi are a very successful group of organisms specialized in inhabiting lichen thalli or apothecia. They are present and diverse everywhere in the world where lichens are found. But still, they were much neglected until recently, as mycologists rarely searched for fungi on lichen thalli, while most lichenologists were not trained to study these fungi. The first major works were Vouaux's '*Synopsis des champignons parasites de lichens*', published in 1912–14, and Karl von Keissler's '*Die Flechtenparasiten*', in 1930. Clauzade & Roux (1976) presented identification keys to lichenicolous fungi, compiled from the literature, with 457 species accepted. The foremost modern treatments were David Hawksworth's '*The Lichenicolous Hyphomycetes*' published in 1979, '*The Lichenicolous Coelomycetes*' in 1981, and eventually '*A key to the lichen-forming, parasitic, parasymbiotic and saprophytic fungi occurring on lichens in the British Isles*', published in 1983. The first lichenicolous fungus I collected and recognized in my life was a specimen of *Phaeophyscia orbicularis* with vertical, black hairs covering the thallus, found in 1979. But only in 1983 was I able to identify it as the lichenicolous hyphomycete *Taeniolella phaeophysciae*, using Hawksworth's keys. I quickly became fascinated by these fungi, collected more of them, was able to identify many specimens, but soon realized how many of them were still undescribed, resulting in my first paper (Diederich 1986) describing five new species, including *Tremella lichenicola*, treated in this volume. During my stay in Uppsala in May 1987, I had the chance to meet Rolf Santesson, author of the monumental *Fungi Lichenicoli Exsiccati*, who supported my research on lichenicolous fungi enormously during the following years. In 1989, I became co-author of the '*Nelikenigintaj fungoj likenlogaj*' (Clauzade et al. 1989), an illustrated identification volume written in Esperanto, that included 662 species. In 1996, I published '*The Lichenicolous Heterobasidiomycetes*', a kind of continuation of Hawksworth's hyphomycetes and coelomycetes monographs. In the meantime, the study of lichenicolous fungi became more popular amongst lichenologists, and most lichen checklists or floristic papers included them. Several colleagues became particularly interested in these fungi and described numerous new species, especially my friends Javier Etayo, who published many major works on South American species, and Mikhail (Misha) Zhurbenko, expert of the arctic lichenicolous fungi. For a long time, I was aware of the need for a new, modern *Flora of Lichenicolous Fungi*, but the increasing number of species (already 2000 in '*The 2018 classification and checklist of lichenicolous fungi*' by Diederich et al. 2018) made this task a huge undertaking. I have eventually decided to take on the challenge of such a giant project, dividing the Flora into several volumes, each treating one taxonomic group. For this first volume on lichenicolous *Basidiomycota*, I am thankful to my friends Ana Millanes, Mats Wedin and James Lawrey for having accepted to co-edit the volume and for being co-authors of a number of chapters, together with experts of the different taxonomic groups.

Paul Diederich, July 2022

Introduction

The discovery of lichenicolous heterobasidiomycetes (= an unnatural group of basidiomycetes with mainly septate basidia and gelatinous basidiomata) in the late 1980^{es} was communicated in August 1990 at the International Mycological Congress IMC-4 in Regensburg by Diederich (1990). Although species of *Tremella* were regarded as being mostly mycoparasitic, the announcement that those common ‘galls’ on lichen thalli were induced by species of *Tremellales*, and further that these species were so numerous, was an unexpected surprise, hard to believe for some notable mycologists from that time. Subsequently, field lichenologists contributed numerous lichen specimens with galls for study, resulting in the monograph ‘*The Lichenicolous Heterobasidiomycetes*’ published six years later (Diederich 1996). Five genera were accepted in that work, viz. *Biatoropsis* (1 species), *Chionosphaera* (2), *Cystobasidium* (2), *Syzygospora* (3) and *Tremella* (40 species, plus 6 not formally described). During the following 25 years, 22 new species were described, but during the same period, c. 500 additional specimens were obtained for study, including many from unknown hosts. Also, molecular phylogenetic studies were initiated in 2006, resulting in a first paper ‘*Phylogeny and character evolution in the jelly fungi (Tremellomycetes, Basidiomycota, Fungi)*’ by Millanes et al. (2011), in which three major lichenicolous clades of *Tremella* were recognized within *Tremellales*, while *Syzygospora* was nested within *Filobasidiales*. In a later paper (Millanes et al. 2014), the *Biatoropsis*-*Usnea* system was used as a model to study the evolution of lichenicolous *Tremellales*, and the authors found that diversity is promoted by host switching as it is in many well-studied host-parasite systems. Further phylogenetic results led Millanes et al. (2016) to conclude that the lichenicolous *Cystobasidium* species belong to *Pucciniomycotina*, and they described the new genus *Cyphobasidium* for them. Very recently, Millanes et al. (2021a) and Diederich et al. (2022) found that the lichenicolous *Chionosphaera* species also belong to *Pucciniomycotina*, describing the new genus *Crittendenia* and family *Crittendeniaceae* for them, and presenting a taxonomic revision that included numerous, mostly semi-cryptic, host-specific species. Numerous species in the heterobasidiomycetes have a dimorphic life-cycle, meaning that they switch between a haploid unicellular yeast phase and a dikaryotic filamentous phase (Bandoni 1995). The unicellular yeast phase reproduces asexually by budding, whereas the sexual dikaryotic mycelium grows associated with another fungus (including lichenized fungi) in nature. The descriptions of lichenicolous species of heterobasidiomycetes are traditionally based on characters of the filamentous phase, although the basidiospores that generate the yeast phase germinating by repetition have also been reported and illustrated in *Filobasidiales* and *Tremellales* (Diederich 1996, Prillinger et al. 1997, Zamora et al. 2016). Yeasts have also been observed in *Crittendenia* (Diederich et al. 2022), but in this case their connection to germinating spores – and therefore if they actually belong to *Crittendenia* – has not been confirmed. In general, since lichenicolous species of heterobasidiomycetes are not easy to grow in culture, the yeast phase of these taxa has been comparatively less studied. Spribille et al. (2016) discovered *Cyphobasidium* yeasts in the cortex of many macrolichens and hypothesized that these yeasts may contribute to the lichen symbiosis. Tuovinen et al. (2019) found that *Tremella* yeasts are as well frequently found in the cortex of lichens, and that this is ‘its dominant stage in nature’. Millanes et al. (2018, 2021b) and Tuovinen et al. (2021) further realized that *Tremella* yeasts are less host-specific than their hyphal stage.

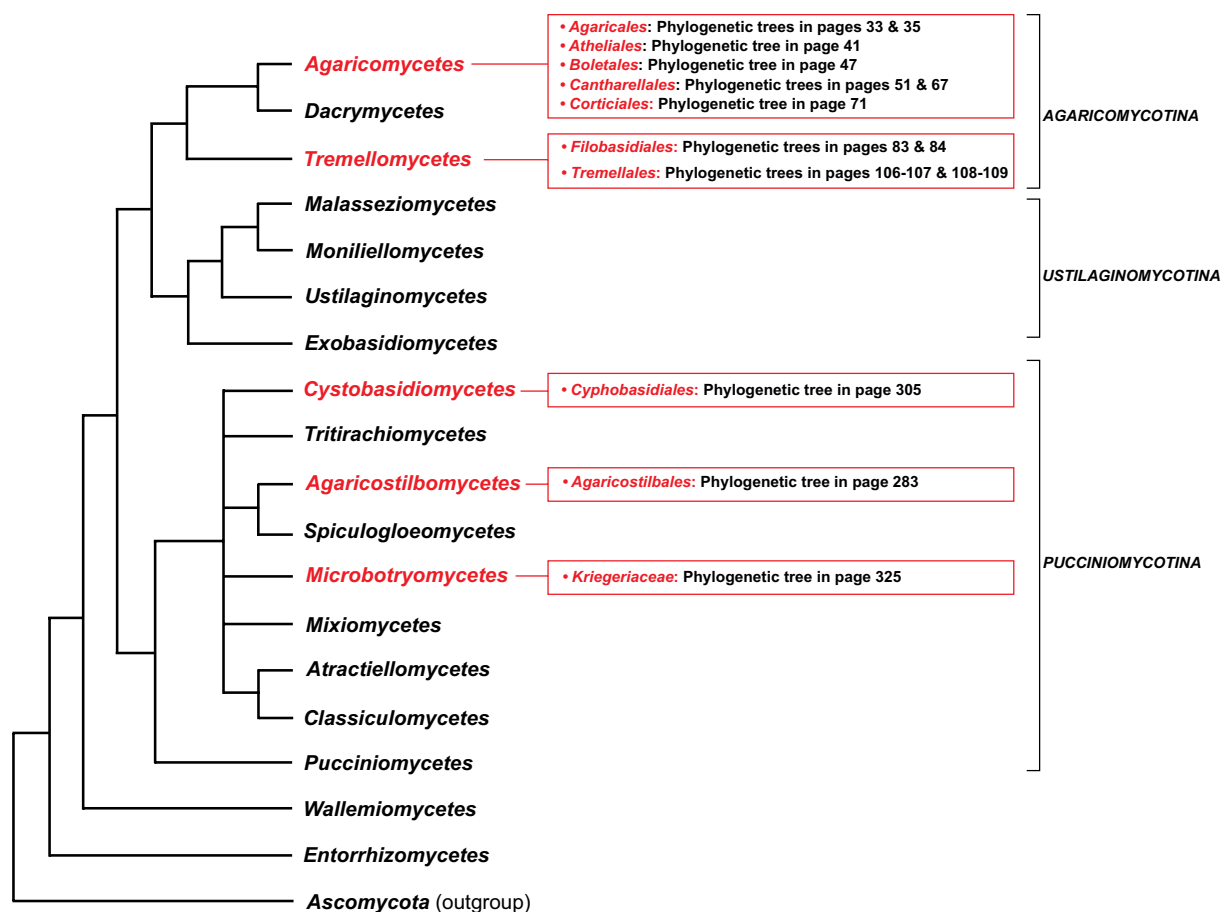
Lichenicolous homobasidiomycetes (= basidiomycetes with aseptate basidia and usually non-gelatinous basidiomata) were similarly neglected until recently. Lawrey et al. (2007) presented a first major contribution ‘*Phylogenetic diversity of lichen-associated homobasidiomycetes*’ with detailed phylogenies comprising lichenicolous species of *Atheliales*, *Boletales*, *Corticiales* and *Cantharellales*, while no sequences of lichen-associated *Agaricales* were available. A number of new species and genera were described in Diederich & Lawrey (2007) and later papers. A recent taxonomic and phylogenetic review of *Corticaceae* by Ghobad-Nejhad et al. (2021) included most lichenicolous taxa. A first phylogeny including lichen-associated *Agaricales* is presented in this volume.

The recent ‘*2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa*’ (Diederich et al. 2018) listed a total of 93 known species of lichenicolous basidiomycetes (+7 facultatively lichenicolous taxa), belonging to *Pucciniomycotina* (4 species) and *Agaricomycotina* (89 species), the latter comprising 68 species of *Tremellomycetes* and 21 of *Agaricomycetes*. They represented c. 5% of all known lichenicolous fungi.

This first volume of the planned *Flora of Lichenicolous Fungi* deals with the lichenicolous *Basidiomycota*. Descriptions and illustrations of all known species are included, and many newly discovered taxa are described. All species are keyed out, mainly in a large host-based key, but also in smaller keys to certain groups. Phylogenies are presented for all taxonomic groups, mostly based on newly obtained sequences. This volume brings the number of known species to almost 200, thus more than twice the number known in 2018, and is thus a major contribution to the knowledge of lichenicolous fungi, and more generally of basidiomycetes. But apart from all these taxonomic and phylogenetic novelties, the main aim of this volume, and the entire *Flora*, is to allow both amateur and professional lichenologists to recognize, collect and identify lichenicolous fungi, to contribute to the overall knowledge of fungal biodiversity, and to promote discovery of the many yet unknown species.

Phylogenetic perspectives in lichenicolous *Basidiomycota*

Within *Basidiomycota*, lichenicolous species are present in two of the three major subphyla in the group (i. e., *Agaricomycotina* and *Pucciniomycotina*). There are lichenicolous representatives in two classes of the *Agaricomycotina* (i. e., *Agaricomycetes* – in five of its eighteen orders viz., *Agaricales*, *Atheliales*, *Boletales*, *Cantharellales* and *Corticiales* – and *Tremellomycetes* – in two of its five orders viz., *Filobasidiales* and *Tremellales*) and in three classes of the *Pucciniomycotina* (i. e., *Agaricostilbomycetes*, *Cystobasidiomycetes* and *Microbotryomycetes*). Discussions on the phylogenies of each particular group are provided in each chapter of this Flora. Still, much work is needed to unravel the phylogenetic relationships of many groups of lichenicolous fungi. The growing access of molecular data in the 1990^{es} resulted in substantial progress in the systematics of fungi in general, and of lichenicolous fungi in particular. However, a challenging aspect to obtain molecular data of lichenicolous fungi is that they often live in intimate association with their hosts and it is not possible to physically separate the lichenicolous fungi (and their DNA) from their linked lichens. This especially applies to the case of heterobasidiomycetes. This has so far been possible to overcome by designing specific PCR primers that allow to selectively amplify and sequencing the basidiomycete partner, avoiding the lichenized host. However, constructing truly comprehensive phylogenies of most lichenicolous groups has been hindered by technical difficulties to obtain protein-coding genes from many taxa. New molecular techniques, in particular next generation sequencing, offer promising opportunities for future studies from a phylogenomic perspective. But in addition to new technologies, it is important to obtain fresh material from rare or little studied species. One of the aims of this first volume is to promote the interest in these still much unknown fungi, boosting field collections often crucial to complete taxon sampling. We predict – and hope – that in the coming years there will be progress in our phylogenetic understanding of many groups, and this will necessarily happen through the collaboration of different experts and enthusiasts, including naturalists, microbiologists, mycologists, lichenologists, taxonomists, systematists and molecular biologists.



Schematic representation of the phylogeny of the *Basidiomycota*, showing the relationships of the 18 classes currently included in the group. The figure is based on a consensus of previous phylogenies published by He et al. (2019), Hibbett et al. (2007), Liu et al. (2015), Wang et al. (2015) and Zhao et al. (2017). Class names in red font indicate the presence of lichenicolous representatives. Orders including lichenicolous taxa in each class are listed to the right, and enclosed in a red box. An indication is also given of the pages of the Flora where detailed phylogenies of particular groups can be viewed. Higher taxonomic ranks are indicated in the right margin.

Host specificity and geographical distribution of lichenicolous *Basidiomycota*

Host specificity

As a rule, most lichenicolous homobasidiomycetes (except species of *Agaricales* that are all confined to *Peltigera* hosts) are generalists, while all known heterobasidiomycetes are host-specific.

The biology of lichenicolous homobasidiomycetes is quite diverse. Some species are virulent pathogens of corticolous lichen communities, especially *Athelia arachnoidea*, *Erythricium aurantiacum*, *Marchandiomyces corallinus* and *Parmeliicida pandemica*. These species show seasonal peaks of their development and are known to be able to kill entire lichen populations. After having killed most lichen thalli, they may be found directly on the bark or over mosses, where they can survive over months as small sclerotia or bulbils, simulating a facultatively lichenicolous way of life. Some species have strong preferences for certain hosts, but still are able to colonize other, often unrelated lichen thalli. For example, *Penttilamyces lichenicola* usually parasitizes terricolous *Cladonia* species in arctic environments, but often also invades populations of *Stereocaulon*. *Erythricium aurantiacum* and *Laetisaria lichenicola* have a predilection for *Physcia adscendens* and *P. tenella* populations, *Bergerella atrofusca* for *P. aipolia* and *P. stellaris*, while *Parmeliicida pandemica* prefers *Parmelia saxatilis* and *P. sulcata*. Thalli of *Physcia* infected by *Burgoa moriformis* rapidly die, while neighbouring inhabited thalli of *Xanthoria parietina* remain uninfected and in good health.

Heterobasidiomycetes, on the contrary, appear to be all strictly host-specific and live on lichens as parasites or facultative lichen symbionts. Most of them are confined to a single host genus, and many are even restricted to a single host species. Some species formerly known to inhabit hosts from several related genera are now regarded as species complexes. A good example is *Syzygospora physciacearum*, reported by Diederich (1996) from *Heterodermia* s. lat., *Physcia* and *Physconia* species, that represents in reality a complex of many species, now included in the new genus *Zyzygomyces*. Another is *Tremella parmeliarum*, described by Diederich (1996) for a species inhabiting both *Parmotrema* and *Rimelia* hosts (the latter now regarded as a synonym of *Parmotrema*), that has subsequently been reported from a wide range of *Parmeliaceae* hosts. This taxon is now split into many morphologically and phylogenetically distinct species, most confined to one host species. Host-specific heterobasidiomycetes are also beginning to be recognized as more is learned about their biology. For example, Diederich (1996) expected that lichenicolous *Chionosphaera* species (now included in the recently described genus *Crittendenia*) may be saprotrophs. However, a recent revision of this genus (Diederich et al. 2022) showed that it includes many parasitic species, all strictly host-specific, all phylogenetically distinct, but most morphologically poorly characterized, and some best regarded as semi-cryptic.

Geographical distribution

Lichenicolous basidiomycetes occur worldwide. With the recent discovery of two species in Antarctica, they are now known from all continents. Nevertheless, the degree of exploration in the various continents is unequal and the known occurrences of lichenicolous basidiomycetes reflects this fact.

The following table gives the number of taxa known from different continents or geographical regions:

• Europe	87
• Macaronesia	23
• North America.....	96
• Central America and Caribbean	13
• South America.....	50
• Africa	6
• Indian Ocean	7
• Asia	24
• Oceania.....	28
• Antarctica	2

It appears that Europe, Macaronesia and North America are quite well explored. However, from the 87 European species, only 18 are here described as new, while 36 from the 96 North American species are newly described in this volume. This shows that the European species are better known than those from North America, where many more additional species are expected to be discovered. South America also appears to harbour a rich flora, with 50 known species, 15 of which are here described as new. Nevertheless, the exploration of South America is far behind that of Europe or North America, having

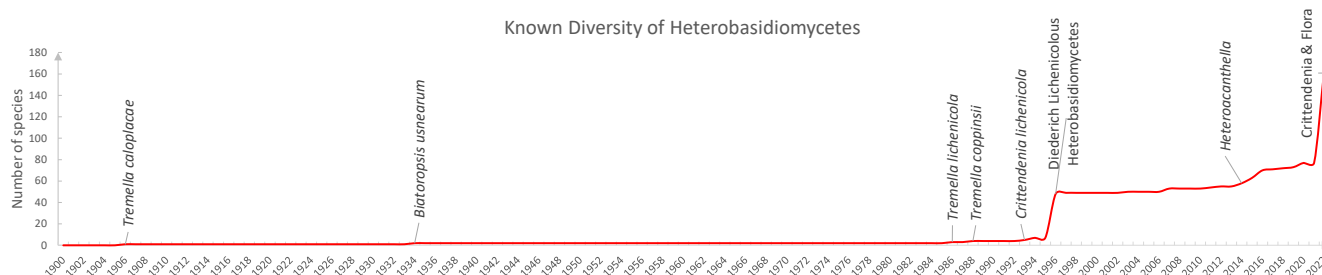
started only in 2000 (Etayo 2002), and this continent will certainly see a dramatic increase of diversity knowledge during the coming decades. Most species known from Oceania have either been collected in Papua New Guinea in 1992 (Diederich 1996), or are based on Australian or New Zealand specimens received for identification. A thorough exploration in Australia and New Zealand has not yet been done, and a very large number of species may be expected. Africa and Asia are poorly explored, and only a small number of species are known from these continents.

Estimation of the global diversity of lichenicolous *Basidiomycota*

Heterobasidiomycetes

Lichenicolous heterobasidiomycetes were discovered only recently. With the exception of *Tremella caloplacae*, described in 1906 as a new genus and species of hyphomycetes, and *Biatoropsis usnearum*, described in 1934 as a new genus and species of ascomycetes, the first lichenicolous species of *Tremella* to be formally described in that genus were *Tremella lichenicola* (Diederich 1986) and *T. coppinsii* (Diederich & Marson 1988). In his monograph of lichenicolous heterobasidiomycetes, Diederich (1996) described 41 new species. During the following 25 years, 22 new species were added, but most of the new species discovered after 1996 are formally described in a recent taxonomic revision of *Crittendenia* (Diederich et al. 2022) and in this volume.

The following graph shows the increase in the number of formally described species (and subspecies) from 1900 until now:



The shape of this graph does not allow estimating how many species really exist. If most species were known, we would expect a logistic curve that becomes more flattened towards to right, while the current graph suggests just the beginning of such a curve.

For an estimation of the global diversity of lichenicolous heterobasidiomycetes, other methods are needed. Here we choose a very simple approach to obtain a first such approximation.

We have observed that there is no way to predict the number of lichenicolous heterobasidiomycete species on a given host genus. E.g., the genus *Peltigera*, known to host an exceptional lichenicolous flora, with 82 species accepted by Diederich et al. (2018), does not harbour a single heterobasidiomycete. The genus *Xanthoparmelia*, with 820 accepted species (Lücking et al. 2016), similarly does not host any heterobasidiomycete. On the contrary, the species-rich genus *Usnea* hosts 15 known species. Amongst the host genera with a crustose thallus, both *Lecanora* (8 heterobasidiomycete species) and *Pertusaria* (7 species) are very rich in lichenicolous species, most newly described in this volume or in recent papers, suggesting many more to be discovered in the near future. Some lichen genera that are rarely recorded or that possess a minuscule thallus are equally chosen by lichenicolous heterobasidiomycetes. E.g., we know two species on *Agonimia*, two on *Byssoloma* and two on *Bacidia*.

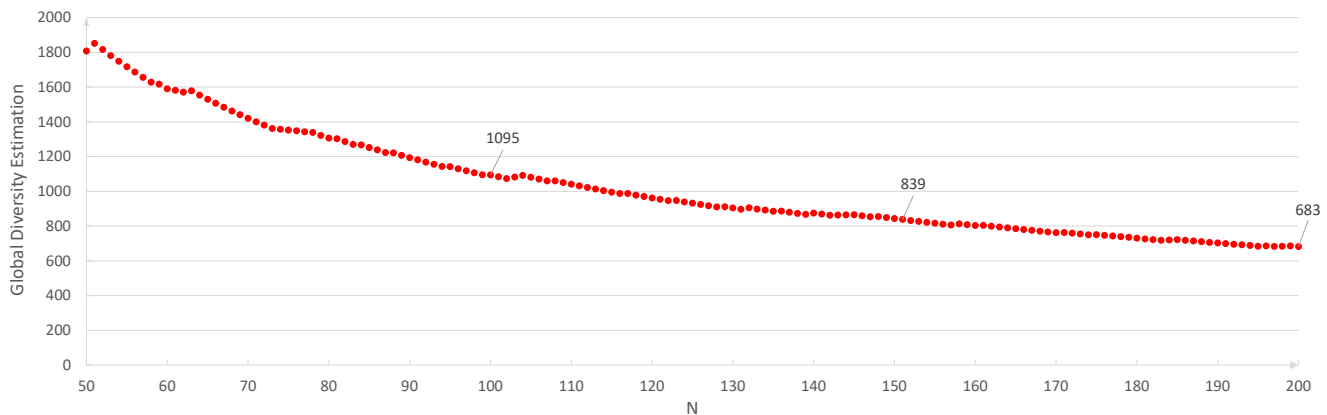
These examples show that lichen genera do not all have a similar probability of harbouring lichenicolous heterobasidiomycetes. For poorly studied genera, however, this probability is unknown and must provisionally be considered as being the same for all genera, regardless of their diversity, frequency or thallus characteristics. The probability of discovering a heterobasidiomycete species on a certain lichen genus would then be proportional to the efforts made by lichenologists to collect, study and investigate the lichenicolous flora on that genus. And these efforts can easily be quantified by the number of occurrences of that lichen genus in the GBIF database (www.gbif.org).

For each of the c. 1000 lichen genera accepted by Lücking et al. (2016), we have obtained the number of occurrences in the GBIF database, then sorted these genera following the decreasing number of occurrences. We considered the first 200 genera, expected to be the best explored hosts for lichenicolous fungi, counted for each of these genera the number of known lichenicolous heterobasidiomycetes inhabiting them, and calculated the average of these numbers. We found that each of these 200 genera harbours an average of 0.68 known species of lichenicolous heterobasidiomycetes. For the 1005 lichen genera

included in our statistics, if we consider an equal probability for all of them to be inhabited, this would give an estimate of $1005 \times 0.68 \approx 683$ heterobasidiomycete species.

However, this estimation is based on the assumption that all heterobasidiomycete species growing on these 200 lichen genera are known and described. But we know that this is not true and that many more species will be discovered on these genera in the future. Therefore, both the average value (0.68) and the resulting estimate (683) need to be multiplied by an unknown factor reflecting our current lack of knowledge. E.g., if the real number of heterobasidiomycete species that grow on these 200 lichen genera is twice the currently known number, then this multiplication factor will be 2, the average value will be 1.36, and the estimate will be 1366 species.

One could argue that the host genus value $N = 200$ has been chosen in an arbitrary way, and that the choice of another value of N would have given another estimate. We have therefore repeated the same calculations with N varying from 50 to 200 and represent the resulting estimates in the following graph:



E.g., if we just considered the 100 most recorded and explored lichen genera, then the resulting estimate would be 1095 heterobasidiomycetes species. However, as the lichenicolous flora of the first 100 genera is better explored than that of the first 200 genera, the multiplication factor needed to express our current lack of knowledge would become smaller, and the estimate obtained, multiplied by this factor, would still remain the same.

As said above, this multiplication factor cannot be identified, and therefore the real number of existing fungi cannot be calculated. However, from our results, we suggest that the global diversity of lichenicolous heterobasidiomycetes is likely to be above 1000.

Homobasidiomycetes

Most lichenicolous homobasidiomycetes are generalists, often with a preference for some hosts, but easily invading neighbouring thalli of unrelated hosts. Many are also able to grow directly on the adjacent bark or mosses, often after the host thallus has been destroyed and disappeared. Given this generalized ecology of most lichenicolous homobasidiomycetes, the above method we used for estimating the number of heterobasidiomycetes cannot be applied to homobasidiomycetes. Instead, we will suggest estimates for each of the known taxonomic groups, based on our knowledge and experience.

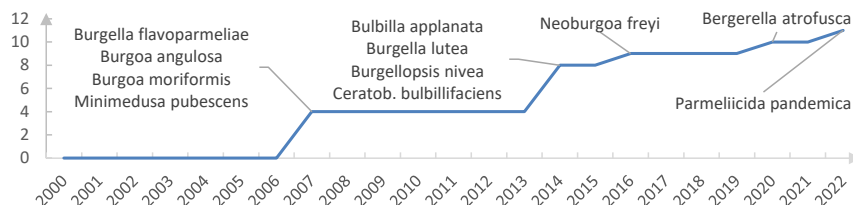
Agaricales. The four known species are all growing on, or loosely associated to *Peltigera* thalli. As no modern treatment of *Gamundia* species, based on morphological and molecular data, is available, and as *G. xerophila* is so variable in colour that it may represent a complex of several species, we estimate the number of lichenicolous species of *Agaricales* to be at least 6.

Atheliales. The common *Athelia arachnoidea* is a virulent pathogen of corticolous lichens, while three members of the *A. epiphylla* species complex occasionally overgrow lichens. As long as no modern treatment of these species is available, supported by phylogenetic analyses, we may expect that a few more obligately or facultatively lichenicolous species will be recognized, thus leading to an estimate of 8 at least facultatively lichenicolous species.

Boletales. The single known species *Penttilamyces lichenicola* is common in arctic environments on *Cladonia* and *Stereocaulon* thalli. Based on our knowledge, there is no reason to expect the existence of more species.

Cantharellales. We currently know 11 lichenicolous species belonging to 9 genera, all asexual with minuscule bulbils. Most of these have rarely been collected, mainly because of their small size, and most also because of their inconspicuous colours.

The following graph shows the increase in the number of described species from 2000 until now:



In our phylogeny, many lichenicolous species occupy an isolated position, with no close relatives known, suggesting a considerable diversity still to be discovered. As new lichenicolous species are regularly being found, although at a very slow pace, and as most lichenologists are not familiar with them, we expect that this trend will continue and we tentatively propose an estimate of 30 lichenicolous species.

Corticiales. Just five species are currently described, including two known exclusively from the sexual stage, two from the asexual, bulbilliferous stage, and one species known from both stages. They all exhibit bright orange to pinkish red colours and are therefore easily detected by field lichenologists. We expect that some more, mostly rarer species will continue to be discovered and we propose an estimate of 15 lichenicolous species.

Seven further endolichenic species of *Lawreymyces* have been invalidly described, as they are known only from DNA sequences. They are all known from South America (Colombia and Ecuador) in thalli of *Agonimia foliacea* and *Normandina* spp. We expect that many more will be discovered through large-scale sequencing of adequate hosts in South America and probably elsewhere, and propose therefore an estimate of over 30 endolichenic species.

The following graph shows the increase in the number of described Corticiales species:



Conclusion

We estimate the global diversity of lichenicolous basidiomycetes as

- > 1000 species of lichenicolous heterobasidiomycetes
- > 60 species of lichenicolous homobasidiomycetes
- > 30 species of endolichenic homobasidiomycetes

Endolichenic heterobasidiomycetes are probably an additional source of diversity but they are not considered here.

Presentation of the Flora

Species included and classification

All fungi that are either strictly lichenicolous, or frequently inhabit lichens, are included. Species that only fortuitously overgrow lichens are thus excluded. As this is a Flora, aiming to identify specimens, we only include species that are macroscopically or microscopically identifiable, and exclude therefore heterobasidiomycete species known only from the yeast stage. However, in the *Corticiales*, we have exceptionally included the endolichenic genus *Lawreymyces*, known only from DNA sequences, as these species are all named, although invalidly, and as they have been included in our phylogenetic tree.

The species are presented following the most recent classification of *Basidiomycota*, mainly following our own phylogenetic results. Each higher-level taxonomic group, especially at the ordinal level, is treated as a separate chapter. Each chapter starts

with a short introduction and phylogenetic tree, an identification key to the species (except the *Tremellales* chapter), followed by the descriptions of genera and species. A host-based key is given in the introductory part of the volume (p. 19).

For each genus, we indicate the existence of molecular data and the number of species in a similar way as given in Diederich et al. (2018). E.g., in ‘Molecular data: yes (T, L)’, ‘yes’ means that sequences exist, ‘T’ that the generic type has been sequenced and ‘L’ that at least one lichenicolous species has been sequenced. ‘Number of species: 23[4]–1–2 (80)’ means that 23 species, subspecies or varieties are obligately lichenicolous (non-lichenized), 4 additional species are known but not formally described, 1 taxon is a lichenicolous lichen, 2 taxa are facultatively (or doubtfully) lichenicolous, while the genus includes a total of c. 80 species (estimation based on recent literature and online databases); the latter number is omitted when all species are lichenicolous.

Hosts, distribution data and references

For each species, we give a list of the known hosts, based on material examined by us or on reliable published data. Similarly, we give a list of countries in which a species has been recorded. The host and the country of the type specimen are written in blue. For most species, we additionally give a distribution map. Data used for these maps comprise (1) our own observations, (2) data found in reliable papers, and (3) non-published data obtained from online databases or atlases. These online resources comprise www.gbif.org/occurrence, www.inaturalist.org/observations, lichenportal.org/cnahl/collections/harvestparams.php (North America), www.lichenology.info (Belgium, Luxembourg and northern France), www.britishlichensociety.org.uk/resources/species-accounts (British Isles), svampe.databasen.org/taxon/44733 (Denmark), elurikkus.ee/bie-hub/search (Estonia), www.verspreidingsatlas.nl/korstmossen (Netherlands), swissfungi.wsl.ch/de/index.html (Switzerland), and others.

For each species, we give a list of the major references, followed by floristic references between square brackets. Despite our efforts to find as many references as possible, we certainly have missed some. Also, for very common species, we sometimes only gave a selection of references.

Illustrations

We made efforts to illustrate all species by macroscopical photos and by microscopical photos or line drawings. While most photos have newly been prepared, we also used our previously published line drawings. A few photos were kindly offered by colleagues. Macroscopical photos have almost all been prepared using a Canon 40D or 6D camera, Nikon BD Plan 5 or 10 objectives, and StackShot (Cognisys) and Helicon Focus (HeliconSoft) for increasing the depth of field. Microscopical photos were prepared using a Leica DMLB microscope, a Leica EC3 camera and Helicon Focus.

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Key to the classes and orders of lichenicolous *Basidiomycota*

- 1 Basidioma a ‘mushroom’, resupinate over the substrate, effuse or floccose; basidia aseptate; or basidiomata absent but sclerotia, bulbils or a white arachnoid mycelium present **AGARICOMYCETES**
- 2 Basidioma a ‘mushroom’, composed of a (sometimes reduced) stipe and a cap (pileus) with fertile lamellae on the lower surface; on *Peltigera* **Agaricales** (33)
- 2’ Basidiomata resupinate over the substrate, effuse or floccose; or basidiomata absent but sclerotia, bulbils or a white arachnoid mycelium present
 - 3 Mycelium sterile, white, arachnoid, covering large areas of bark; or basidiomata present, white or cream-coloured, very thin and pellicular; or compact, mat, brownish sclerotia up to 0.5 mm diam. present **Atheliales** (41)
 - 3’ Mycelium poorly developed; basidiomata, when present, not white; sclerotia or bulbils, when present and brown, less than 0.2 mm diam. (not to be confused with very young, developing sclerotia of *Athelia*)
 - 4 Hymenium meruloid, i. e., with deep fissures and rounded wrinkles when fresh (but smooth when dry), pastel yellow to orange yellow; sclerotia pale yellow to bright orange, 1–3(–5) mm diam.; mainly between podetia of terricolous *Cladonia* or *Stereocaulon* **Boletales** (47)
 - 4’ Hymenium different or basidiomata absent; bulbils less than 0.5 mm diam.
 - 5 Basidiomata or bulbils pastel to coral red or orange (carrot red); bulbils mat **Corticiales** (71)
 - 5’ Bulbils differently coloured, white, pale brown, orange brown, bright yellow or dark reddish brown, mat or shiny; basidiomata unknown. **Cantharellales** (51)
- 1 Basidiomata synnemata-like; basidia tubular, aseptate **AGARICOSTILBOMYCETES · Agaricostilbales** (283)
- 1 Basidiomata gelatinous, often inducing gall formation, in some species reduced and immersed in host apothecia or thallus; basidia septate or not; or basidia missing but conidiophores present
 - 2 Basidiospores obliquely attached to the sterigmata, probably actively released; tremelloid haustorial branches, with a subspherical mother cell and a haustorial filament, usually present; asteroconidia observed in many lichenicolous species; basidia subspherical, ellipsoid, claviform or cylindrical, often with longitudinal, oblique or transverse septa, with elongate sterigmata or epibasidia; or basidia missing but conidiophores present **TREMELLOMYCETES**
 - 3 Basidia cylindrical, aseptate, with 2–4 apical subulate sterigmata, always present; basidiospores ellipsoid or ovoid to almost limoniform, with a refractive basal apiculus **Filobasidiales** (83)
 - 3’ Basidia subspherical, ellipsoid, claviform or cylindrical, usually with longitudinal, oblique or transverse septa and elongate epibasidia, or missing but conidiophores present; basidiospores subglobose to ellipsoid, with a non-refractive lateral apiculus **Tremellales** (105)
 - 2’ Basidiospores symmetrically attached to the sterigmata, passively released; tremelloid haustorial branches usually absent; asteroconidia absent; basidia always present
 - 3 Basidia of two parts, a lower thick-walled ellipsoid or claviform probasidium, and an upper, cylindrical, transversely 1–3-septate, thin-walled meiosporangium with short perpendicular epibasidia **CYTOBASIDIOMYCETES · Cyphobasidiales** (305)
 - 3’ Basidia of one part, clavate to subcylindrical, 0–3-transseptate
 - 4 Basidia with 3 transverse septa, without epibasidia or sterigmata; basidiospores elongate ellipsoid, 10–18 × 3.5–5 µm, formed laterally at the upper edge of each of the three lower basidial cells (i. e., just below the septum) and at the lower edge of the upper cell (i. e., just above the upper septum), resulting in the two upper spores being adjacent; on *Tetramelas* aff. *graminicola* in Antarctica **MICROBOTRYOMYCETES** (325)
 - 4’ Basidia with 0–2 transverse septa and short epibasidia; basidiospores ellipsoid, 4–5.5 × 3–4 µm; on *Hypotrachyna* ‘*Syzygospora*’ (331)
- 1’ Bulbils, sclerotia, basidiomata, conidiomata and mycelium unknown; endolichenic fungi detectable by DNA sequencing
 - 2 Yeast stage unknown **AGARICOMYCETES · Corticiales (Lawreymyces)** (79)
 - 2’ Yeast stage present, also detectable using Fluorescence in situ hybridization (FISH)
 **TREMELLOMYCETES or CYTOBASIDIOMYCETES**

Host-based key to the lichenicolous *Basidiomycota* and bacterial galls

This key includes all host-specific species. Some generalist species are keyed out under their main hosts. For the identification of species with bulbils or sclerotia that may grow on diverse hosts, the key to the lichenicolous classes and orders of lichenicolous *Basidiomycota*, and the keys to the species of *Atheliales*, *Cantharellales* and *Corticiales* should be used. This key also includes galls resembling *Tremella* basidiomata, probably induced by bacteria.

The microscopical examination of heterobasidiomycetes basidiomata is often difficult, as basidia are frequently poorly distinguishable, and basidiospores are often extremely few, or difficult to detect, or overmature and collapsed. Adequate staining of microscopical preparations is therefore essential. Although many techniques of staining exist, we suggest the following for routine examinations (used also for galls containing bacteria):

- Deposit a drop of 5% KOH and a drop of phloxine on a microscopical slide, distant from each other by c. 1 cm.
- With a sharp razor blade, cut a horizontal section of the upper part of a basidioma, c. 50 µm thick, to obtain as many basidia as possible, while avoiding too many host cells.
- Put the section in the drop of KOH and wait for one minute.
- With a needle, transfer the section to the drop of phloxine and wait for one minute until the stain entered the cells.
- With the same needle, transfer the section back to the drop of KOH, remove the drop of phloxine with tissue paper, and wait for one minute.
- Add the cover glass. Under a binocular microscope, press laterally on the cover glass until most air drops are gone, then, at the highest magnification, press with a blunt needle on the cover glass, together with slight lateral movements, until the basidia are all separated. Exaggerated pressure may destroy basidia and basidiospores. Cover the glass with a thick layer of tissue paper and press on it until all the excessive liquid is gone.
- Examine under the microscope through the ×100 objective; when available, also use phase contrast or DIC optics.

ABROTHALLALES

Abrothallaceae – Abrothallus

Basidiomata intrahymenial; basidia transversely 1-septate, 17–21 × 7–8 µm; basidiospores 5.5–8 × 5–6.5 µm; on *Abrothallus parmeliarum* *Tremella abrothalli* (131)

ACAROSPORALES

Acarosporaceae – Acarospora

Basidiomata intrahymenial, apothecia becoming swollen, convex, waxy-gelatinous, 0.3–0.8 mm diam.; basidia transversely 1-septate, 16–29 × 5.5–8.5 µm; on *Acarospora* *Tremella acarosporae* (132)

ARTHONIALES

Arthoniaceae

1 Basidiomata synnemata-like; basidia tubular, aseptate; on *Bryostigma muscigenum* *Crittendenia bryostigmatis* (288)

1' Basidiomata convex, waxy-gelatinous; basidia septate

2 Basidia 2-celled

3 Basidiomata gelatinous, flat to slightly convex, orange-brown, 0.3–0.6 mm diam.; basidia with a longitudinal or oblique septum, 11–20 × 7.5–11 µm; basidiospores 6–9.5 × 5.5–7.5 µm; on *Synarthonia inconspicua* *Tremella synarthoniae* (259)

- 3' Basidiomata non-gelatinous, matt, convex, pale yellowish brown to dark grey, 0.1–0.6 mm diam.; basidia with a longitudinal, oblique or transverse septum, $12\text{--}22 \times 6.5\text{--}10\text{ }\mu\text{m}$; basidiospores $6\text{--}7.5 \times 4.5\text{--}7\text{ }\mu\text{m}$; on *Herpothallon*..... ***Tremella herpothalli*** (180)
- 2' Basidia 4-celled, with longitudinal septa, $11\text{--}20 \times 8\text{--}13.5\text{ }\mu\text{m}$; basidiospores $5.5\text{--}6.5 \times 5\text{--}5.5\text{ }\mu\text{m}$; basidiomata gelatinous, convex, pale brown, 0.2–0.45 mm diam.; on *Coniocarpon cinnabarinum*..... ***Tremella coniocarpi*** (161)

Roccellaceae

- 1 Basidia of two parts, a lower thick-walled elongate ellipsoid probasidium, $11\text{--}19.5 \times 7.5\text{--}12\text{ }\mu\text{m}$, and an upper, cylindrical, transversely septate, thin-walled meiosporangium; basidiomata pulvinate, subspherical or irregular, not gelatinous, whitish to pale brown, 0.2–0.35 mm diam.; on *Enterographa pallidella* ***Cyphobasidium enterographicola*** (311)
- 1' Basidia of one part, ellipsoid to claviform, 2–4-celled, with longitudinal septa
 - 2 Basidiomata applanate to pulvinate, gelatinous, often confluent, pale orange brown, 0.1–0.5 mm diam.; basidia $14.5\text{--}17 \times 11\text{--}12.5\text{ }\mu\text{m}$; basidiospores $5.5\text{--}7 \times 3.5\text{--}5\text{ }\mu\text{m}$; on *Graphidastra multiformis*..... ***Tremella graphidastrae*** (175)
 - 2' Basidiomata inducing large, convex, basally constricted galls with a matt surface, up to 4 mm diam.
 - 3 Basidiomatal galls strongly convex, whitish, 0.5–4 mm diam.; basidia $17\text{--}24 \times 14\text{--}23\text{ }\mu\text{m}$; basidiospores $7\text{--}9 \times 7\text{--}8\text{ }\mu\text{m}$; on *Dendrographa* species with a fruticose thallus..... ***Tremella dendrographae*** (163)
 - 3' Basidiomatal galls subspherical, medium brown, 0.2–1 mm diam., when confluent, up to 4 mm; basidia $12\text{--}20 \times 12.5\text{--}18\text{ }\mu\text{m}$; basidiospores c. $7 \times 7.5\text{ }\mu\text{m}$; on *Dendrographa franciscana*..... ***Tremella robusta*** (252)

CALICIALES

Caliciaceae

- 1 Basidia aseptate, elongate, subcylindrical, with 3–4 sterigmata; on *Pyxine* ***Zyzygomyces* sp. 4** (101)
- 1' Basidia septate
 - 2 Basidia elongate claviform to subcylindrical, with 3 transverse septa; epibasidia and sterigmata missing; basidiospores elongate ellipsoid, without apiculus; basidiomata pulvinate, blackish with a rough surface; on *Tetramelas* aff. *graminicola*..... ***Kriegeriopsis livingstonensis*** (326)
 - 2' Basidia with elongate epibasidia; basidiospores with a lateral apiculus
 - 3 Basidia 2-celled, ellipsoid, base often attenuated
 - 4 Basidiomata pulvinate, black, 0.25–0.35 mm diam.; basidia transversely septate, $17\text{--}24 \times 6.5\text{--}10\text{ }\mu\text{m}$; basidiospores $6\text{--}8 \times 5.5\text{--}6.5\text{ }\mu\text{m}$; on *Dirinaria aegialita*..... ***Tremella dirinariae*** (166)
 - 4' Basidiomata resupinate, brown, 0.3–6 mm diam.; basidia longitudinally or obliquely, rarely transversely septate, $16\text{--}30 \times 10\text{--}17.5\text{ }\mu\text{m}$; basidiospores $8.5\text{--}10 \times 7\text{--}9\text{ }\mu\text{m}$; on *Dirinaria purpurascens*.. ***Tremella purpurascensis*** (243)
 - 3' Basidia 4-celled, longitudinally septate, subspherical, $11\text{--}14.5 \times 10\text{--}16\text{ }\mu\text{m}$, endolichenic; basidiomata missing; on *Tetramelas* aff. *graminicola* ***Tremella* sp. 12** (275)

Physciaceae

- 1 Basidiomata and conidiomata absent
 - 2 Bulbils present, orange or dark brown
 - 3 Bulbils dark reddish brown, shiny, 25–35 μm diam.; on *Physcia aipolia* and *P. stellaris*..... ***Bergerella atrofusca*** (54)
 - 3' Bulbils orange (carrot red), matt, 100–150 μm diam.; on *Physcia adscendens*, *P. tenella* and other lichens ***Erythricium aurantiacum*** (74)
 - 2' Galls present, orange brown, either subspherical, or pustular and apothecium-like, containing no lichenicolous fungus but numerous bacteria; on *Hyperphyscia adglutinata* or *Physcia*..... **Bacterial galls on *Hyperphyscia* and *Physcia*** (338)
- 1' Basidiomata present

- 2 Basidiomata resupinate, floccose, loosely attached to the substratum, orange or pinkish; on *Physcia adscendens*, *P. tenella* and other lichens
- 3 Basidiomata orange (carrot red), up to 1 cm diam.; mature basidia clavate to suburniform, $25\text{--}40 \times 12\text{--}15 \mu\text{m}$, with 4 sterigmata; basidiospores pyriform or lacrimiform, $13\text{--}17.5 \times 8\text{--}11.5 \mu\text{m}$ *Erythricium aurantiacum* (74)
- 3' Basidiomata pink to coral, up to 2 mm diam.; mature basidia clavate to suburniform, $30\text{--}35 \times 9.5\text{--}12 \mu\text{m}$, with 2 sterigmata; basidiospores pyriform or lacrimiform, $14.5\text{--}18.5 \times 10.5\text{--}12.5 \mu\text{m}$ *Laetisaria lichenicola* (78)
- 2 Basidiomata synnemata-like; basidia tubular, aseptate..... *Crittendenia* (284)
- 2' Basidiomata waxy-gelatinous, often gall-inducing
 - 3 Basidia aseptate, elongate, subcylindrical, with 3–4 sterigmata *Zyzygomyces* (85)
 - 3' Basidia septate
 - 4 Basidia 2-celled
 - 5 Basidia cells elongating laterally at maturity, septum longitudinal, $10\text{--}18 \mu\text{m}$ diam., near septum $10\text{--}17 \mu\text{m}$ long, individual cells up to $30 \mu\text{m}$ long; basidiospores $9\text{--}12 \times 8.5\text{--}10.5 \mu\text{m}$; basidiomata inducing galls on the host thallus, $0.4\text{--}2 \text{ mm}$ diam., or galls on apothecia resembling an agglomeration of many small apothecia; on *Physcia*..... *Tremella christiansenii* (150)
 - 5' Basidia cells not elongating at maturity
 - 6 Basidia stalked, $15\text{--}20 \times 10\text{--}15 \mu\text{m}$ (without stalk), stalk $2\text{--}21 \mu\text{m}$ long; basidiospores $5.5\text{--}9 \times 5\text{--}9 \mu\text{m}$; basidiomata waxy-gelatinous, pale brown to black, $0.2\text{--}2 \text{ mm}$ diam.; on *Anaptychia ciliaris* *Tremella anaptychiae* (135)
 - 6' Basidia not or indistinctly stalked, $< 10 \mu\text{m}$ wide
 - 7 Basidiomata intrahymenial, appearing as dark brown swellings of host apothecia; basidia $20\text{--}26 \times 8\text{--}10 \mu\text{m}$; basidiospores $7\text{--}9 \times 5\text{--}8 \mu\text{m}$; on *Rinodina oleae* *Tremella rinodinae* (251)
 - 7' Basidiomata inducing brown galls on the host thallus, $0.4\text{--}2 \text{ mm}$ diam.; basidia $15\text{--}27 \times 4.5\text{--}8 \mu\text{m}$; basidiospores $6\text{--}8 \times 5.5\text{--}7.5 \mu\text{m}$; on *Phaeophyscia* *Tremella phaeophysciae* (232)
 - 4' Basidia 2–4-celled
 - 5 Basidiomata inducing brown roundish galls on the host thallus, $0.4\text{--}2 \text{ mm}$ diam.; basidia $15\text{--}27 \times 4.5\text{--}8 \mu\text{m}$; basidiospores $6\text{--}8 \times 5.5\text{--}7.5 \mu\text{m}$; on *Phaeophyscia* *Tremella phaeophysciae* (232)
 - 5' Basidiomata not gall-inducing, dark brown to black when mature, elongate, $0.3\text{--}1.5 \text{ mm}$ long
 - 6 Basidia $9\text{--}16 \times 4.5\text{--}7 \mu\text{m}$; basidiospores $5\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$; on *Leucodermia*.. *Tremella leucodermiae* (192)
 - 6' Basidia $13.5\text{--}22.5 \times 8\text{--}14.5 \mu\text{m}$; basidiospores c. $5 \times 5 \mu\text{m}$; on *Tornabea scutellifera* *Tremella tornabeae* (261)

CANDELARIALES

Candelariaceae – Candelariella

Basidiomata reduced, inducing yellow galls, $0.1\text{--}0.8 \text{ mm}$ diam., or intrahymenial; basidia 2–4-celled, septa longitudinal or oblique, $18\text{--}23 \times 10\text{--}12 \mu\text{m}$; basidiospores $6.5\text{--}8 \times 5\text{--}6 \mu\text{m}$; on *Candelariella*..... *Tremella candelariellae* (142)

LECANORALES

Cladoniaceae – Cladonia

- 1 Orange bulbils or sclerotia present, sometimes accompanied by orange meruloid basidiomata
- 2 Basidiomata meruloid (wrinkled or folded), orange, up to 10 mm diam.; sclerotia orange, up to 5 mm diam.; on *Cladonia*, more rarely *Stereocaulon* *Penttilamyces lichenicola* (48)

- 2' Basidiomata absent; bulbils immersed, erumpent, pale yellow to orange, 150–300(–700) µm diam.; on *Cladonia* and other lichens *Neoburgoa freyi* (64)
- 1' Bulbils and sclerotia absent; basidiomata waxy-gelatinous, often gall-inducing
 - 2 Basidia aseptate, elongate, subcylindrical, with 3–4 sterigmata; basidiomata waxy-gelatinous, reddish brown, rarely dark brown, inducing gall formation, up to 5 mm long; on *Cladonia* *Zyzygomyces bachmannii* (88)
 - 2' Basidia 1-septate
 - 3 Basidia subspherical to ellipsoid, longitudinally, rarely obliquely or transversely septate, 8.5–14 × 7–8.5 µm; basidiospores 5.5–7.5 × 4–5.5 µm; basidiomata waxy-gelatinous, pale to dark reddish brown, 0.2–0.8 mm diam.; on *Cladonia macroceras* *Tremella macroceratis* (197)
 - 3' Basidia transversely septate, 20–36 × 4.5–8 µm; basidiospores 7–10 × 6–8 µm; basidiomata inducing concolorous to reddish brown galls, 0.1–2.2 mm diam.; on *Cladonia*. *Tremella cladoniae* (152)

Haematommaceae – Haematomma

- Basidiomata waxy-gelatinous, amber-coloured, convex, 0.1–0.8 mm diam.; basidia 4-celled, septa longitudinal or oblique, 15–36 × 11–20 µm; basidiospores 7–10 × 6.5–9.5 µm; in or on the hymenium, or on the thallus of *Haematomma persoonii* *Tremella haematommatis* (178)

Lecanoraceae

- 1 Basidiomata synnemata-like; basidia tubular, aseptate; on *Lecanora* or *Lecidella elaeochroma* *Crittendenia* (284)
- 1' Basidiomata waxy-gelatinous or intrahymenial
 - 2 Basidia aseptate; intrahymenial, later inducing galls over apothecia of *Lecanora carpinea*
 - 3 Basidia smooth-walled, not or shortly stalked, 17–40 × 9.5–17 µm (stalk included); hyphidia absent; basidiospores subspherical to broadly ellipsoid, with a lateral apiculus, 9.5–15.5 × 10–16 µm *Tremella endosporogena* (168)
 - 3' Basidia with an acanthoid ornamentation, mostly stalked, 10–15 × 7.5–12 µm (stalk not included), stalk 1–7 µm long; hyphidia acanthoid, 8–23 × 5–12 µm; basidiospores ellipsoid, with a refractive apiculus at the proximal end, 10–14 × 6.5–9.5 µm *Heteroacanthella ellipsospora* (130)
 - 2 Basidia 2-celled, transversely septate; basidiomata intrahymenial
 - 3 Basidia 16.5–29 × 6–10 µm; basidiospores 8.5–11 × 6.5–9 µm; basidiomata visible as convex brown swellings of the host apothecia; on *Lecanora* gr. *polytropa* *Tremella pyrenaica* (245)
 - 3' Basidia 15–21 × 5–7 µm; basidiospores 7.5–8 × 5–5.5 µm; basidiomata reduced; on *Lecanora rimicola*. *Tremella* sp. 2 (273)
 - 2' Basidia 2–4-celled, longitudinally septate
 - 3 Individual basidial cells elongating at maturity
 - 4 Basidiomata intrahymenial, visible as small convex swellings on the apothecial disk; on *Lecanora allophana* *Tremella mayrhoferi* (198)
 - 4' Basidiomata distinct, on the host thallus, pale to orange-brown, waxy-gelatinous, 0.2–0.7 mm diam.
 - 5 Basidial cells at maturity 40–72 × 6.5–19 µm; basidiospores 11.5–17.5 × 10.5–18 µm; on *Lecanora louisianae* *Tremella zamorae* (270)
 - 5' Basidial cells at maturity up to 85 × 4.5–8.5 µm; on *Lecanora nothocaesiella* *Tremella* aff. *zamorae* (272)
 - 3' Basidial cells not elongating at maturity
 - 4 Basidiomata intrahymenial, later convex, waxy-gelatinous; basidia 20–51 × 12–24 µm; basidiospores 7–12.5 × 7.5–13 µm; on *Lecanora chlarotera* *Tremella macrobasidiata* (196)
 - 4' Basidiomata distinct, pulvinate, waxy-gelatinous, on the host thallus or apothecial margin
 - 5 Basidiomata 0.2–1.3 mm diam., pale brown; basidia 12–19.5 × 8.5–13.5 µm; on *Lecanora appalachensis* *Tremella* sp. 9 (274)
 - 5' Basidiomata < 0.7 mm diam.; basidia larger

- 6 Basidiomata 0.1–0.4 mm diam., pale to medium yellow to orange brown; basidia $19\text{--}32 \times 13\text{--}23\ \mu\text{m}$; on *Lecidella elaeochroma* ***Tremella lecidellae*** (187)
- 6' Basidiomata larger, 0.1–0.7 mm diam., pale brown
- 7 Basidia $15\text{--}26 \times 12\text{--}22\ \mu\text{m}$; basidiospores $7\text{--}10.5 \times 7\text{--}11\ \mu\text{m}$ diam.; on *Lecanora varia* ***Tremella variae*** (266)
- 7' Basidia $20\text{--}30 \times 17\text{--}24\ \mu\text{m}$; basidiospores $9\text{--}10 \times 7.5\text{--}10\ \mu\text{m}$; on *Lecanora intumescens* ***Tremella* aff. *variae*** (267)

Parmeliaceae

- 1 On *Alectoria sarmentosa*; basidiomatal galls visible as concolorous swellings of the thallus, 0.3–1.5 mm diam.; basidia 2-celled, septum longitudinal or rarely oblique, $7.5\text{--}14.5 \times 7\text{--}11\ \mu\text{m}$; basidiospores $6\text{--}6.5 \times 5\text{--}5.5\ \mu\text{m}$ ***Tremella alectoriae*** (133)
- 1 On *Brodoa intestiniformis*; basidiomatal galls concolorous to dark brown or black, with a smooth and shiny surface, 0.5–4.5 mm diam.; basidia of narrowly ellipsoid to ampulliform cells fixed together only at the base, with an attenuated apex devoid of epibasidia and basidiospores, producing ellipsoid conidia, $12.5\text{--}15.5 \times 2.5\text{--}3.5\ \mu\text{m}$ ***Tremella brodoae*** (140)
- 1 On *Bryoria*, over ascomata of *Raesaenenia huuskonenii*; basidiomata gelatinous, black, convex, elongate, up to 1.2×0.5 mm; basidia 2-celled, septum transverse or rarely oblique, $13.5\text{--}18 \times 5.5\text{--}7\ \mu\text{m}$; basidiospores $6.5\text{--}8.5 \times 5\text{--}6.5\ \mu\text{m}$ ***Tremella huuskonenii*** (182)
- 1 On *Canoparmelia cryptochlorophaea*; basidiomata, conidiomata and bulbils absent; subpherical galls present, medium brownish, rapidly turning dark brown to black, 0.1–0.5 mm diam., containing no lichenicolous fungus but numerous bacteria **Bacterial galls on *Canoparmelia cryptochlorophaea*** (337)
- 1 On *Cetraria*
- 2 Basidiomatal galls dark brown to black, with a smooth and shiny surface, 1–2 mm diam.; basidia of narrowly ellipsoid to ampulliform cells fixed together only at the base, with an attenuated apex devoid of epibasidia and basidiospores, producing ellipsoid conidia, $4\text{--}9.5 \times 2.5\text{--}3.5\ \mu\text{m}$; on *Cetraria ericetorum* ***Tremella cervina*** (145)
- 2' Basidiomatal galls pustular, surface rough with irregular openings; basidia subspherical to shortly ellipsoid, not constricted at the septa, devoid of epibasidia and of basidiospores, producing sessile, ellipsoid conidia
- 3 Conidia $2.5\text{--}4 \times 2\text{--}3\ \mu\text{m}$; on *Cetraria aculeata* ***Tremella cetraculeata*** (146)
- 3' Conidia $5.5\text{--}7.5 \times 2\text{--}3\ \mu\text{m}$; on *Cetraria islandica* ***Tremella cetrariae*** (147)
- 1 On *Cetrariella delisei*; basidiomata waxy-gelatinous, pale to dark brown or black, convex to subglobose, often tuberculate, 0.1–1.5 mm diam.; basidia 2–4-celled, septa longitudinal, oblique or transverse, $10\text{--}31 \times 4\text{--}11\ \mu\text{m}$; basidiospores $4\text{--}8 \times 4\text{--}8\ \mu\text{m}$ ***Tremella cetrariellae*** (148)
- 1 On *Evernia*
- 2 Basidiomata inducing large bullate galls reaching 15 mm diam.; basidia 2–4-celled, septa longitudinal, $9\text{--}14 \times 9\text{--}13\ \mu\text{m}$; basidiospores $5\text{--}7 \times 5\text{--}6\ \mu\text{m}$; on *Evernia mesomorpha* ***Tremella everniae*** (171)
- 2' Basidiomata inducing superficial galls, brown, slightly convex, basally not constricted, up to 1 mm diam.; basidia 2-celled, septum longitudinal or slightly oblique, $14\text{--}24 \times 10\text{--}13\ \mu\text{m}$; on *Evernia prunastri* [known from California; similar, common galls on European *E. prunastri* never contain basidia and are not this species!] ***Tremella* sp. 8** (273)
- 1 On *Flavoparmelia*
- 2 Basidiomata absent; bulbils yellow to ochraceous or orange, 60–110 μm diam.; on *Flavoparmelia baltimorensis* and *Parmotrema* ***Burgella flavoparmeliae*** (56)
- 2' Basidiomata present, inducing strongly convex to bullate galls, up to 10 mm diam.; bulbils absent; basidia 2-celled, septum longitudinal, $16\text{--}22 \times 11\text{--}17.5\ \mu\text{m}$; basidiospores $8.5\text{--}11.5 \times 8.5\text{--}11\ \mu\text{m}$ on *Flavoparmelia caperata* ***Tremella flavoparmeliae*** (173)
- 1 On *Hypogymnia*
- 2 Basidia of two parts, a lower thick-walled ellipsoid probasidium, $11\text{--}22 \times 4\text{--}11\ \mu\text{m}$, and an upper, cylindrical, transversely 3-septate, thin-walled meiosporangium

- 3 Basidiomata inducing convex, later bullate galls up to 17 mm diam.; on *Hypogymnia physodes* and other *Hypogymnia* species..... ***Cyphobasidium hypogymniicola*** (312)
- 3' Basidiomata inducing small, subspherical galls, 0.1–1.2 mm diam.; on *Hypogymnia hultenii*
..... ***Cyphobasidium* aff. *hypogymniicola*** (313)
- 2' Basidia of one part, ellipsoid, 2-celled, septum longitudinal, oblique or transverse
 - 3 Basidiomata absent; basidia endolichenic, 11–17 × 7–13 µm; basidiospores 6.5–7.5 × 5–7 µm; in the necrosed, blackened thallus of *Hypogymnia physodes*..... ***Tremella pinaultii*** (233)
 - 3' Basidiomata or basidiomatal galls present
 - 4 Basidiomata waxy-gelatinous, not gall-inducing; basidia 11–15 × 6.5–8.5 µm; basidiospores 6–7.5 × 3.5–6 µm; on several *Hypogymnia* species..... ***Tremella papuana*** (210)
 - 4' Basidiomata inducing convex galls, 0.2–1.8 mm diam.
 - 5 Galls pale brown to pinkish, occasionally becoming blackish; basidia 11–20 × 7–14 µm; basidiospores 7–10 × 5.5–7 µm; on *Hypogymnia physodes*..... ***Tremella hypogymniae*** (184)
 - 5' Galls pale to dark brown or blackish; basidia 10–17(–23) × 8–11 µm; basidiospores 6–8 × 5–7 µm; on *Hypogymnia tubulosa* ***Tremella tubulosae*** (262)
- 1 On *Hypotrachyna*
 - 2 Basidiomata synnemata-like; basidia tubular, aseptate..... ***Crittendenia hypotrachynae*** (292)
 - 2' Basidiomata resupinate, waxy-gelatinous, or gall inducing
 - 3 Basidia of two parts, a lower thick-walled ellipsoid probasidium, 12–23 × 3.5–8 µm, and an upper, cylindrical, transversely 1–3-septate, thin-walled meiosporangium ***Cyphobasidium hypotrachynicola*** (314)
 - 3' Basidia of one part, ellipsoid, clavate or subcylindrical, aseptate, or transversely 1–2-septate, with very short epibasidia; basidiospores ellipsoid, 4–5.5 × 3–4 µm
 - 4 Basidia aseptate, 10–18 × 3–5.5 µm; basidiomata inducing subspherical to bullate or lobate brownish galls
..... ***Syzygospora parmeliicola*** (331)
 - 4' Basidia transversely 1–2-septate, 15.5–27 × 3.5–5.5 µm; basidiomata inducing dark brown to black galls, 0.3–0.7 mm diam., becoming cerebriform to tuberculate, up to 5 mm diam. ***Syzygospora septata*** (332)
- 1 On *Imshaugia aleurites*; basidiomata gelatinous, amber-coloured, convex, 0.1–1 mm diam.; basidia 2–4-celled, septa longitudinal or rarely oblique, 15.5–21.5 × 13–16.5 µm; basidiospores 6.5–9 × 6.5–8.5 µm .. ***Tremella imshaugiae*** (185)
- 1 On *Letharia vulpina*; basidiomata inducing small orange galls, 0.2–1.5 mm diam.; basidia 4-celled, septa longitudinal, 15–20 × 10–16 µm; basidiospores 6–8 × 5.5–7.5 µm ***Tremella lethariae*** (191)
- 1 On *Melanelixia* and *Melanohalea*; basidiomata synnemata-like; basidia tubular, aseptate ***Crittendenia*** (284)
- 1 On *Menegazzia*, gall-inducing; basidia of two parts, a lower thick-walled ellipsoid probasidium, and an upper, cylindrical, transversely septate, thin-walled meiosporangium ***Cyphobasidium* sp. 1** (322)
- 1 On *Nephromopsis orbata*; basidiomata inducing galls with a narrow base and a flat upper surface, pale to medium brown, 0.3–1.2 mm diam.; basidia 2-celled, septum longitudinal or rarely oblique, 10–17 × 5–9 µm; basidiospores c. 6 × 6.5 µm ***Tremella nephromopsidis*** (203)
- 1 On *Parmelia*; basidiomata absent
 - 2 Bulbils present, dark reddish brown, slightly translucent, 150–270(–400) × 120–200 µm ***Parmeliicida pandemica*** (65)
 - 2' Subpherical to irregular galls present, pinkish to brownish, then blackish, 0.3–0.8 mm diam., containing no lichenicolous fungus but numerous bacteria; on *Parmelia saxatilis* **Bacterial galls on *Parmelia saxatilis*** (340)
- 1 On *Parmelina quercina*; basidiomata synnemata-like; basidia tubular, aseptate ***Crittendenia* sp. 1** (302)
- 1 On *Parmelinella amazonica*; basidiomata absent; conidiomata immersed, breaking through the cortex, flat to slightly convex, pale brown, rapidly dark brown to black, gelatinous, 0.4–1.2 mm diam.; conidia clamped, ellipsoid, c. 4.5–5.5 × 3.5–4.5 µm ***Tremella conidiopunctelia* subsp. *parmelinellae*** (159)

- 1 On *Parmotrema*
 - 2 Basidiomata absent
 - 3 Bulbils present, yellow to ochraceous or orange, 60–110 µm diam.; on *Flavoparmelia baltimorensis* and *Parmotrema* ***Burgella flavoparmeliae*** (56)
 - 3' Stipitate, apically enlarged galls present, pinkish to brownish, rarely blackish, apically 0.1–1 mm diam., containing no lichenicolous fungus but numerous bacteria **Bacterial galls on *Parmotrema*** (341)
 - 2' Basidiomata or conidiomata present; bulbils absent
 - 3 Conidiomata convex, gelatinous, pale to dark reddish brown, 0.15–0.5 mm diam.; conidia clamped, ellipsoid, $5\text{--}6.5 \times 4.5\text{--}5$ µm; basidia occasionally present; on *Parmotrema* ***Tremella conidioparmotrema*** (155)
 - 3' Conidiomata absent; basidiomata present
 - 4 Basidia of two parts, a lower thick-walled ellipsoid probasidium, and an upper, cylindrical, transversely septate, thin-walled meiosporangium; basidiomata inducing convex, brown galls; on *Parmotrema reticulatum* ***Cyphobasidium* aff. *hypotrachynicola*** (317)
 - 4' Basidia of one part, septate
 - 5 Basidia 2-celled
 - 6 Basidiomatal galls convex with a constricted base, medium to dark chestnut brown, 0.25–5 mm diam.; basidia subspherical to ellipsoid, septum longitudinal or oblique, $10\text{--}22 \times 6.5\text{--}13$ µm; basidiospores $6\text{--}8 \times 5\text{--}6$ µm; on *Parmotrema reticulatum* ***Tremella parmeliarum*** (211)
 - 6' Basidiomata resupinate, flat or very slightly convex, well delimited, medium to dark brown, waxy-gelatinous, 1–4 mm diam.; basidia elongate ellipsoid, septum transverse, $16\text{--}28 \times 6\text{--}10$ µm; basidiospores $6\text{--}8 \times 5\text{--}7$ µm; on *Parmotrema gardneri* ***Tremella parmogardneri*** (214)
 - 5' Basidia 2–4-celled
 - 6 Basidiomatal galls strongly convex, basally constricted, often with a central depression, sometimes tuberculate, pale to dark brown, often with a greyish tinge, 0.3–5 mm diam.; basidia ellipsoid, septa longitudinal, oblique or transverse, $17\text{--}36 \times 12\text{--}18$ µm; basidiospores $7.5\text{--}9.5 \times 7\text{--}9$ µm
 - 7 On *Parmotrema hypotropum* ***Tremella parmohypotropi*** (215)
 - 7' Basidiomatal galls often darker; on *Parmotrema hypoleucinum* ***Tremella* aff. *parmohypotropi*** (216)
 - 6' Basidiomatal galls slightly convex, basally not constricted, pale to medium brown, 0.4–2 mm diam.; basidia subspherical to ellipsoid, septa longitudinal, $11\text{--}17.5 \times 8.5\text{--}14$ µm; basidiospores $5\text{--}7.5 \times 3.5\text{--}7$ µm; on *Parmotrema perforatum* ***Tremella parmoperforati*** (217)
 - 1 On *Platismatia*; basidiomata waxy-gelatinous, pinkish to reddish orange, applanate or pulvinate, 0.3–0.7 mm diam.; basidia 2–4-celled, septa longitudinal, $8\text{--}13 \times 5\text{--}12$ µm; basidiospores $6\text{--}10 \times 4\text{--}6.5$ µm ***Tremella coppinsii*** (162)
 - 1 On *Protoparmelia*
 - 2 Basidiomata intrahymenial, not visible; basidia 2-celled, transversely septate, narrowly ellipsoid to subcylindrical, $29\text{--}39 \times 8\text{--}10$ µm; basidiospores $8.5\text{--}9.5 \times 6.5\text{--}8$ µm; on *Protoparmelia badia* ***Tremella protoparmeliae*** (236)
 - 2' Basidiomata pulvinate, gelatinous, pale to dark greyish brown, 0.15–0.5 mm diam.; basidia 2–4-celled, subspherical to ellipsoid, $18\text{--}24 \times 12\text{--}18$ µm; basidiospores $9\text{--}10.5 \times 8\text{--}10$ µm; on *Protoparmelia hypotremella* and *P. oleaginea* ***Tremella wirthii*** (268)
 - 1 On *Punctelia*
 - 2 Basidiomata absent; conidiomata immersed, breaking through the cortex, flat to slightly convex, pale to dark brown or blackish, gelatinous, 0.4–1.8 mm diam.; conidia clamped, ellipsoid, c. $5\text{--}7 \times 4\text{--}5$ µm; on *Punctelia caseana* and *P. subrudecta* ***Tremella conidiopunctelia*** (157)
 - 2' Basidiomata present, waxy-gelatinous or gall-inducing

- 3 Basidia of two parts, a lower thick-walled ellipsoid probasidium, $9\text{--}17 \times 5.5\text{--}11\ \mu\text{m}$, and an upper, cylindrical, transversely 2–3-septate, thin-walled meiosporangium; basidiomata inducing convex, brown galls; on *Punctelia graminicola* ***Cyphobasidium puncteliicola*** (318)
- 3' Basidia of one part, ellipsoid, 2-celled, septum longitudinal, rarely oblique
 - 4 Basidiomata strongly convex, often with a constricted base, medium to dark brown, 0.3–5 mm diam.; basidia $11.5\text{--}23.5 \times 8\text{--}11.5\ \mu\text{m}$; basidiospores $6\text{--}10 \times 6\text{--}10\ \mu\text{m}$
 - 5 On *Punctelia borrieri* ***Tremella puncteliae*** (240)
 - 5' On *Punctelia caseana* ***Tremella* aff. *puncteliae*** (241)
 - 4' Basidiomata resupinate, thin, medium brown, up to 5 mm diam.; basidia $20\text{--}32 \times 9\text{--}14.5\ \mu\text{m}$; basidiospores $9\text{--}10.5 \times 7\text{--}10.5\ \mu\text{m}$; on *Punctelia borrieri* ***Tremella puncteliotegens*** (242)
- 1 On *Raesaenenia huuskonenii*; basidiomata gelatinous, black, convex, elongate, up to $1.2 \times 0.5\ \text{mm}$; basidia 2-celled, septum transverse or rarely oblique, $13.5\text{--}18 \times 5.5\text{--}7\ \mu\text{m}$; basidiospores $6.5\text{--}8.5 \times 5\text{--}6.5\ \mu\text{m}$ ***Tremella huuskonenii*** (182)
- 1 On *Sulcaria sulcata*; basidiomata subspherical, black, 0.2–0.4 mm diam.; basidia 2-celled, septum longitudinal, $9\text{--}14 \times 6\text{--}8.5\ \mu\text{m}$; basidiospores $7\text{--}8 \times 4\text{--}6\ \mu\text{m}$ ***Tremella sulcariae*** (259)
- 1 On *Tuckermannopsis*; basidiomata waxy-gelatinous, reddish or greyish brown, convex, often with a constricted base and a typical central depression, 0.4–1.8 mm diam.; basidia 2- or 4-celled, septa longitudinal or oblique, rarely transverse, $12\text{--}18 \times 7\text{--}11\ \mu\text{m}$; basidiospores ellipsoid to limoniform, $6.5\text{--}8 \times 4.5\text{--}4.5\ \mu\text{m}$ ***Tremella cetrariicola*** (149)
- 1' On *Usnea* or *Protousnea*
 - 2 Basidiomata absent; conidiomata pulvinate to subspherical, gelatinous, black, 0.15–0.5 mm diam.; conidia clamped, ellipsoid, c. $5.5\text{--}8 \times 4\text{--}6\ \mu\text{m}$; on *Usnea longissima* ***Tremella confluens*** (154)
 - 2' Basidiomata present
 - 3 Basidia of two parts, a lower thick-walled ellipsoid probasidium, $20\text{--}35 \times 5.5\text{--}6\ \mu\text{m}$, and an upper, cylindrical, transversely septate, thin-walled meiosporangium; basidiomata inducing convex galls; on *Usnea* ***Cyphobasidium usneicola*** (321)
 - 3' Basidia of one part, septate, 2–4-celled
 - 4 Basidia longitudinally, rarely obliquely septate, subspherical to ellipsoid; on *Usnea*
 - 5 Basidiomata applanate to pulvinate, roundish, pale to dark reddish brown, 0.15–0.5 mm diam.; basidia $9\text{--}12 \times 7.5\text{--}9\ \mu\text{m}$; basidiospores $5.5\text{--}6.5 \times 4.5\text{--}5.5\ \mu\text{m}$; conidiophores frequent, situated between basidia, consisting of a $9\text{--}21\ \mu\text{m}$ long conidiogenous cell, bearing in the upper part 5–30 ellipsoid conidia ***Tremella stevensiana*** (255)
 - 5' Basidiomata subspherical or more often elongate, very pale to rarely dark brown, $0.3\text{--}2.5 \times 0.2\text{--}0.7\ \text{mm}$; basidia $8\text{--}20 \times 8.5\text{--}12\ \mu\text{m}$; basidiospores $5\text{--}8 \times 4\text{--}6\ \mu\text{m}$; asexual stage unknown ***Tremella nashii*** (201)
 - 4' Basidia transversely septate
 - 5 Basidia 1-septate, elongate ellipsoid, constricted at the septum, $16\text{--}21 \times 8\text{--}9\ \mu\text{m}$; basidiomata pulvinate, discoid, waxy-gelatinous, reddish brown to almost black, 0.2–0.4 mm diam.; basidiospores $6.5\text{--}8 \times 5.5\text{--}7\ \mu\text{m}$; on *Usnea* ***Tremella santessonii*** (253)
 - 5' Basidia 1–3-septate, clavate to subcylindrical, $20\text{--}70\ \mu\text{m}$ long; on *Usnea* or *Protousnea* ***Biatoropsis*** (110)

Pilocarpaceae

- Basidiomata synnemata-like; basidia tubular, aseptate; on *Byssoloma*, *Fellhanera* or *Micarea* ***Crittendenia*** (284)

Ramalinaceae

- 1 Basidiomata synnemata-like; basidia tubular, aseptate; on *Bacidia* or *Bacidina* ***Crittendenia*** (284)
- 1' Basidiomata resupinate or convex, waxy-gelatinous or gall-inducing; basidia septate
 - 2 Basidia of two parts, a lower thick-walled elongate ellipsoid probasidium, and an upper, cylindrical, transversely septate, thin-walled meiosporangium; on *Lecania naegelia* or *Ramalina fraxinea* ***Cyphobasidium*** (37)
 - 2' Basidia of one part, subspherical, ellipsoid to pyriform, 2–4-celled

- 3 Basidiomata resupinate; basidia longitudinally or rarely obliquely septate; basidia 2(–4)-celled; on *Ramalina*
- 4 Basidia 2-celled, 10.5–15.5 µm diam., 12–17 µm long near the septum, both cells elongating at maturity up to 30 µm long; basidiospores 7.5–9 × 6.5–8 µm *Tremella tuckerae* (264)
- 4' Basidia 2(–4)-celled, 9–18 × 7.5–11.5 µm, individual cells not elongating at maturity; basidiospores 5.5–7 × 5.5–7 µm; on *Ramalina fraxinea* *Tremella celata* (143)
- 3' Basidiomata strongly convex, or inducing the formation of convex galls; basidia 4-celled
- 4 Basidia pyriform, often with 2 transverse septa, the upper part with an additional longitudinal septum, 23–34 × 8–14 µm; basidiospores 5–6.5 × 4–6 µm; basidiomata subspherical-applanate, with a constricted base, pale to reddish brown, on some hosts gall-inducing, 0.4–3 mm diam.; on *Ramalina lacera* (type) and other *Ramalina* species *Tremella ramalinae* s. lat. (247)
- 4' Basidia with longitudinal, rarely oblique septa, 11–28 × 8.5–15 µm; basidiospores 4–5.5 × 4–5.5 µm; basidiomata inducing convex, subspherical or bullate galls, 0.8–10 mm diam.; on *Niebla* *Tremella nieblae* (205)

Ramboldiaceae – Ramboldia

Basidiomata waxy-gelatinous, amber-coloured, 0.15–0.3 mm diam.; basidia 2–4-celled, septa longitudinal, oblique or transverse, 18–41 × 14–19 µm; basidiospores 9–11 × 7.5–9.5 µm; on *Ramboldia haematites* *Tremella ramboldiae* (248)

Sphaerophoraceae – Bunodophoron

Basidia aseptate, elongate, subcylindrical, 20–42 µm long, with 3–4 sterigmata; basidiomata waxy-gelatinous, reddish brown, roundish to elongate, up to 5 mm long; on *Bunodophoron* *Zyzygomyces bunodophori* (90)

Stereocaulaceae

- 1 Basidiomata meruloid (wrinkled or folded), orange, up to 10 mm diam.; sclerotia orange, up to 5 mm diam.; on *Cladonia*, more rarely *Stereocaulon* *Penttilamyces lichenicola* (48)
- 1' Basidiomata waxy-gelatinous, orange-brown, 0.1–0.3 mm diam.; basidia with 1 longitudinal, rarely oblique or transverse septum, 15–21.5 × 7–10 µm; basidiospores 6–8.5 × 5.5–7 µm; on *Lepraria finkii* *Tremella leprariae* (189)

Tephromelataceae – Violella

Basidiomata strongly gelatinous, dark brown to black, 0.2–1 mm diam.; basidia 2–4-celled, with longitudinal septa, 16–23 × 10–19 µm; basidiospores 7–11 × 7–9.5 µm; on *Violella fucata* *Tremella lichenicola* (193)

LECIDEALES

Lecideaceae

- 1 Basidiomata synnemata-like; basidia tubular, aseptate; on *Lopadium disciforme* *Crittendenia lopadii* (296)
- 1' Basidiomata convex, waxy-gelatinous, pale cream to pale brown, 0.05–0.5 mm diam.; basidia 2–4-celled, with longitudinal septa, individual cells elongating separately, each 14.5–34 × 6–13 µm; basidiospores 10–12.5 × 10–14 µm; on *Lecidea* aff. *erythrophaea* *Tremella diderichiana* (164)

OSTROPALES

Graphidaceae

- 1 Basidiomata, conidiomata and bulbils absent; subpherical to elongate galls present, orange brown, later dark brown to black, 0.1–0.2 mm diam., containing no lichenicolous fungus but numerous bacteria; on *Graphis scripta* **Bacterial galls on *Graphis scripta*** (338)
- 1' Basidiomata present

- 2 Basidia 2-celled
 - 3 Basidia very long and narrow, $30\text{--}38 \times 4\text{--}5\ \mu\text{m}$, septum transverse; basidiospores $6\text{--}7 \times 5\text{--}6\ \mu\text{m}$; basidiomata intrahymenial; on *Graphis* ***Tremella graphidis*** (177)
 - 3' Basidia shorter and broader
 - 4 Basidia $8\text{--}16.5\ \mu\text{m}$ long
 - 5 Basidia subspherical, $10.5\text{--}15.5 \times 10.5\text{--}14.5\ \mu\text{m}$, septum longitudinal; basidiospores c. $8 \times 5.5\ \mu\text{m}$; basidiomata waxy-gelatinous, brown, $0.2\text{--}1\ \text{mm}$ diam.; on *Rhabdodiscus inalbescens* ***Tremella rhabdodisci*** (249)
 - 5' Basidia ellipsoid, $8\text{--}16.5 \times 5\text{--}10.5\ \mu\text{m}$, septum longitudinal, oblique or transverse; basidiospores $4.5\text{--}5 \times 4\text{--}4.5\ \mu\text{m}$; basidiomata waxy-gelatinous, brown, $0.1\text{--}0.5\ \text{mm}$ diam.; on *Graphis* ***Tremella graphidicola*** (175)
 - 4' Basidia $14\text{--}30\ \mu\text{m}$ long
 - 5 Basidiospores $5.5\text{--}7.5 \times 5\text{--}6\ \mu\text{m}$; basidia $16\text{--}24 \times 8\text{--}12\ \mu\text{m}$; basidiomata waxy-gelatinous, pale to dark brown, $0.4\text{--}0.7\ \text{mm}$ diam.; on *Phaeographis* s. lat. ***Tremella phaeographidis*** (229)
 - 5' Basidiospores larger
 - 6 Basidiomata waxy-gelatinous, pale (rarely dark) brown, up to $0.5\ \text{mm}$ diam.; basidia $20\text{--}28.5 \times 9\text{--}10.5\ \mu\text{m}$, septum transverse; basidiospores $7.5\text{--}9.5 \times 6.5\text{--}8.5\ \mu\text{m}$; on *Glyphis scyphulifera* ***Tremella wedinii*** (267)
 - 6' Basidiomata gall-inducing, brown, dark brown or black, $0.3\text{--}0.9\ \text{mm}$ diam.; basidia $14\text{--}30 \times 8\text{--}14\ \mu\text{m}$, septum longitudinal, oblique or transverse; basidiospores $7\text{--}9 \times 6\text{--}9\ \mu\text{m}$; on *Diploschistes* ***Tremella diploschistina*** (165)
 - 2' Basidia 2–4-celled
 - 3 Basidia 3-celled, with one transverse and one oblique or longitudinal septum, $22\text{--}32 \times 9.5\text{--}11\ \mu\text{m}$; basidiospores $5.5\text{--}7.5 \times 5\text{--}6.5\ \mu\text{m}$; basidiomata intrahymenial, soon superficial, convex, waxy-gelatinous, reddish brown, $0.3\text{--}1.2 \times 0.2\text{--}0.5\ \text{mm}$; on *Phaeographis* s. lat. ***Tremella phaeographinae*** (231)
 - 3' Basidia 2–4-celled, septa transverse or oblique, $13\text{--}24.5 \times 8\text{--}12\ \mu\text{m}$; basidiospores $4.5\text{--}7 \times 4.5\text{--}6\ \mu\text{m}$; basidiomata waxy-gelatinous, medium brown, $0.4\text{--}1.3\ \text{mm}$ diam.; on *Sarcographa medusulina* ***Tremella sarcographae*** (254)

Phlyctidaceae – Phlyctis

Basidiomata, conidiomata and bulbils absent; roundish to irregular galls present, dark reddish brown to black, $0.1\text{--}0.5\ \text{mm}$ diam., containing no lichenicolous fungus but numerous bacteria; on *Phlyctis argena* ... **Bacterial galls on *Phlyctis argena*** (342)

PELTIGERALES

Coccocarpiaceae – Coccocarpia

Basidiomata waxy-gelatinous, subspherical, pale brownish, $0.05\text{--}0.2\ \text{mm}$ diam.; basidia longitudinally or obliquely 1-septate; on *Coccocarpia* ***Tremella coccocarpiiae*** (153)

Collemataceae – Leptogium

- 1 Basidia aseptate, distinctly stalked, with one epibasidium; basidiomata waxy-gelatinous, slightly convex, pale brown, $0.1\text{--}0.6\ \text{mm}$ diam.; on *Leptogium* ***Tremella monospora*** (200)
- 1' Basidia 2–4-celled, with longitudinal of slightly oblique septa, not stalked; basidiomata waxy-gelatinous, subglobose, orange-brown, $0.12\text{--}0.22\ \text{mm}$ diam.; on *Leptogium* ***Tremella leptogii*** (190)

Lobariaceae

- 1 Basidiomata absent; bulbils $200\text{--}400\ \mu\text{m}$ diam., pale beige, greyish yellow or greyish orange, translucent, flattened; on *Lobariella*, *Peltigera*, *Pseudocyphellaria* or *Sticta* ***Bulbilla applanata*** (55)
- 1' Basidiomata present

- 2 Basidiomata synnemata-like; basidia tubular, aseptate; on *Sticta fuliginosa* s. lat. ***Crittendenia stictae*** (300)
- 2' Basidiomata convex, waxy-gelatinous or gall-inducing; basidia septate
 - 3 Basidia of two parts, a lower thick-walled ellipsoid or claviform probasidium, and an upper, cylindrical, transversely 3-septate, thin-walled meiosporangium with short perpendicular epibasidia; on *Crocodia rubella* ***Cyphobasidium crocodiicola*** (309)
 - 3' Basidia of one part, ellipsoid to claviform, with one longitudinal or oblique septum
 - 4 Basidiospores large, $9.5\text{--}13.5 \times 7.5\text{--}11.5 \mu\text{m}$, pale to medium or dark reddish brown; on *Crocodia aurata* ***Tremella flakusii*** (172)
 - 4' Basidiospores smaller, $5\text{--}10 \times 4\text{--}7.5 \mu\text{m}$
 - 5 Basidiomata relatively small, $< 0.5 \text{ mm}$ diam.
 - 6 Basidia $10\text{--}16 \times 6\text{--}8.5 \mu\text{m}$; basidiomata pale to dark brown; on *Sticta* (incl. dendriscocauloid species) ***Tremella stictae*** (256)
 - 6' Basidia longer, $14.5\text{--}26 \times 4.5\text{--}9 \mu\text{m}$; basidiomata pale brown; on *Emmanuelia* (cephalodia) ***Tremella emmanueliae*** (167)
 - 5' Basidiomata becoming much larger, up to 1.6 mm diam. [two genetically distinct, but morphologically similar species]
 - 6 On *Lobaria* ***Tremella lobariacearum*** s. lat. (195)
 - 6' On *Pseudocyphellaria* ***Tremella pseudocyphellariae*** (237)

Nephromataceae – Nephroma

Basidia 2-celled; basidiomata waxy-gelatinous, dark reddish brown, subspherical, later often irregular, lobate or tuberculate, $0.6\text{--}4 \text{ mm}$ diam.; on *Nephroma parile* ***Tremella nephromatis*** (203)

Pannariaceae

- 1 Basidiomata $0.1\text{--}0.3 \text{ mm}$ diam., pale brownish (type specimen; in a second specimen, $0.2\text{--}0.6 \text{ mm}$ diam., black); basidia with one longitudinal, oblique or transverse septum, $14\text{--}22 \times 5\text{--}9 \mu\text{m}$; basidiospores $5\text{--}8 \times 4\text{--}6 \mu\text{m}$; on *Parmeliella foliicola* ***Tremella parmeliellae*** (214)
- 1' Basidiomata larger, medium brown, $0.2\text{--}0.8 \text{ mm}$ diam.
 - 2 Basidia with one longitudinal or oblique septum, $13\text{--}17 \times 8\text{--}12 \mu\text{m}$; basidiospores $6.5\text{--}7.5 \times 5.5\text{--}6.5 \mu\text{m}$; on *Pannaria papuana* ***Tremella cephalodiicola*** (144)
 - 2' Basidia with one transverse or slightly oblique septum, $17\text{--}24 \times 8.5\text{--}11.5 \mu\text{m}$; basidiospores $7\text{--}9 \times 6.5\text{--}8 \mu\text{m}$, on *Psoroma* ***Tremella psoromicola*** (240)

Peltigeraceae – Peltigera

- 1 Basidioma a 'mushroom', composed of a (sometimes reduced) stipe and a cap (pileus) with fertile lamellae on the lower surface; on *Peltigera* ***Agaricales*** (34)
- 1' Basidiomata absent; bulbils $200\text{--}400 \mu\text{m}$ diam., pale beige, greyish yellow or greyish orange, translucent, flattened; on *Lobariella*, *Peltigera*, *Pseudocyphellaria* or *Sticta* ***Bulbilla applanata*** (55)

PERTUSARIALES

Icmadophilaceae – Thamnolia

Basidiomata effused, thin, floccose, pale pink, up to > 1 cm diam.; basidia aseptate, clavate to suburniform, 30–45 µm long, up to 8 µm diam., with 3–4 sterigmata; basidiospores pyriform or lacrimiform, 8.5–10.5 × 6–7.5 µm; on *Thamnolia* ***Corticium silviae*** (72)

Megasporaceae – Aspicilia

Basidiomata inducing concolorous pustular galls, not gelatinous, 0.2–0.45 mm diam.; basidia ellipsoid, 4-celled, septa longitudinal, 9–14 × 6–9 µm; epibasidia deciduous, acting as diaspores, 9–17 × 1.8–2.5 µm; on *Aspicilia caesiocinerea* ***Tremella aspiciliae*** (138)

Ochrolechiaceae – Lepra

Basidiomata applanate, dark brown to blackish, gelatinous, 0.3–2 mm diam.; basidia 2–4-celled, septa mainly longitudinal, 17–36 × 16–25 µm; basidiospores 10–11.5 × 8.5–10 µm; on *Lepra* ***Tremella leprae*** (188)

Pertusariaceae – Pertusaria

- 1 Basidia elongate claviform to subcylindrical, transversely 1-septate, 25–45 × 3.5–6.5 µm; basidiospores 5–8.5 × 5–6.5 µm; basidiomata subspherical, pale brown, waxy-gelatinous; on isidiate *Pertusaria* species ***Tremella ertzii*** (169)
- 1' Basidia subspherical to ellipsoid, in some species stalked, 2–4-celled, septa mainly longitudinal to oblique
 - 2 Basidiomata dark brown to black, gelatinous, immersed and erumpent to superficial, 0.3–0.8 mm; basidia 21–40 × 10–19 µm (short stalk included); basidiospores 10–11.5 × 8.5–10 µm; on *Pertusaria* cf. *rigida* ***Tremella pertusariicola*** (223)
 - 2' Basidiomata pale coloured, or some becoming blackish when old
 - 3 Basidia usually with a long and narrow stalk-like base
 - 4 Basidiomata inducing concolorous to beige, convex galls, basally often constricted, becoming cerebriform when old, 0.2–2.5 mm diam.; basidia 27–52 × 15–26 µm (stalk included), upper part (without stalk) 19–29 µm long; basidiospores 9.5–11.5 × 8.5–10 µm; on *Pertusaria pertusa* ***Tremella pertusae*** (220)
 - 4' Basidiomata waxy-gelatinous, not gall inducing
 - 5 Basidiomata applanate to slightly convex, almost resupinate, pale pinkish brown, up to 2.5 mm diam.; basidiospores 7.5–8 × 6.5–8 µm; basidia 13.5–33 × 11–16 µm (stalk included), upper part (without stalk) 13.5–23 µm long; on *Pertusaria* ***Tremella pertuceracea*** (219)
 - 5' Basidiomata applanate to strongly convex and then basally constricted, pale orange-brown, 0.3–1.5 mm diam.; basidiospores 9.5–12 × 8–10.5 µm; basidia 17–48 × 12–17 µm (stalk included), upper part (without stalk) 17–22 µm long; on *Pertusaria tetralthalamia* ***Tremella pertuthalamiae*** (238)
 - 3' Most basidia without a stalk (but if present, up to 20 µm long)
 - 4 Basidiomata intrahymenial, soon convex, waxy-gelatinous, pale pinkish, rarely dark brown, 0.3–0.8 mm diam.; basidia 22–45 × 15–28 µm; basidiospores 8.5–9 × 8–8.5 µm; on *Pertusaria hymenea* ***Tremella pertusariae*** (222)
 - 4' Basidiomata on the host thallus, applanate to pulvinate and then with a constricted base, waxy-gelatinous, pale pinkish brown, greyish brown to blackish, 0.15–0.5 mm diam.; basidia 26–50 × 11–25 µm; basidiospores slightly larger, 9–12 × 8–11.5 µm; on *Pertusaria texanae* ***Tremella pertutexanae*** (225)

PYRENULALES

Pyrenulaceae – Pyrenula

Basidiomata pulvinate, waxy-gelatinous, pale pinkish brown, up to 0.5 mm diam.; basidia 2-celled, septum longitudinal, 13–17 × 9.5–13 µm; basidiospores 7–8 × 6.5–7.5 µm; on *Pyrenula ochraceoflavens* ***Tremella pyrenulae*** (246)

RHIZOCARPALES***Rhizocarpaceae – Rhizocarpon***

Basidiomata intrahymenial, visible as swellings of the host apothecia; basidia narrowly ellipsoid to subcylindrical, 2-celled, septum transverse, $17\text{--}44 \times 7\text{--}12\ \mu\text{m}$; basidiospores $7.5\text{--}9.5 \times 6\text{--}8.5\ \mu\text{m}$; on *Rhizocarpon lavatum* ***Tremella rhizocarpicola*** (251)

STRIGULALES***Strigulaceae – Strigula***

Basidiomata flat and thin, often poorly delimited, sometimes pulvinate, waxy-gelatinous, yellowish brown, 0.2–0.5 mm diam.; basidia 2-celled, septum transverse or oblique, $14\text{--}22 \times 7.5\text{--}12\ \mu\text{m}$; basidiospores $6.5\text{--}7.5 \times 6\text{--}6.5\ \mu\text{m}$; on *Strigula stigmatella* ***Tremella strigulae*** (258)

TELOSCHISTALES***Letrouitiaceae – Letrouitia***

Basidiomata intrahymenial, host apothecia not or slightly swollen; basidia 2-celled, septum transverse, $21\text{--}40 \times 5.5\text{--}9\ \mu\text{m}$; on *Letrouitia domingensis* ***Tremella* sp. 10** (274)

Megalosporaceae – Megalospora

Basidiomata waxy-gelatinous, pale yellowish or reddish brown, becoming darker when old, pulvinate, 0.04–0.2 mm diam.; basidia 2-celled, septum longitudinal or oblique, $9.5\text{--}12.5 \times 7\text{--}11\ \mu\text{m}$, or stalked, $17\text{--}20 \times 8\text{--}10.5\ \mu\text{m}$; basidiospores $5.5\text{--}8.5 \times 4.5\text{--}7\ \mu\text{m}$; on a sterile sorediate crust, possibly belonging to *Megalospora* ***Tremella microcarpa*** (199)

Teloschistaceae

- 1 Basidiomata synnemata-like; basidia tubular, aseptate; on *Teloschistes exilis* and *T. flavicans* ***Crittendenia teloschistis*** (301)
- 1' Basidiomata intrahymenial, convex and waxy-gelatinous, or gall-inducing; basidia septate
 - 2 Basidia devoid of epibasidia, producing sessile conidia instead of basidiospores; basidia subspherical to ellipsoid, 4-celled, with longitudinal septa, $8.5\text{--}11.5 \times 8\text{--}10.5\ \mu\text{m}$; conidia $4.5\text{--}5.5 \times (3.5\text{--})4\text{--}4.5\ \mu\text{m}$; on the lower thallus surface of *Xanthoria parietina* ***Tremella occultixanthoriae*** (206)
 - 2' Basidia with epibasidia producing basidiospores; basidia ellipsoid, 2-celled
 - 3 Basidiomata intrahymenial, host apothecia slightly to strongly swollen (a phylogenetically diverse group that will be treated in detail elsewhere)
 - 4 Basidia transversely, more rarely obliquely or longitudinally septate, $16\text{--}25 \times 7\text{--}10\ \mu\text{m}$; basidiospores $7\text{--}8 \times 6\text{--}6.5\ \mu\text{m}$; on *Variospora* (type) and other species of *Teloschistaceae* ***Tremella caloplacae* s. lat.** (141)
 - 4 Basidia transversely septate, $17\text{--}24 \times 7\text{--}10\ \mu\text{m}$; basidiospores slightly broader, $6.5\text{--}8.5 \times 6.5\text{--}7.5\ \mu\text{m}$; on *Pisutiella* ***Tremella pisutiellae*** (234)
 - 4' Basidia transversely septate, shorter, $12\text{--}18 \times 7\text{--}9\ \mu\text{m}$; on *Pyrenodesmia chalybaea* ***Tremella* sp. 12** (275)
 - 3' Basidiomata inducing orange, waxy-gelatinous galls on the host thallus
 - 4 Basidiomatal galls elongate, curved swellings of the host thallus, base usually not constricted, up to $1 \times 0.3\ \text{mm}$; basidia transversely septate, $12\text{--}23 \times 5.5\text{--}10\ \mu\text{m}$; basidiospores $5\text{--}7.5 \times 4.5\text{--}6.5\ \mu\text{m}$; on *Teloschistes exilis* ***Tremella teloschistis*** (260)
 - 4' Basidiomatal galls pulvinate, subspherical, often with a constricted base, 0.15–0.6 mm diam.; basidia transversely or obliquely septate, $13\text{--}22 \times 5.5\text{--}9\ \mu\text{m}$; basidiospores $5\text{--}7.5 \times 4.5\text{--}6\ \mu\text{m}$; on *Xanthomendoza weberi* ***Tremella xanthomendozae*** (269)

TRAPELIALES

Trapeliaceae – Placynthiella

Basidiomata waxy-gelatinous, pale brown, subspherical, 0.04–0.16 mm diam.; basidia 2-celled, septum longitudinal, oblique or transverse, $6.5\text{--}12 \times 5.5\text{--}9\ \mu\text{m}$; basidiospores $5\text{--}6.5 \times 4.5\text{--}6.5\ \mu\text{m}$; on *Placynthiella icmalea*... ***Tremella placynthiellae*** (235)

TRYPETHELIALES

Trypetheliaceae

- 1 Basidiomata subglobose, medium to dark brown, 0.15–0.3 mm in diam.; basidia 2–4-celled, septa longitudinal or oblique, $15\text{--}22 \times 11\text{--}16\ \mu\text{m}$, not or shortly stalked; basidiospores $6\text{--}7.5 \times 5.5\text{--}6.5\ \mu\text{m}$; on *Polymeridium catapastum* s. lat. ***Tremella harrisii*** (179)
- 1' Basidiomata subglobose, soon slightly applanate, centrally depressed, marginally lobed to almost tuberculate, pale to dark reddish brown or blackish, 0.1–1.5 mm diam.; basidia 2–4-celled, septa mainly oblique, often with a long stalk-like base 3–25 μm long, upper part (without stalk) $13\text{--}20 \times 9\text{--}18\ \mu\text{m}$; basidiospores $4.5\text{--}9.5 \times 5.5\text{--}8.5\ \mu\text{m}$; on *Astrothelium* ***Tremella aptrootii*** (135)

UMBILICARIALES

Ophioparmaceae – Hypocenomyce

Basidiomata strongly gelatinous, dark brown to black, often tuberculate or cerebriform, 0.2–2 mm diam.; basidia 2(–4)-celled, septa longitudinal, near the septa 8–14 μm long, individual cells elongating separately, 10–17 μm diam., up to 24 μm long; basidiospores subspherical, 5.5–7.5 μm diam.; on *Hypocenomyce scalaris* ***Tremella hypocenomycis*** (183)

Umbilicariaceae – Umbilicaria

Basidiomata inducing convex galls basally not or slightly constricted, dark brown to blackish, 0.6–2.5 mm diam.; basidia 2-celled, septum transverse, $19\text{--}25 \times 7\text{--}8\ \mu\text{m}$; basidiospores $7.5\text{--}9.5 \times 6\text{--}7.5\ \mu\text{m}$; on *Umbilicaria* ... ***Tremella umbilicariae*** (265)

VERRUCARIALES

Verrucariaceae

All species with waxy-gelatinous basidiomata and 1-septate basidia.

- 1 Basidiospores $< 6\ \mu\text{m}$ long; basidiomata subspherical
 - 2 Basidiomata pale brown, 0.1–0.3 mm diam.; basidia longitudinally septate, $7.5\text{--}15.5 \times 5\text{--}8\ \mu\text{m}$; basidiospores $3.5\text{--}4.5 \times 3.5\text{--}4\ \mu\text{m}$; on *Agonimia pacifica* ***Tremella pacifica*** (209)
 - 2' Basidiomata medium brown, 0.1–0.45 mm diam.; basidia longitudinally or slightly obliquely septate, $10\text{--}16 \times 7\text{--}10\ \mu\text{m}$; basidiospores $4\text{--}5 \times 3.5\text{--}4.5\ \mu\text{m}$; on *Psoroglaena* ***Tremella psoroglaenae*** (239)
- 1' Basidiospores $> 6\ \mu\text{m}$ long
 - 2 Basidia transversely, obliquely or rarely longitudinally septate, $12\text{--}17 \times 7\text{--}9\ \mu\text{m}$; basidiomata subspherical, later tuberculate to cerebriform, reddish brown, 0.1–1.4 mm diam.; basidiospores $6\text{--}7 \times 5\text{--}6\ \mu\text{m}$; on *Normandina simodense* ***Tremella montis-wilhelmii*** (200)
 - 2' Basidia broader, 8–13 μm wide; basidiomata subspherical, $< 0.6\ \text{mm}$ diam.; basidiospores $> 6\ \mu\text{m}$ wide
 - 3 Basidiomata pale to medium brown, 0.15–0.35 mm diam.; basidia longitudinally septate, $9\text{--}16.5 \times 8\text{--}13\ \mu\text{m}$; basidiospores $6\text{--}7 \times 6.5\text{--}7.5\ \mu\text{m}$; on *Agonimia octospora* ***Tremella octosporae*** (208)
 - 3' Basidiomata pale or pinkish brown, 0.2–0.6 mm diam.; basidia transversely, obliquely or longitudinally septate, $14.5\text{--}21 \times 8.5\text{--}11.5\ \mu\text{m}$; basidiospores $6.5\text{--}8.5 \times 6\text{--}7\ \mu\text{m}$; on *Normandina pulchella*.... ***Tremella normandinae*** (206)

Class *AGARICOMYCETES*

Order *AGARICALES*

by P. Diederich, M. Garnier-Delcourt, R. Lücking, D. Ertz & J. D. Lawrey

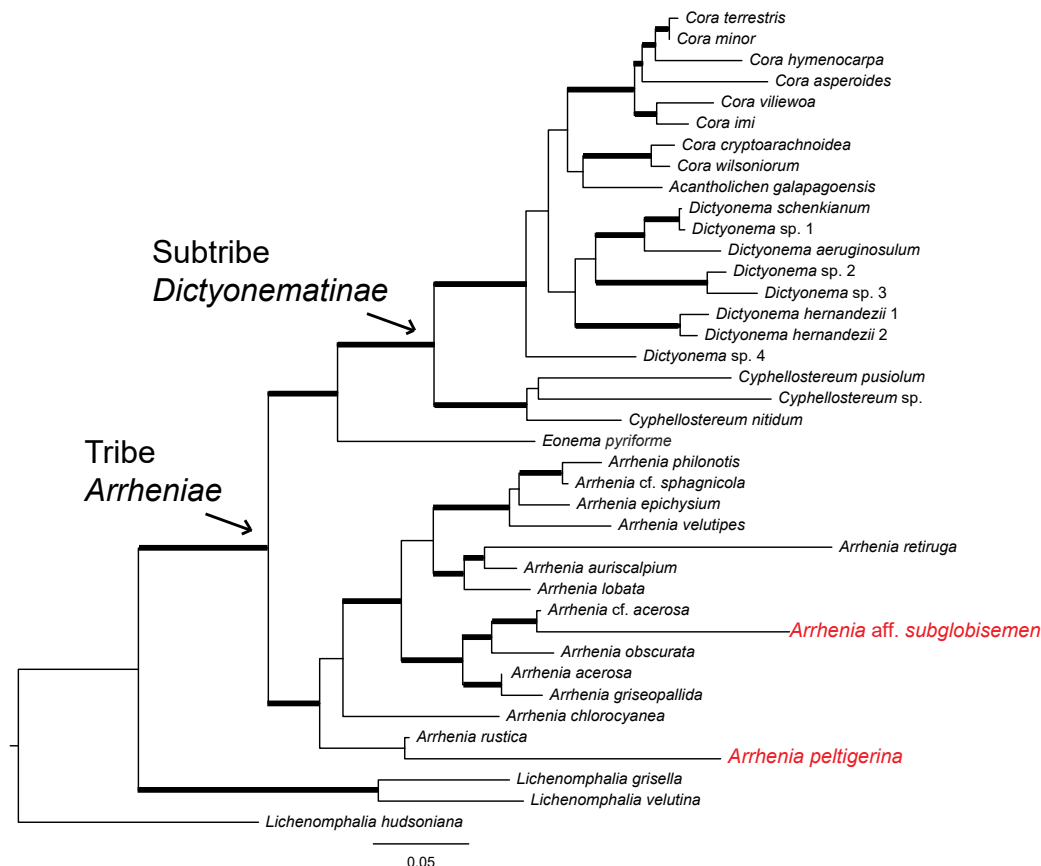
Diederich, P., M. Garnier-Delcourt, R. Lücking, D. Ertz & J. D. Lawrey. 2022. Class *Agaricomycetes*, order *Agaricales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 33–40.

Introduction and phylogeny

The *Agaricales* is the largest order of *Agaricomycetes* with over 13,000 described species (Kirk et al. 2008; Hibbett et al. 2014). Most are pileate-stipitate forms with lamellate hymenophores, but there is much diversity of fruit-body morphology as well as microscopic characters. Most species are saprotrophic or ectomycorrhizal, but plant pathogens, mycoparasites and basidiolichens are also known.

Several lichenicolous species are known in the *Hygrophoraceae*, a molecular phylogeny of which was

published by Lodge et al. (2014). They include species of *Arrhenia*, a largely bryophilous genus, which is sister to a clade comprising *Eonema pyriforme* and the entirely lichenized *Dictyonema* s. lat. clade. In addition to these lichenicolous members of the *Hygrophoraceae*, two *Gamundia* species of the *Tricholomataceae* are reported to be regularly associated to *Peltigera* thalli, but no phylogenetic analysis of the *G. striatula* complex has ever been done.



Phylogeny (nucLSU + ITS) of the tribe *Arrheniae*, *Agaricales*, *Hygrophoraceae* (with members of *Lichenomphalia* used as an outgroup) obtained under ML with the positions of several lichenicolous species indicated. The tribe includes *Arrhenia*, *Eonema pyriforme* and the cyanolichen subtribe *Dictyonematinae*. The lichen-associated *Gamundia* species (*Tricholomataceae*) are not shown. Branches are thickened for all bootstrap (BS) values >70.

Key to the lichenicolous species of *Agaricales*

- 1 Conspicuous cheilo- and pleurocystidia present; basidiospores minutely verruculose; loosely associated with *Peltigera* thalli
 - 2 Basidiomata dark brown to black; smell indistinct; basidiospores ellipsoid to broadly ellipsoid, $6\text{--}7\text{--}(8) \times 4.5\text{--}5.5\text{--}(6)$ μm , ratio length/breadth 1.2–1.5 ***Gamundia arctica*** (37)
 - 2' Basidiomata medium brown; smell farinaceous; basidiospores ellipsoid, $(6\text{--})7\text{--}8.5\text{--}(9) \times (4\text{--})4.2\text{--}5\text{--}(6)$ μm , ratio length/breadth 1.4–1.9 ***Gamundia xerophila*** (38)
- 1' Cystidia absent; basidiospores smooth; on *Peltigera* thalli
 - 2 Basidiomata omphalinoid, cap (pileus) with a central depression, with a distinct stipe; on *Peltigera* species with cyanobacteria ***Arrhenia peltigerina*** (36)
 - 2' Basidiomata pleurotoid, i. e., laterally-attached, with a reduced stipe; on *Peltigera* species with green algae or cyanobacteria ***Arrhenia* aff. *subglobisemen*** (34)

AGARICOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: *Agaricus* L.

AGARICALES Underw.

Moulds, mildews and mushrooms: 97 (1899). Type: *Agaricus* L.

Hygrophoraceae Lotsy

Vorträge über botanische Stammesgeschichte: 706 (1907). Type: *Hygrophorus* Fr.

Notes. Lodge et al. (2014) revised the molecular phylogeny and morphology in *Hygrophoraceae*, described the new subfamily *Lichenomphalioidae* Lücking & Redhead typified on the lichenized genus *Lichenomphalia*, and within this subfamily the tribe *Arrhenieae* Lücking. This tribe appeared as a strongly supported monophyletic clade and includes the non-lichenized *Arrhenia* and *Eonema*, and the lichenized *Acantholichen*, *Cora*, *Corella*, *Cyphellostereum* and *Dictyonema*. *Eonema pyriforme* (M. P. Christ.) Redhead, Lücking & Lawrey has once been reported as overgrowing a thallus of *Cetraria aculeata* (Khodosovtsev et al. (2018), but is not further treated here.

ARRHENIA Fr.

Summa Veg. Scand., Section Post.: 312 (1849). Type: *A. auriscalpium* (Fr.) Fr.

Molecular data: yes (T, L). **Number of species:** 2–0–0 (45).

A morphologically poorly characterized genus with omphalinoid or pleurotoid, greyish or brownish basidiomata, a paler, lamellate, cantharelloid, meruloid or smooth hymenium.

Notes. The genus *Arrhenia* is rather heterogeneous morphologically, as the hymenium is variable, and as it in-

cludes both species with pleurotoid basidiomata, such as the generic type *A. auriscalpium* and the *A. subglobisemen* treated below, and species with omphalinoid basidiomata, such as the lichenicolous *A. peltigerina*. Over forty species are known worldwide, amongst which eight had been included in a phylogenetic analysis, whilst the others had been included in the genus based on morphological characters (Lodge et al. 2014, Redhead et al. 2002). The *Arrhenia acerosa* complex has recently been studied phylogenetically (Voitk et al. 2020), with the recognition of several new species, amongst which some were not formally described, and several groups of unresolved species.

Ecology. Bryophilous, more rarely phycophilous or lichenicolous, the *A. acerosa* complex on plant debris, wood, etc.

Arrhenia aff. *subglobisemen* Corriol

Bull. Mycol. Bot. Dauphiné-Savoie 222: 14 (2016). Type. France, Haute-Savoie, La Chapelle-Rimbaud, near la Roche-sur-Foron, 23 Oct. 1938, C. Poluzzi (G 9922 – holotype). France, Hautes-Pyrénées, Ancizan, plateau de Payolle, vallon de la Prade, 9 Oct. 2015, G. Corriol (BBF GC15100901 – epitype).

Basidiomata pleurotoid, growing on the thallus of *Peltigera*. **Pileus** thin, up to 40 mm wide, umbilicate, margin undulate and striate, glabrous, medium brown; pileipellis loose to dense, not gelatinized, of subcylindrical, $45\text{--}65$ μm long and $4\text{--}10$ μm wide, hyaline hyphae; pileitrama of occasionally branched hyphae, $7\text{--}14$ μm wide. **Lamellae** decurrent, distant, $8\text{--}15$ mm long, thick, forked, somewhat veined, pinkish brown; lamellar trama irregular, with branched hyphae, $3\text{--}7$ μm wide. **Cystidia** absent. **Stipe** reduced, white tomentose. **Basidia** $16\text{--}23 \times 5.5\text{--}7$ μm , subclaviform to claviform; sterigmata not observed. **Basidiospores** dacryoid to subglobose, $(5.5\text{--})5.9\text{--}6.9\text{--}(7.5) \times (4\text{--})4.5\text{--}5.4\text{--}(6.5)$ μm , ratio length/breadth $(1.0\text{--})1.1\text{--}1.4\text{--}(1.8)$ ($n = 45$), with a prominent apiculus, smooth, non-amyloid. All tissues with clamp connections. [Description based on the lichenicolous specimen.]

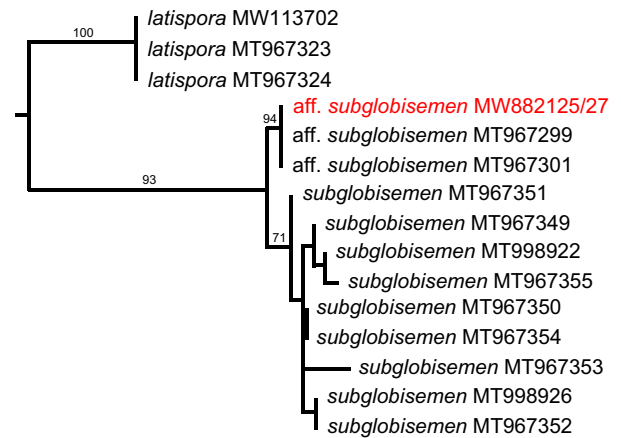


Arrhenia aff. *subglobisemen*, Canada, Björk 19420. Basidiomata on *Peltigera chionophila*. Photo: Curtis Björk.



Arrhenia aff. *subglobisemen*, Canada, Björk 19420. Basidiomata on *Peltigera chionophila*. Photo: Curtis Björk.

Notes. An ITS sequence of the lichenicolous specimen studied here is identical to those of two Norwegian specimens named AC-1 in Voitek et al. (2020). They are very close to *Arrhenia subglobisemen* and probably represent a distinct, yet undescribed species. No description of the two Norwegian specimens was given, except that the pileus is pleurotoid and grey, and a stipe is present, thus differing slightly from the lichenicolous specimen. A further specimen of '*A. acerosa*' on *Peltigera rufescens* from Russia



Phylogeny (ITS) of the *Arrhenia latispora* - *subglobisemen* clade, obtained under ML, with the position of the lichenicolous specimen indicated in red. Bootstrap support values of main branches are indicated. Analysis based on Voitek (2020), after adding a sequence of the lichenicolous specimen. GenBank accession numbers are explained in Voitek (2020).

[www.gbif.org/occurrence/3347247725, www.ncbi.nlm.nih.gov/nucleotide/MT380845.1] is genetically identical and obviously represents the same taxon.

Ecology and hosts. One population on the healthy thallus of *Peltigera chionophila*, one over *P. rufescens*, one over bryophytes on gravel, and one on wood in a coniferous forest. The relations to *Peltigera* need to be further studied when more lichenicolous populations are known.

Distribution. Peltigericolous specimens known from Europe (Russia) and North America (Canada: British Columbia). Genetically identical, non-lichenicolous populations are known from Norway.

Specimen examined. **Canada:** British Columbia: central Coast Ranges, Bute Inlet area, Southgate River Canyon, shortly upstream from the mouth of the Bishop River, 50°58.85'N, 124°21.80'W, 260 m, on *Peltigera chionophila*, 2009, Björk 19420 (BR, UBC).

References. Corriol 2016, Voitek et al. 2020.



Arrhenia aff. *subglobisemen* (peltigericolous populations)

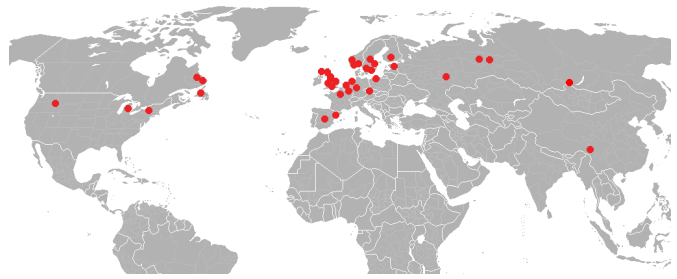
***Arrhenia peltigerina* (Peck) Redhead, Lutzoni, Moncalvo & Vilgalys**

Mycotaxon 83: 48 (2002); *Agaricus peltigerinus* Peck, *Annual Rep. New York State Mus. Nat. Hist.* 30: 38 (1878) [as “*Agaricus (Clitocybe) peltigerinus*”]; *Clitocybe peltigerina* (Peck) Sacc., *Syll. Fung.* 5: 184 (1887); *Clitocybe peltigerina* (Peck) Peck, *New York State Mus. Bull.* 157: 87 (1912) [superfl. comb.]; *Omphalina peltigerina* (Peck) P. Collin, in Collin & Lauron, *Bull. Soc. Mycol. France* 110: 11 (1994). *Type*: USA, New York State, Oneida, on *Peltigera* sp., H. A. Warne (NYS 2308 – lectotype, selected by Barrasa & Rico 2010).

= *Omphalina cupulatoidea* P. D. Orton, *Kew Bull.* 31: 712 (1977). *Type*: UK, Scotland, Perthshire, Rannoch, Dall, Sawmill Site, on *Peltigera* sp., 29 Sept. 1971, P. D. Orton 4192 (E 157979 – holotype; K – isotype).

= *Cantharellus peltigerae* Velen., *Věda Přírodní* 1: 270 (1920). *Type*: Czech Republic, Prague, Chuchle, on old thalli of *Peltigera* cf. *rufescens*, Apr. 1910, O. Reisner (PRC 336[a] [parte cum *Peltigera*]) – lectotype, selected by Hawksworth et al. 2009).

Basidiomata omphalinoid, 8–30 mm tall, growing in moribund, necrosed thalli of *Peltigera* sp. *Pileus* thin, 5–20 mm wide, convex, plane or umbilicate, margin undulate and striate, glabrous to pubescent, brown to dark brown or yellowish red, light brown to brown when dry; pileipellis a cutis of hyaline or slightly encrusted, cylindrical, branched, clamped hyphae with ascending free ends, (2.5–) 3–10 µm wide, with intracellular and slightly extracellular encrusted pigment. *Lamellae* decurrent, distant, 8–12(–15) mm long, thick, forked near the cap, somewhat veined, pinkish, ± concolorous with stipe; lamellar trama irregular, with branched hyphae, (1.5–)2.5–6 µm wide, with slightly encrusted pigment. *Cystidia* absent. *Stipe* cylindrical with a slightly thicker base, pinkish, pruinose-tomentose to pubescent, floccose-tomentose at the base, 8–20 × 0.7–3 mm; stipitipellis a cutis of cylindrical or flexuous hyphae, 4–14 µm wide. *Flesh* concolorous, whitish when dry. *Basidia*



Arrhenia peltigerina

sidia subclaviform, (25–)27–40 × 5–10 µm, 4-spored; sterigmata 3–10 µm long; basidioles 25–35 × 4–8 µm, subclaviform to claviform. *Basidiospores* elongate ellipsoid, 6–11 × 4–6.5 µm, with a prominent apiculus, smooth, non-amyloid. All tissues with clamp connections. [Description modified from Barrasa & Rico 2010.]

Notes. A phylogenetic tree including *Arrhenia peltigerina* was first published by Voitek et al. (2020).

Ecology and hosts. On moribund, necrosed parts of *Peltigera* sp., *P. lactucifolia*, *P. cf. membranacea*, *P. cf. polydactylon* and *P. rufescens*.

Distribution. Europe (Czech Republic; Denmark; Estonia, Finland; France; Germany; Luxembourg; Netherlands; Norway; Poland; Spain; Sweden; UK: England, Scotland, Wales), North America (Canada: Quebec; USA: Idaho, Michigan, New York) and Asia (China; Russia).

References. Barrasa & Rico 2010, Collin & Lauron 1994, Garnier-Delcourt 2008, Hawksworth et al. 2009, Orton 1977 [Santesson 1993, Vila 2002, Zhurbenko 2009].

***Tricholomataceae* R. Heim ex Pouzar**

Ceská Mykologie 37: 175 (1983). *Type*: *Tricholoma* (Fr.) Staude



Arrhenia peltigerina, Luxembourg, Dudelange. Basidiomata on *Peltigera rufescens*.



Arrhenia peltigerina, France, Charente-Maritime. Basidiomata on *Peltigera*. Photo: Patrice Tanchaud.

Notes. *Rimbachia bryophila* (Pers.) Redhead, an almost exclusively bryophylous species, has been reported as lichenicolous on *Lathagrium undulatum* var. *granulosum* in Iceland (Svane & Alstrup 2004), but will not be treated here.

GAMUNDIA Raitelh.

Metrodiana 8: 34 (1979). Type: *G. pseudoclusilis* (Joss. & Konrad) Raitelh.

Molecular data: yes. *Number of species:* 2–0–0 (10).

Basidiomata omphalinoid. *Pileus* often translucently striate, greyish to dark brown, surface hygrophanous or not; pileipellis a cutis of radially arranged, cylindrical, thin-walled, smooth or minutely incrustated hyphae. *Lamellae* decurrent, with fimbriate edge. *Cheilocystidia* and *pleurocystidia* present, similar. *Stipe* same colour as pileus. *Basidia* clavate. *Basidiospores* ellipsoid to broadly ellipsoid, thin-walled, hyaline, non-amyloid. *Clamp connections* present in all tissues.

Notes. The generic type of *Gamundia* is a saprotrophic fungus that may be a synonym of *G. striatula* (Kühner) Raitelh.

Although *Peltigera*-associated *Gamundia* populations have frequently been observed in many countries, their taxonomy and nomenclature are still unsettled. While most authors have included them in *G. striatula* s. lat. (e.g., Bigelow 1979), they obviously represent distinct species (Moreau 2005). Antonín (2004) revised most types of European *Fayodia* and *Gamundia* species and cited *G. arctica* as the only name available for specimens associated to *Peltigera* thalli. This author considered *Fayodia xerophila* Luthi & Röllin to be almost surely a synonym of *G. striatula*, without mentioning that it had also been described from *Peltigera* thalli.

The true *Gamundia striatula* s. str. is characterized by having a strongly hygrophanous, greyish brown pileus and by growing in coniferous forests (L. Krieglsteiner, pers. comm.). On the contrary, *G. arctica*, with a dark brown to black pileus, and *G. xerophila*, with a medium brown pileus usually without a greyish tinge, both with a less hygrophanous pileus, have been described from sandy soil, not under conifers, and are regularly associated with *Peltigera* thalli, although the trophic relations with the lichens are not yet understood.

Unfortunately, few molecular data are currently available for this species complex, and therefore our current treatment of lichen-associated *Gamundia* species should be regarded as provisional.

Ecology. Terricolous, in forests, parklands, grasslands, or in arctic environments, often under conifers, two species associated with *Peltigera* thalli.

Gamundia arctica (Gulden) E. Ludw.

Pilzkompendium 1: 140 (2001); *Fayodia arctica* Gulden, *Sydowia* 40: 52 (1988 [‘1987’]); *Gamundia leucophylla* var. *arctica* (Gulden) Bon, *Doc. Mycol.* 26 (102): 19 (1996). Type: Norway, Svalbard, Kongsfjord distr., Ossian Sars-fjella, 7 Aug. 1986, K. M. Jensen & G. Gulden 262/86 (O 72600 – holotype).

Basidiomata omphalinoid. *Pileus* 13–35 mm diam., thin-fleshed, convex to applanate, later with a slight central depression, margin down bent, neither hygrophanous nor translucently striate, dark brown, surface glabrous, shiny; pileipellis a cutis of radially arranged, cylindrical, thin-walled, smooth or minutely incrustated, up to 8 µm wide hyphae. *Lamellae* slightly decurrent, moderately close, with many lamellulae inserted from the margin and becoming interveined, thin, up to 4 mm high, whitish, becoming brownish or greyish. *Cheilocystidia* and *pleurocystidia* sparse, subcylindrical, clavate to subfusiform, 42–80(–98) × 6.5–13 µm, thin-walled, hyaline. *Hymenophoral hyphae* cylindrical, thin-walled, smooth, up to 15 µm wide. *Stipe* cylindrical, basally slightly broadened, 14–50 mm long, 2–3.5 mm wide, first concolorous with pileus, later paler brown, smooth and glabrous, except base white tomentous. *Flesh* whitish; smell indistinct. *Basidia* clavate, 25–32(–42) × 8–10 µm, 4-spored; basidioles cylindrical-clavate, 10–34 × 3–10 µm. *Basidiospores* ellipsoid to broadly ellipsoid, 6–7(–8) × 4.5–5.5(–6) µm, ratio length/breadth 1.2–1.5, thin to slightly thick-walled, indistinctly minutely echinulate, hyaline. *Clamp connections* present in all tissues. [Description modified from Antonín 2004 and Gulden 1987.]

Notes. Distinguished from *Gamundia xerophila* by the dark brown pileus and several other characters (see under *G. xerophila*).

Ecology and hosts. From the three specimens collected by Gulden (1987), “small pieces of ± moribund *Peltigera* (cf.)



Gamundia arctica, Svalbard, type population. Basidiomata on *Peltigera* (not visible on the photo). Photo: Kolbjørn Mons Jenssen.



Gamundia arctica

leucophlebia were found on and at the base of two specimens". Following Gulden & Torkelsen (1996), "the fruit-bodies were in all cases associated with moribund thalli of the lichen genus *Peltigera*". Jalink & Nauta (2004) wrote that "near the base of its stem dying pieces of lichens of the genus *Peltigera* could always be found. On one occasion *Fayodia arctica* was even attached to the lichen."

Distribution. With certainty known from Europe (Norway: Svalbard) and North America (Greenland), all other reports being unreliable.

References. Antonín 2004, Gulden 1987 [Borgen et al. 2006, Gulden & Torkelsen, Jalink & Nauta 2004, www.gbif.org/occurrence/2991049992].

***Gamundia xerophila* (Luthi & Röllin) P.-A. Moreau & Courtec.**

Doc. Mycol. 34 (135–136): 50 (2008); *Fayodia xerophila* Luthi & Röllin, *Bull. trimestr. Soc. mycol. Fr.* 88: 174 (1973 [1972]), nom. inval., Art. 40.1; *Fayodia xerophila* Luthi & Röllin, *Doc. Mycol.* 29 (116): 14 (2000). Type: Switzerland, Boucle du Rhône, Moulin de Vert, 5 Dec. 1971, O. Röllin 6507 (G 5714 – holotype).

Basidiomata omphalinoid. *Pileus* 15–45 mm diam., first hemispherical, then convex with a slight central depression, strongly translucently striate, pale to medium brown, surface glabrous, smooth, shiny; pileipellis a cutis of radially arranged, cylindrical, thin-walled, smooth or minutely incrustate, 3–10 µm wide hyphae, externally often gelatinized and diverticulate. *Lamellae* adnate to slightly decurrent, moderately distant, whitish, becoming slightly brownish. *Cheilocystidia* and *pleurocystidia* present, sparse to numerous, subcylindrical, clavate to subfusiform, 32–92 × 9–15 µm, thin-walled, hyaline. *Hymenophoral hyphae* cylindrical, thin-walled, smooth, up to 15 µm wide. *Stipe* cylindrical, basally or apically sometimes slightly broadened, 25–40 mm long, 2–8 mm wide, brownish, often paler than pileus, smooth and glabrous. *Flesh* whitish; smell farinaceous. *Basidia* clavate, 25–33 × 8.5–10 µm, 4-spored; basidioles cylindrical-clavate, 14–32 × 3–10 µm. *Basidiospores* ellipsoid, (6–)7–8.5(–9) × (4–)4.2–5(–6) µm, ratio length/breadth 1.4–1.9, thin-walled, minutely echinulate, hyaline. *Clamp connections* present in all tissues. [Description modified from Antonín 2004 and Luthi & Röllin 1973].

Notes. Following Gulden (1987), *Gamundia xerophila* material from the type locality is "more omphaloid, more yellow-brown, distinctly striate and distinctly hygrophanous, has not been observed with brown edged lamellae and has a somewhat particular smell ... slightly more ellipsoid spores" than *G. arctica*. We have observed that the pileus colour is rather variable, including almost white populations that may represent a distinct, yet undescribed species.

Without microscopical examination, a confusion with *Arrhenia peltigerina* is possible; however, species of *Gamundia* clearly differ from *Arrhenia* by the conspicuous cheilo- and pleurocystidia. Additionally, basidiospores of peltigericolous *Gamundia* species are minutely echinulate, although this character may be difficult to recognize by light microscopy.



Gamundia xerophila, Belgium, Koksijde. Basidioma on *Peltigera*. Photo: Bernard Clesse.



Gamundia xerophila, Belgium, Koksijde. Basidioma on *Peltigera*. Photo: Bernard Clesse.



Gamundia xerophila, Canada, Newfoundland and Labrador. Basidiomata on *Peltigera*. Photo: Andrus Voitk.



Gamundia cf. *xerophila*, Luxembourg, Dudelange. Unusually pale basidiomata on *Peltigera*. Photo: Marie Garnier-Delcourt.

Ecology and hosts. On or close to *Peltigera aphthosa*, *P. didactyla*, *P. cf. elizabethae*, *P. hymenina*, *P. polydactylon* and *P. praetextata*, often on decayed thalli, usually on dry sandy soil or mosses, mainly in late autumn or winter.

Distribution. As *Gamundia* populations on *Peltigera* have commonly been included within a larger concept of *G. striatula*, little is known on the geographical distribution of *G. xerophila*. A careful search in the literature, in online databases and forums, considering only reliable data with photos showing the presence of *Peltigera* thalli, have revealed the presence of *G. xerophila* in Europe (Austria; Belgium; Denmark; France; Germany; Luxembourg; Sweden; [Switzerland](#)) and North America (Canada: Newfoundland and Labrador; Greenland).

Specimens examined. **Luxembourg:** Dudelange, Haardt, 2007, Garnier-Delcourt 071018.1; Steinfort, Schwaarzenhaff, 2012, Garnier-Delcourt 121125.3.

References. Antonín 2004, Bigelow 1979, Luthi & Rölli 1973 [Alstrup 1993, Alstrup & Hawksworth 1990, Lamoure et al. 1982, *Omphalina* 1(5) 2010: cover page, Roux 2020, Zimmermann & Feusi 2021].



Gamundia xerophila

Acknowledgments

C. Björk (specimen and photos of *Arrhenia* aff. *subglobisemen*), B. Clesse (photos of *Gamundia xerophila*), G. Gulden (information on *A. aff. subglobisemen*), K. M. Jenssen (photo of *G. arctica*), L. Krieglsteiner (information on *G. striatula* s. str.), P. Tanchaud (photo of *A. peltigerina*), A. Voitk (photo of *G. xerophila*; information on *A. aff. subglobisemen*).

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *AGARICOMYCETES*

Order *THELIALES*

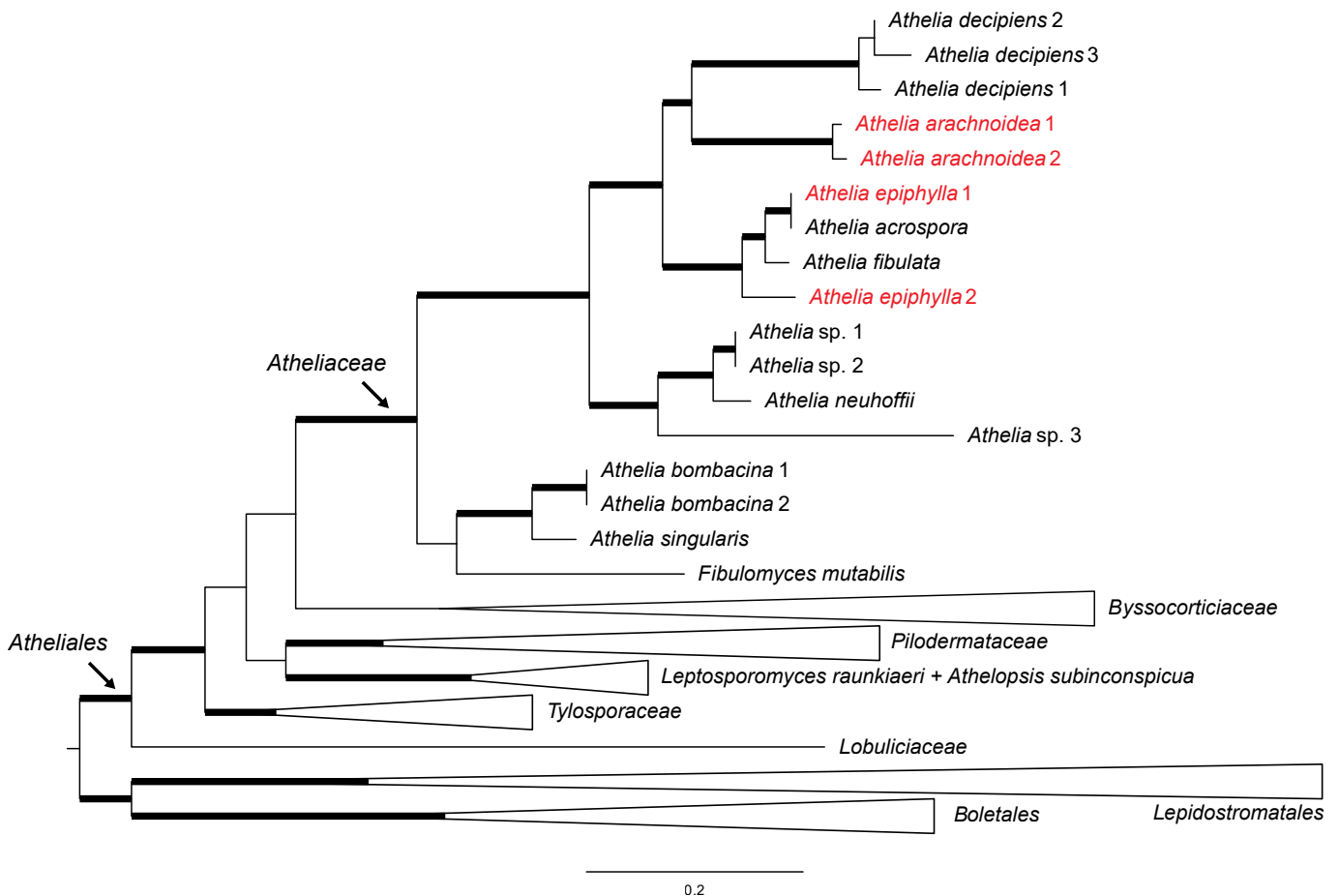
by P. Diederich, B. P. Sulistyo, D. Haelewaters, A. C. Dirks & J. D. Lawrey

Diederich, P., B. P. Sulistyo, D. Haelewaters, A. C. Dirks & J. D. Lawrey. 2022. Class *Agaricomycetes*, order *Atheliales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 41–46.

Introduction and phylogeny

Atheliales is a small order of around 100 described species in 20 genera (He et al. 2019, Sulistyo et al. 2021). Most species are inconspicuous with simple resupinate fruiting bodies lacking morphological differentiation. Ecologically, they are remarkably diverse and include ectomycorrhizal forms, white-rot saprotrophs, insect symbionts, and parasites of cyanobacteria, green algae and lichens. The genus *Athelia* includes a number of species that Jülich (1972) reported to be facultatively lichen-

icolous and two of them are treated here, *Athelia arachnoidea*, which has been collected from a wide variety of lichens as well as green algae, mosses, dead leaves and wood, and *A. epiphylla*, which is mainly corticolous and lignicolous, but also occasionally found on lichens. In the recent *Atheliales* phylogeny of Sulistyo et al. (2021), the two species are in separate but related clades in the *Atheliaceae*, but *A. epiphylla* is obviously heterogeneous and (as it is the type species) in need of delimitation.



Phylogenetic relationships of *Atheliales* and *Atheliaceae* based on nLSU, 5.8S, ITS1, ITS2, *rpb2* and *tef1*, with *Lepidostromatales* and *Boletales* as outgroups, showing the position of the lichenicolous *Athelia arachnoidea* and the facultatively lichenicolous *A. epiphylla* (modified from Sulistyo et al. 2021). Thickened branches indicate BS \geq 75 and PP \geq 0.95.

Key to the lichenicolous species of *Atheliales*

- 1 Basidia with 2(–4) sterigmata, (14–)20–30 × 5–7 µm; sterigmata mostly 4–7 µm long; basidiomata often missing; sterile, white, arachnoid mycelium and/or brown sclerotia frequently present and abundant *A. arachnoidea* (43)
- 1' Basidia with (2–)4 sterigmata, 10–25 × 5–6 µm; sterigmata frequently shorter; basidiomata usually present; arachnoid mycelium absent or poorly developed around basidiomata; sclerotia absent *A. epiphylla* s. lat. (44)
 - 2 Basidia 15–25 µm long, always with 4 sterigmata; sterigmata 3.5–5.5 µm long *A. alnicola*
 - 2' Basidia 10–18 µm long, with (2–)4 sterigmata
 - 3 Basidiospores narrow, almost cylindrical, 6–7.5(–9) × 2.8–3.2 µm; sterigmata 4–5 µm long *A. epiphylla* s. str.
 - 3' Basidiospores wider, (5.5–)6–7.5(–8.5) × 3.5–4.5 µm; sterigmata 2.5–3.5 µm long *A. salicum*

AGARICOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: *Agaricus* L.

ATHELIALES Jülich

Bibliotheca Mycologica 85: 343 (1982). Type: *Athelia* Pers.

Atheliaceae Jülich

Bibliotheca Mycologica 85: 355 (1982). Type: *Athelia* Pers.

ATHELIA Pers.

Traité sur les champignons comestibles: 57 (1818). Type: *A. epiphylla* Pers.

= *Fibularhizoctonia* G. Adams & B. Kropp, *Mycologia* 88: 464 (1996). Type: *Rhizoctonia carotae* Rader

Molecular data: yes (T, L). Number of species: 1–0–1 (32).

Basidiomata white or cream-coloured, thin, pellicular, easily separable from the substrate. *Hymenium* often wrinkled, smooth when dry; *subbasidial (subhymenial) hyphae* thin-walled; *basal (subicular) hyphae* slightly wider and more thick-walled; clamps present or absent. *Basidia* shortly claviform, with 2–4 sterigmata. *Basidiospores* subspherical, ellipsoid or narrowly ovate, smooth, non-amyloid. *Sclerotia* known in at least one species.

Notes. Although the genus *Athelia* includes many common species, and the microscopical and anatomical characters are particularly easy to study because of the thin, pellicular basidiomata, the taxonomy and phylogeny within the genus are still poorly known. Jülich (1972) presented a worldwide monograph of *Athelia*, in which he accepted over 20 species. His taxonomy mainly used the number of sterigmata per basidium, the absence or presence of clamps, and the form and size of basidiospores for species delimitation. He found that at least four species are facultatively lichenicolous, *A. alnicola*, *A. arachnoidea*, *A. epiphylla* and *A. salicum*. He reported that lichen-inhabiting species frequently

do not produce mature basidiospores, but instead preferably reproduce by sclerotia, and therefore cannot be identified with certainty. He did not use the presence or absence of sclerotia as a taxonomic character and did not indicate which species produce them. Eriksson & Ryvarden (1973) mainly agreed with the taxonomic treatment by Jülich (1972), but found it difficult to distinguish some species that they preferred therefore to consider as *A. epiphylla* in a larger sense, provisionally including the facultatively lichenicolous *A. alnicola* and *A. salicum*. Other authors, such as Bernicchia & Gorjón (2010), followed more or less Eriksson & Ryvarden (1973) by calling this the *A. epiphylla* complex, although they distinguished and keyed out the different members of this complex. As the taxa of the *A. epiphylla* complex seem to be only rarely lichenicolous, and thus not so important in the context of the present flora, we follow the view of these authors, by accepting one lichenicolous species, *A. arachnoidea*, and one facultatively lichenicolous species complex, *A. epiphylla* s. lat., of which we shortly mention the lichenicolous members.

A further problem is the distinction of *A. arachnoidea* and *A. epiphylla*, based on the number of sterigmata per basidium. Eriksson & Ryvarden (1973) even wondered whether *A. arachnoidea* should also be included in the *A. epiphylla* complex, comprising those populations with mainly 2-spored basidia. In the phylogeny by Lawrey et al. (2007), including a very small number of *Athelia* sequences, two clades were obtained (but with a low support): one comprising sequences of *A. arachnoidea* and *A. epiphylla*, and another comprising *A. arachnoidea* and *A. decipiens*. In a recent phylogenetic study of the *Atheliales* (Sulistyó 2021), *A. arachnoidea* was sister to *A. decipiens*, and both were sister to a clade comprising *A. epiphylla* (two sequences not grouping together), *A. acrospora* and *A. fibulata*. A widescale phylogenetic study of a much larger number of both lichenicolous and non-lichenicolous *Athelia* populations will be essential for a better understanding of the taxonomy of *Athelia*.

Ecology. Mainly on dead wood, also on bark, at least one lichenicolous species frequently overgrowing and killing entire corticolous lichen communities.

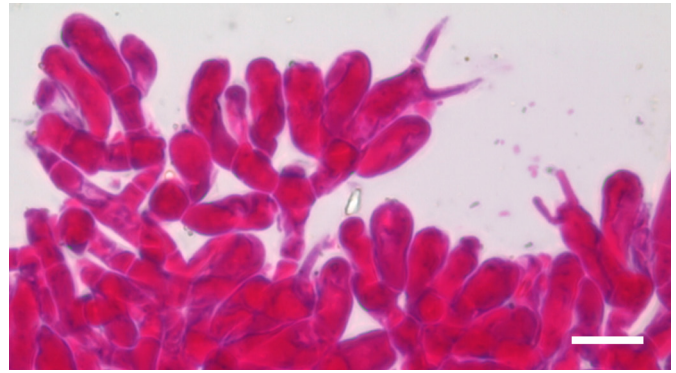
Athelia arachnoidea (Berk.) Jülich

Willdenowia, Beiheft 7: 53 (1972); *Corticium arachnoideum* Berk., *Annals and Magazine of Natural History* 13: 345 (1844); *Terana arachnoidea* (Berk.) Kuntze, *Revisio generum plantarum* 2: 872 (1891); *Athelia epiphylla* var. *arachnoidea* (Berk.) Krieglst., *Beiträge zur Kenntnis der Pilze Mitteleuropas* 12: 40 (1999). *Type*: UK, Northampton, c. 24 mi. SW of King's Cliffe, Blatherwycke Park, 1879, M. J. Berkeley (K).

= *Fibularhizoctonia carotae* (Rader) G. Adams & B. Kropp, *Mycologia* 88: 464 (1996); *Rhizoctonia carotae* Rader, *Phytopathology* 38: 444 (1948). *Type*: USA, New York, Freeport, Freeport storage, on *Daucus carota* in storage, 11 Jan. 1946, W. E. Rader (CUP 37972 – lectotype, selected by Adams & Kropp 1996).

Mycelium white, arachnoid, circular, eventually forming rings over the bark with the central zone composed of dying remnants of the hosts, rings often discontinuous, reaching over 1 m diam. *Basidiomata* white or cream-coloured, thin (c. 0.1 mm thick), pellicular. *Hymenium* often sterile, consisting of basidioles only; *subbasidial hyphae* 2.5–3.5(–5) μm diam., without clamps; *basal hyphae* 3.5–5 μm , with scattered clamps. *Basidia* (14–)20–30 \times 5–7 μm when mature, with 2(–4) sterigmata, basal clamps absent; sterigmata mostly 4–7 μm long. *Basidiospores* narrowly ellipsoid to narrowly ovate, 6–7.5 \times 2.7–3.7 (Yurchenko & Golubkov 2003) or 8–10 \times 4–5 μm (Eriksson & Ryvarden 1973). *Sclerotia* developing on the mycelium, initially forming white mycelial knots with radiating hyphae, 0.1–0.2 mm; when mature, brownish, up to 0.5 mm diam., with a smooth and matt surface, composed of a compact mass of short-segmented to pseudoparenchymatic cells, 6–15.5 \times 5–15 μm . [From Eriksson & Ryvarden 1973, Jülich 1972, Yurchenko & Golubkov 2003 and own observations.]

Notes. Following Yurchenko & Golubkov (2003), the main mycelial growth and destruction of epiphytic hosts occurred during the cold part of the year. Young or mature sclerotia were found in 14% of the specimens. The formation of



Athelia arachnoidea, Luxembourg, Diederich 8591. Hymenium with 2-sterigmate basidia. In phloxine. Scale bar: 10 μm .

fertile basidiomata was very rare, often on the bark away from lichen thalli, and mostly occurred from August to November. The identification of *Athelia arachnoidea* populations is therefore rarely done using microscopic examination, but mostly based on the presence of large, whitish mycelial rings on the bark, rarely associated with sclerotia. Phylogenetic data are currently not sufficient for identifying whether all those populations represent the same species.

Ecology and hosts. Usually lichenicolous on epiphytic lichens, also on green coccoid algae and mosses, dead leaves, bark or wood. Further reported as a pathogen of carrots in cold storage (Adams & Kropp 1996). Best developed in areas with considerable air pollution, and therefore formerly extremely common in Europe (e.g., in the 1980s).

Distribution. Widely distributed in Europe (including UK) and probably common in all countries, also known from North America (Canada; USA) and Africa (Tunisia).

References. Adams & Kropp 1996, Arvidsson 1976, Eriksson & Ryvarden 1973, Gilbert 1988, Jülich 1972, Motiejūnaitė & Jucevičienė 2005, Yurchenko & Golubkov 2003.



Athelia arachnoidea, Luxembourg, Diederich 8591. Basidiomata on bark of *Fagus* over remnants of host lichens. Scale bar: 1 mm.



Athelia arachnoidea, Luxembourg, Diederich 8591. Mature sclerotia on bark of *Fagus* over remnants of host lichens. Scale bar: 0.5 mm.



Athelia arachnoidea, Luxembourg, Diederich 19588. Arachnoid mycelium with sclerotial initials on *Physcia adscendens*. Scale bar: 0.2 mm.



Athelia arachnoidea, Luxembourg, Diederich 19588. Arachnoid mycelium with young, developing sclerotia. Scale bar: 0.2 mm.



Athelia arachnoidea, Luxembourg, Diederich 19588. Immature, brownish sclerotia. Scale bar: 0.2 mm.



Athelia arachnoidea, Luxembourg, Diederich 17756. Mature, brown sclerotia on *Xanthoria parietina*. Scale bar: 0.2 mm.

Athelia epiphylla Pers. s. lat.

Mycol. Europ. I: 84 (1822). *Type*: Unknown origin (L 910.262–268).

= *Fibularhizoctonia centrifuga* (Lév.) G. Adams & B. Kropp, *Mycologia* 88: 466 (1996); *Rhizoctonia centrifuga* Lév., *Ann. sci. Nat. Bot.*, Ser. 2, 20: 225 (1843); *Corticium centrifugum* (Lév.) Bres., *Annales Mycologici* 1: 96 (1903), nom. illeg., non *Corticium centrifugum* (Weinm.) Fr., *Hymenomycetes europaei*: 658 (1874). *Type*: ? (G – lectotypus, fide Jülich 1972).

incl. *Athelia alnicola* (Bourd. & Galz.) Jülich, *Willdenowia* Beih. 7: 47 (1972); *Corticium centrifugum* subsp. *alnicola* Bourd. & Galz., *Hymén. de France*: 198 (1928). *Type*: Germany, “Norddeutschland, Bredent. Teich”, Oct. 1908, O. Jaap (PC, UPS).

incl. *Athelia salicum* Pers., *Mycol. Europ.* I: 84 (1822). *Type*: Unknown origin (L 910.262–281).

Basidiomata white to light yellowish, thin. *Subbasidial hyphae* 3–5 µm diam., without clamps; *basal hyphae*

somewhat wider, 5–8 µm wide, with scattered clamps. *Basidia* 10–25 × 5–6 µm, with (2–)4 sterigmata, basal clamps absent. *Basidiospores* subcylindrical, narrowly ellipsoid or ovate, 6–8.5 × 3–5 µm. [From Eriksson & Ryvarden 1973 and Jülich 1072.]

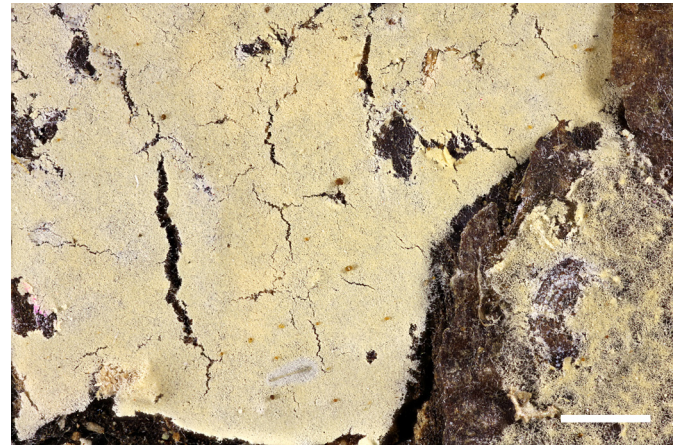
- *Athelia alnicola*: basidia 15–25 µm long; sterigmata 3.5–5 µm long; basidiospores 6.5–8.5 × 3.5–4.5 µm.
- *Athelia epiphylla* s. str.: basidia 13–18 µm long; sterigmata 4–5 µm long; basidiospores, (5.5–)6–7.5(–9) × 2.8–3.2 µm.
- *A. salicum*: basidia 10–16 µm long; sterigmata 2.5–3.5 µm long; basidiospores (5.5–)6–7.5(–8) × 3.5–4.5 µm.

Notes. The complicated nomenclature around *Corticium centrifugum*, *Sclerotium lichenicola* Svendsen and other taxa based on sterile fungi belonging to *Athelia* has been thoroughly discussed by Jülich (1972).

Ecology and hosts. Corticolous and lignicolous, facultatively lichenicolous (host choice poorly documented).



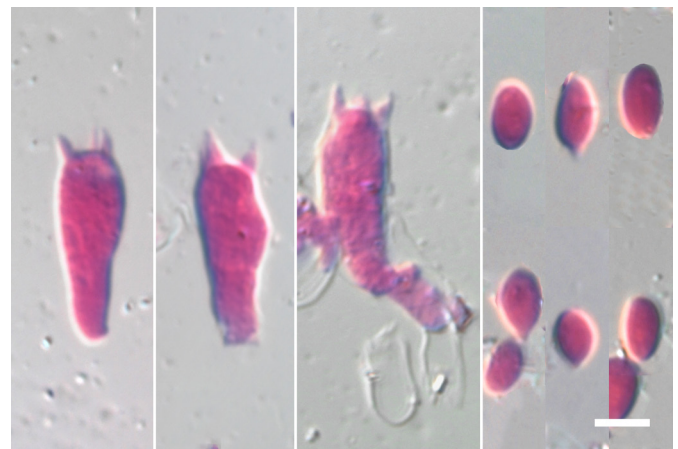
Athelia salicum, Luxembourg, Diederich 8640. Lichenicolous basidiomata on *Lepraria incana*. Scale bar: 0.5 mm.



Athelia salicum, Luxembourg, Schultheis 12-87. Non-lichenicolous basidiomata on wood. Scale bar: 1 mm.



Athelia salicum, Belgium, Diederich 15118. Lichenicolous basidiomata on *Xanthoria parietina*. Scale bar: 0.5 mm.



Athelia salicum, Belgium, Diederich 15118. Basidia with 3 short sterigmata, and basidiospores. In phloxine. Scale bar: 5 µm.

Distribution. Members of the *A. epiphylla* complex have been reported by Jülich (1972) from Europe, North America and South America. Because of the uncertain taxonomy, countries are not enumerated here.

References. Eriksson & Ryvarden 1973, Jülich 1972.

Acknowledgments

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Class *AGARICOMYCETES*

Order *BOLETALES*

by P. Diederich & J. D. Lawrey

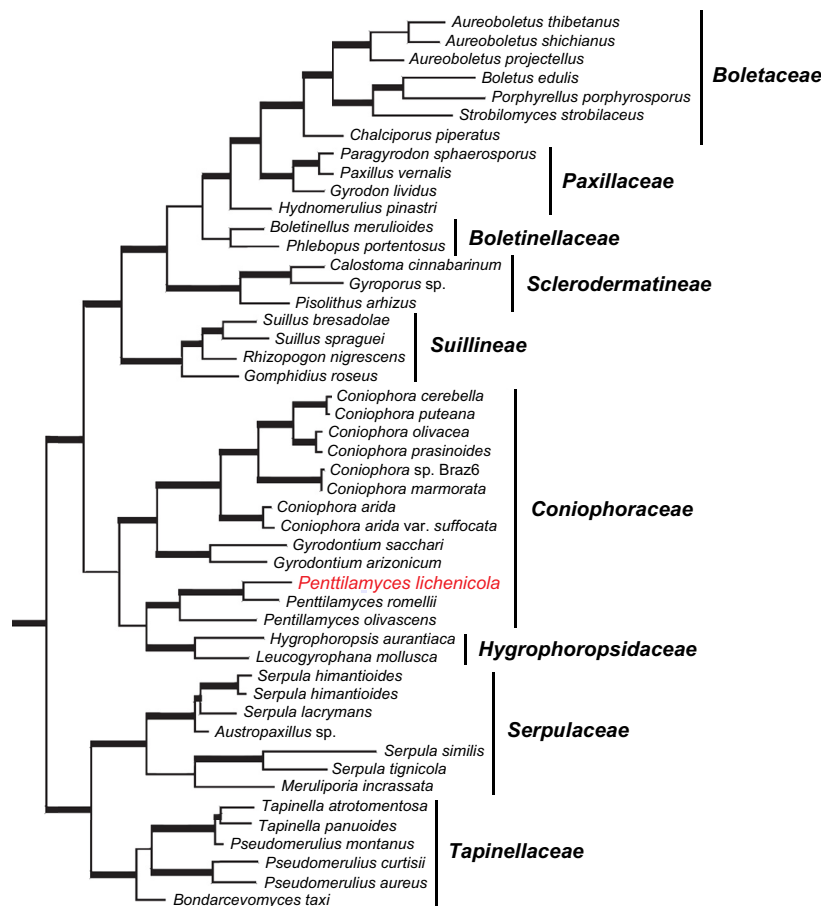
Diederich, P., & J. D. Lawrey. 2022. Class *Agaricomycetes*, order *Boletales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 47–49.

Introduction and phylogeny

The *Boletales* is a relatively large and morphologically diverse order of *Basidiomycota* that includes typically piliate-stipitate forms with a tubular hymenophore (in the *Boletineae*/*Sclerodermatineae*/*Suillineae*) but also resupinate to effused reflexed forms especially in the *Tapinellineae*, *Coniophorineae*, *Serpulaceae* and *Hygrophoropsidaceae* (Hibbett et al. 2014). *Boletales* include brown-rot saprotrophs, diverse ectomycorrhizal forms and mycoparasites.

In recent molecular phylogenies, a single resupinate lichenicolous species, originally named *Leucogyrophana lichenicola*,

is consistently resolved in the *Coniophoraceae* along with most other named species of *Leucogyrophana* (Lawrey et al. 2007; Binder et al. 2010). However, *Leucogyrophana* is known to be polyphyletic (Jarosch and Besl 2001; Binder et al. 2010) and the type species of the genus, *L. mollusca*, is in the *Hygrophoropsidaceae*. *L. lichenicola* was recently placed in the new genus *Penttilamyces*, along with *L. romellii* and *L. olivascens*. Although we believe this group of fungi requires more work to delimit and name natural groups, we adopt the new genus name for the lichenicolous species here.



Phylogenetic relationships of *Boletales* and *Coniophoraceae*, showing the position of the lichenicolous *Penttilamyces lichenicola* (modified from Binder et al. 2010). Thickened branches indicate Bayesian posterior probability = 1.0.

AGARICOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: Agaricus L.

BOLETALES E.-J. Gilbert

Les Livres du Mycologue, Tome III: Les Bolets: 83 (1931). Type: Boletus Fr.

Coniophoraceae Ulbr.

Krypt.-Fl. für Anfänger: 120 (1928). Type: Coniophora DC.

PENTTILAMYCES Zmitr., Kalinovskaya & Myasnikov

Folia Cryptogamica Petropolitana 7: 8 (2019). Type: P. romellii (Ginns) Zmitr., Kalinovskaya & Myasnikov

Molecular data: yes (T, L). Number of species: 1–0–0 (3).

Basidiomata resupinate, effused, surface smooth, wrinkled or folded (merulioid), easily detached from the substrate, orange or orange to olivaceous brown. *Hyphae* nodose-septate, with clamps, those in the subiculum sparsely branched, under the hymenium densely packed and richly branched; leptocystidia fusoid or hyphoid. *Basidia* aseptate, narrowly clavate to utriculate, 4-spored, with a basal clamp. *Basidiospores* ellipsoid-cylindrical, smooth, brownish. *Sclerotia* known in some species.

Notes. Following Zmitrovich et al (2019), this genus is distinguished from *Leucogyrophana* by the “predominance of nodose-septate hyphae and brown-walled small ellipsoid basidiospores with strong dextrinoid reaction”.

Ecology. Saprotrophic, on rotten coniferous wood, one species lichenicolous.



Penttilamyces lichenicola, Canada, Ontario. Basidiomata over *Cladonia rangiformis*. Photo: D. Malloch.

Penttilamyces lichenicola (Thorn, Malloch & Ginns)

Zmitr., Kalinovskaya & Myasnikov

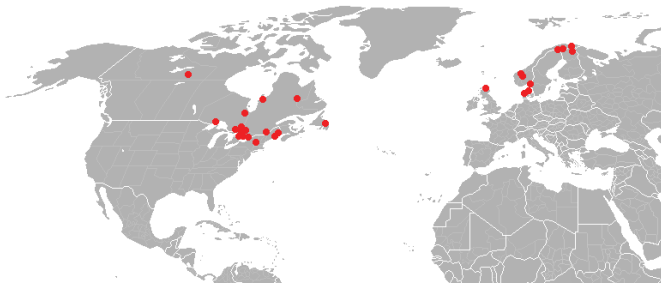
Folia Cryptogamica Petropolitana 7: 8 (2019); Leucogyrophana lichenicola Thorn, Malloch & Ginns, *Can. J. Bot.* 76: 687 (1998). *Type:* Canada, Ontario, Nipissing District, Algonquin Provincial Park, Canisbay Township, Lake of Two Rivers, old airfield, under *Cladonia* sp., 1 Oct. 1988, R.G. Thorn, D.W. Malloch & J. Ginns 9440 (DAOM 194172 – holotype).

Basidiomata developing on a pale yellow cottony mycelium, becoming pellicular to soft membranous, merulioid, with deep fissures and rounded wrinkles when fresh, smooth when dry, continuous, pastel yellow to orange-yellow, drying concolorous or yellow-orange, 2–10 mm broad; margins white to pale yellow. *Subicular hyphae* thin-walled, 2–7.5 μm broad, with simple clamps; hyphal strands present in subiculum and margin, approximately 25 μm broad. *Hymenium* containing numerous clavate basidioles; cystidia none, or present as clavate-mucronate cells the size of basidioles, apically rounded. *Basidia* clavate, 4-spored, (19–)22.5–29.5 \times 5.5–7.5(–10) μm , with a basal clamp; sterigmata short, conical, 2.5–5 μm long, 1–1.8 μm broad at their base. *Basidiospores* ellipsoid or ovate, smooth, weakly to strongly dextrinoid, (4–)4.5–5.5(–7) \times (2.5–)3–3.5(–4.5) μm , wall 0.3–0.6 μm thick. *Sclerotia* subspherical, 1–3 mm diam., or elongate, to 5 mm long, dense, often breaking into smaller parts, pale yellow to bright orange, ecorticate, composed of inflated, clamped, short-celled hyphae, 13–43 \times 5–17 μm , thin to slightly thick-walled. [Description modified from Thorn et al. 1998.]

Notes. This species is very similar to the generic type *Penttilamyces romellii* Ginns that differs in habitat (decayed wood and rotting bark of gymnosperms), basidiospores germinating more quickly, missing hyphal strands in cul-



Penttilamyces lichenicola, Canada, Ontario, Thorn 87102401. Basidioma over *Cladonia* subgen. *Cladina*. Scale bar: 1 mm.



Penttilamyces lichenicola

ture, and missing sclerotia (Thorn et al. 1998). Phylogenetically, both species were sister in an analysis by Lawrey et al. (2007).

Ecology and hosts. Over podetia of terricolous *Cladonia* and *Stereocaulon* species, incl. *C. arbuscula*, *C. cristatella*, *C. rangiferina*, *C. rangiformis*, *C. stellaris*, *S. paschale*, *S. saxatile* and *S. tomentosum*, rarely below neighbouring leaves and other litter.

Distribution. N Europe (Denmark; Finland; Norway; Sweden; UK: Scotland) and North America (Canada: Newfoundland and Labrador, New Brunswick, Northwest Territories, Ontario, Quebec; USA: Maine, New York), common in northern latitudes. A report from Hungary on *Cladonia foliacea* (Varga et al. 2021) needs verification.

References. Lawrey et al. 2007, Thorn et al. 1998 [Burzynski & Voitek 2018, Hitch 2013, Varga et al. 2021].

Acknowledgments

D. Malloch (photo of *Penttilamyces lichenicola*).

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Class *AGARICOMYCETES*

Order *CANTHARELLALES*

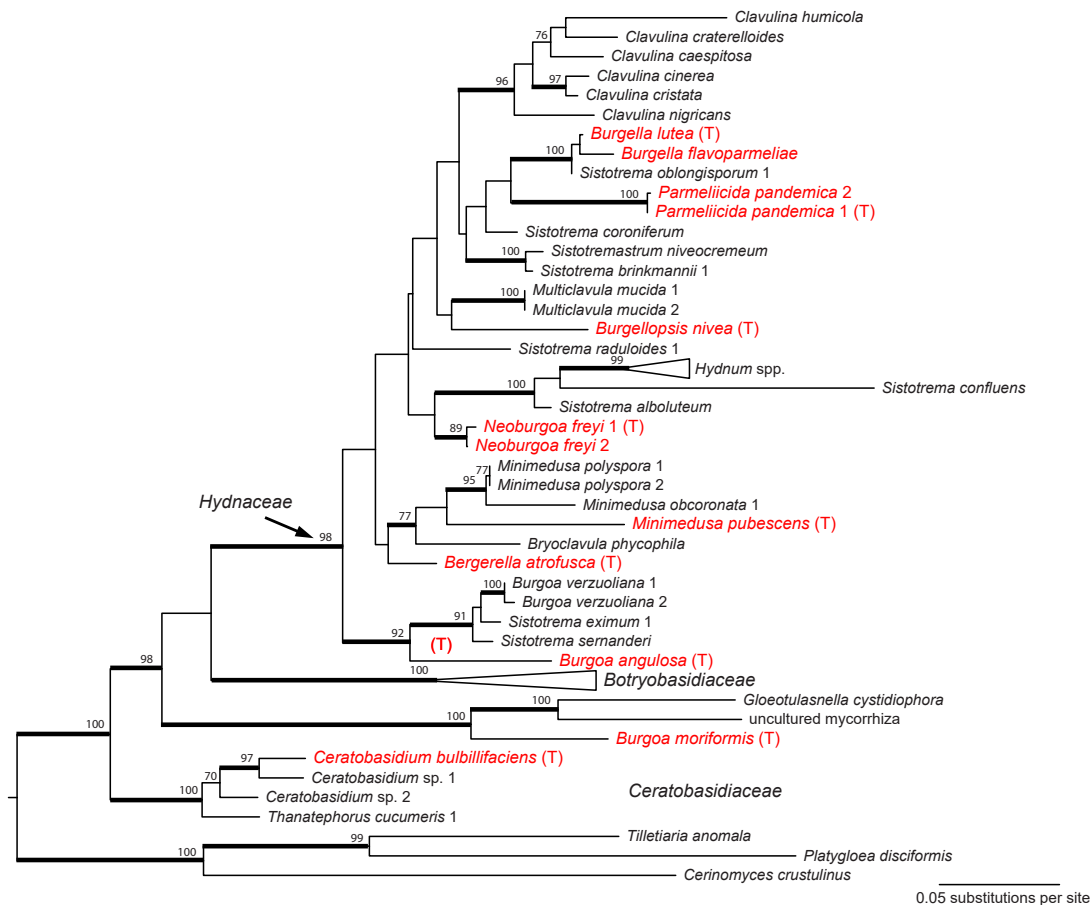
by P. Diederich, M. Sikaroodi & J. D. Lawrey

Diederich, P., M. Sikaroodi & J. D. Lawrey. 2022. Class *Agaricomycetes*, order *Cantharellales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 51–69.

Introduction and phylogeny

The *Cantharellales* is a small order of around 300 described species recently circumscribed using molecular approaches (Hibbett & Thorn 2001, Binder et al. 2005, Moncalvo et al. 2006). It is remarkably diverse morphologically, with the chanterelles (*Cantharellus*) and other well-known mushroom-forming (*Hydnum*, *Clavulina*) fungi included along with familiar resupinate (*Botryobasidium*, *Sistotrema*, *Ceratobasidium*) forms. The order is also nutritionally diverse, including saprotrophic, parasitic and mutualistic (mycorrhizal and lichen-forming) species.

Lichenicolous species were first recognized in the order by Sikaroodi et al. (2001) using molecular approaches, and new species have been discovered throughout the order since then. All known lichenicolous species in the order are bulbilliferous, forming tightly coiled masses usually on the lichen thallus surface. Similar structures are also commonly produced by lichenicolous species in the *Corticiales* and other basidiomycete orders (Lawrey et al. 2007), which indicates the need for molecular approaches to accurately determine their phylogenetic placement.



Best-scoring nuLSU RAXML phylogram of sequences used to place lichenicolous species (in red) in the *Cantharellales*. Internal branches in bold-face indicate posterior probabilities ≥ 0.95 and numbers are ML-BS values ≥ 70 . Sequences representing *Cantharellus* are known to exhibit high levels of rate heterogeneity in nuDNA (Moncalvo et al. 2006, Matheny et al. 2007) and were therefore left out of the analysis. Type specimen of lichenicolous species are indicated with '(T)'.

Key to the lichenicolous species of *Cantharellales*

- 1 Bulbils subspherical, 60–80 µm diam., pubescent, entirely covered by radially oriented ‘hairs’ with a ± pointed apex and a relatively broad base; on various lichens *Minimedusa pubescens* (63)
- 1’ Bulbils with a more or less smooth surface; externally without specialized cells
 - 2 Bulbils (20–)25–35(–45) µm diam., dark reddish brown, shiny; composed of cells 6–15 µm diam. not separating easily (damaged with pressure on cover glass); mainly on *Physcia* *Bergerella atrofusca* (54)
 - 2’ Bulbils larger
 - 3 Bulbils yellow or orange; with yellow oil droplets emerging when observed in lactophenol cotton blue
 - 4 Bulbils 150–300(–700) µm diam., pale yellow to orange; externally covered by an amorphous layer 3–15 µm thick; internally cells thick-walled 10–20 µm diam., separating rather easily (with pressure on cover glass); on the thallus of terricolous macrolichens (*Cladonia* subgen. *Cladina* and *Cetraria*) *Neoburgoa freyi* (64)
 - 4’ Bulbils less than 110 µm diam.; externally without an amorphous layer, cells in surface view polyhedral; internal cells thin-walled, strongly adherent, 6–15 µm diam., separating only with difficulty
 - 5 Bulbils 50–80 µm diam., yellow to orange yellow; facultatively lichenicolous over various lichens *Burgella lutea* (57)
 - 5’ Bulbils 60–110 µm diam., yellow to ochraceous or orange (honey-coloured); on *Flavoparmelia baltimor-ensis* and perhaps *Parmotrema* *Burgella flavoparmeliae* (56)
 - 3’ Bulbils differently coloured; without or with colourless oil droplets emerging when observed in lactophenol cotton blue
 - 4 Bulbils 35–250 µm diam., white, brown or dark reddish brown
 - 5 Bulbils dark reddish brown, sometimes flattened, 150–270 µm diam.; cell content in old herbarium specimens with a cyanophilous granulation (dark blue in lactophenol cotton blue); on *Parmeliaceae* *Parmeliicida pandemica* (65)
 - 5 Bulbils greyish yellow when young, brown when mature, dark brown when old, 100–200 µm diam.; facultatively lichenicolous over various lichens *Ceratobasidium bulbillifaciens* (53)
 - 5’ Bulbils white; on various lichens
 - 6 Bulbils 35–65 µm diam., white, with a moriform, slightly shiny surface, made of an agglomeration of hyaline, subspherical, ballooned cells 7–12 µm diam. *Burgoa moriformis* (61)
 - 6 Bulbils 100–250 µm diam., whitish to slightly translucent, matt, irregular in form, surface uneven, often slightly to distinctly angular; external cells in surface view roundish, 6–9 µm diam.; internally of elongate, straight or curved, septate hyphae; individual cells 5–30 × 4.5–11 µm *Burgoa angulosa* (60)
 - 6’ Bulbils 100–220 µm diam., white, slightly shiny, not translucent, roundish to shortly ellipsoid, surface not angular; external cells in surface view polyhedral, 8–15 µm diam.; internal cells indistinctly catenate, ±roundish to ellipsoid or polyhedral, 8–15 µm diam. *Burgellopsis nivea* (59)
 - 4’ Bulbils 200–400 µm diam., pale beige, greyish yellow or greyish orange, translucent, flattened, c. 200 µm tall; external cells in surface view polyhedral, 5–12 µm diam.; internal cells strongly adherent, roundish to ellipsoid or polyhedral, 4–11(–14) µm diam., separating with difficulty; on *Peltigerales* *Bulbilla applanata* (55)

AGARICOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: *Agaricus* L.

CANTHARELLALES Gäum.

Vergleichende Morphologie der Pilze: 495 (1926). Type: *Cantharellus* Juss.

Ceratobasidiaceae G.W. Martin

Lloydia 11: 114 (1948). Type: *Ceratobasidium* D. P. Rogers

CERATOBASIDIUM D. P. Rogers

University of Iowa Studies in Natural History 17: 4 (1935). Type: *C. calosporum* D. P. Rogers

Molecular data: yes (L). *Number of species:* 1–0–0 (10).

Basidiomata effused, thin, ceraceous or pellicular. *Hymenium* with a smooth surface. *Subicular hyphae* hyaline or brownish, without clamps. *Basidia* hyaline, aseptate, thin-walled, globose to broadly clavate or ellipsoid, usually with 2–4 sterigmata. *Basidiospores* hyaline, thin-walled, smooth, globose to ellipsoid or vermiform, not amyloid.

Asexual stages: monilioid hyphae with chains of swollen, ellipsoid cells; sclerotia or bulbils present in many species.

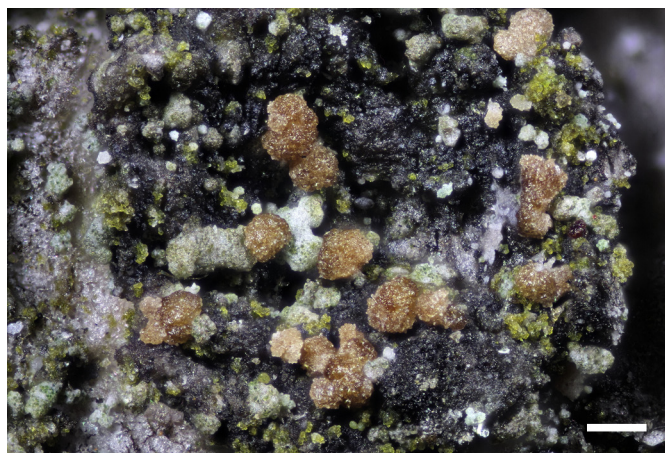
Notes. The phylogenetic analysis of *Ceratobasidiaceae* by Diederich et al. (2014a) resulted in a well-supported clade including the generic type *Thanatephorus cucumeris* and another unidentified *Thanatephorus*, and a non-supported clade including several *Ceratobasidium* sequences, *Thanatephorus fusisporus* and the lichenicolous *C. bulbillifaciens*, but unfortunately not the type of *Ceratobasidium*, for which no sequences are available yet. Taxonomic treatments are available, e. g., in Roberts (1999), Stalpers & Andersen (1996).

Ecology. Saprotrophic or parasitic on plants and wood, one species at least facultatively lichenicolous, also soil-inhabiting and mycorrhizal.

Ceratobasidium bulbillifaciens Diederich & Lawrey

in Diederich et al., *Lichenologist* 46: 345 (2014). *Type:* Germany, Hessen, Gießen, Parkplatz bei Sporthalle im Süden von Heuchelheim, 155 m, on *Acer platanoides*, on unidentified, dying lichenized crust, also on young thalli of *Physcia tenella*, 6 Sept. 2010, R. Cezanne & M. Eichler 8193 (BR – holotype and isotype).

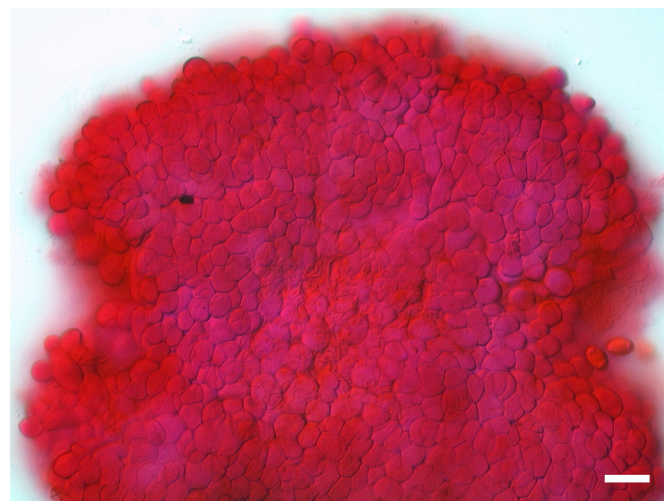
Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed bulbils growing over or between corticolous lichen thalli. *Mycelium* not observed. *Bulbils* superficial, dispersed, roundish to shortly ellipsoid, greyish yellow when young, brown when mature, dark brown when old, matt, not translucent, without hairs, 100–200 µm diam.; bulbils externally without specialized cells; bulbils internally composed of branched chains of subspherical to elongate, hyaline cells, 7–23 × 6–10 µm, septa without clamps, crystals absent in polarized light.



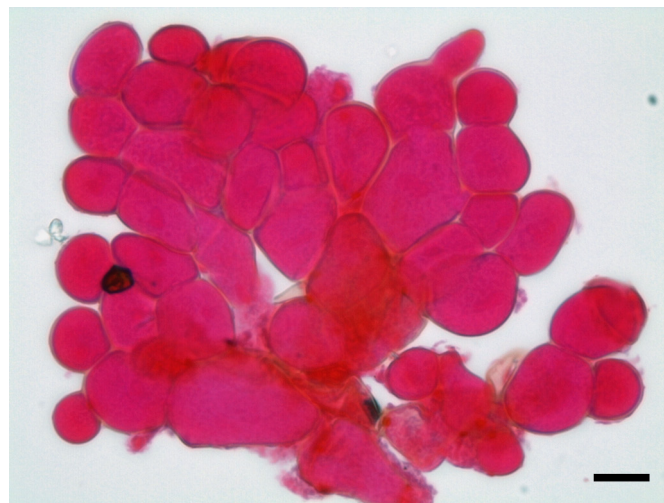
Ceratobasidium bulbillifaciens, Germany, holotype. Bulbils over corticolous lichens. Scale bar: 200 µm.

Notes. This species is characterized by small, brown, dispersed bulbils, less than 200 µm diam., internally composed of branched chains of subspherical to elongate, hyaline cells, and by the absence of clamps. The species may be confused with similarly-coloured sclerotia of *Athelia arachnoidea* that are typically much larger, over 500 µm diam., and often associated with a superficial white mycelium or thin, resupinate basidiomata.

Ecology and hosts. Bulbils develop over or between lichen thalli, e.g., *Candelariella* spp., *Phaeophyscia orbicularis*, *Physcia tenella* and *Xanthoria parietina*, frequently on unidentified, lichenized crusts, not visibly damaging the lichen thalli, usually in Xanthorion communities. Most specimens have been collected on the bark of various trees, but one, from the Netherlands, was growing over concrete.



Ceratobasidium bulbillifaciens, Germany, holotype. Bulbil in Congo red + phloxine. Scale bar: 20 µm.



Ceratobasidium bulbillifaciens, Germany, holotype. Squashed bulbil in Congo red + phloxine. Scale bar: 10 µm.



Ceratobasidium bulbilifaciens

Owing to the inconspicuous colour of the small bulbils, the species is difficult to recognize in the field and certainly much overlooked.

Distribution. Europe (Belgium; France; Germany; Luxembourg; Netherlands; Slovakia; Sweden; UK; Ukraine).

References. Diederich & Lawrey 2007 (as ‘*Burgoa*-like species of *Ceratobasidiaceae*’), Diederich et al. 2014a [Darmostuk 2022, Hitch 2015, Khodosovtsev & Darmostuk 2016].

Hydnaceae Chevall.

Flore générale des environs de Paris 1: 270 (1826). Type: *Hydnum* L.

References. Lawrey et al. 2016.

BERGERELLA Diederich & Lawrey

in Lawrey et al., *Bryologist* 123: 159 (2020). Type: *B. atrofusca* Diederich & Lawrey

Molecular data: yes (T, L). **Number of species:** 1–0–0.

Notes. As the genus is currently monospecific, no generic description is given here.

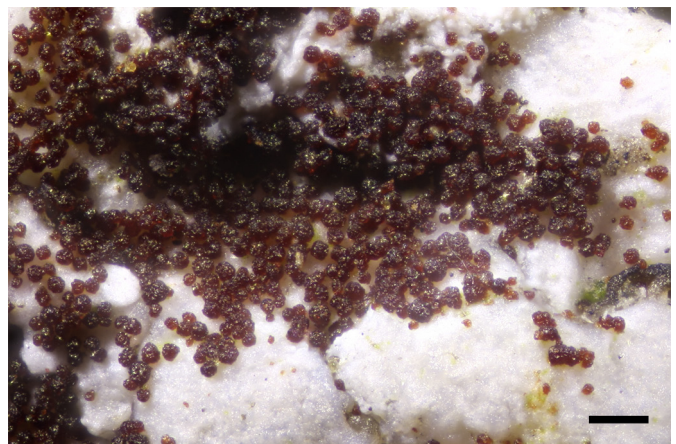
Bergerella atrofusca Diederich & Lawrey

in Lawrey et al., *Bryologist* 123: 159 (2020). Type: Austria, Osttirol, Matrei in Osttirol, Matreier Tauernhaus, 47°07'12"N, 12°29'36"E, 1510 m, on young *Larix* near river, on thallus of *Physcia aipolia*, 12 Sept. 2019, F. Berger 34240 (BR – holotype; herb. Berger – isotype).

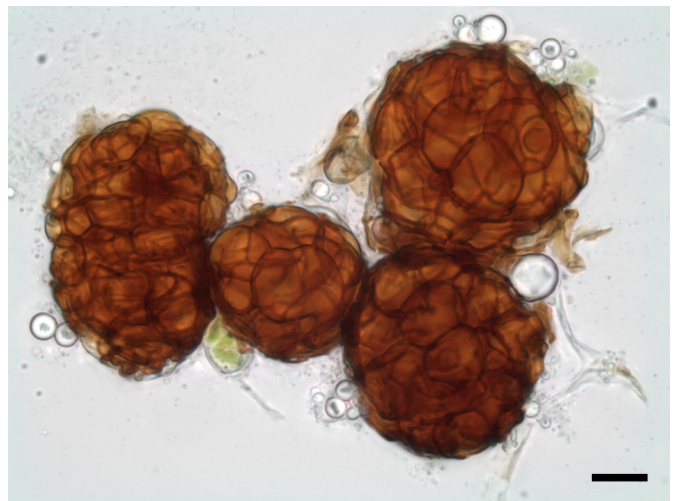
Basidiomata and **conidiomata** unknown. Colonies appearing as dispersed or more often densely aggregated bulbils overgrowing thalli of *Physcia* species. **Mycelium**

sparse around bulbils, hyaline, 3.5–5 µm diam. **Bulbils** superficial from the beginning, dark reddish brown, shiny, without hairs, surface smooth, with individual cells indistinctly visible at a very high magnification, roundish to ellipsoid, (20–)25–35(–45) µm diam., externally without specialized cells, not covered by an amorphous layer, composed of more or less roundish to ellipsoid cells not separating easily (damaged with pressure on the cover glass), 6–15 µm diam.; cell wall thin, c. 0.5 µm thick; clamps not observed; content of cells colourless, with hyaline oil droplets emerging from slightly damaged bulbils when observed in water; no crystals visible in polarized light.

Notes. *Bergerella atrofusca* is mainly characterized by the extremely small, dark reddish brown and shiny bulbils that develop superficially as a virulent pathogen on the thallus of *Physcia* species. All other known



Bergerella atrofusca, Austria, holotype. Bulbils over *Physcia aipolia*. Scale bar: 100 µm.



Bergerella atrofusca, Austria, holotype. Bulbils in water. Scale bar: 10 µm.

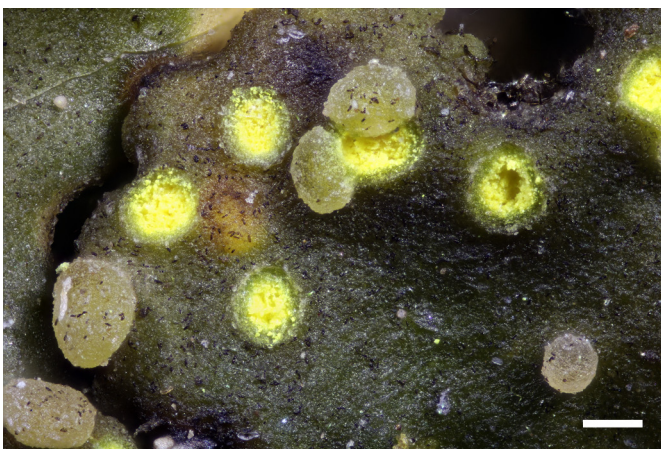
*Bergerella atrofusca*

lichenicolous bulbilliferous fungi have larger bulbils, and all except *Ceratobasidium bulbillifaciens* are paler, ranging from white, ochraceous, honey-colored, yellow and orange to pink (Diederich et al. 2014a). Bulbils of *C. bulbillifaciens* are greyish yellow to dark brown, matt, 100–200 µm in diam., internally composed of branched chains of cells.

Ecology and hosts. A virulent pathogen of *Physcia aipolia* and *P. stellaris* thalli, always along subalpine rivers. Colonized thalli quickly become white and much thinner, and eventually get reduced to a thin film of thallus remnants or disappear entirely. In the latter case, bulbils remain present on the bark of the tree, frequently over other corticolous lichens; e. g., it has been collected once on *Thelotrema lepadinum* (Berger, pers. comm.).

Distribution. Europe (Austria; Switzerland).

References. Lawrey et al. 2020 [Kray & Weber 2021].



Bulbilla applanata, Bolivia, holotype. Bulbils on *Pseudocyphellaria*. Scale bar: 200 µm.

BULBILLA Diederich, Flakus & Etayo

in Diederich et al., *Lichenologist* 46: 340 (2014). Type: *B. applanata* Diederich, Flakus & Etayo

≡ *Adamflakia* Diederich & Lawrey, in Lawrey et al. 2016, *Bryologist* 119: 347 (2016), nom. inval. et nom. illeg. superfl.

Molecular data: yes (T, L). **Number of species:** 1–0–0.

Notes. As the genus is currently monospecific, no generic description is given here. ITS sequences from 454 pyrosequencing clearly included the species within the *Cantharellales*, but excluded it from the genus *Burgella*. No cultures have been obtained.

The nomenclature of the genus is confusing. Lawrey et al. (2016) introduced the new name *Adamflakia*, stating that *Bulbilla* is invalid following ICN, Art. 20.2, as a generic name ‘may not coincide with a Latin technical term in use in morphology’. However, He et al. (2019) explained that the Latin technical term for bulbil is ‘*bulbillus*’ and not ‘*bulbilla*’, and that only the exact spelling ‘*Bulbillus*’ is thus not allowed for a genus. Although the term ‘*bulbilla*’ has been used by Weresub & LeClair (1971) for the Latin description of bulbils in the new genus *Minimedusa*, this has to be regarded as a grammatical error, and does not make of ‘*bulbilla*’ a technical term in use.

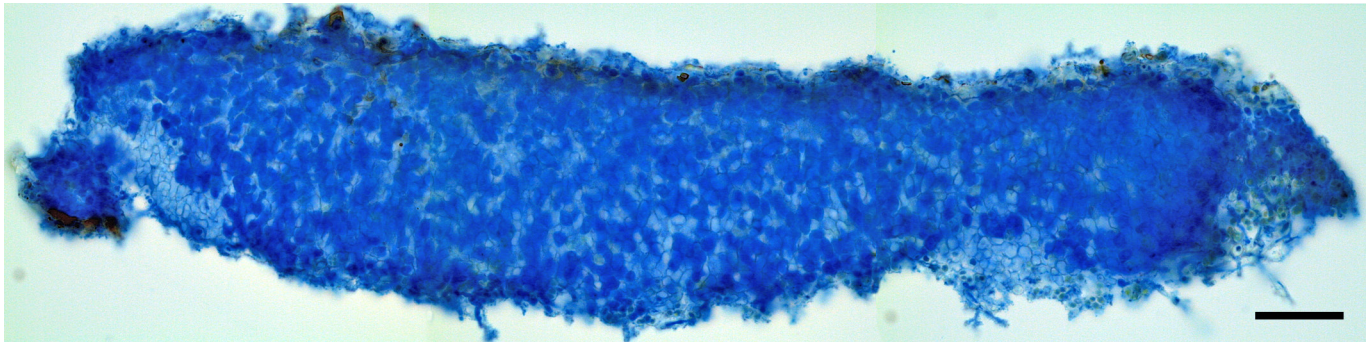
Bulbilla applanata Diederich, Flakus & Etayo

in Diederich et al., *Lichenologist* 46: 340 (2014). Type: Bolivia, Dept. La Paz, Prov. Nor Yungas, Coroico village, Yungas montane forest, 16°11’10”S, 67°43’16”W, 1550 m, on epiphytic *Pseudocyphellaria*, 6 June 2010, A. Flakus 16422 & P. Rodrigues-Flakus (KRAM – holotype; BR, LPB – isotypes).

≡ *Adamflakia applanata* Diederich & Lawrey, in Lawrey et al. 2016, *Bryologist* 119: 347 (2016), nom. inval.



Bulbilla applanata, Ecuador, Etayo 26437. Bulbils on *Sticta*, leaving distinct scars on the host thallus. Scale bar: 200 µm.



Bulbilla applanata, Bolivia, holotype. Section through bulbil, in lactophenol cotton blue. Scale bar: 50 µm.

Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed bulbils overgrowing lichen thalli or more rarely apothecia. *Mycelium* not observed. *Bulbils* slightly to distinctly immersed in the host thallus, usually leaving conspicuous scars in the thallus when removed, pale beige, greyish yellow or greyish orange, translucent, and colour consequently varying with the colour of the host thallus, not or faintly shiny, without hairs, roundish to shortly ellipsoid, 200–400(–500) µm diam., sometimes confluent and up to 700 µm, flattened, c. 200 µm tall, basally strongly constricted; bulbils externally without specialized cells, cells in surface view polyhedral, smooth, mainly 5–12 µm diam.; bulbils internally composed of strongly adherent, more or less roundish to ellipsoid or polyhedral cells separating only with difficulty, 4–11(–14) µm diam., clamps not observed; agglomerations of small crystals visible in polarized light present on the bulbil surface in some specimens examined.

Notes. The species differs from other lichenicolous, bulbil-forming basidiomycetes (other than the sclerotia-forming *Athelia arachnoidea* and *Penttilamyces lichenicola*) by the particularly large bulbils, typically reaching 400 µm in diam. Bulbils are slightly translucent, show some variability in colour, and are often, but not always, applanate. They leave conspicuous scars in the host thallus when removed.



Bulbilla applanata

Ecology and hosts. On the thallus, more rarely apothecia, of *Peltigerales*: *Pseudocyphellaria* sp., *P. faveolata*, *Lobariella crenulata*, *Peltigera* sp., *Sticta* sp.). Infected thalli often, but not always, change colour, suggesting a virulent parasite on some hosts.

Distribution. South America (Bolivia; Chile; Ecuador).

References. Diederich et al. 2014a, Lawrey et al. 2016 [Etayo 2017].

BURGELLA Diederich & Lawrey

Mycol. Progress 6: 62 (2007). Type: *B. flavoparmeliae* Diederich & Lawrey

Molecular data: yes (T, L). *Number of species:* 2–0–0.

Colonies appearing as dispersed or rarely agglomerate bulbils. *Bulbils* honey-colored or bright yellow, ±shiny, without hairs, roundish to shortly ellipsoid or irregular in form, partly immersed to superficial, externally without specialized cells, cells in surface view polyhedral, internally of strongly adherent, more or less roundish to ellipsoid or polyhedral cells separating only with difficulty; clamps not observed.

Notes. The genus *Burgella* belongs to the same clade as the sexual species *Sistotrema oblongisporum*, from which no bulbils have been reported (Hallenberg 1984), and which is only distantly related to the generic type *S. confluens* Pers.

Ecology. Both known species are lichenicolous on the thallus of *Parmeliaceae*.

Burgella flavoparmeliae Diederich & Lawrey

Mycol. Progress 6: 64 (2007). Type: USA, Missouri, Wayne Co., Sam A. Bakker State Park, Shut-Ins Trail, 37°15'42"N, 90°30'28"W, T.30N, R.5E, sec. 20, 21, 125 m, floodplain forest along Big Creek with dolomite ledges and rhyolite bluffs, on *Flavoparmelia baltimorensis*, 15 Oct. 2003, W. R. Buck 45360 (NY – holotype; BR – isotype).

Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed or rarely agglomerate bulbils overgrowing lichen



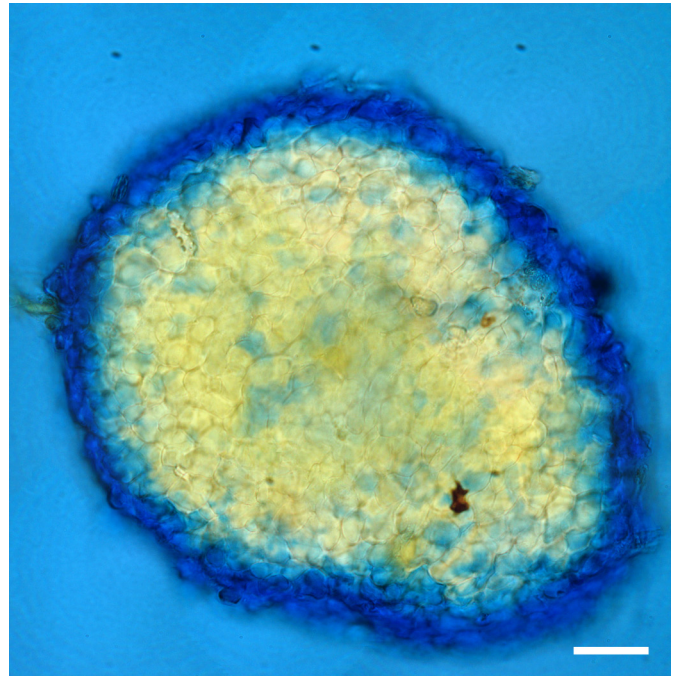
Burgella flavoparmeliae, USA, isotype. Bulbils on *Flavoparmelia baltimorensis*. Scale bar: 200 µm.

thalli. *Mycelium* not observed. *Bulbils* slightly immersed in the host thallus to superficial, dispersed, yellow to ochraceous or orange (honey-coloured), ±shiny, without hairs, roundish to shortly ellipsoid or rarely irregular in form, 60–110 µm diam.; bulbils externally without specialized cells, cells in surface view polyhedral, smooth 6–12 µm diam.; bulbils internally composed of strongly adherent, more or less roundish to ellipsoid or polyhedral cells separating only with difficulty, 6–12 µm diam., clamps not observed; large, orange-coloured oil drops are present in these cells and emerge from them when examined in lactophenol cotton blue; agglomerations of small crystals visible in polarized light present on the surface of all specimens examined.

Notes. This species is rather well-characterized by the yellowish to orange, honey-coloured bulbils, 60–110 µm diam. It was originally described from North America on *Flavoparmelia baltimorensis*. Morphologically similar populations from South America on *Parmotrema* need more study: sequences from both hosts group together in phylogenetic analyses (Lawrey et al. 2007), but form two rather long branches on a short, unsupported branch, leaving some doubt as to whether they are really conspecific.



Burgella flavoparmeliae



Burgella flavoparmeliae, USA, Buck 30461. Bulbil in lactophenol cotton blue. Scale bar: 20 µm.

Ecology and hosts. On the thallus of *Flavoparmelia baltimorensis* and *Parmotrema* sp. Bulbils are frequently slightly immersed in the host thallus, with the host cortex sometimes a little raised around them, and some leave distinct holes in the cortex when removed.

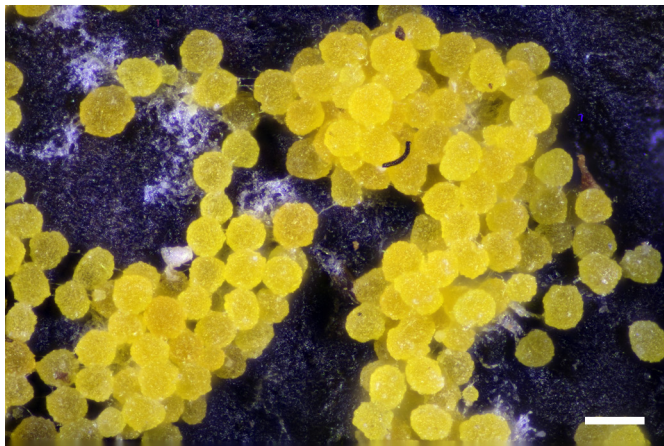
Distribution. North America (USA: North Carolina, Missouri, Oklahoma) and South America (Bolivia; Ecuador).

References. Diederich & Lawrey 2007, Diederich et al. 2014a, Lawrey et al. 2007.

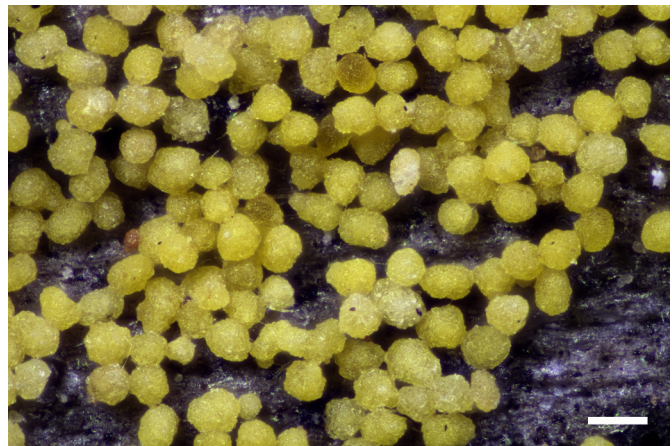
Burgella lutea Diederich, Capdet, A. I. Romero & Etayo

in Diederich et al., *Lichenologist* 46: 343 (2014). *Type:* Bolivia, Dept. La Paz, Prov. Franz Tamayo, near Apolo village, small valley amongst meadows, 14°50'15"S, 68°26'58"W, 1430 m, pre-Andean Amazon forest, on corticolous lichens, 17 May 2011, J. Etayo 27623, A. Flakus, M. Kukwa & U. Schiefelbein (LPB – holotype; BR, hb. Etayo – isotypes).

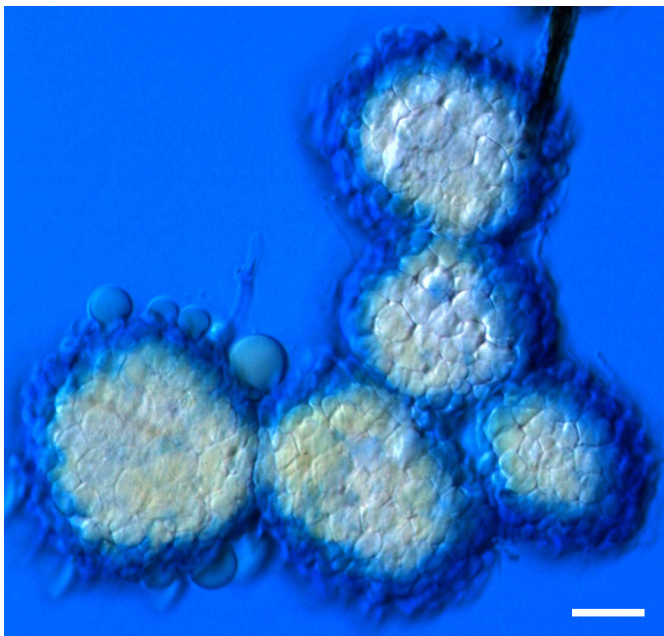
Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed or agglomerated bulbils overgrowing lichen thalli, ascomycete perithecia or rotten woody parts of palms. *Mycelium* superficial, 3.0–3.5 µm thick, with clamps. *Bulbils* superficial, yellow to orange-yellow, without hairs, surface at a high magnification (×50) rather rough, with individual convex cells slightly distinguishable, slightly shiny, roundish to shortly ellipsoid, 50–80 µm diam.; bulbils externally without specialized cells; cells in surface view polyhedral, smooth, mainly 7–15 µm diam.; bulbils internally composed of strongly adherent,



Burgella lutea, Bolivia, holotype. Bulbils on corticolous lichens. Scale bar: 100 µm.



Burgella lutea, Argentina, Capdet 51690. Non-lichenicolous bulbils on *Butia yatay*. Scale bar: 100 µm.



Burgella lutea, Argentina, isotype. Bulbils in lactophenol cotton blue, with emerging oil drops (left). Scale bar: 20 µm.

more or less roundish to ellipsoid or polyhedral cells, 7–15 µm diam., clamps not observed; large, orange-coloured oil drops are present in these cells and emerge from them when examined in lactophenol cotton blue; no crystals visible in polarized light.

Notes. The species is characterized by the abundant, yellow to orange-yellow bulbils, 50–80 µm diam., covering the substratum. *Burgella flavoparmeliae* differs in the slightly larger (60–110 µm diam.), honey-coloured bulbils that appear to be strictly lichenicolous over parmelioid lichens, on the thallus of which they leave distinct scar-like holes when removed.



Burgella lutea

Ecology and hosts. Lichenicolous over corticolous, sometimes necrosed thalli of *Sticta weigeli*, *Heterodermia* sp., *Hypotrachyna* sp. and cf. *Pertusaria* sp., or directly on the supporting bark; in the Argentinian material, not associated with lichens, but bulbils densely covering the rotten fallen foliar rachis and spathe of *Butia yatay* and also the ascomycete *Cannonia australis* developing on the spathe.

Distribution. South America (Argentina; [Bolivia](#)).

Reference. Diederich et al. 2014a.

BURGELLOPSIS Diederich & Lawrey

in Diederich et al., *Lichenologist* 46: 344 (2014). Type: *B. nivea* Diederich & Lawrey

Molecular data: yes (T, L). **Number of species:** 1–0–0.

Notes. As the genus is currently monospecific, no generic description is given here. In the phylogenetic analysis by Diederich et al. (2014a), this species is sister to the clade containing *Burgella*, but with very low support.

Burgellopsis nivea Diederich & Lawrey

in Diederich et al., *Lichenologist* 46: 344 (2014). *Type*: Great Britain, Scotland, VC 82, East Lothian, Lammermuir Hills, Lamb Burn, on small stone in scree, over sterile, sorediate, crustose lichen, 36(NT)604.630, 350 m, 6 Apr. 2006, A. M. & B. J. Coppins 21845 (E – holotype).

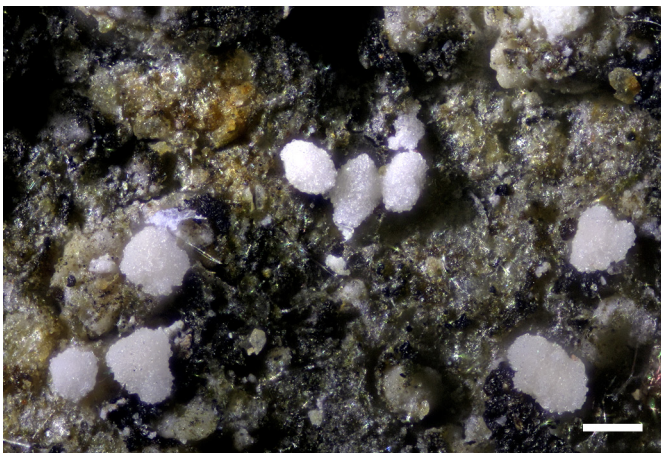
Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed bulbils overgrowing lichen thalli. *Mycelium* not observed. *Bulbils* superficial, white, without hairs, surface at a high magnification ($\times 50$) rather rough, with individual convex cells slightly distinguishable, slightly shiny, roundish to shortly ellipsoid or rarely irregular in form, 100–220 μm diam.; bulbils externally without specialized cells, cells in surface view polyhedral, smooth, mainly 8–15 μm diam.; bulbils internally composed of indistinctly catenate, more or less roundish to ellipsoid or polyhedral cells, 8–15 μm diam., clamps not observed; no oil droplets emerging from cells when observed in lactophenol cotton blue; no crystals visible in polarized light.

Notes. This species differs from *Burgella* by the absence of any yellowish or ochraceous pigments and consequently the absence of yellow oil drops emerging from cells in microscopical preparations, and by the distinctly larger bulbils (60–110 μm in *B. flavoparmeliae* and 50–80 μm in *B. lutea*). *Burgoa angulosa*, another species producing white bulbils, differs by the more irregular, often angulose bulbils, and anatomically by the distinctly catenate arrangement of cells and the presence of clamps.

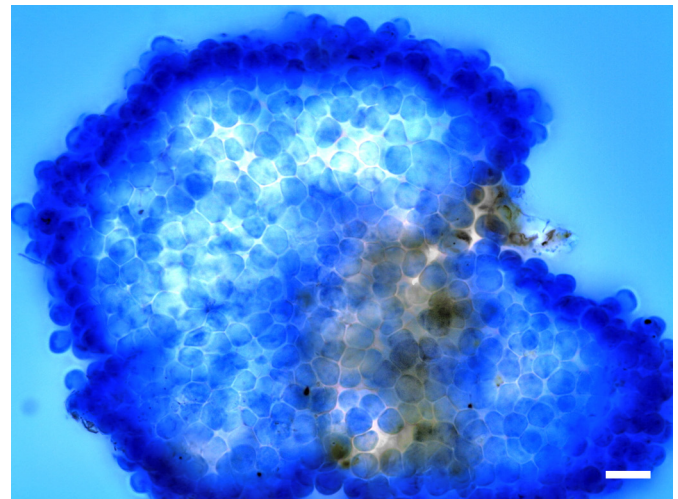
Ecology and host. On the thallus of a **sterile, crustose saxicolous lichen**.

Distribution. Europe (**UK: Scotland**).

References. Diederich et al. 2014a.



Burgellopsis nivea, Scotland, holotype. Bulbils over sterile saxicolous lichen. Scale bar: 200 μm .



Burgellopsis nivea, Scotland, holotype. Bulbil in lactophenol cotton blue. Scale bar: 20 μm .



Burgellopsis nivea

BURGOA Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 354 (1938). *Type*: *B. verzuoliana* Goid.

Molecular data: yes (T, L). *Number of species*: 2–0–0 (7).

Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed or agglomerate bulbils, saprotrophic or lichenicolous. *Mycelium* composed of hyphae with clamp connections. *Bulbils* roundish, ellipsoid or elongate, without hairs, externally without specialized cells, internally composed of elongate, straight or curved, rarely ramified, septate hyphae, septa with clamp.

Notes. This asexual, bulbil-forming genus is closely related to the sexual species *Sistotrema eximum* (H. S. Jacks.) Ryvarden & Solheim and *S. sernanderi* (Litsch.) Donk, (Lawrey et al. 2007), but not to the generic type *S. confluens*. A detailed description of the genus *Burgoa*, the delimitation with reference to other genera and the mode of development of bulbils are given by Weresub & LeClair (1971).

Ecology. Over decaying plant tissues and degraded plant products, especially timber, also lichenicolous.

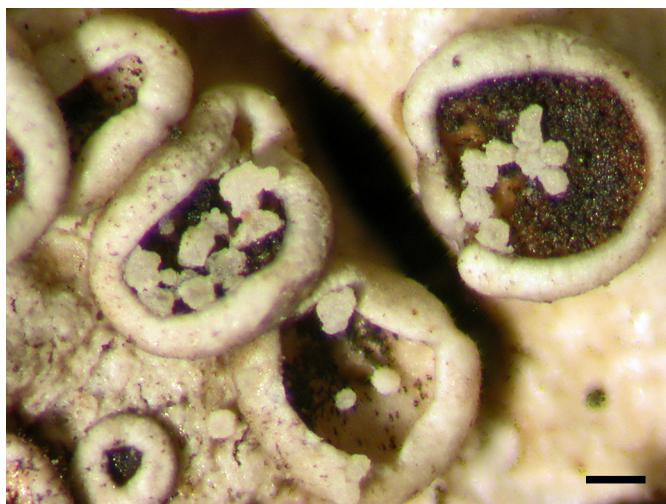
***Burgoa angulosa* Diederich, Lawrey & Etayo**

in Diederich & Lawrey, *Mycol. Progress* 6: 66 (2007). *Type*: Spain, Huesca, Panticosa, balneario de Panticosa, in garden, on *Acer*, on *Physcia aipolia*, 11 Oct. 1998, J. Etayo 16256 (MA – holotype).

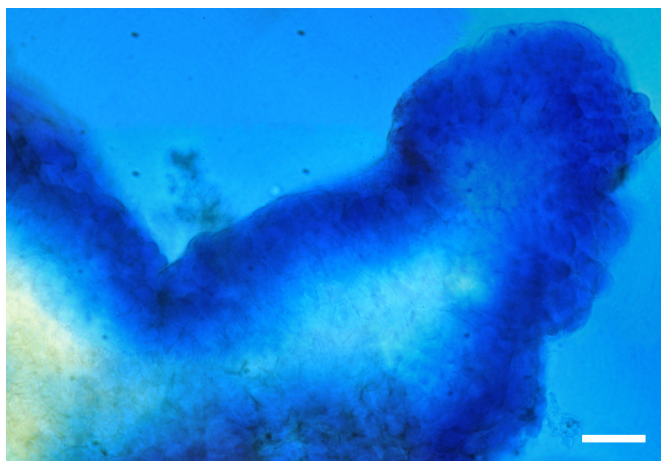
Basidiomata and *conidiomata* unknown. *Colonies* appearing as dispersed or agglomerate bulbils overgrowing lichen thalli or apothecia. *Mycelium* absent in most specimens; septa with clamp connections. *Bulbils* usually lichenicolous, superficial, dispersed or in short straight or ramified chains of several bulbils, irregular in form, roundish, ellipsoid or elongate, surface uneven, often slightly to distinctly angular, whitish to slightly translucent, matt, without hairs, $100\text{--}250 \times 80\text{--}160 \mu\text{m}$; bulbils externally without specialized cells, cells appearing in surface view as roundish, $6\text{--}9 \mu\text{m}$ diam.; bulbils internally composed of elongate,



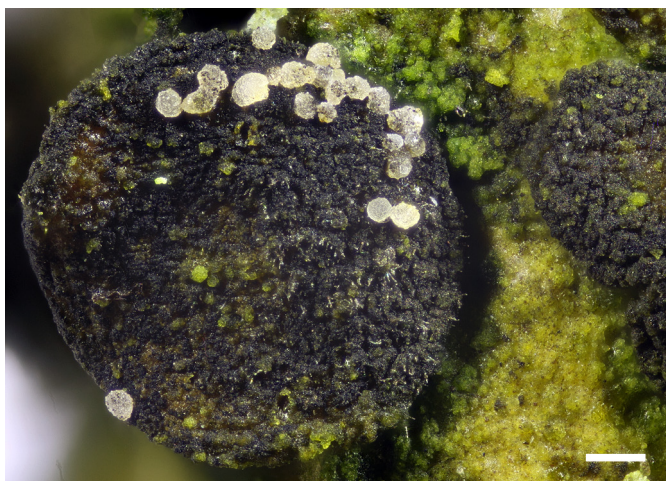
Burgoa angulosa, Luxembourg, Diederich 19585. Bulbils on *Physcia tenella*. Scale bar: 200 μm .



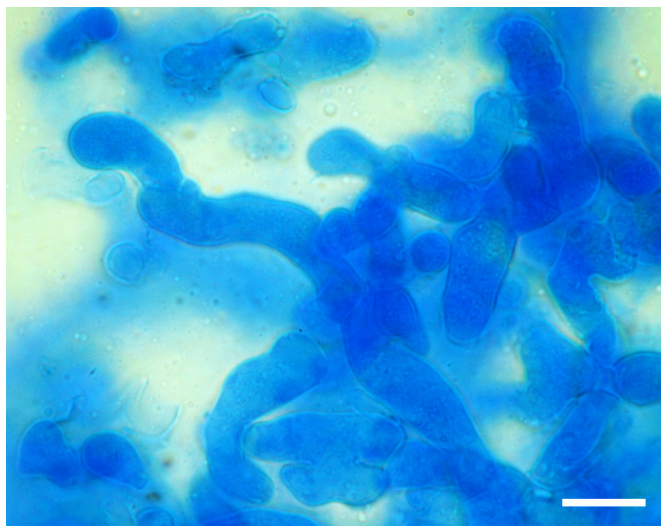
Burgoa angulosa, Spain, holotype. Bulbils on *Physcia aipolia*. Scale bar: 200 μm .



Burgoa angulosa, Spain, holotype. Bulbil in lactophenol cotton blue. Scale bar: 10 μm .



Burgoa angulosa, France, Diederich 17718. Bulbils over dead apothecia of *Xanthoria parietina*. Scale bar: 200 μm .



Burgoa angulosa, Spain, holotype. Squashed bulbil in lactophenol cotton blue. Scale bar: 10 μm .



European distribution of *Burgoa angulosa*

straight or curved, rarely ramified, septate hyphae, 4.5–11 μm thick, individual cells 5–30 μm long, cell wall c. 0.5 μm thick, septa with clamps; crystals absent in most specimens (polarized light), rarely abundant on the surface of the bulbils.

Notes. *Burgoa angulosa* is characterized by whitish bulbils with an irregular shape and an often angular surface, no specialized external cells and elongate internal hyphae.

Ecology and hosts. On the thallus and/or apothecia of *Physcia aipolia*, *P. tenella*, *Lecanora* sp., *Lobarina scrobiculata*, *Peltigera didactyla*, *Scytinium lichenoides*, *Xanthoria parietina*, etc., also frequent in mixed epiphytic vegetations of granulose lichen thalli (e.g., *Bacidina* spp.), mosses or algae, or directly on the bark, possibly after the host lichen has been killed. The species may not be obligately lichenicolous, but more studies are needed to ascertain this.

Distribution. Europe (Belgium; France; Hungary; Italy; Luxembourg; Netherlands; Poland; [Spain](#); UK: Wales) and North America (North Carolina).

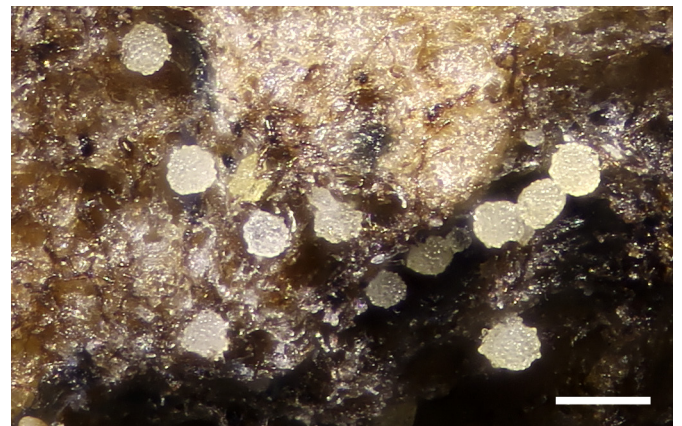
Additional specimens examined. **Germany:** *Bayern*: Mehlmäisel, 2010, Eichler & Cezanne 8194 (BR); *Hessen*, Kühkopf, 2009, Eichler & Cezanne (BR). *Rheinland-Pfalz*: Ringels-Berg W von Frankweiler, 2012, Eichler & Cezanne 8549 (BR). **Netherlands:** Noord-Brabant, Aalst, churchyard, on *Peltigera didactyla*, 2012, van den Boom 48271 (herb. van den Boom). **Poland:** Beskid Niski Mts, Magurski National Park, 49°27'41"N, 21°32'23"E, 2009, Kukwa (UGDA L-15834, BR). **USA:** *North Carolina*: Pender Co., Holly shelter Game Land, Trumpeter Swamp N of Blossom Creek, S of Tram/trumpeter Road 2.5 mi SW of jct with Lodge Road, 34°25'28"N, 77°44'15"W, 25 ft, on *Acer rubrum*, over hepatic, 2013, Harris 59325-A (NY).

References. Diederich & Lawrey 2007, Lawrey et al. 2007 [Bielecyk et al. 2020, Brackel & Puntillo 2016, Van den Broeck et al. 2012].

Burgoa moriformis Diederich, Ertz & Coppins

in Diederich & Lawrey, Mycol. Progress 6: 67 (2007). *Type:* Ireland, VC H33 (Fermanagh), Crom, Inisherk, 50 m, over moribund bryophytes and lichens on *Salix*, 12 July 1993, B. J. Coppins 15829 & A. M. O'Dare (E – holotype; BR – isotype).

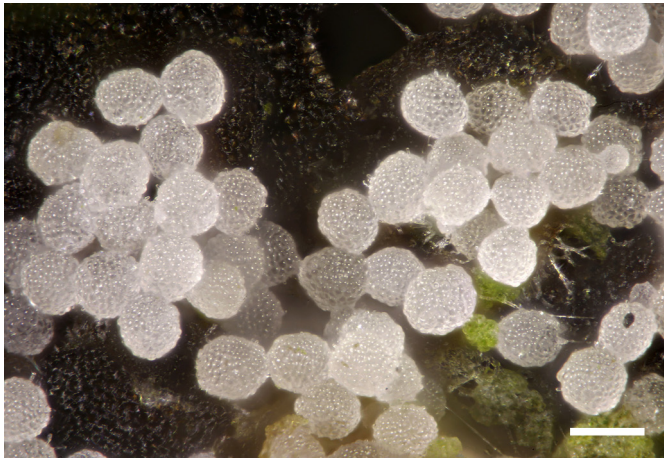
Basidiomata and *conidiomata* unknown. *Colonies* developing over corticolous lichens, several cm diam., appearing as numerous bulbils. *Mycelium* immersed, with clamps. *Bulbils* superficial, dispersed or indistinctly in short chains or agglomerations of several bulbils, white, with a moriform, slightly shiny surface, without hairs, translucent when dry, roundish to shortly ellipsoid, 35–65 μm diam.; bulbils externally moriform, appearing as an agglomeration of hyaline, subspherical, ballooned, smooth cells of 7–12 μm diam.; bulbils internally composed of catenate, subspherical to ellipsoid cells of 7–12 μm diam., 12–18 μm long, septa with small, often poorly distinct clamps, crystals absent (polarized light).



Burgoa moriformis, Ireland, isotype. Bulbils on unidentified dying lichen thallus. Scale bar: 100 μm .



Burgoa moriformis, France, Pinault. Bulbils on dying thallus of *Physcia*. Scale bar: 200 μm .



Burgoa moriformis, Belgium, Clesse. Bulbils over corticolous bryophytes. Scale bar: 100 µm.

Notes. *Burgoa moriformis* is characterized by small, white, shiny bulbils entirely composed of subspherical, ballooned cells.

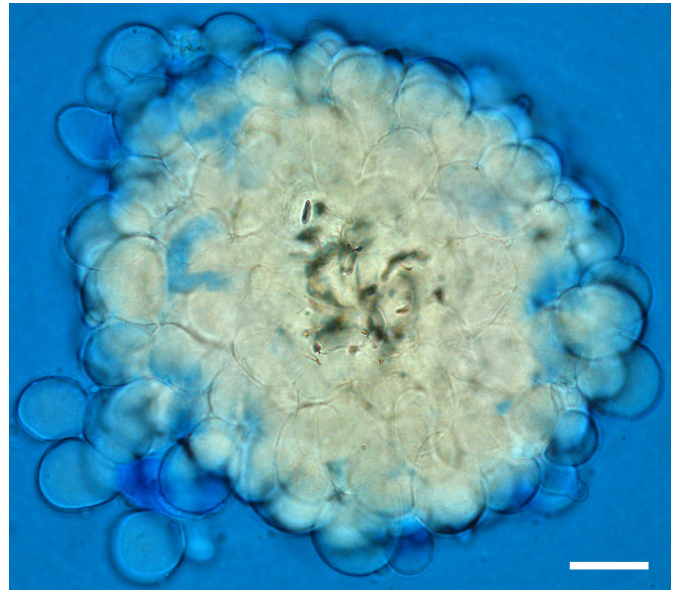
nuLSU sequences from the type place the species in a clade that also comprises *Gloeotulasnella cystidiophora* (Höhn. & Litsch.) Jülich and an uncultured mycorrhiza. More sequences will be needed to confirm the position of *Burgoa moriformis*, and also to identify to which family this clade belongs, the *Hydnaceae* or the *Tulasnellaceae*. The species was therefore only provisionally described within *Burgoa*.

Ecology and hosts. This rarely collected species is known from thalli and apothecia of corticolous *Lecanora*, *Physcia*, *Xanthoria* and [unidentified dead lichens](#), also invading neighbouring thalli, bark or liverworts. Infected thalli of *Physcia* are dying, suggesting a virulent parasite on this host genus, while thalli of *Xanthoria* covered by bulbils are in good health.

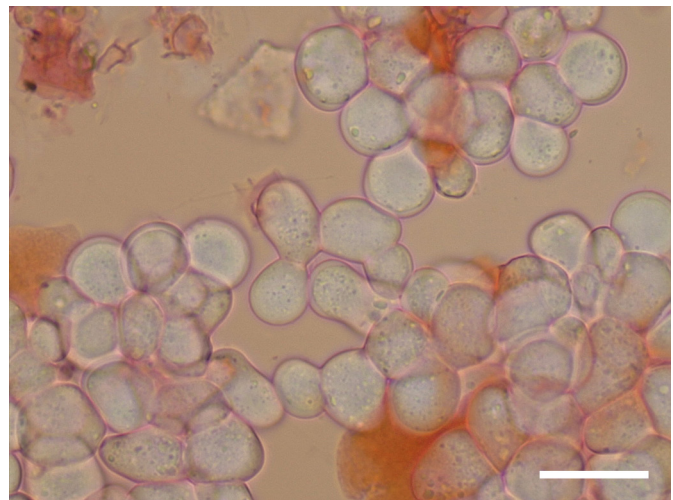
Distribution. Europe (Belgium; France; [Ireland](#)).



Burgoa moriformis



Burgoa moriformis, Ireland, holotype. Slightly squashed bulbil in lactophenol cotton blue. Scale bar: 10 µm.



Burgoa moriformis, France, Pinault. Squashed bulbil in ammoniacal Congo red. Photo: Pinault. Scale bar: 20 µm.

Additional specimens examined. Belgium: Dourbes, on leaves of *Frullania dilatata* and *Radula complanata*, 2022, Clesse (BR).

France: Puy-de-Dôme: Saint-Ours-les-Roches, Beauregard, 900 m, sur thalles corticales de *Lecanora*, *Physcia*, *Xanthoria*, 2020, Pinault (BR).

References. Diederich & Lawrey 2007

MINIMEDUSA Weresub & P. M. LeClair

Can. J. Bot. 49: 2210 (1971). *Type: M. polyspora* (Hotson) Weresub & P. M. LeClair

Molecular data: yes (T, L). *Number of species:* 1–0–0 (3).

Basidiomata and *conidiomata* unknown. Colonies appearing as dispersed or agglomerate bulbils, saprotrophic or lichenicolous. *Mycelium* composed of hyphae with clamp connections. *Bulbils* roundish or reduced with few cells, without or with external hairs, internally composed of globose cells.

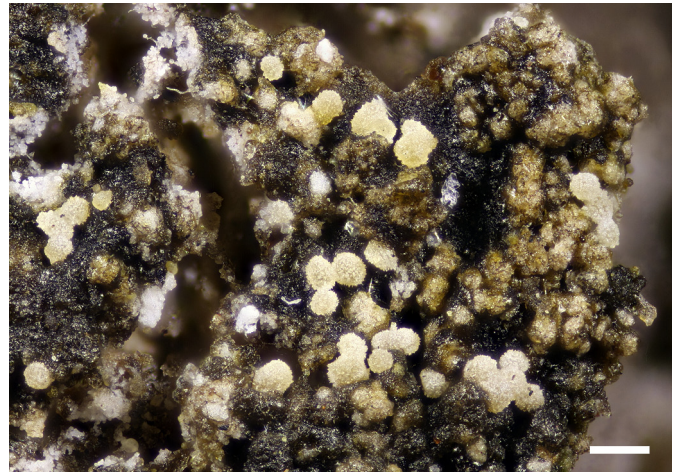
Notes. Phylogenetic results (Lawrey et al. 2007) place the only lichenicolous species in a clade with *Minimedusa polyspora*, *M. obcoronata* (B. Sutton, Kuthub. & Muid) Diederich & Lawrey and *Sistotrema coronilla* (Höhn.) Donk.

Ecology. The type species has been isolated from soil, straw, old paper, oat seed and cotton flowers, while *M. obcoronata* has been described from leaves. One species is lichenicolous.

Minimedusa pubescens Diederich, Lawrey & Heylen

in Diederich & Lawrey, *Mycol. Progr.* 6: 71 (2007). *Type:* Belgium, prov. Antwerp, Heist-op-den-Berg, comm. Booischot, medieval park “Hof ter Laken”, on *Frangula alnus*, on *Scliosporum chlorococcum*, 23 May 2003, O. Heylen L03/117 (BR – holotype; BR, E, LG, NY, UPS, herb. Heylen-Walraevens – isotypes).

Basidiomata and *conidiomata* unknown. Colonies appearing as whitish, \pm rounded areas over poorly distinct, corticolous, lichenized crusts, several cm diam., with numerous bulbils covering the inner, necrosed parts of the host, externally with poor or abundant mycelial growth. *Mycelium* hyaline, \pm straight, 2.5–3.5 μm thick, wall c. 0.5 μm thick, septa with clamps. *Bulbils* superficial, dispersed or in straight or ramified chains of several bulbils, roundish to ellipsoid, pubescent,



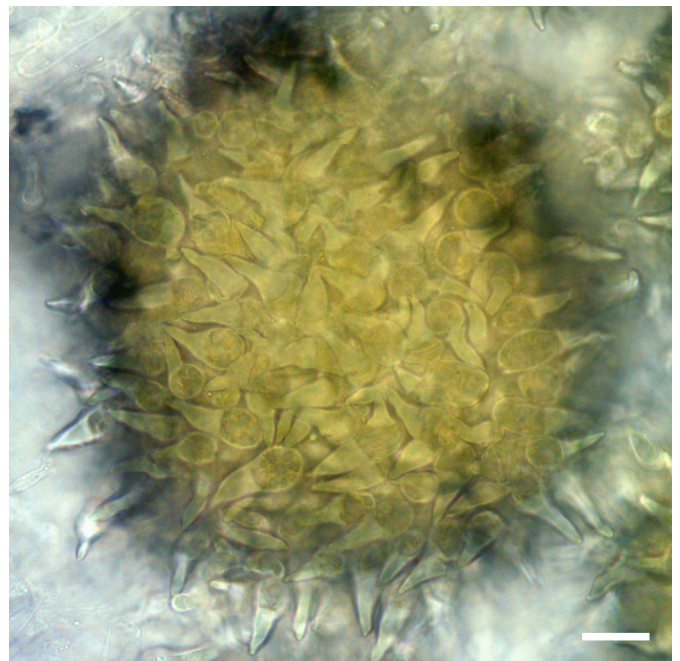
Minimedusa pubescens, Belgium, isotype. Bulbils on *Scliosporum chlorococcum*. Scale bar: 200 μm .

whitish or pale yellowish to brownish white (exceptionally reddish), mainly due to the whitish ‘hairs’, pale brownish and slightly translucent when ‘hairs’ abraded, 60–100 μm diam.; bulbils externally composed of radially oriented, hyaline ‘hairs’ with a more or less pointed apex and a thin to relatively broad base, sometimes almost ampulliform, 15–21 \times 3–8 μm , thin-walled, except at the apex, where the wall is up to 6 μm thick; bulbils internally composed of subglobose cells of 5.5–12 μm diam., crystals absent (polarized light).

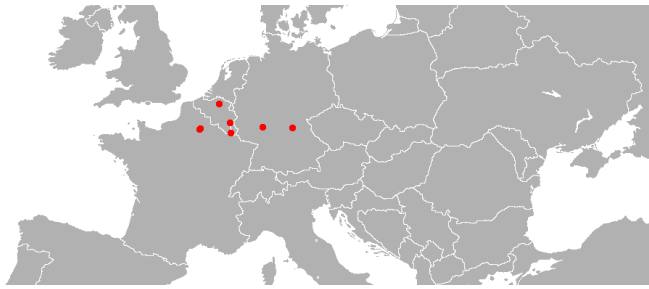
Notes. This species is distinguished by pale, roundish to ellipsoid bulbils covered by characteristic aseptate ‘hairs’



Minimedusa pubescens, Belgium, holotype population. Colony over *Scliosporum chlorococcum*. Modified from Diederich & Lawrey (2007).



Minimedusa pubescens, Belgium, ex-type culture. Bulbil in water. Scale bar: 10 μm .



Minimedusa pubescens

with a swollen base, a pointed apex and an apically thickened cell wall.

Ecology and hosts. This species is frequently overgrowing corticolous lichens (*Bacidina* spp., *Candelariella refl-exa*, *Melanohalea exasperatua*, *Physcia tenella*, *Scoliciosporum chlorococcum*), sometimes killing their thalli, but might be only facultatively lichenicolous.

Distribution. Europe (Belgium; France; Germany; Luxembourg).

References. Diederich & Lawrey 2007, Lawrey et al. 2007 [Brackel 2014, Cezanne & Eichler 2015, Van den Broeck et al. 2012, 2017].

NEOBURGOA Diederich, E. Zimm. & Lawrey

in Lawrey et al., *Bryologist* 119: 344 (2016). Type: *N. freyi* Diederich, E. Zimm. & Lawrey

Molecular data: yes (T, L). **Number of species:** 1–0–0.

Notes. As the genus is currently monospecific, no generic description is given here.

Neoburgoa freyi Diederich, E. Zimm. & Lawrey

in Lawrey et al., *Bryologist* 119: 344 (2016). Type: Switzerland, Kanton Wallis, Oberwald, Grimselpass, westlich vom Totensee (Swiss

grid 6680600, 1560800), 2200 m, alpinen Rasen, Windkantenrasen (Elynion), Silikat, on *Cladonia rangiferina*, Sept. 2015, E. Zimmermann LF1256 (G – holotype; BR – isotype).

Basidiomata and conidiomata unknown. **Colonies** appearing as dispersed bulbils overgrowing the thallus of the hosts. **Mycelium** not observed. **Bulbils** entirely immersed when young, later becoming superficial, pale yellow to orange, without hairs, surface smooth, with no individual cells visible, roundish to ellipsoid or irregular in form, 150–300(–700) µm diam.; bulbils externally without specialized cells, covered by an amorphous layer 3–15 µm thick; bulbils internally composed of more or less roundish to ellipsoid or polyhedral cells separating rather easily (with pressure on the cover glass), 10–20 µm diam.; cell wall 0.8–1.7 µm thick; clamps not observed; content of cells occasionally yellowish, with yellow oil droplets emerging when observed in lactophenol cotton blue; no crystals visible in polarized light.

Notes. *Neoburgoa freyi* is mainly characterized by the yellow to orange bulbils that are first immersed and then become superficial on the thallus of terricolous macrolichens. *Burgella* species are similar in colour, but bulbils are much smaller and superficial from the beginning: those of *B. flavoparmeliae* are honey-colored, 60–110 µm diam., while those of *B. lutea* are yellow to orange yellow, 50–80 µm diam. *Erythricium aurantiacum*, a species belonging to the *Corticaceae*, is distinguished by orange (carrot red) bulbils. Microscopically, *N. freyi* is distinguished from most lichenicolous, bulbilliferous fungi by the roundish to ellipsoid or polyhedral cells with a particularly thick wall.

Ecology and hosts. On the thallus of *Cladonia rangiferina*, *C. stellaris* and *Flavocetraria nivalis*.

Distribution. Europe (Austria; Russia; Switzerland).

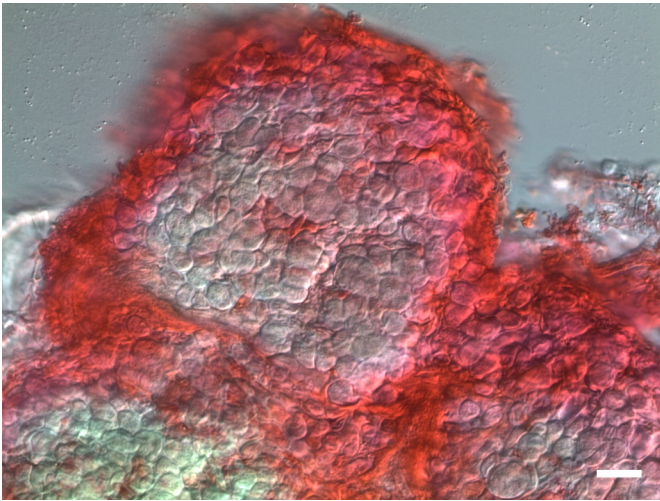
References. Lawrey et al. 2016 [Berger & Zimmermann 2021, Zhurbenko & Pino-Bodas, Zimmermann 2020].



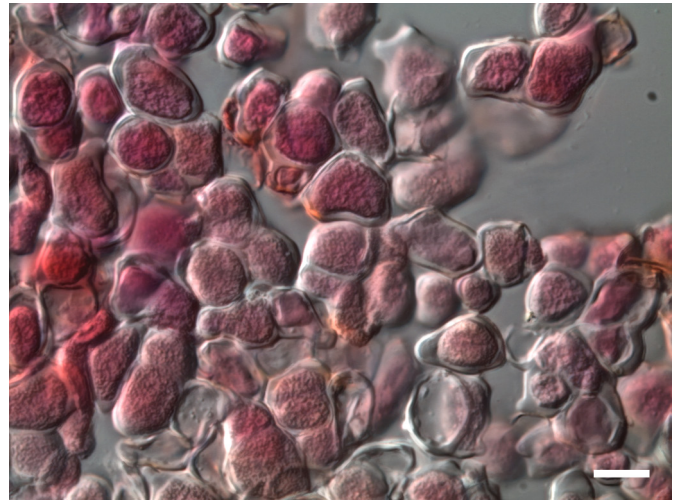
Neoburgoa freyi, Switzerland, holotype. Bulbils on *Cladonia rangiferina*. Scale bar: 200 µm.



Neoburgoa freyi, Switzerland, Zimmermann 4455. Bulbils on *Cetraria nivalis*. Scale bar: 200 µm.



Neoburgoa freyi, Switzerland, holotype. Bulbil in Congo red + phloxine. Scale bar: 20 µm.



Neoburgoa freyi, Switzerland, holotype. Squashed bulbil in Congo red + phloxine. Scale bar: 10 µm.



Neoburgoa freyi



Parmeliicida pandemica, France, holotype. Bulbils on the necrosed thallus of *Parmelia saxatilis*, showing mycelium attaching young bulbils to the host thallus. Scale bar: 200 µm.

***PARMELIICIDA PANDEMICA* Diederich, F. Berger, Etayo & Lawrey, gen. et sp. nov.**

Diagnosis: Characterized by dark reddish brown, superficial licheniculous bulbils 150–270 × 120–200 µm, no specialized external cells, and roundish to ellipsoid internal cells 8–17 µm diam.

Etymology: From *Parmelia* (the most common host lichen of the type species), the Latin suffix *-cida* (one who kills), and the Latin adjective *pandemicus* (pandemic).

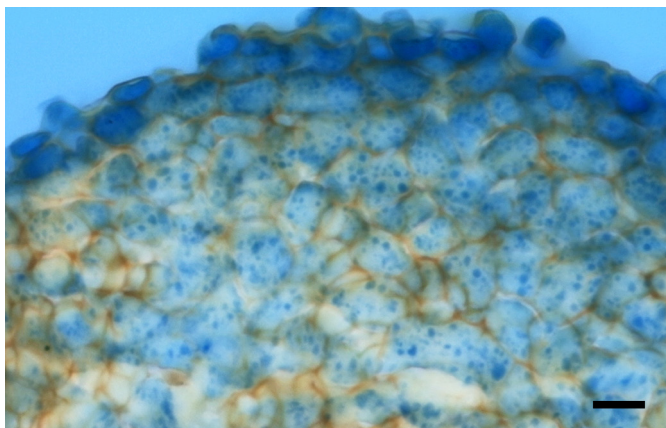
Type: France, Pyrénées-Atlantiques, à 20 km au SE de Saint-Jean-Pied-de-Port, forêt d'Iraty, à 500 m au S du Chalet Pedro, 43.0313°N (±200 m), 1.0796°W (±100 m), 1000–1030 m, on *Fagus*, on *Parmelia saxatilis* and *P. sulcata*, 3 Sept. 2015, P. Diederich 18144 (BR – holotype; GMUF – isotype).

Mycobank: MB844615 (genus) and MB844616 (species)

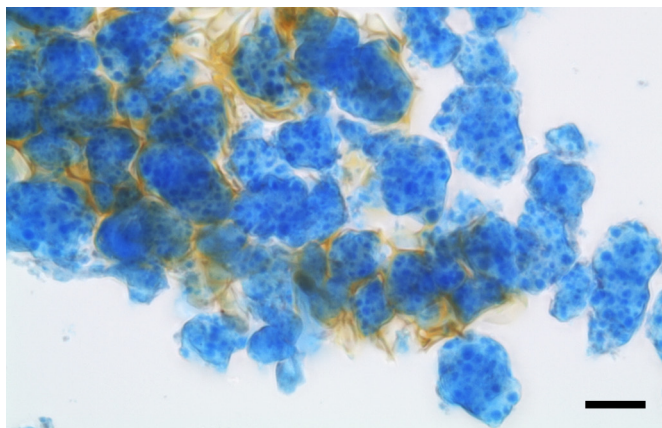
Molecular data: yes (T, L). **Number of species:** 1–0–0.



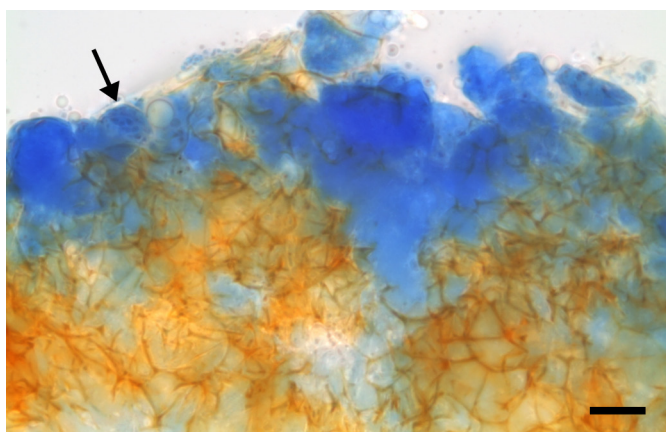
Parmeliicida pandemica, Austria, Berger 35564. Bulbils on the necrosed thallus of *Parmelia sulcata*. Scale bar: 1 mm.



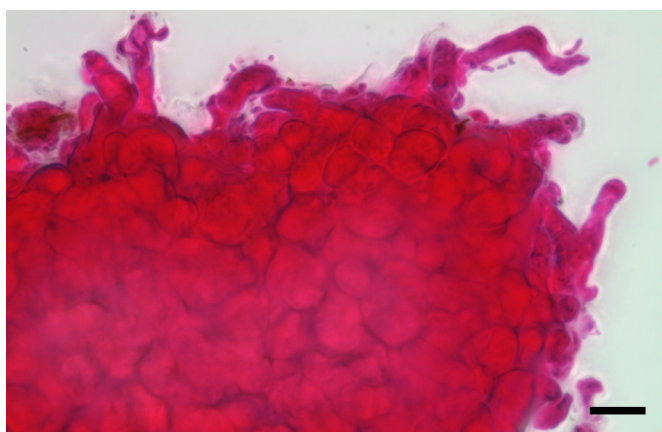
Parmeliicida pandemica, France, holotype. Section through bulbil in lactophenol cotton blue. Scale bar: 10 µm.



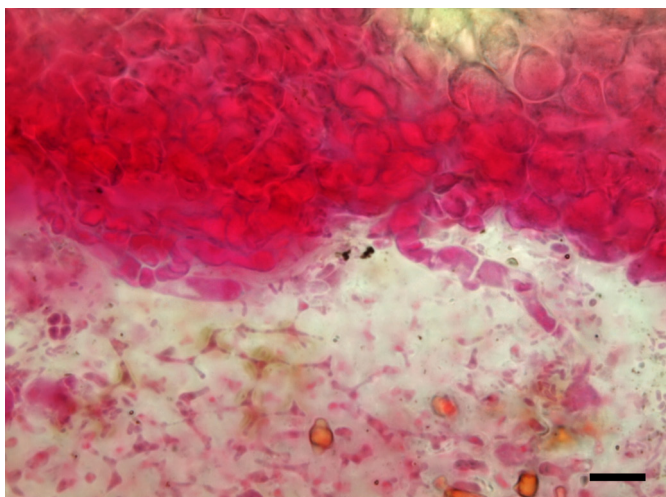
Parmeliicida pandemica, France, holotype. Squashed bulbil in lactophenol cotton blue showing cyanophilous granulation of dead cell content. Scale bar: 10 µm.



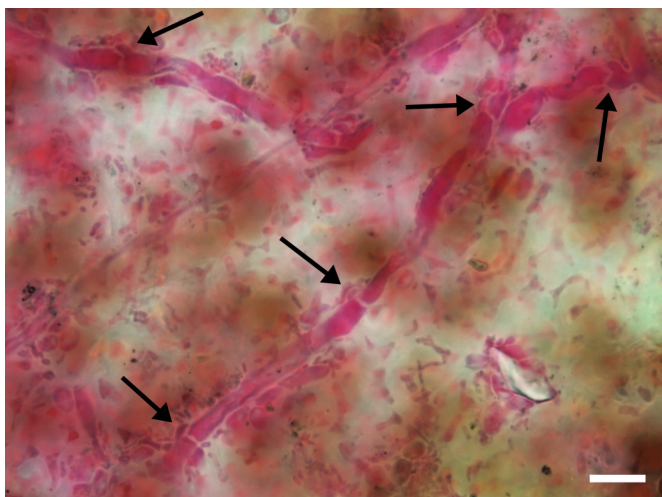
Parmeliicida pandemica, Austria, Berger 35564. Squashed bulbil in lactophenol cotton blue with cyanophilous granulation in one cell (arrow). Scale bar: 10 µm.



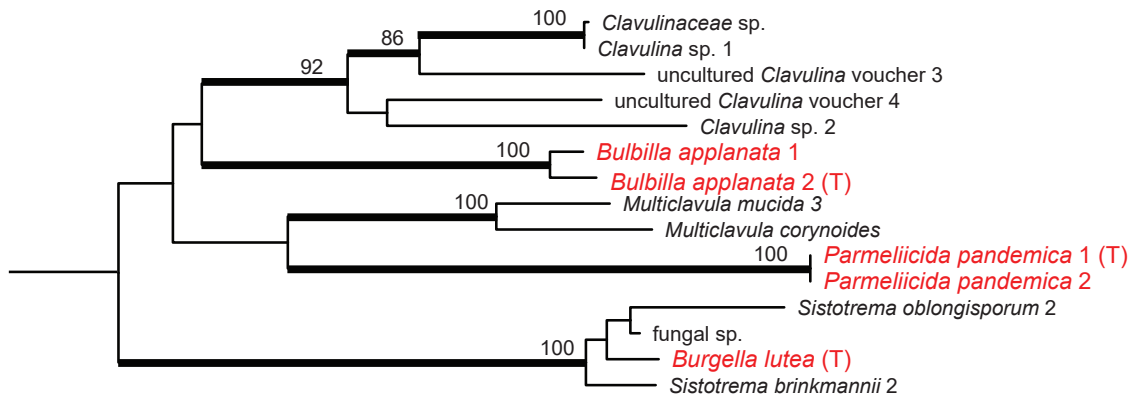
Parmeliicida pandemica, France, holotype. Bulbil in phloxine, with superficial hyphae that may attach laterally to the host thallus. Scale bar: 10 µm.



Parmeliicida pandemica, France, holotype. Bulbil in phloxine, showing the region of attachment to the host thallus. Scale bar: 10 µm.



Parmeliicida pandemica, France, holotype. Hyphae with clamps (arrows) in the thallus of *Parmelia saxatilis*, in phloxine. Scale bar: 10 µm.



Portion of the ITS phylogeny of the *Cantharellales* obtained under ML, showing the position of lichenicolous species in *Burgella* and *Bulbilla*, and the new species *Parmeliocida pandemica*, all indicated in red. Internal branches in boldface indicate posterior probabilities ≥ 0.95 and numbers are ML-BS values ≥ 70 . Type specimen of lichenicolous species are indicated with ‘(T)’.

Basidiomata and *conidiomata* unknown. Colonies appearing as dispersed or slightly agglomerated bulbils overgrowing lichen thalli or more rarely apothecia. *Mycelium* arising superficially, but most commonly laterally from young bulbils and attaching them to the host thallus; immersed mycelium present below bulbils; hyphae 3–6 μm thick; septa all with clamps. *Bulbils* superficial, slightly immersed in the host thallus, not leaving scars when removed, reproducing laterally by budding and thus sometimes irregularly catenate, when young yellowish brown, quickly turning dark reddish brown, slightly translucent and shiny, without hairs (but with superficially arising mycelium when young), surface at a high magnification slightly rough because of the convexity of the individual outer cells, roundish to more frequently ellipsoid, 150–270(–400) \times 120–200 μm , sometimes distinctly flattened, 100–170 μm tall, basally constricted; bulbils externally without specialized cells, although outer cells may be flattened in section view, cells in surface view roundish to ellipsoid or polyhedral, sometimes more elongate, smooth, mainly 8–11 μm diam., wall yellowish brown, 1–2.5 μm thick; bulbils internally composed of more or less adherent, roundish to ellipsoid cells separating only with difficulty, 8–17 μm diam., wall yellowish brown, clamps not observed; cell content of old herbarium specimens (rarely of freshly collected specimens) with a cyanophilous (dark blue in lactophenol cotton blue) granulation, granules 1–2.5 μm diam.; colourless oil droplets emerge from bulbil cells of freshly collected specimens when examined in lactophenol cotton blue; crystals not observed in polarized light.

Notes. The new taxon differs from other bulbilliferous *Cantharellales* species and genera by the relatively large and dark reddish brown superficial bulbils confined to *Parmelia* thalli. The cells of old herbarium specimens contain a cyanophylous granulation, which is rarely observed in



Parmeliocida pandemica

fresh specimens. In our phylogenetic analyses, the species appeared as closely related to the lichenicolous genera *Bulbilla* and *Burgella*, to the lichenized genus *Multiclavula* and to the mainly ectomycorrhizal genus *Clavulina*, although most main branches had a low support.

The epithet refers to the COVID-19 pandemic, as the species has been discovered and recognized as new by F. B. in the park of a rehabilitation centre where he recovered from a severe infection.

Ecology and hosts. On the thallus and rarely the apothecia of corticolous *Parmelia saxatilis* and *P. sulcata* in forests and parklands, more rarely on *Cetrelia olivetorum* and *Menegazzia terebrata*. Entire host populations are rapidly killed and turn reddish brown, suggesting a virulent parasite.

Distribution. Europe (Austria; France; Spain).

Additional specimens examined. **Austria:** *Niederösterreich:* Bezirk Scheibbs, Wildnisgebiet Dürrenstein, Windischbachau, 47°45'37"N, 15°00'04"E, 665 m, Grauerlenwald, on *Parmelia sulcata*, 2021, Berger 35701 (herb. Berger); *ibid.*, on *Cetrelia olivetorum*, Berger 35700 (herb. Berger); *Bezirk Lilienfeld*, St. Aegydam Neuwalde, Urwald "Lahnsattel", 47°46'17"N, 15°31'14"E, 940 m, on *Menegazzia terebrata*, 2021, Berger 35911 (herb. Berger). *Oberösterreich:* Bez. Steyr Land, Weyer, Rehazentrum,

Park, 47°51'26"N, 14°40'53"E, 520 m, on *P. sulcata*, 2021, Berger 35564 (GMUF, herb. Berger); Bez. Rohrbach, Rannatal, 48°29'28"N, 13°46'50"E, 340 m, on *P. sulcata*, 2022, Berger 36298 (herb. Berger). **Spain:** *Cataluña:* Lleida prov., Val d'Aran, Bausen, Carlac *Fagus*-wood, 42°50'24"N, 00°43'14"E, 1120 m, on *P. sulcata*, 2021, Etayo 33497 (herb. Etayo). *Navarra:* Orbaiceta, selva de Irati, 200 m ahead of refugio de Azpegui, track to the east, *Fagus* forest below Mendilaz, 43°01'30"N, 01°13'27"W, 1050 m, on *P. saxatilis*, 2018, Etayo 31407, 31414 (herb. Etayo); Oronoz-Mugaire, Bertizarana valley, Señorío de Bértiz, 200 m, *P. sulcata*, 2016, Etayo 29984 (herb. Etayo); *ibid.*, suspiro track, 43°09'48"N, 01°36'49"W, 200–300 m, on *P. saxatilis*, 2001, Etayo 23924 (herb. Etayo); Puerto de Lizarrusti between Etxarri-Aranaz and Beasain, oak park with large *Quercus robur*, 42°57'20"N, 2°05'00"W, 565 m, on *P. saxatilis* and *P. sulcata*, Etayo 31138 (herb. Etayo); Roncesvalles way to col de Lindux, 43°01'17"N, 01°17'46"W, 1110 m, on *P. sulcata*, 1992, Etayo 6013 (PAMP); S. Miguel de Aralar, carretera de ascenso NA-7510, entre km 8-9, 42°58'N, 1°58'W, 940 m, on *P. saxatilis*, 2018, Etayo 31726. *Pais Vasco:* Guipúzcoa, surroundings caserio del alto de Lizarrusti, *Fagus* wood with some dispersed oaks, 42°58'N, 2°06'W, 630 m, on *P. saxatilis* and *P. sulcata*, 2011, Etayo 27164 (BR, VIT, herb. Etayo); S^a de Aralar, track Lizarrusti to Otxondo, 42°58'N, 02°06'W, 650–900 m, on *P. saxatilis*, 2011, Etayo 27174 (herb. Etayo).

Acknowledgments

F. Berger and J. Etayo (description of *Parmeliicida pandemica*), R. Cezanne, B. Clesse, M. Eichler, M. Kukwa, P. Pinault, P. van den Boom (loan of specimens), P. Pinault (photo of *Burgoa moriformis*).

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *AGARICOMYCETES*

Order *CORTICIALES*

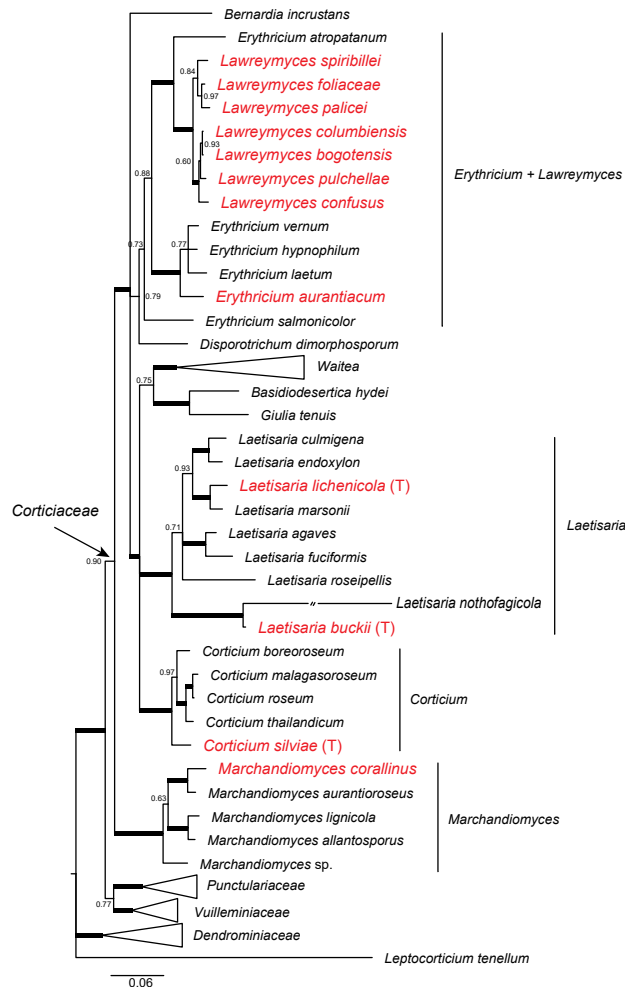
by P. Diederich, M. Ghobad-Nejhad & J. D. Lawrey

Diederich, P., M. Ghobad-Nejhad & J. D. Lawrey. 2022. Class *Agaricomycetes*, order *Corticiales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 71–81.

Introduction and phylogeny

Corticiales is a small order of about 17 genera and 86 species (He et al. 2019, Ghobad-Nejhad et al. 2021). The order consists of four families and the form of its basidiomata is simple, resupinate, corticioid, with low morphological differentiation. The three families *Vuilleminiaceae*, *Punctulariaceae*, and *Dendrominiaceae* are entirely white rot saprotrophs. *Corticaceae* is the largest family in this order and is nutritionally diverse, includ-

ing plant pathogens, saprotrophs, as well as lichenicolous and endolichenic species. The family is also noteworthy in its high tendency to form asexual structures, with several taxa lacking any known sexual forms (Ghobad-Nejhad et al. 2021). Currently, there are five lichenicolous species in the *Corticaceae* belonging to the genera *Corticium*, *Erythrimum*, *Laetisaria*, and *Marchandiomyces*, besides seven endolichenic species in *Lawreymyces*.



Phylogenetic relationships of *Corticiales* and *Corticaceae* based on nuLSU and ITS regions, showing the position of the lichenicolous species as well as the endolichen species in *Lawreymyces*. The tree was rooted with one member of *Russulales*. Thickened branches indicate PP ≥ 0.99. Type specimen of lichenicolous species are indicated with '(T)'.

Key to the lichenicolous species of *Corticiales*

- 1 Basidiomata present; bulbils present or absent
 - 2 Sterigmata 2 per basidium; basidiomata light pink to coral; basidiospores $14.5\text{--}18.5\text{--}(20.0) \times (8\text{--})10.5\text{--}12.5 \mu\text{m}$; clamps unknown; on *Physcia*..... *Laetisaria lichenicola* (78)
 - 2' Sterigmata 3–4 per basidium
 - 3 Basidiomata light orange (carrot red); bulbils abundant, concolorous; basidiospores $13\text{--}17.5\text{--}(18.5) \times 8\text{--}11.5\text{--}(13.5) \mu\text{m}$; clamps unknown; on *Physcia* and other lichens in Xanthorion communities *Erythricium aurantiacum* (74)
 - 3' Basidiomata pale pink; bulbils absent; basidiospores $(8\text{--})8.5\text{--}10.5\text{--}(14) \times (5.5\text{--})6\text{--}7.5\text{--}(8.5) \mu\text{m}$; septa with clamps; on *Thamnolia* *Corticium silviae* (72)
- 1 Basidiomata absent; bulbils present
 - 2 Bulbils orange (carrot red), $100\text{--}150 \mu\text{m}$ diam.; on *Physcia* and other lichens in Xanthorion communities, developing over the host thallus and almost entirely degrading it, with only the host cortex left..... *Erythricium aurantiacum* (74)
 - 2' Bulbils pale to pastel red; on various hosts
 - 3 Bulbils regularly subspherical to ellipsoid, $70\text{--}100 \mu\text{m}$ diam., composed of radially oriented, frequently branched and occasionally septate, thick-walled, smooth, hyaline, elongate hyphae, mainly $3\text{--}4 \mu\text{m}$ diam., some of which are apically 2–6-furcate *Laetisaria buckii* (77)
 - 3' Bulbils subspherical, ellipsoid or irregular with a slightly or distinctly angular surface, $80\text{--}250 \mu\text{m}$, composed of large, subspherical to elongate, catenate cells, mainly $5\text{--}12 \times 3.5\text{--}7 \mu\text{m}$, not visibly radiating and not apically furcate *Marchandiomyces corallinus* (80)
 - 1' Basidiomata, bulbils and mycelium unknown; endolichenic fungi known only from DNA sequences *Lawreymyces* (79)

AGARICOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: Agaricus L.

CORTICIALES K.-H. Larss.

in Hibbett et al., *Mycological Research* 111: 540 (2007). *Type: Corticium Pers.*

Corticiaceae Herter

Kryptogamen-Flora der Mark Brandenburg 6: 70 (1910), nom. cons. *Type: Corticium Pers.*

Notes. A synopsis, phylogeny and key to the genera of *Corticiaceae* have been published by Ghobad-Nehjad et al. (2021).

CORTICIUM Pers.

Neues Magazin für die Botanik 1: 110 (1794). *Type: C. roseum Pers.*
Molecular data: yes (T, L). *Number of species.* 1–0–0 (14).

Basidiomata usually pale pink, resupinate, effused, thin, firmly attached to the substrat. *Hyphae* hyaline, with clamps. *Hymenium* comprising one layer of basidia on vertically branching, thin-walled hyphae; dendrohyphidia

common; cystidia lacking; probasidia ellipsoid, thick-walled, with a basal clamp. *Basidia* clavate-cylindrical, thin-walled, sometimes with a basal lateral, ellipsoid probasidial bladder; sterigmata 3–4 per basidium. *Basidiospores* hyaline, smooth, aseptate, not repetitive, ellipsoid, pyriform or lacrimiform, with a prominent truncate apiculus.

Notes. Keys to the species of *Corticium* have been published by Duhem & Michel (2006) and Ghobad-Nehjad et al. (2021).

Ecology. Saprotrophic on wood, bryophytes or litter, one species lichenicolous.

Corticium silviae Diederich, E. Zimm. & Lawrey

in Diederich et al., *Bull. Soc. Nat. luxemb.* 120: 52 (2018). *Type:* Switzerland, Valais, Arolla, La Follisses, $46^{\circ}00'07''$ N, $7^{\circ}29'27''$ E, 2126 m, on *Thamnolia*, 5 June 2017, S. Feusi (G – holotype; BR – isotype).

Basidiomata pale pink, effused, thin, adnate, floccose, margin poorly distinct, up to 0.1 mm thick, reaching more than 1 cm diam. *Basal hyphae* hyaline, thin-walled, smooth, straight, 2–3 mm wide, septa with clamps. *Subhymenial hyphae* hyaline, thin-walled, smooth, 2–4 μm thick, septa with clamps. *Hymenium* comprising one layer of basidia on vertically branching, thin-walled hyphae, without crystals; dendrohyphidia common in hymenium, with few rather



Corticium silviae, Switzerland, holotype. Basidioma on *Thamnia*. Scale bar: 1 mm.

short side branches, 2–2.5(–3) μm diam., hyaline; cystidia and other sterile hymenial elements lacking; probasidia ellipsoid, 13–16 \times 6–7 μm , with a basal clamp. *Basidia* initially elongate, cylindrical, c. 38–60 \times 4–6 μm , sometimes with a basal lateral, ellipsoid probasidial bladder; when mature, clavate to suburniform, 30–45(–55) μm long, up to 8 μm in the upper part, exceptionally with a thin, transverse septum in the upper third; wall c. 0.5 μm thick; sterigmata 3–4 per basidium, to 4 μm long and 2 μm wide at the base, curved. *Basidiospores* hyaline, smooth, aseptate, not repetitive, pyriform or lacrimiform, one side frequently flattened or slightly concave, with a prominent truncate apiculus of 1–2 μm , (8–)8.5–10.5(–14) \times (5.5–)6–7.5(–8.5) μm , ratio length/breadth (1.1–)1.2–1.5(–1.6); wall c. 0.5 μm thick; germ tubes 1.5–2 μm thick. *Asexual stage*: conidial and bulbiferous morphs unknown.

Notes. The similar *Laetisaria lichenicola* is distinguished by pink to coral basidiomata, shorter basidia, c. 30–35 \times 9.5–12 μm when mature, 2 sterigmata per basidium, larger basidiospores, 14.5–18.5(–20) \times (8–)10.5–12.5 μm , and a different host selection (*Phycia adscendens* and *P. tenella*). *Erythricium aurantiacum* differs by orange basidiomata, the absence of clamp connections, shorter and broader basidia, 25–40 \times 12–15 μm , larger basidiospores,



Corticium silviae, Switzerland, holotype. Basidia and basidiospore. In Congo red + phloxine. Scale bar: 5 μm .

13–17.5(–18.5) \times 8–11.5(–13.5) μm , and a different ecology (on corticolous *Phycia*, *Xanthoria*, etc.).

Ecology and host. On the not or slightly damaged (swollen and bent) thallus of *Thamnia vermicularis*.

Distribution. Europe (Austria; [Switzerland](#); Italy).

References. Diederich et al. 2018 [Zimmermann & Berger 2021].

ERYTHRICIUM J. Erikss. & Hjortstam

Svensk Botanisk Tidskrift 64: 165 (1970). *Type*: *E. laetum* (P. Karst.) J. Erikss. & Hjortstam

= *Marchandiobasidium* Diederich & Schultheis, in Diederich et al., *Mycol. Res.* 107: 524 (2003). *Type*: *M. aurantiacum* Diederich & Schultheis

Molecular data: yes (T, L). *Number of species*: 1–0–0 (6).

Basidiomata resupinate, effused, floccose, rather loosely attached to the substratum. *Hyphae* hyaline; basal hyphae straight, thick-walled, sparsely branched; subhymenial hyphae short-celled, richly branched. *Hymenium* smooth, vividly rose or orange coloured; hyphidia, cystidia and other sterile hymenial elements lacking. *Basidia* more or less cylindrical, centrally slightly constricted and basally widened; sterigmata 4 per basidium, bent. *Basidiospores* hyaline, smooth, ellipsoid, non-amyloid, with prominent apiculus. *Bulbils* present and abundant in one species.

Notes. The genus *Erythricium* was described for two former *Corticium* species, distinguished by the rather soft texture and the basidiomata only loosely attached to the substratum (Eriksson & Hjortstam 1970). Phylogenetic results (Lawrey et al. 2007, 2008, Ghobad-Nejhad et al. 2010) showed that the lichenicolous *Marchandiobasidium aurantiacum* grouped with *Erythricium laetum*, a salmon-colored resupinate fungus overgrowing dead stems and branches, and *E. salmonicolor*, a fungus causing pink disease in citrus, coffee and rubber trees, the latter with



Corticium silviae

lower support, and Hawksworth & Henrici (2015) formally transferred *M. aurantiacum* to *Erythrimum*. A synopsis and key to the six currently known species is given by Ghobad-Nehjad et al. (2021).

Ecology. Saprotrophic on dicotyledonous herbs, plant debris or bryophytes, parasitic on trees, one species lichenicolous.

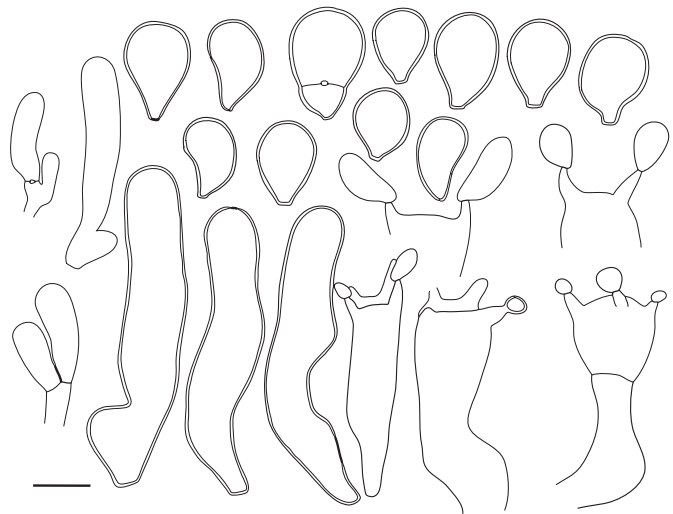
***Erythrimum aurantiacum* (Lasch) D. Hawksw. & A. Henrici**

Marchandiomyces aurantiacus (Lasch) Diederich & Etayo, in Etayo & Diederich, *Mycotaxon* 60: 421 (1996); *Illosporium aurantiacum* Lasch, in Rabenhorst, *Fungi Eur.*, cent. I, no. 74 (1859). *Type*: Poland, in lichenibus trunci Pyri mali pr. Driesen, on *Physcia adscendens*, G. W. Lasch, Rabenhorst *Fungi Eur.*, cent. I, no. 74 (K, M, UPS – isotypes).

= *Marchandiobasidium aurantiacum* Diederich & Schultheis, in Diederich et al., *Micol. Res.* 107: 524 (2003). *Type*: Belgium, Lischert, on *Physcia tenella*, 21 Dec. 2001, P. Diederich 15133 & D. Thoen (LG – holotype; BR – isotype).

=? *Aegerita physciae* Vouaux, *Bull. trimestr. Soc. mycol. Fr.* 30: 314 (1914). *Types*: (1) France, Meurthe-et-Moselle, Laitre-sous Amance, on *Physcia adscendens*, Vouaux; (2) France, Nord, Begues, on *P. adscendens*, M. Bouly de Lesdain; both specimens lost (Hawksworth 1979).

Basidiomata light orange (carrot red), effused, thin, adnate, granulose, floccose, margin indeterminate, reaching 1 cm diam. **Basal hyphae** hyaline, occasionally contorted, 3.5–6 µm thick, cells 7–25 µm long, wall 0.5–1 µm thick; dolipores (observed in phase contrast) 0.5–1 µm diam.; subhymenial (superior) hyphae hyaline, thin-walled, lacking clamps, septate, 2–4 µm thick. **Hymenium** comprising one or several layers of basidia on vertically branching, thin-walled hyphae; hyphidia, cystidia and other sterile hymenial elements lacking. **Basidia** initially elongate cylindrical, sometimes



Erythrimum aurantiacum, Belgium, Diederich 15570. Basidia and basidiospores. Modified from Diederich et al. (2003). Scale bar: 10 µm.

with a basal, lateral, ellipsoid probasidial bladder, to 57 × 11 µm; when mature, generally becoming clavate to suburniform, 25–40 × 12–15 µm, distinctly wider than the supporting hyphae; wall 0.6–0.8 µm thick; basal clamps lacking; basal septum with dolipore visible by light microscopy; sterigmata 4 per basidium, to 6.5 µm long and 3 µm wide at the base, curved. **Basidiospores** hyaline, smooth, usually aseptate, non-amyloid, not repetitive, pyriform or lacrimiform, one side frequently flattened or slightly concave, with a prominent truncate apiculus of 1.5–3 µm diam, 13–17.5(–18.5) × 8–11.5(–13.5) µm; wall 0.5–1 µm thick. **Bulbils** abundant, at first partly to almost completely immersed, rapidly becoming superficial, orange (carrot red), the same colour as the basidiomata, subspherical, ellipsoid or irregular in form, matt,



Erythrimum aurantiacum, Luxembourg. Bulbils invading and killing entire corticolous *Physcia adscendens* and *P. tenella* populations.



Erythrimum aurantiacum, Belgium, Diederich 15570. Bulbils (left) and basidioma (right) on *Physcia tenella*. Scale bar: 200 µm.



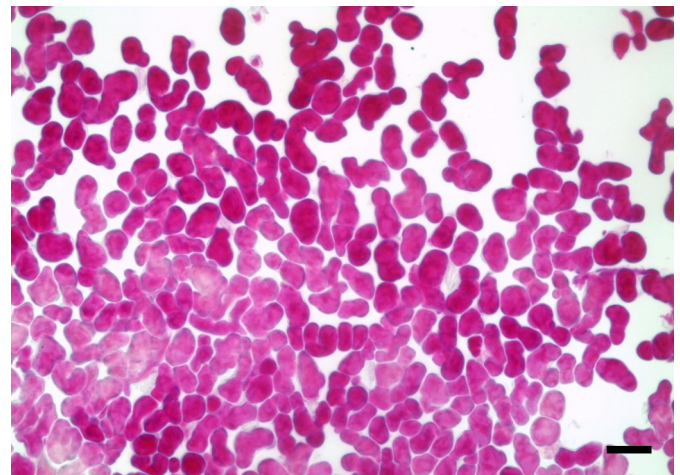
Erythricium aurantiacum, Luxembourg, Diederich 19591. Bulbils on *Physcia adscendens*. Scale bar: 200 μm .



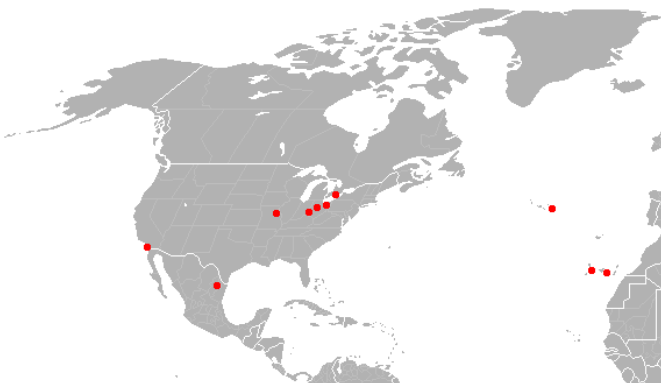
Erythricium aurantiacum, Luxembourg, Diederich 19591. Bulbils on *Physcia adscendens* remnants. Scale bar: 200 μm .

with an uneven surface, mostly 100–150 μm diam., regularly multiplying by enlargement and division, never covered by host thallus remnants; externally without specialized cells; internally composed of large, subspherical to elongate, occasionally catenate cells, mainly $12\text{--}28 \times 7\text{--}14 \mu\text{m}$; cell wall c. 0.7–1 μm thick; clamps not observed.

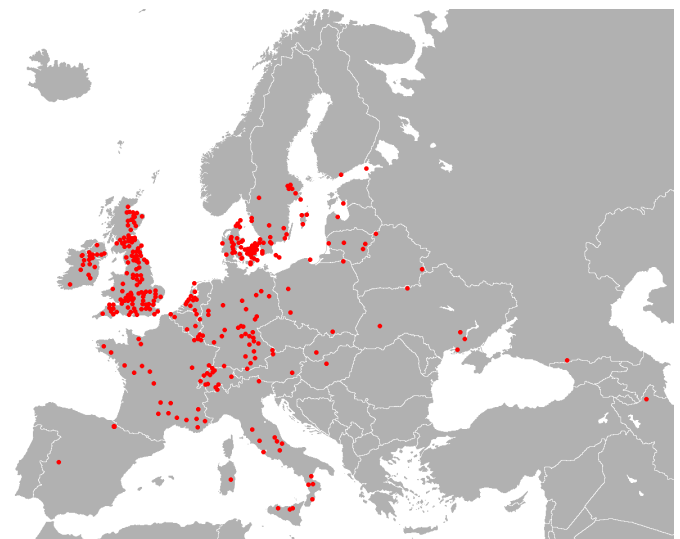
Notes. *Erythricium aurantiacum* is a very common basidiomycete that can easily be recognized in the field by its numerous orange, subspherical bulbils, 50–150 μm diam., and the parasitic behaviour on corticolous lichens of Xanthorion communities, mostly on *Physcia* species. Basidiomata are rare and have hitherto been recognized only in a few specimens. It differs from *Marchandiomyces corallinus*, with which has been confused until recently, by the colour of the bulbils: they are orange (carrot red) in *E. aurantiacum* and pastel to coral red in *M. corallinus*. Also the biology and ecology of both are distinct: bulbils of *E. aurantiacum* almost entirely degrade the host thalli, of which only the cortical layers remain after an invasion by the parasite, while bulbils of *M. corallinus* never degrade the host thalli in such a way.



Erythricium aurantiacum, Luxembourg, Diederich 19591. Squashed bulbil in phloxine. Scale bar: 20 μm .



American and Macaronesian distribution of *Erythricium aurantiacum*



European and Asian distribution of *Erythricium aurantiacum*

Ecology and hosts. This species is a virulent parasite of corticolous *Physcia* species, especially *Physcia adscendens* and *P. tenella*, occasionally also attacking neighbouring thalli of other lichens (extensive list of hosts in Brackel 2014). It develops mainly in autumn and is able to kill entire *Physcia* populations within several weeks. Infections result in the thalli shrinking in thickness, leaving at the end the discoloured, film-like, cortical remnants of the hosts.

Distribution. Europe (Austria; Belarus; Belgium; Denmark; Estonia; Finland; France; Germany; Hungary; Ireland; Latvia; Lithuania; Luxembourg; Netherlands; Poland; Russia; Slovakia; Spain; Sweden; Switzerland; UK; Ukraine), Macaronesia (Azores: São Miguel; Canary Islands: Gran Canaria, La Gomera), North America (Canada: Ontario; USA: California, Missouri, Ohio) and Asia (Iran).

Additional specimens. **Azores:** São Miguel: Ponta Delgada, on *Physcia adscendens*, 2010, Diederich 17001 (BR). **Canary Islands:** La Gomera: Hermigua, Wanderweg von La Laja zum Roque de Agando, Waldrand in Laurisilva, 28°06'24"N, 17°12'33"W, 1028 m, on *Erica arborea*, on *Teloschistes chrysophthalmus*, 2021, Winkler s. n. (herb. Berger 35507; det. and comm. F. Berger). **Spain:** Navarra: Valle de Erro, carretera de Zalba a Erro (pueblo), 42°55'09"N, 1°27'48"W, 640 m, on *Buxus* leaves, on *P. tenella*, 2018, Etayo 31425 (herb. Etayo).

Selected references. DePriest et al. 2005, Diederich & Lawrey 2007, Diederich et al. 2003, Etayo and Diederich 1996, Hawksworth & Henrici 2015 [Berger 2019, Brackel 2008a, 2008b, 2013, 2015, Brackel & Berger 2019, Brackel & Puntillo, Brinker in prep., Darmostuk & Sira 2020, Diederich 1990, Esnault et al. 2021, Etayo & Pérez-Ortega 2016, Kapets 2016, Kukwa & Jabłońska 2008, Motiejūnaitė et al. 2016, Rettig 2016, 2018, Roberts 2011, Schiefelbein et al. 2017, Søchting et al. 2007, Sohrabi & Alstrup 2007, Stepanchikova et al. 2019, Tsurykau et al. 2013, Urbanavichus & Urbanavichene 2014, van den Boom & Clerc 2015, Varga et al. 2016, Yatsyna 2011, Zhurbenko & Kobzeva 2014, Zimmermann & Feusi 2021].

LAETISARIA Burds.

Trans. Brit. Mycol. Soc. 72: 420 (1979). Type: *L. fuciformis* (McAlpine) Burds.

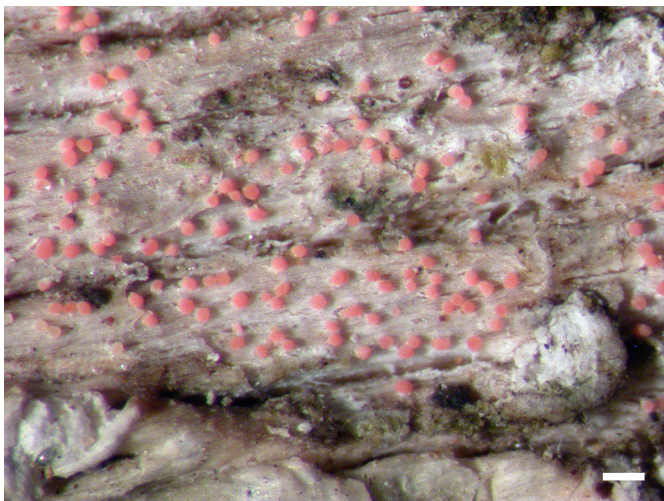
= *Limonomyces* Stalpers & Loer., *Canad. J. Bot.* 60: 533 (1982). Type: *L. roseipellis* Stalpers & Loer.

Molecular data: yes (T, L). **Number of species:** 2–0–0 (10).

Basidiomata annual, corticioid, thin, pink to pale red, resupinate crustose to membranaceous, smooth. **Hyphal system** monomitic, hyphae with or without clamps; cystidia absent, hyphidia occasionally present. **Basidia** first bladder-like, then subcylindrical to clavate, with 2–4 sterigmata. **Basidiospores** large ovoid, thin to moderately thick-walled, not reacting in Melzer's reagent. **Asexual stage**, when present, consisting of small pink to pale red bulbils.

Notes. *Laetisaria fuciformis*, *Limonomyces roseipellis* and *Limonomyces culmigenus* (R.K. Webster & D.A. Reid) Stalpers & Loer are pathogens and endophytes of grasses and form red or coral basidiomata or sclerotia. Phylogenetic results have shown that they belong to the same highly supported clade that also includes two lichenicolous species (see below) and two species growing on wood or *Pandanus* leaves described in *Marchandiomycetes* (Diederich et al. 2011). These were eventually all transferred to the now monophyletic *Laetisaria* by Diederich et al. (2018). A synopsis, new combinations and a key to all known species is given by Ghobad-Nehjad et al. (2021).

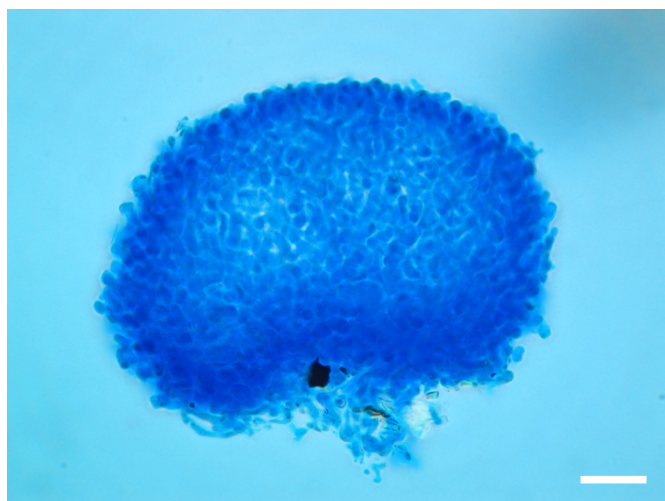
Ecology. Mostly parasitic on leaves of monocotyledons (*Poaceae*, *Agave*, *Pandanus*), on lichen thalli or lignicolous.



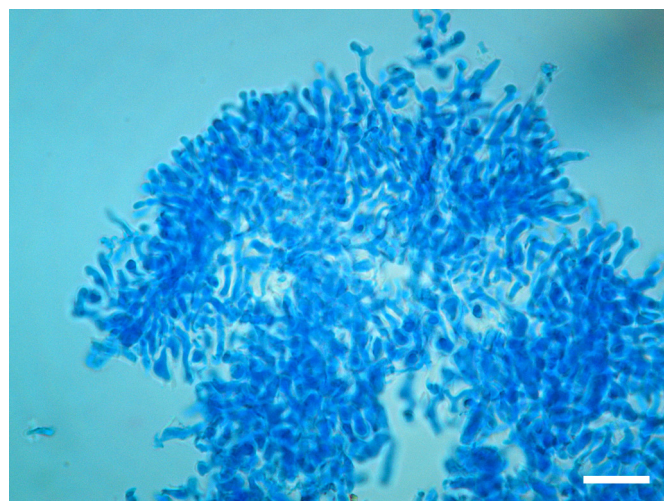
Laetisaria buckii, USA, Missouri, Buck 44504. Bulbils on *Pertusaria hypothamnica*. Scale bar: 200 µm.



Laetisaria buckii, USA, North Carolina, holotype. Bulbils on apothecia of *Bacidia hetreochroa*. Scale bar: 200 µm.



Laetisaria buckii, USA, holotype. Bulbil in lactophenol cotton blue. Scale bar: 20 μ m.

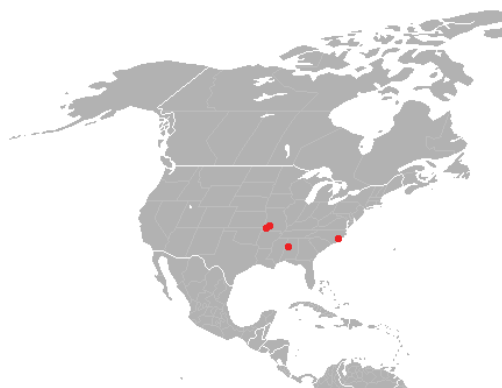


Laetisaria buckii, USA, holotype. Squashed bulbil in lactophenol cotton blue. Scale bar: 20 μ m.

Laetisaria buckii (Diederich & Lawrey) Diederich, Lawrey & Ghobad-Nejhad

in Diederich et al., *Bull. Soc. Nat. luxemb.* 120: 53 (2018); *Marchandiomyces buckii* Diederich & Lawrey, *Mycol. Progr.* 6: 70 (2007). Type: USA, North Carolina, Carteret Co., Cape Lookout National Seashore, Shackleford Banks, 34°41'01"N, 76°38'22"W, maritime forest dominated by *Quercus virginiana* and *Juniperus silicicola*, on *Bacidia heterochroa*, 19 March 2003, W. R. Buck 43835 (NY – holotype).

Basidiomata and *conidiomata* unknown. Colonies lichenicolous, appearing as numerous bulbils. *Mycelium* not observed. *Bulbils* developing in the host hymenium, soon becoming superficial, densely covering the apothecia and touching each other, or dispersed over the host thallus, subspherical to ellipsoid, 70–100 μ m diam., pale to pastel red; bulbils composed of radially oriented, frequently branched and occasionally septate, thick-walled, smooth, hyaline, elongate hyphae, mainly 3–4 μ m diam., some of which are apically typically 3–6-furcate, but not distinctly swollen; septa with clamps.



Laetisaria buckii

Notes. Macroscopically, this species looks similar to *Marchandiomyces corallinus*. The bulbils are distinctly smaller, more regularly subspherical to ellipsoid and more pale pinkish. Microscopically, both are very distinct: bulbils of *M. corallinus* are composed of large, subspherical to elongate, catenate cells, mainly 5–12 \times 3.5–7 μ m, not typically radiating and not furcate. Phylogenetically, both belong to two distinct clades (Diederich et al. 2018).

Ecology and hosts. On the apothecia and more rarely the thallus of *Bacidia heterochroa*, and on the thallus of *Huneckia pollinii* and *Pertusaria hypothamnolica*. Uninfected apothecia of *B. heterochroa* have a dark brown to blackish brown hymenial disk; after infection, apothecia become paler, being finally reddish brown; bulbils are initially immersed and concolorous to the hymenial disk; they rapidly become erumpent and change to red; when they are removed from the host apothecia, they leave distinct, often decolorized scars. We have seen an additional lignicolous, apparently non-lichenicolous specimen from Alabama, morphologically typical, and with identical nLSU and ITS sequences.

Distribution. North America (USA: Alabama, Missouri, North Carolina).

Additional specimen examined. USA: Alabama: Bibb Co., Bibb County Glades TNC Preserve, E of Fullman Lane, 0.7 mi S of jet with CR 65/Bulldog Bend Road, 4.3 mi NW of AL 25, E-facing slopes above W shore of Little Chahaba River, 33°03'29" N, 87°02'18" W, c. 100 m, on lignum of *Juniperus virginiana*, 2017, Buck 64594 (NY).

References. Diederich & Lawrey 2007, Diederich et al. 2018a.

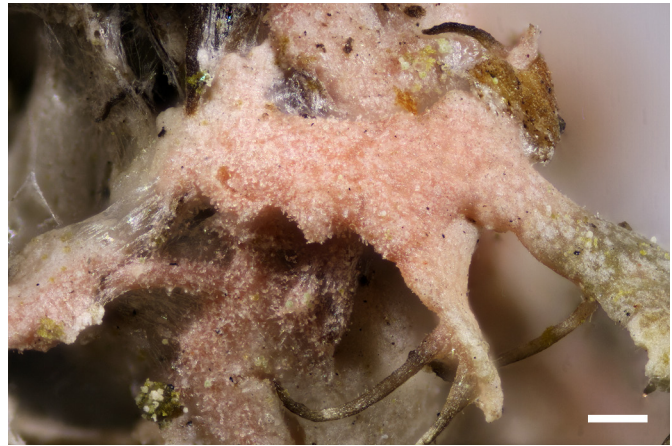
Laetisaria lichenicola Diederich, Lawrey & Van den Broeck

in Diederich et al., *Mycologia* 103: 530 (2011). *Type*: Luxembourg, Dudelange, centre of city, trees on parking along Schwaarze Wee, on *Platanus*, on *Physcia tenella* and *P. adscendens*, 15 Febr. 2010, P. Diederich 16900 (BR – holotype; BR, GMUF – isotypes).

Basidiomata light pink to coral, effused, thin, adnate, granulose, floccose, margin indeterminate, reaching 2 mm diam. *Basal hyphae* hyaline, straight or occasionally contorted, clamps observed in some specimens, smooth, 2.5–3 µm wide, wall c. 0.5 µm; dolipores c. 0.5 µm; subhymenial hyphae hyaline, thin-walled, clamps observed in some specimens, septate, smooth, 2.5–4 µm wide. *Hymenium* comprising one layer of basidia on vertically branching, thin-walled hyphae; hyphidia, cystidia and other sterile hymenial elements lacking. *Basidia* initially elongate cylindrical, c. 25–40 × 7.5–9 µm, basally up to 11.5 µm wide, without basal, lateral probasidial bladder; when mature, generally becoming clavate to suburniform, aseptate, c. 30–35 × 9.5–12 µm, distinctly wider than the supporting hyphae; wall 0.6–1.0 µm; basal clamps observed in some specimens; sterigmata two per basidium, 6.5–11.5 µm long and 3–3.5 µm wide at the base, curved. *Basidiospores* hyaline, smooth, aseptate, non-amyloid, pyriform or lac-riform, one side frequently flattened or slightly concave, with a prominent truncate apiculus of 1.5–3 µm diam., 14.5–18.5(–20.0) × (8–)10.5–12.5 µm; wall 0.4–0.7 µm. *Bulbils* unknown.

Notes. This species may be confused with the rare sexual morph of *Erythrimum aurantiacum*, from which it differs by the colour of the basidiomata (pink versus orange), the basidia with only two sterigmata (vs four) and the absence of bulbils, which are always present and abundant in *E. aurantiacum*.

Ecology and hosts. On the thallus of *Physcia adscendens* and *P. tenella*, rarely on adjacent thalli of *Xanthoria pariet-*



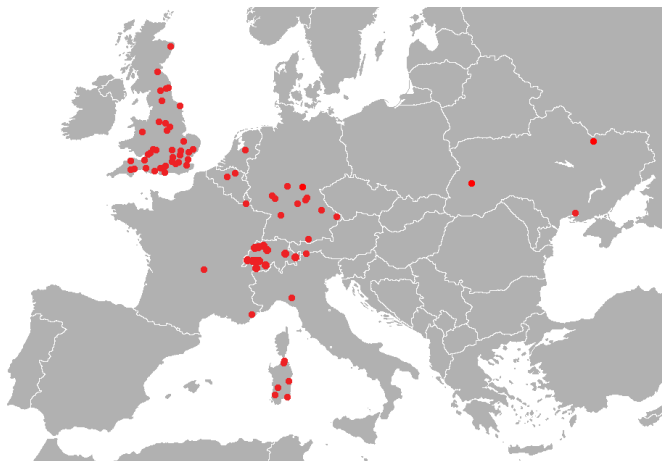
Laetisaria lichenicola, Germany, Heklau (STU). Basidioma on *Physcia tenella*. Scale bar: 200 µm.

ina and other lichens. A virulent parasite that kills the host thalli that become very thin, shiny, varnish-like. Remnants of host thalli often fuse together, sometimes resulting in mixed *Physcia/Xanthoria* thalli.

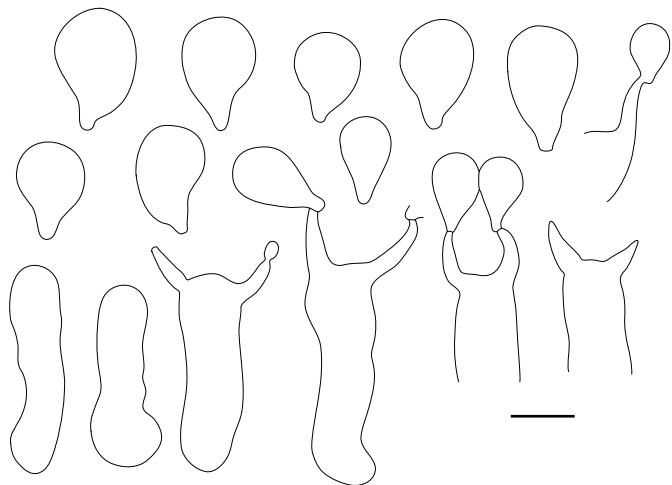
Distribution. Europe (Austria; Belgium; France; Germany; Italy [incl. Sardinia]; Luxembourg; Netherlands; UK; Ukraine) and North America (USA: Washington).

Additional specimens examined. **France**: Puy-de-Dôme: Châteaugay, c. 1 km au NE des Caves, on *Physcia adscendens*, 2020, Pinault (herb. Diederich). **Germany**: Baden-Württemberg: Stuttgart, Botnang, 2010, Heklau (STU).

References. Diederich et al. 2011 [Brackel 2014, 2015, Brackel & Berger 2019, Cezanne & Eichler 2015, Darmostuk 2021, Darmostuk & Khodosovtsev 2017, Darmostuk & Sira 2020, Diederich et al. 2012, Eckstein et al. 2021, Haldeman 2021, John et al. 2014, Khodosovtsev & Darmostuk 2017, Van den Broeck 2012, van der Kolk 2020, Zimmermann & Berger 2018].



European distribution of *Laetisaria lichenicola*



Laetisaria lichenicola, Luxembourg, holotype. Basidia and basidiospores. Reproduced from Diederich et al. (2011). Scale bar: 10 µm.

LAWREYMYCES Lücking & Moncada

Fungal Diversity 84: 133 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: *L. palicei* Lücking & Moncada

Molecular data: yes (T, L). *Number of species*: 7–0–0.

Notes. Sexual, asexual, hyphal and yeast stages unknown. Endolichenic. Cannot be detected or identified without DNA sequences, thus morphological descriptions of genus and of species not available. Not validly published (Hawksworth et al. 2017). DNA sequences obtained from the host of the generic type (*Agonimia foliacea*) led previous authors to erroneously conclude that the host was a lichenized member of *Corticiaceae*.

Ecology. All known species are endolichenic.

Lawreymyces bogotensis Lücking & Moncada

Fungal Diversity 84: 133 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7A in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Normandina* sp.

Distribution. South America (Colombia).

References. Lücking & Moncada 2017.

Lawreymyces columbiensis Lücking & Moncada

Fungal Diversity 84: 133 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7B in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Normandina columbiensis*.

Distribution. South America (Colombia).

References. Lücking & Moncada 2017.

Lawreymyces confusus Lücking & Moncada

Fungal Diversity 84: 133 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7C in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Normandina* aff. *columbiensis*.

Distribution. South America (Colombia).

References. Lücking & Moncada 2017.

Lawreymyces foliaceae Lücking & Moncada

Fungal Diversity 84: 133 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7D in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Agonimia foliacea*.

Distribution. South America (Colombia).

References. Lücking & Moncada 2017.

Lawreymyces palicei Lücking & Moncada

Fungal Diversity 84: 135 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7E in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Agonimia foliacea*.

Distribution. South America (Ecuador).

References. Lücking & Moncada 2017.

Lawreymyces pulchellae Lücking & Moncada

Fungal Diversity 84: 135 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7F in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Normandina pulchella*.

Distribution. South America (Colombia).

References. Lücking & Moncada 2017.

Lawreymyces spribillei Lücking & Moncada

Fungal Diversity 84: 135 (2017), nom. inval., Art. 38.1 (a), 40 (Ex. 6). *Type*: Fig. 7G in Lücking & Moncada (2017).

Ecology and host. Endolichenic in *Agonimia foliacea*.

Distribution. South America (Colombia).

References. Lücking & Moncada 2017.

MARCHANDIOMYCES Diederich & D. Hawksw.

in Diederich, *Mycotaxon* 37: 311 (1990). *Type*: *M. corallinus* (Roberge) Diederich & D. Hawksw.

= *Marchandiopsis* Ghobad-Nejhad & Hallenb., *Taxon* 59: 1530 (2010). *Type*: *Marchandiopsis quercina* (J. Erikss. & Ryvarden) Ghobad-Nejhad (a synonym of *Marchandiomyces aurantioroseus* (P. Karst.) Ghobad-Nejhad)

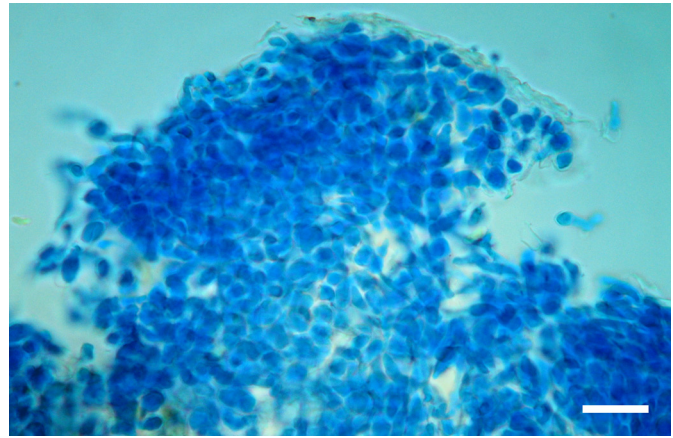
Molecular data: yes (T, L). *Number of species*: 1–0–0 (5).

Basidiomata known in one fungicolous species, resupinate, closely adnate, orbicular, reddish-pink, smooth, gelatinous. *Hyphae* hyaline, thin-walled, without clamps. *Basidia* elongate clavate, developing from a bladder-like probasidium; sterigmata 2 per basidium; cystidia absent; dendrohyphidia few, little branched. *Basidiospores* ellipsoid, smooth, thin-walled, non-amyloid, with a prominent apiculus. *Bulbils* known in two species, at first partly to almost completely immersed, becoming superficial, subspherical to ellipsoid, pastel red; internally composed of hyaline hyphae that are either subspherical, elongate and catenate, or radially orientated, branched, with bi- or trifurcate apices.

Notes. The type species is a rather common lichenicolous fungus with pastel red bulbils. A similar lignicolous species with much smaller bulbils, *M. lignicola* Lawrey & Diederich (DePriest et al. 2005), and two sexual species, *M. allantosporus* Ghobad-Nejhad and *M. aurantioroseus*



Marchandiomyces corallinus, Germany, Diederich 19582. Bulbils breaking through the cortex of *Parmelia sulcata*. Scale bar: 200 μ m.



Marchandiomyces corallinus, Luxembourg, Diederich 16339. Squashed bulbil in lactophenol cotton blue. Scale bar: 20 μ m.

all proved to be phylogenetically closely related (Ghobad-Nejhad et al. 2010, 2021). Several other, morphologically similar species belong to the genus *Laetisaria* (Diederich et al. 2018).

Ecology. Most species saprotrophic lignicolous, one species lichenicolous.

***Marchandiomyces corallinus* (Roberge) Diederich & D. Hawksw.**

in Diederich, *Mycotaxon* 37: 312 (1990); *Illosporium corallinum* Roberge, in Demazières, *Pl. crypt. Fr.*, Ed. 1, fasc. 32 no. 1551 (1847). *Type*: France, on *Physcia tenella*, J. Desmazières, *Pl. crypt. Fr.*, Ed. 1, fasc. 32 no. 1551 (K – syntype).

Basidiomata unknown. **Bulbils** at first partly to almost completely immersed, becoming superficial, subspherical, ellipsoid or irregular with a slightly or distinctly angular surface, pastel red, matt, \pm smooth, 80–250 μ m, often covered by host thallus remnants; externally without specialized cells, but covered by a hyaline amorphous layer 3–5 μ m thick; internally composed of large, subspherical to elongate, catenate cells, mainly 5–12 \times 3.5–7 μ m; cell wall c. 0.5 μ m thick; clamps not observed.



Marchandiomyces corallinus
(Chile, China, India and Japan are not shown)

Notes. This species has for a long time been confused with *Erythrimum aurantiacum* (for differences, see under that species), and therefore most older reports may refer to one of these two species.

Ecology and hosts. On the thallus *Acarospora*, *Allantoparmelia*, *Cetraria*, *Chrysothrix*, *Cladonia*, *Diploschistes*, *Evernia*, *Flavoparmelia*, *Flavopunctelia*, *Heterodermia*, *Hypotrachyna*, *Hypogymnia*, *Imshaugia*, *Lasallia*, *Lecanora*, *Lecidea*, *Lepra*, *Lepraria*, *Melanelia*, *Melanelixia*, *Melanohalea*, *Montanelia*, *Ochrolechia*, *Pannaria*, *Parmelia*, *Parmelina*, *Parmeliopsis*, *Parmotrema*, *Pertusaria*, *Phaeophyscia*, *Physcia*, *Physconia*, *Porpidia*, *Protoparmelia*, *Pseudephebe*, *Placynthiella*, *Ramalina*, *Teloschistes*, *Tephromela*, *Trapeliopsis*, *Umbilicaria*, *Usnea*, *Xanthoparmelia* and *Xanthoria*.

Distribution. Europe (Austria; Belgium; Bulgaria; Czech Republic; Denmark; Germany; Estonia; Finland; France; Hungary; Italy; Luxembourg; Netherlands; Norway; Portugal; Russia; Sweden; Slovakia; Spain; Switzerland; UK), Macaronesia (Canary Islands: La Gomera), North America (Canada: Ontario, Quebec; Greenland; Mexico; USA: Alabama, Arkansas, Georgia, Illinois, Iowa, Kentucky, Maine, Minnesota, Missouri, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Virginia, Wisconsin), South America (Chile) and Asia (China; India; Japan [GenBank LC462852]).

Selected references. DePriest et al. 2005, Diederich 1990, Diederich & Lawrey 2007, Hawksworth 1979, Lawrey et al. 2007, Molina et al. 2005 [Brackel 2021, Farkas et al. 2013, Shivarov et al. 2021; see Brackel 2014 for older references].

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *TREMELLOMYCETES*Order *FILOBASIDIALES*

by P. Diederich, A. M. Millanes, A. Flakus, P. Rodriguez-Flakus, J. Etayo & M. Wedin

Diederich, P., A. M. Millanes, A. Flakus, P. Rodriguez-Flakus, J. Etayo & M. Wedin. 2022. Class *Tremellomycetes*, order *Filobasidiales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 83–104.

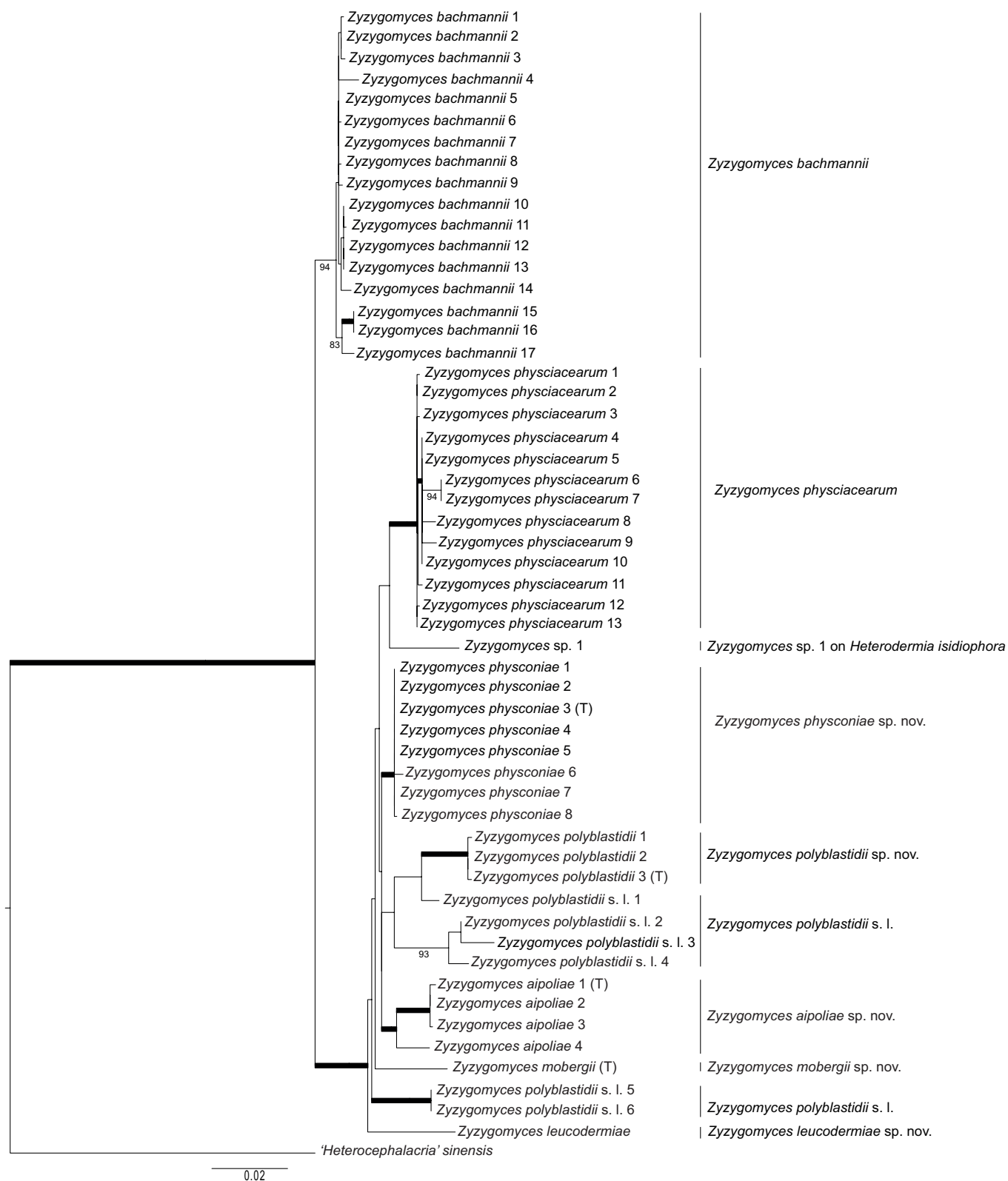
Introduction and phylogeny

Filobasidiales is an order of the *Tremellomycetes* that was originally introduced by Jülich (1981) to include fungi lacking proper basidiocarps and having holobasidia with passively released basidiospores. The presence of dolipore septa without paranthosomes was reported in several species (Moore & Kreger-

van Rij 1972, Rhodes et al. 1981), although the structure of the septal pore is not a good diagnostic character for the group (Wells 1994, Wells & Bandoni 2001). The *Filobasidiales* was recently re-circumscribed by Liu et al. (2015a, b) to include two families, *Filobasidiaceae*, with the genera *Filobasidium* (tele-



Phylogeny based on ITS and nuLSU sequences, representing the *Filobasidiales*. Branches in boldface indicate nodes supported by both Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . When nodes received support only from one of the two methods, Bayesian posterior probabilities values ≥ 0.95 are indicated over branches and ML-BS values ≥ 70 , below branches. Branch lengths are scaled to the expected number of substitutions per site. Generic assignments are indicated in the right margin. Red font used for *Zyzygomycetes* indicates that this genus includes only lichenicolous species. See tree on next page for a larger taxon sampling within *Zyzygomycetes*.



Phylogeny based on ITS and nuLSU sequences, with an enlarged taxon sampling focusing on *Zyzygomyces*. Branches in boldface indicate nodes supported by both Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . When nodes received support only from one of the two methods, Bayesian posterior probabilities values ≥ 0.95 are indicated over branches and ML-BS values ≥ 70 , below branches. Species names are indicated in the right margin. The type specimen of each new species is indicated with '(T)'. Branch lengths are scaled to the expected number of substitutions per site.

omorph), *Goffeauzyma* (yeasts), *Heterocephalacria* (teleomorph), *Naganishia* (yeasts) and *Syzygospora* (teleomorph), and *Piskurozymaceae* with the genera *Piskurozyma* (yeasts) and *Solicoccozyma* (yeasts). Two lichenicolous species were originally described in *Syzygospora* (Diederich 1996), and later combined into *Heterocephalacria* based mainly on molecular results excluding them from *Syzygospora*, and on partial similarities to the generic type, *H. solida* (Liu et al. 2015b). That decision was, however, premature, as the two lichenicolous species possess a different basidium type that is entire, not cruciately septate at the apex, and there was at that time no molecular data for *Heterocephalacria* s. str. We have been able to sequence a specimen of *Heterocephalacria solida* and found it to belong to the *Tremellales* (see phylogenetic tree on pages 106–107), confirming that the two lichenicolous species cannot stay in that genus. Consequently, the new genus *Zyzygomyces* is introduced here for the lichenicolous species. Several yeast species in the *Filobasidiales* were also transferred to – or later described in – *Heterocephalacria*, based on molecular results (Kachalkin et al.

2019, Crous et al. 2020), and they do not belong to this genus either. We temporarily refer to them here as ‘*Heterocephalacria*’. Although a new generic assignment is needed for these yeast taxa, this is beyond the aims of this Flora.

Phylogenetically, the genus *Zyzygomyces* is strongly supported and nested within the *Filobasidiales*, and is the sister group of the yeast clade currently included in ‘*Heterocephalacria*’ (Crous et al. 2020). This relationship has also high phylogenetic support, which allows placing the new genus in the *Filobasidiaceae* (Liu et al. 2015b). Our dataset, however, does not let us explore further family assignments in the *Filobasidiales*. Our molecular analyses support 7 of the 8 described species in *Zyzygomyces* as independently evolving lineages, viz., *Z. aipoliae*, *Z. bachmannii*, *Z. leucodermiae*, *Z. mobergii*, *Z. physciacearum*, *Z. physconiae* and *Z. polyblastidii*. In addition, one still unnamed lineage (*Zyzygomyces* sp. 1 on *Heterodermia isidiophora*) is also supported, and several specimens, tentatively assigned to *Z. polyblastidii* s. lat., appear scattered along the phylogeny.

Key to the lichenicolous species of *Filobasidiales*

As most species on *Physciaceae* are poorly characterized morphologically, some being semi-cryptic, we use host-specificity to key out these species, more reliable and easier to use than a purely morphology-based key.

- 1 On *Bunodophoron*; basidia 20–42 µm long; basidiomata reddish brown, pulvinate to slightly tuberculate, 0.2–0.6 mm diam. *Zyzygomyces bunodophori* (90)
- 1 On *Cladonia*; basidia 50–90 µm long; basidiomata reddish brown, often irregular, sometimes tuberculate, up to 5 mm *Zyzygomyces bachmannii* (88)
- 1' On *Physciaceae*
 - 2 On *Heterodermia* s. str.; basidiomata medium to dark reddish brown, not tuberculate *Zyzygomyces* sp. 1 (100)
 - 2 On *Heterodermia* gr. *comosa*; basidiomata whitish to pale brown, tuberculate *Zyzygomyces* sp. 2 (100)
 - 2 On *Leucodermia*; basidiomata pale to medium brown, rapidly turning almost black, subspherical to more often strongly tuberculate; basidia 29–34 µm long *Zyzygomyces leucodermiae* (91)
 - 2 On *Physcia*; basidiomata never tuberculate
 - 3 Basidiomata pale brown, often concolorous with the host thallus, frequently unevenly pigmented, being darker in central areas, rarely becoming dark brown to blackish, roundish; basidia 22–68 µm long; on the thallus or rarely apothecia of *Physcia adscendens*, *P. biziana*, *Physcia dubia* (incl. *P. teretiuscula*), *P. leptalea*, *P. stellaris* and *P. tenella* *Zyzygomyces physciacearum* (93)
 - 3 Basidiomata pale to medium reddish brown, often irregular; basidia 45–68 µm long; on the thallus and apothecia of *Physcia aipolia*, rarely intrahymenial *Zyzygomyces aipoliae* (86)
 - 3' Basidiomata reddish brown; basidia 65–90 µm long; on *Physcia albinea* *Zyzygomyces* sp. 3 (101)
 - 2 On *Physconia*; basidiomata medium to dark reddish brown, convex to subspherical, not tuberculate; basidia 28–50 µm long *Zyzygomyces physconiae* (96)
 - 2 On *Polyblastidium* gr. *japonicum*
 - 3 Basidioma orange-brown, 0.2–0.7 mm diam., mostly agglomerate to almost tuberculate, agglomerations up to 1.8 mm diam.; basidia basally broad, 31–65 × 8–11.5 µm; basidiospores 9–12.5 × 5–7.5 µm *Zyzygomyces mobergii* (92)
 - 3' Basidiomata medium orange to dark brown, 0.3–1.5 mm diam., not agglomerate or tuberculate; basidia narrower, 35–54 × 3.5–7.5 µm; basidiospores smaller, 6.5–8.5 × 4.5–5.5 µm *Zyzygomyces polyblastidii* (98)
- 2' On *Pyxine*; basidiomata medium to dark brown, convex, not tuberculate *Zyzygomyces* sp. 4 (101)

TREMELLOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: *Tremella* Pers.

FILOBASIDIALES Jülich

Bibliotheca Mycologica 85: 347 (1981). Type: *Filobasidium* L. S. Olive

Filobasidiaceae L. S. Olive

Journal of the Elisha Mitchell Scientific Society 84: 261 (1968).
Type: *Filobasidium* L. S. Olive

= *Syzygosporaceae* Jülich, *Persoonia* 11: 426 (1982). Type: *Syzygospora* G. W. Martin

ZYZYGOMYCES Diederich, Millanes & Wedin, gen. nov.

Diagnosis: Characterized by the waxy to gelatinous, often gall-inducing, whitish to brown or blackish, applanate pulvinate to subspherical or tuberculate, lichenicolous basidiomata, tremelloid haustoria, ellipsoid, at least in some species clamped probasidia, the absence of hyphidia and cystidia, aseptate, cylindrical, 2–4 sterigmate basidia, subulate sterigmata with a refractive apex, and ellipsoid or ovoid to almost limoniform basidiospores obliquely attached to sterigmata.

Etymology: From *zy[ma]*, yeast, as the closest relatives of the new genus are all yeast-forming fungi, [*Sy*]zygo[*spora*], a genus very similar and related to *Zyzygomyces*, and *myces*, fungus.

Type: *Zyzygomyces bachmannii* (Diederich & M. S. Christ.) Diederich & Millanes

Mycobank: MB844617

Molecular data: yes (T, L). **Number of species:** 8[4]–0–0.

Basidiomata waxy-gelatinous, often gall inducing, whitish, pale to dark brown, often reddish brown, or blackish, applanate pulvinate to almost subspherical, sometimes tuberculate. **Context hyphae** thin-walled, with clamp connections; tremelloid haustoria frequent, at least in some species with clamp connections, mother cell subspherical to ellipsoid, 2.5–4 µm diam., haustorial filament 0.5 µm diam. **Hymenium** hyaline, containing numerous probasidia; probasidial initials ellipsoid, proliferations (at least in some species) occurring through the basal clamp; hyphidia and cystidia absent. **Basidia**, when mature, cylindrical, aseptate, with 2–4 sterigmata; sterigmata subulate, apex refractive. **Basidiospores** ellipsoid or ovoid to almost limoniform, obliquely attached to sterigmata, refractive at the point of attachment. **Asexual stage** of two kinds: lunate germination conidia are present in many specimens; catenulate conidia with individual conidia subspherical to elongate, 2.5–5 µm diam., have been observed in some specimens.

Notes. The genus *Syzygospora* Martin [type species *S. alba* Martin] had been used in a wide sense by Ginns (1986) to include mycoparasitic heterobasidiomycetes with unique holobasidia and basidiospores germinating by yeast-like budding, and this author included as synonyms the genera *Carcinomyces* Oberw. & Bandoni [type *C. effibulatus* (Ginns & Sunhede) Oberw. & Bandoni], *Christiansenia* Hauerslev [type *C. pallida* Hauerslev] and *Heterocephalacria* Berthier [type *H. solida* Berthier]. Two lichenicolous species of *Syzygospora* were described by Diederich (1996), and an additional species, *S. parmeliicola* Diederich was provisionally described there.

The types of *Carcinomyces*, *Syzygospora* and *Christiansenia*, and also the two lichenicolous *Syzygospora bachmannii* and *S. physciacearum* were for the first time included in a phylogenetic analysis by Millanes et al. (2011) who found that *Christiansenia* is a synonym of *Syzygospora*. *Syzygospora* s. str. currently includes these two species, characterized by the production of zygoconidia, aseptate basidia, haustoria of the *Tremella*-type and basidiospores asymmetrically attached to horn-shaped sterigmata. *Syzygospora* s. str. and the two lichenicolous *Syzygospora* species belong to the *Filobasidiaceae* in the *Filobasidiales*, while *Carcinomyces* belongs to the *Tremellales*. The two lichenicolous species were later combined in *Heterocephalacria* by Liu et al. (2015b). As said above, newly obtained sequences of the generic type *H. solida* place that genus in the *Tremellales*, and consequently, the new genus *Zyzygomyces* is described here for the two lichenicolous species.

Ecology. All species are lichenicolous.

Zyzygomyces aipoliae Diederich, Millanes, F. Berger & Ertz, sp. nov.

Diagnosis: Characterized by the waxy-gelatinous, often gall inducing, pale to medium reddish brown basidiomata on the thallus, apothecial margin or disk of *Physcia aipolia*, 0.15–0.6 mm diam., the 2–3-sterigmate basidia, 45–68 × 4.5–6.5 µm, and the ellipsoid basidiospores, 7–9 × 4.5–5.5 µm.

Etymology: From *Physcia aipolia*, the host lichen.

Type: Sweden, Västra Götaland, Trollhättan, Brandsbo Naturreservat, X6465670, Y1290076, 11 m, mixed forest with *Quercus*, *Corylus*, *Salix*, *Picea*, *Alnus*, along stream, on *Corylus*, on *Physcia aipolia*, 14 April 2013, A. Millanes 726 & J. Olsson (S – holotype; BR – isotype).

Mycobank: MB844618

Basidiomata waxy-gelatinous, often gall inducing, pale to medium reddish brown, convex, often with a constricted base, never tuberculate but often with an irregular surface, 0.15–0.6 mm diam., or confluent and then spreading over the host thallus and poorly delimited, up to 1.5 mm diam., frequently on the apothecial margin that becomes strongly swollen, or reduced, intrahymenial, the disk showing indistinct to distinct swellings. **Subbasidial hyphae** thick-walled,

4–6 µm diam.; haustoria frequent, with a basal clamp. *Hymenium* containing numerous ellipsoid probasidia, basal clamp not observed, and/or numerous asteroconidia-producing conidiophores. *Basidia*, when mature, 45–68 × 4.5–6.5 µm, with 2–3 sterigmata, 1.5–2.5 µm diam., 5–8 µm long. *Basidiospores* ellipsoid or ovoid to almost limoniform, 7–9 × 4.5–5.5 µm. *Asexual morph*: asteroconidia, lunate conidia and catenulate conidia have been observed in one specimen.

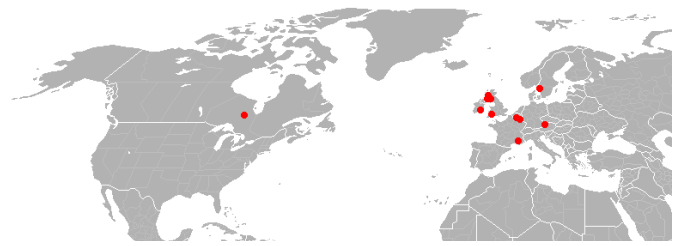
Notes. This species is phylogenetically distinct from the more common *Zyzygomyces physciacearum* and seems to be confined to *Physcia aipolia*, although a larger number of specimens will be needed to confirm this. Contrarily to *Z. physciacearum*, this species typically grows not only on the host thallus, but also on the apothecial margin, where it causes conspicuous irregular swellings, and even in the hymenium, but this observation may simply result from the rarity of apothecia on the most common hosts of the other two species. Diederich (1996) reported that in two Canadian specimens of ‘*Zyzygospora physciacearum*’ on *P. aipolia* (Ahti 3730 and 3973),



Zyzygomyces aipoliae, Sweden, holotype. Basidiomatal galls on the thallus and apothecia of *Physcia aipolia*. Scale bar: 500 µm.



Zyzygomyces aipoliae, Luxembourg, Diederich 18185. Basidiomatal galls on the thallus and apothecia of *Physcia aipolia*. Scale bar: 500 µm.



Zyzygomyces aipoliae

‘most basidiomata are reduced and grow in the hymenium of the lichen apothecia’. We provisionally include here all specimens on *Physcia aipolia* reported by Diederich (1996), but not those from that host reported in other papers.

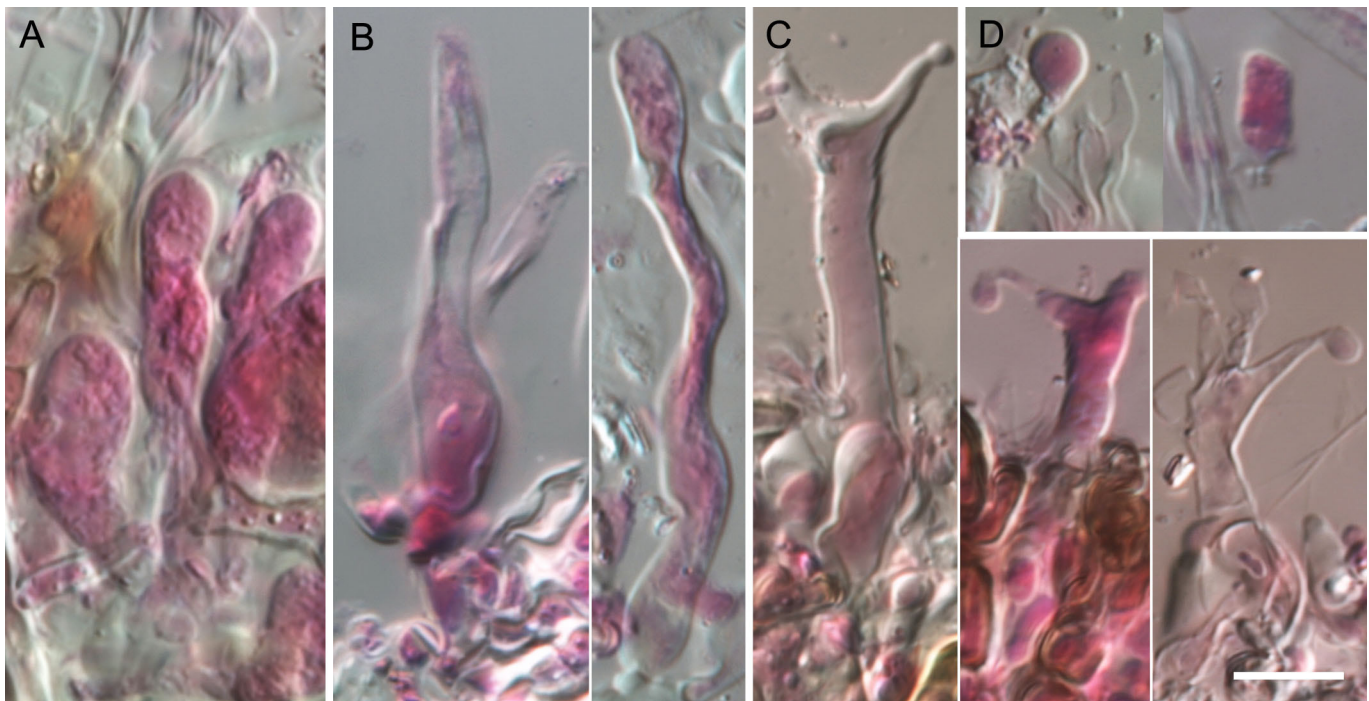
Ecology and host. On the thallus, apothecial margin and more rarely in the hymenium of corticolous *Physcia aipolia*.

Distribution. Europe (Austria; France; Ireland; Luxembourg; Sweden; UK: England, Scotland) and North America (Canada: Ontario).

Additional specimens examined (all on *Physcia aipolia*; *specimens seen by P. D. before 2000, not re-examined in 2022). **Austria:** ‘M. Alm’, 1988, Berger 8643 (h)*. **Oberösterreich:** Engelhartzell, Oberanna, 48°28’27”N, 13°46’20”E, 290 m, 2017, Berger 31521 (herb. Berger). **Belgium:** Olloy-sur-Viroin, ruisseau de Nouée, 50°03’20”N, 4°35’18”E, 240 m, 2021, Ertz 25889 (BR). **Canada:** *Ontario*: Cochrane Dist., Martison Lake, 1958, Ahti 3730, 3973 (H)*. **France:** *Alpes-de-Haute-Provence*: N St-Etienne-les-Orgues, vers notre Dame de Lure, 1996, Diederich 12962 (BR). **Ireland:** Waterford Co., 7 km NE Ardmore, Ballymacart Bridge, Durwael & Fox (DBN 35:1999)*. **Luxembourg:** Steinfort, carrières, 49.6672°N, 5.9045°E, 315 m, 2015, Diederich 18185 (BR). **UK:** *England*: VC 4, N Devon, Arlington, Court Park, 1994, Coppins 16316 (E)*. *Scotland*: VC 73, Kirkcudbright, New Galloway, Water of Ken Woods, Long Wood, 1991, Coppins 14222 (E)*; VC 97, Westerness, Morvern, Rhemore, Dun Bàn, 1992, Coppins 14869 (E)*; VC 101, Kintyre, 7 km SE of Campbeltown, Balnabraid Glen, 1994, Coppins 16211 (E)*.



Zyzygomyces aipoliae, Austria, Berger 31521. Basidiomatal galls on the thallus and apothecia of *Physcia aipolia*. Scale bar: 500 µm.



Zyzygomyces aipoliae, holotype. A, Probasidia. B, Immature basidia. C, Mature basidia. D, Immature (left) and mature basidiospore. In phloxine. Scale bar: 10 μm .

Zyzygomyces bachmannii (Diederich & M. S. Christ.)
Diederich, Millanes & Wedin, comb. nov.

Syzygospora bachmannii Diederich & M. S. Christ., in Diederich, *Bibl. Lichenol.* 61: 30 (1996); *Heterocephalacria bachmannii* (Diederich & M. S. Christ.) Millanes & Wedin, in Liu et al., *Studies in Mycology* 81: 120 (2016). *Type*: Luxembourg, E of Ernster, Warschent, on *Cladonia subrangiformis*, 25 Nov. 1990, P. Diederich 9153 (LG – holotype; BR, H – isotypes).

Mycobank: MB844619

Basidiomata waxy-gelatinous, reddish brown, sometimes pale or dark brown, roundish or more frequently elongate, often irregular, sometimes tuberculate, inducing gall formation, up to 5 mm long. *Context hyphae* thin-walled, with clamp connections, 2–3.5 μm diam.; haustoria frequent, tremelloid, with clamp connections, mother cell subspherical to ellipsoid, 2.5–4 μm diam., haustorial filament 0.5 μm diam., 1–7 μm long. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, 50–90 \times 4–6.5 μm , with (2–)4 sterigmata, 1–2 μm diam., 5–12 μm long. *Basidiospores* ellipsoid or ovoid to almost limoniform, 7–9 \times 4.5–6 μm . *Asexual stage* of three kinds: asteroconidia, lunate conidia and catenulate conidia with individual conidia subspherical to elongate, 2.5–5 μm diam., have been observed in some specimens.

Notes. This taxon is distinguished from most other *Zyzygomyces* species by having particularly long basidia. It is con-

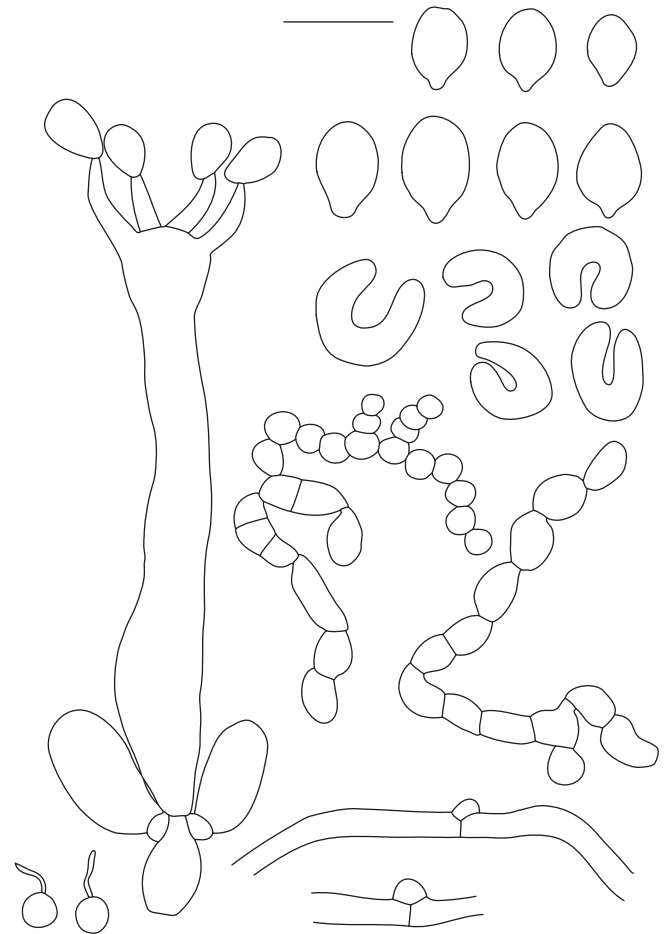
fined to thalli of *Cladonia*, growing mainly on the podetia but also on the primary thallus, where it typically causes deformations. Contrarily to a common belief, *Zyzygomyces bachmannii* cannot be distinguished from *Tremella cladoniae* without a microscopical examination of the basidia, and therefore some of the published or databased records may represent misidentifications. Also, both *Tremella cladoniae* and *Zyzygomyces bachmannii* can be simultaneously present in the same gall (personal observation).

Ecology and hosts. On the thallus of *Cladonia subrangiformis*, *C. acuminata*, *C. amaurocraea*, *C. artuata*, *C. bacillaris*, *C. bacilliformis*, *C. cervicornis*, *C. chlorophaea*, *C. coccifera*, *C. coniocraea*, *C. cornuta*, *C. corymbescens*, *C. crispata*, *C. deformis*, *C. ecmocyna*, *C. foliacea*, *C. floerkeana*, *C. furcata*, *C. glauca*, *C. gracilis*, *C. granulosa*, *C. macilenta*, *C. macroceras*, *C. macrophylla*, *C. mitis*, *C. monomorpha*, *C. phyllophora*, *C. cf. pleurota*, *C. pocillum*, *C. pyxidata*, *C. ramulosa*, *C. rangiferina*, *C. rangiformis*, *C. scabriuscula*, *C. squamosa*, *C. stereoclada*, *C. stygia*, *C. subulata*, *C. sulphurina*, *C. symphylicarpa*, *C. turgida*, *C. uliginosa*, *C. umbricola*, *C. uncialis* and *C. verticillata*, usually inducing conspicuous deformations of the host podetia.

Distribution. Europe (Austria; Belgium; Croatia; Czech Republic; Denmark; Estonia; Faeroe Islands; Finland; France; Germany; Greece; Hungary; Iceland; Ireland; Italy; Luxembourg; Netherlands; Norway; Portugal; Russia; Spain; Sweden; Switzerland; Türkiye; UK; Ukraine),

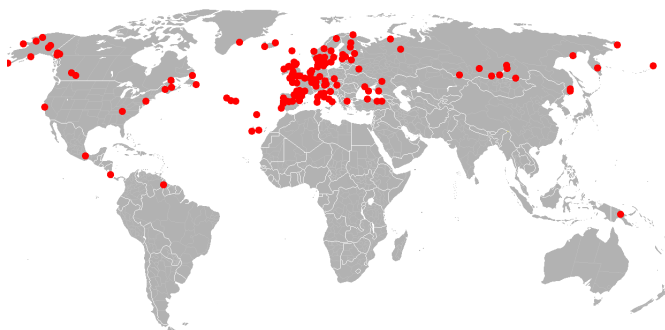


Zyzygomycetes bachmannii, Luxembourg, Diederich 19595. Basidiomata on the strongly deformed thallus of *Cladonia rangiformis*. Scale bar: 2 mm.



Zyzygomycetes bachmannii, Luxembourg, holotype, except catenulate conidia: Germany, Lettau (modified from Diederich 1996). Basidium, basidiospores, hyphae with clamp connections, catenulate and lunate conidia and haustoria. Scale bar: 10 μ m.

Macaronesia (Azores; Canary Islands; Madeira), North America (Canada: British Columbia, New Brunswick, Newfoundland and Labrador, Quebec, Yukon; Greenland; Mexico; USA: Alaska, California, Maine, Tennessee, New York), Central America (Panama), South America (Guyana), Asia (Mongolia; Russia; Türkiye) and Oceania



Zyzygomycetes bachmannii

(Papua New Guinea). This species may be cosmopolitan and should be searched for in Africa, Australia, China, etc.

Selected additional specimens examined. **Canada:** *British Columbia:* Wells Gray Provincial Park, Trophy Mountains, 51°45'34"N, 119°56'15"W, 1740 m, on *Cladonia sulphurina*, 2008, Diederich 17286 (BR). **Canary Islands:** *Tenerife:* Las Montanas de Anaga, Monte de las Mercedes, W of Cruz del Carmen, 28°32'N, 16°17'W, 910 m, on *C. furcata*, 2007, Diederich 16472 (BR).

Selected references. Diederich 1996, Pino-Bodas et al. 2017, Zhurbenko & Pino-Bodas 2017 [Alstrup 2004, Brackel 2019, Brackel & Berger 2019, Diederich 2003, Etayo & López de Silanes 2020, Frisch et al. 2020, Hafellner 2016, 2018b, 2019, Himmelbrant et al. 2018, Khodosovtsev & Darmostuk 2017, Kocourková & van den Boom 2005, Kocourková et al. 2012, Kukwa & Kowalewska 2007, Roux 2016, Roux 2020, Spribille et al. 2020, Urbanavichus et al. 2020, van den Boom & Giralte 2012, Varga et al. 2021, Zhurbenko & Yakovchenko 2014, Zhurbenko & Zheludeva 2015, Zhurbenko et al. 2019, Zimmermann & Berger 2018].

Zyzygomyces bunodophori Diederich, Etayo & Palice,
sp. nov.

Diagnosis: Characterized by the reddish brown, pulvinate to slightly tuberculate, gelatinous basidiomata, 0.2–0.6 mm diam., developing over the thallus of *Bunodophoron*, and the relatively short basidia, $20\text{--}42 \times 3.5\text{--}6.5\ \mu\text{m}$.

Etymology: From *Bunodophoron*, the host lichen.

Type: Ecuador, Prov. Tungurahua, Parque Nacional Llanganates, El Triunfo, valley of Quebrada de Plata, $1^{\circ}18'05''\text{S}$, $78^{\circ}22'30\text{--}35''\text{W}$, 3000 m, on *Alnus acuminata*, on *Bunodophoron* sp., 21 March 2003, Z. Palice 8397 (PRA – holotype; BR, hb. Etayo 28156 – isotypes).

Mycobank: MB844620

Basidiomata waxy-gelatinous, reddish brown, sometimes pale or dark brown, roundish or more frequently elongate, often irregular, sometimes tuberculate, inducing gall formation, up to 5 mm long. **Context hyphae** thin-walled, with clamp connections, $2\text{--}3.5\ \mu\text{m}$ diam.; subbasidial hyphae thick-walled, $3\text{--}5\ \mu\text{m}$ diam.; haustoria frequent, with a basal clamp. **Hymenium** containing numerous subspherical to pyriform probasidia with a basal clamp. **Basidia**, when mature, $20\text{--}42 \times 3.5\text{--}6.5\ \mu\text{m}$, with 3 sterigmata, $1.5\text{--}2.5\ \mu\text{m}$ diam., $5.5\text{--}8.5\ \mu\text{m}$ long. **Basidiospores** ellipsoid to ovoid, $10\text{--}10.5 \times 7\text{--}7.5\ \mu\text{m}$. **Asexual stage** of three kinds: asteroconidia, lunate conidia and catenulate conidia with individual conidia subspherical to elongate, $2.5\text{--}5\ \mu\text{m}$ diam., have been observed in some specimens.

Notes. This species is distinguished from most other *Zyzygomyces* species by the reddish brown, pulvinate to slightly tuberculate basidiomata, and the relatively short basidia.



Zyzygomyces bunodophori, Ecuador, holotype. Basidiomatal galls on the thallus of *Bunodophoron* sp. Scale bar: 500 μm .

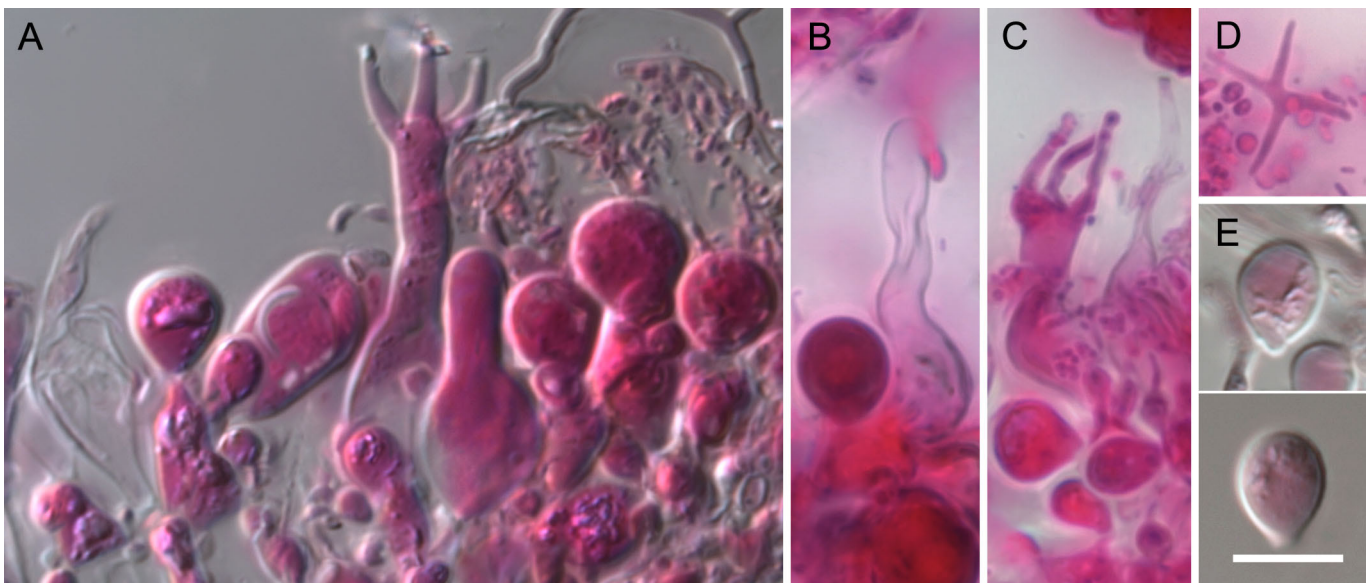


Zyzygomyces bunodophori

Ecology and host. Gall-inducing on sterile thalli of unidentified corticolous *Bunodophoron* species.

Distribution. Central America (Panama) and South America (Ecuador).

Additional specimen examined. **Panama:** Chiriquí province, Chiriquí, way to Las Brujas from El Quetzal Station, on corticolous *Bunodophoron* sp., 1997, Etayo 16829 (hb. Etayo).



Zyzygomyces bunodophori, Ecuador, holotype. A, Probasidia and mature basidium. B, Probasidium and immature basidium. C, Mature basidium. D, Asteroconidium. E, Basidiospores. In phloxine. Scale bar: 10 μm .

Zyzygomyces leucodermiae Diederich, Millanes, Ertz, Etayo & Flakus, sp. nov.

Diagnosis: Characterized by the waxy-gelatinous, pale to medium brown, often blackish basidiomata, frequently becoming tuberculate, on the thallus of *Leucodermia* species, the 2–3-sterigmate basidia, $29\text{--}34 \times 4\text{--}9 \mu\text{m}$, and the basidiospores, $8.5\text{--}11 \times 4.5\text{--}6 \mu\text{m}$.

Etymology: From *Leucodermia*, the host lichen.

Type: Rwanda, Parc national de l'Akagera, rive sud-ouest du lac Ihema, 1300 m, on *Leucodermia leucomelos*, 1972, J. Lambinon 72/175 (BR – holotype).

Mycobank: MB844621

Basidiomata waxy-gelatinous, pale to medium brown, rapidly turning almost black, convex, often with a constricted base, at first hemispherical, 0.1–0.7 mm diam., frequently becoming tuberculate and then 0.2–1.2 mm diam., composed of 'granules' of 0.05–0.13 mm diam., not clearly gall-inducing. **Context hyphae** thin-walled, 2.5–4 μm thick,

septa with clamps. **Haustoria** frequent. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, $29\text{--}34 \times 4\text{--}9 \mu\text{m}$, with 2–3 sterigmata, 1.5–2.5 μm diam., 5–8 μm long. **Basidiospores** ellipsoid or ovoid to almost limoniform, $8.5\text{--}11(13) \times 4.5\text{--}6 \mu\text{m}$. **Asexual morph:** catenulate conidia observed in one specimen.

Notes. This species typically has tuberculate, blackish basidiomata when old and is further distinguished by the particularly short basidia.

Ecology and hosts. On the thallus of *Leucodermia leucomelos*, *L. cf. vulgaris* and *L. sp.*

Distribution. South America (Bolivia; Ecuador), Africa (Malawi; Rwanda), Indian Ocean (Mauritius) and Oceania (Papua New Guinea).

Additional specimens examined (all on *Leucodermia*). **Bolivia:** Dept. Cochabamba, Prov. Carrasco, Parque Nacional Carrasco, Wayra Mayu close to Monte Punku, $17^{\circ}33'30''\text{S}$, $65^{\circ}16'08''\text{W}$, 2750 m, on *L. leucomelos*, 2014, Flakus 25848 (KRAM, LPB). Dept. Tarija, Prov. Burnet O'Connor, close to Los Pinos, old road between Entre



Zyzygomyces leucodermiae, Rwanda, holotype. Basidiomata on the thallus of *Leucodermia leucomelos*. Scale bar: 1 mm.



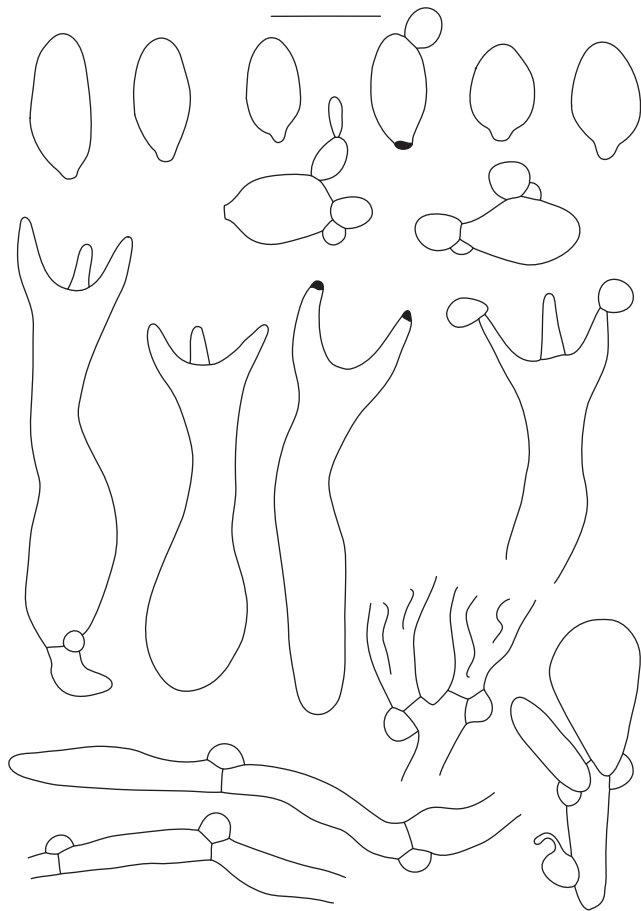
Zyzygomyces leucodermiae, Malawi, Chapman s. n. Basidiomata on the thallus of *Leucodermia leucomelos*. Scale bar: 1 mm.



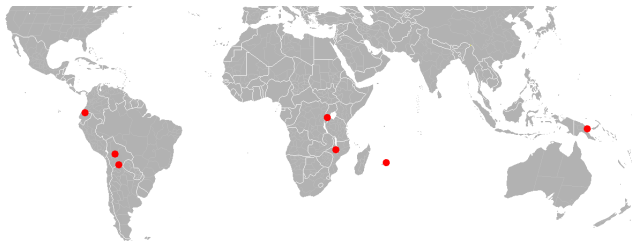
Zyzygomyces leucodermiae, Mauritius, Ertz 23499. Young basidiomata on the thallus of *Leucodermia* sp. Scale bar: 500 μm .



Zyzygomyces leucodermiae, Mauritius, Ertz 23499. Mature basidiomata on the thallus of *Leucodermia* sp. Scale bar: 500 μm .



Zyzygomycetes leucodermiae, Rwanda, holotype (modified from Diederich 1996, as *Syzygospora physciacearum*). Basidia, basidiospores, and hyphae with clamp connections. Scale bar: 10 μ m.



Zyzygomycetes leucodermiae

Ríos and Tarija, 21°25'07"S, 64°18'50"W, 2190 m, on *L. cf. vulgaris*, 2015, Flakus 27448 (KRAM, LPB). **Ecuador:** Prov. Imbabura, Chachimbiro, vallonada desde las piscinas naturales hasta bosque secundario arbustivo, 2800 m, on *L. leucomelos*, 2003, Etayo 25512 (herb. Etayo). **Malawi:** Mt Mulanjaa, above Fort Lister on the Sombani path, 1120 m, on *L. leucomelos*, 1986, Chapman 7745B (BR, E). **Mauritius:** Savanne district, Black River Gorges National Park, along the trail to Mt Cocotte, 20°26'30"S, 57°28'16"E, 720–750 m, dense evergreen mountain forest, 2019, Ertz 23499 (BR, MAU). **Papua New Guinea:** Madang Prov., Huon Peninsula, Finisterre Range, Yupna valley, Teptep village, 5.95°S, 146.55°E, 2500 m, on *L. leucomelos*, 1992, Diederich 10828 (BR).

References. [Diederich 1996 as *Syzygospora physciacearum*].

Zyzygomycetes mobergii Diederich & Millanes, sp. nov.

Diagnosis: Characterized by the waxy-gelatinous, medium orange-brown, often agglomerate basidiomata on the thallus of *Polyblastidium cf. japonicum*, 0.2–0.7 mm diam., the 3–4-sterigmate basidia, 31–65 \times 8–11.5 μ m, and the large basidiospores, 9–12.5 \times 5–7.5 μ m.

Etymology: Named after Roland Moberg, Swedish lichenologist.

Type: Australia, New South Wales, Minnamurra Nat. Park, 12 km NW of Kiama, 34°36'S, 150°43'E, 180 m, stream surrounded by temperate forest, on *Polyblastidium cf. japonicum*, 16 March 1992, R. Moberg A74:11 & B. Owe-Larsson (UPS L-124437 – holotype; BR – isotype).

Mycobank: MB844622

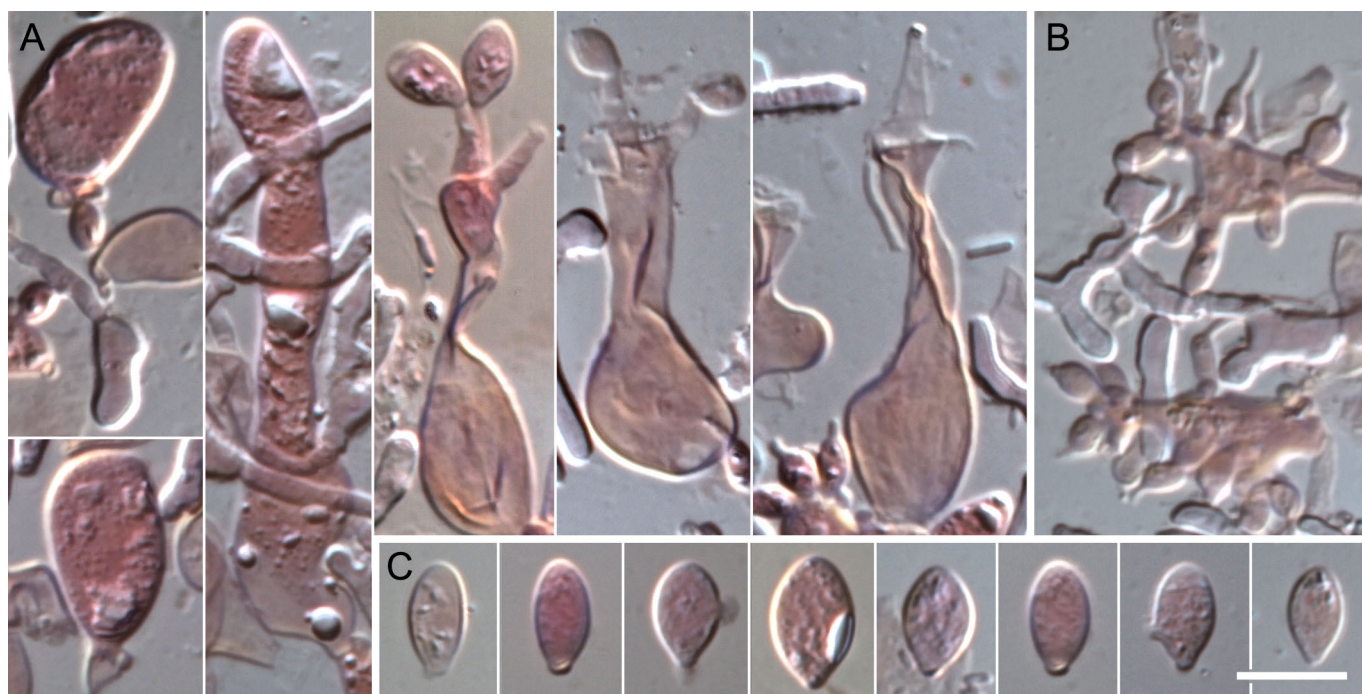
Basidiomata waxy-gelatinous, medium orange-brown, convex, with a slightly constricted base, mostly agglomerate to almost tuberculate, inducing gall formation, 0.2–0.7 mm diam., agglomerations up to 1.8 mm diam. **Sterile hyphae** thick-walled, 2–6 μ m diam., subbasidial hyphae 3–4 μ m diam., without clamps; haustoria frequent, with a basal clamp. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, broadest near the basis, 31–65 \times 8–11.5 μ m, with 3–4 sterigmata, 2–2.5 μ m diam., 5–9 μ m long. **Basidiospores** ellipsoid or ovoid to almost limoniform, 9–12.5 \times 5–7.5 μ m. **Asexual stage** not observed.

Notes. This species is distinguished from the other *Polyblastidium*-inhabiting species by the relatively small, agglomerate basidiomata and the particularly large basidiospores (they are 6.5–8.5 \times 4.5–5.5 μ m in *Z. polyblastidii*). Phylogenetically, this species is distinct from all other known *Zyzygomycetes* species.

It is a pleasure for us to dedicate the new species to Roland Moberg, Swedish lichenologist, world expert of *Physciaceae* and collector of the new species.



Zyzygomycetes mobergii, Australia, Moberg A74:11. Basidiomatal galls on the thallus of *Polyblastidium cf. japonicum*. Scale bar: 1 mm.



Zyzygomycetes mobergii, Australia, holotype. A, Probasidia and mature basidia in various stages of development. B, Hyphae with haustoria. C, Basidiospores. In ammoniacal Congo red pre-stained with phloxine. Scale bar: 10 μ m.



Zyzygomycetes mobergii

Ecology and host. On the thallus of *Polyblastidium* cf. *japonicum*.

Distribution. Oceania (Australia: New South Wales) known only from the type locality.

***Zyzygomycetes physciacearum* (Diederich) Diederich, Millanes & Wedin, comb. nov.**

Heterocephalacria physciacearum (Diederich) Millanes & Wedin, in Liu et al., *Studies in Mycology* 81: 120 (2016); *Syzygospora physciacearum* Diederich, *Bibl. Lichenol.* 61: 38 (1996). **Type:** Sweden, Närke, St. Mellösa par., Mellersta Gundholmen, on saxicolous *Physcia dubia*, 27 Aug. 1929, R. Johansson & E. Julin s. n. (UPS – holotype; BR – isotype).

Mycobank: MB844623

Basidiomata waxy-gelatinous, pale to dark brown, typically with a darker granular pigmentation in the central part,

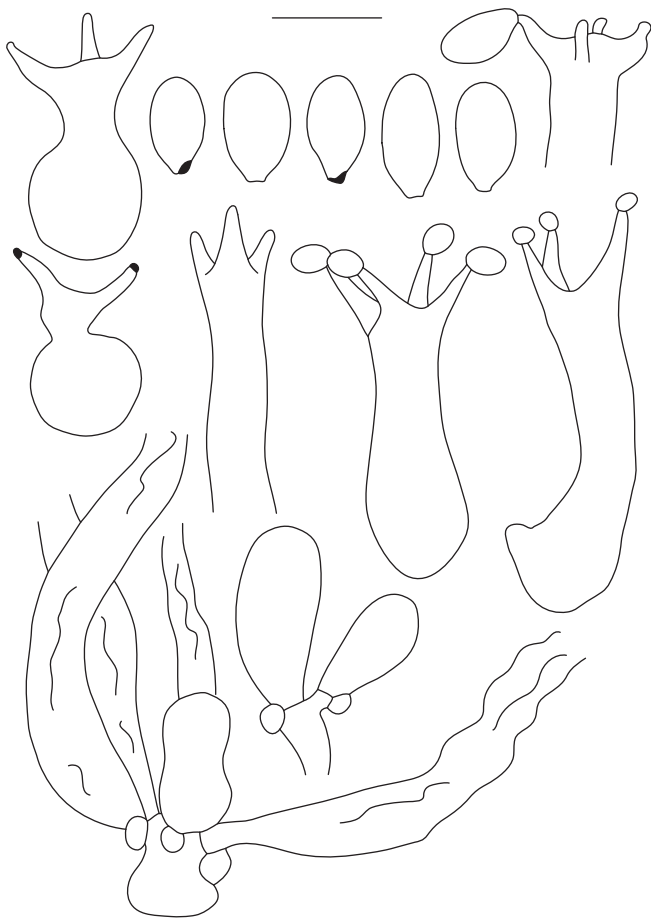
rarely dark brown to black, convex, often with a constricted base, not or indistinctly tuberculate when old, inducing gall formation, 0.15–0.75 mm diam. *Subbasidial hyphae* 3.5–5.5 μ m thick; *haustoria* present, with a basal clamp. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp, and/or numerous asteroconidia-producing conidiophores. *Basidia*, when mature, 22–68(–82) \times 4–7 μ m, with 2–4 sterigmata, 1–2.5 μ m diam., 5–8 μ m long. *Basidiospores* ellipsoid or ovoid to almost limoniform, 8–12.5 \times 4.5–7.5 μ m. *Asteroconidia* abundant in some specimens, with 4 arms 5–7.5 μ m long; *conidiogenous cells* thick-walled, 19–37 \times 3–5 μ m, the upper half attenuated, apically with numerous small ramifications, each having produced a conidium.

Notes. This species was described for an assemblage of specimens growing on different *Physciaceae* hosts. Diederich (1996) realized that the material was heterogeneous, but without the support of molecular phylogenetics, a splitting in several species was hardly possible at that time. Here we consider that *Zyzygomycetes physciacearum* s. str. is confined to *Physcia* species (except *P. aipolia*) and is characterized by the convex, never distinctly tuberculate basidiomata that are typically pale to dark brown, exceptionally black.

Ecology and hosts. On the thallus of corticolous and saxicolous *Physcia tenella*, *P. adscendens*, *P. biziana*, *P. dubia* (incl. var. *teretiusscula*), *P. leptalea* and *P. stellaris*. In W Europe, the species became very abundant during the past 20 years, in some regions being present on most isolated trees in urban environments.



Zyzygomyces physciacearum, Sweden, isotype. Basidiomata on the thallus of *Physcia dubia*. Scale bar: 500 µm.



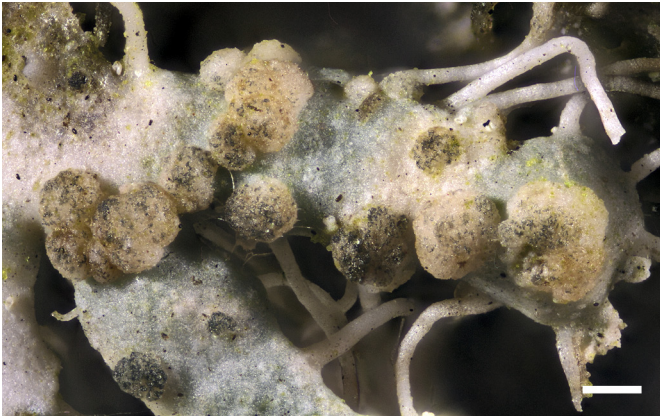
Zyzygomyces physciacearum, Sweden, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 µm.

Distribution. Europe (Austria; Belarus; [Belgium](#); Denmark; Estonia; Finland; France; Germany; Greece; Hungary; Ireland; Italy; Latvia; Liechtenstein; Lithuania; Luxembourg; Netherlands; Norway; Poland; Russia; Spain; Sweden; Switzerland; UK), Macaronesia (Canary Islands) and North America (Canada: Ontario; USA: California, Oregon, Washington).

Selected additional specimens examined. **Austria:** Oberösterreich: Donautal, Schlögener Schlinge, Steiner Felsen, on *Physcia dubia* var. *teretiusscula*, 1994, Berger 7409 (BR, herb. Berger); id., Donaublockwurf bei Stkm 2185.5, 2014, Berger 28744 (herb. Berger). **Belgium:** Lischert, on *P. tenella*, 2001, Diederich 15122 (BR; S). **Canary Islands:** Tenerife: S of Los Silos, Erjos, 28°19'N, 16°48'W, 1100 m, on *Physcia adscendens*, 2007, Diederich 16568 (BR). **France:** Jura: S Champagnole, W Ilay, cadscades de l'Hérissou, on *P. tenella*, 2007, Diederich 16668 (BR). **Italy:** Basilicata, Prov. di Potenza, Monticchio Bagni, 450 m, on *P. biziana*, 2010, Brackel 5663 (herb. Brackel). Lazio, Prov. di Latina, Monti Lepini, Saiano WSW Privesno, 215 m, on *P. biziana*, 2013, Brackel 6830 (herb. Brackel). **Luxembourg:** Between Grevenmacher and Pötschberg,



Zyzygomyces physciacearum



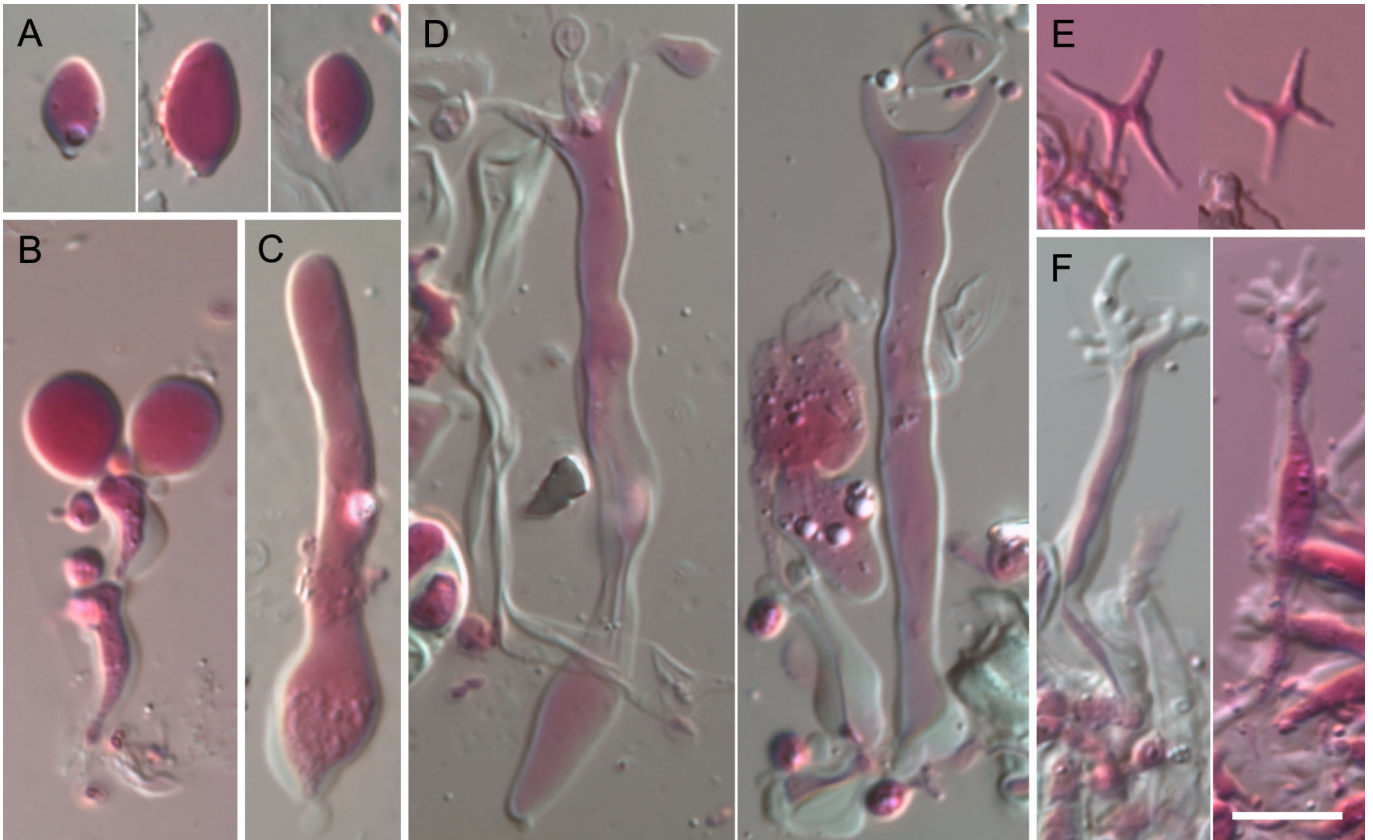
Zyzygomyces physciacearum, Luxembourg, Diederich 17715. Basidiomatal galls on the thallus of *Physcia adscendens*. Scale bar: 200 μ m.



Zyzygomyces physciacearum, Italy, Brackel 5663. Basidiomatal galls on the thallus of *Physcia biziana*. Scale bar: 500 μ m.

49.6730°N, 6.4142°E, 212 m, on *P. adscendens*, 2013, Diederich 17715 (BR). **Netherlands:** Friesland, Ameland, E of Nes, on *P. tenella*, 1995, van den Boom 17529 (BR, herb. van den Boom). **Spain:** Mallorca: NW Bunyola, 1.5 km SW Orient, 39°42'30"N, 2°44'50"E, 430 m, on *P. adscendens*, 2010, Diederich 16913 (BR). **Sweden:** Västmanland, Arboga, Nedre Löten, W of Säby, on a roof of tiles, on *P. dubia*, 1950, Kjellmert, Magnusson *Lich. sel. scand. exs.* 414 (as '*Physcia dubia* f. *angustata*') (BR, UPS). Långelän-

da, Svanesund, on saxicolous '*P. teretiuscula*', 1930, Magnusson 12246 (BR, UPS). **UK:** Scotland: Argyll, N of Tighnabruaich, on saxicolous *P. tenella*, 2003, Diederich 15631 (BR). **USA:** California: Santa Barbara Co., South Fork, La Brea Canyon, on *P. adscendens*, 1985, Bratt 4595 (SBBG). Minnesota: Chippewa National Forest, c. 14.58 km W of Federal Dam and 15.59 km S of Schley, on Ottertail Point, 47.2289°N, 94.4022°W, on *P. adscendens*, 2014, Thayer 41 (BR).



Zyzygomyces physciacearum. A–D, UK, Scotland, Diederich 15631, E–F, Belgium, Diederich 15122. A, Basidiospores. B, Probasidia with basal clamps, and haustoria. C, Immature basidium. D, Mature basidia and old basidium remnants (left). E, Asteroconidia. F, Asteroconidia-producing conidiogenous cells. In phloxine. Scale bar: 10 μ m.

Selected references (all as *Syzygospora/Hetereocephalacria physciacearum* on *Physcia adscendens*, *P. leptalea* or *P. tenella*). Diederich 1996 [Berger 2019, Brackel 2011, 2013, 2015, 2020, Brackel & Berger 2019, Brackel & Puntillo 2016, Brinker 2020, Czarnota & Kukwa 2010, Diederich 2003, Eckstein et al. 2021, Etayo 2010, Hafellner 2018a, 2020, Hafellner & van den Boom 2018, John et al. 2011, Kocourková et al. 2012, Kukwa et al. 2013, Rettig 2016, 2018, Roux 2000, Schiefelbein et al. 2018, Suija et al. 2020, Thor & Söchting 2018, Tsurukau et al. 2016, Urbanavichene et al. 2013, van den Boom 2015, van den Boom & Ertz 2012, van den Boom & Etayo 2014, Varga et al. 2021, Zimmermann & Feusi 2021].

***Zyzygomyces physconiae* Diederich, Millanes, P. Pinault & Brackel, sp. nov.**

Diagnosis: Characterized by the waxy-gelatinous, uniformly reddish brown basidiomata, mainly on the thallus of *Physconia* species, 0.15–0.8 mm diam., the 2–4-sterigmate basidia, $28\text{--}50 \times 4.5\text{--}7\text{ }\mu\text{m}$, and the broadly ellipsoid basidiospores, $7.5\text{--}9.5 \times 6\text{--}8\text{ }\mu\text{m}$.

Etymology: From *Physconia*, the host lichen.

Type: France, Puy-de-Dôme, Châteaugay, c. 1 km NE des Caves, 45.8614°N, 3.1082°E, 520 m, on *Quercus*, on *Physconia grisea*, 10 May 2020, P. Pinault s. n. (BR – holotype).

Mycobank: MB844624

Basidiomata waxy-gelatinous, uniformly medium to dark reddish brown, often covered by a whitish pruina from the host, convex, often with a constricted base, often irregular in form but never tuberculate, inducing gall formation, 0.15–0.8 mm diam., occasionally developing a basidioma on each soredium of parasitized soralia, resulting in an agglomeration of numerous small basidiomata resembling a large tuberculate basidioma, up to 2 mm diam. *Subbasidial hyphae* thick-walled, $3\text{--}6\text{ }\mu\text{m}$ diam., clamp connections not observed; haustoria frequent, with a basal clamp. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp, and/or numerous asteroconidia-producing conidi-

ophores. *Basidia*, when mature, $28\text{--}50 \times 4.5\text{--}7\text{ }\mu\text{m}$, with 2–4 sterigmata, $1.5\text{--}2.5\text{ }\mu\text{m}$ diam., $4\text{--}8\text{ }\mu\text{m}$ long. *Basidiospores* broadly ellipsoid or ovoid to almost limoniform, $7.5\text{--}9.5 \times 6\text{--}8\text{ }\mu\text{m}$. *Asteroconidia* abundant in some specimens, with 4 arms $5\text{--}7.5\text{ }\mu\text{m}$ long; *conidiogenous cells* thick-walled, $21\text{--}41 \times 3\text{--}8\text{ }\mu\text{m}$, the upper half attenuated, apically with numerous small ramifications, each having produced a conidium.

Notes. This species is phylogenetically distinct from all other sequenced *Zyzygomyces* species. It is distinguished from the other *Physcia*-inhabiting species by the reddish brown basidiomatal galls. We include here all specimens seen by us or reported in the literature from *Physconia* hosts.

Ecology and hosts. On the thallus of *Physconia grisea*, *P. americana*, *P. californica*, *P. detersa*, *P. distorta*, *P. enteroxantha*, *P. fallax*, *P. isidiigera*, *P. perisidiosa* and *P. venusta*.

Distribution. Europe (France; Germany; Italy; Netherlands; Spain) and North America (USA: California, Oregon, Washington).

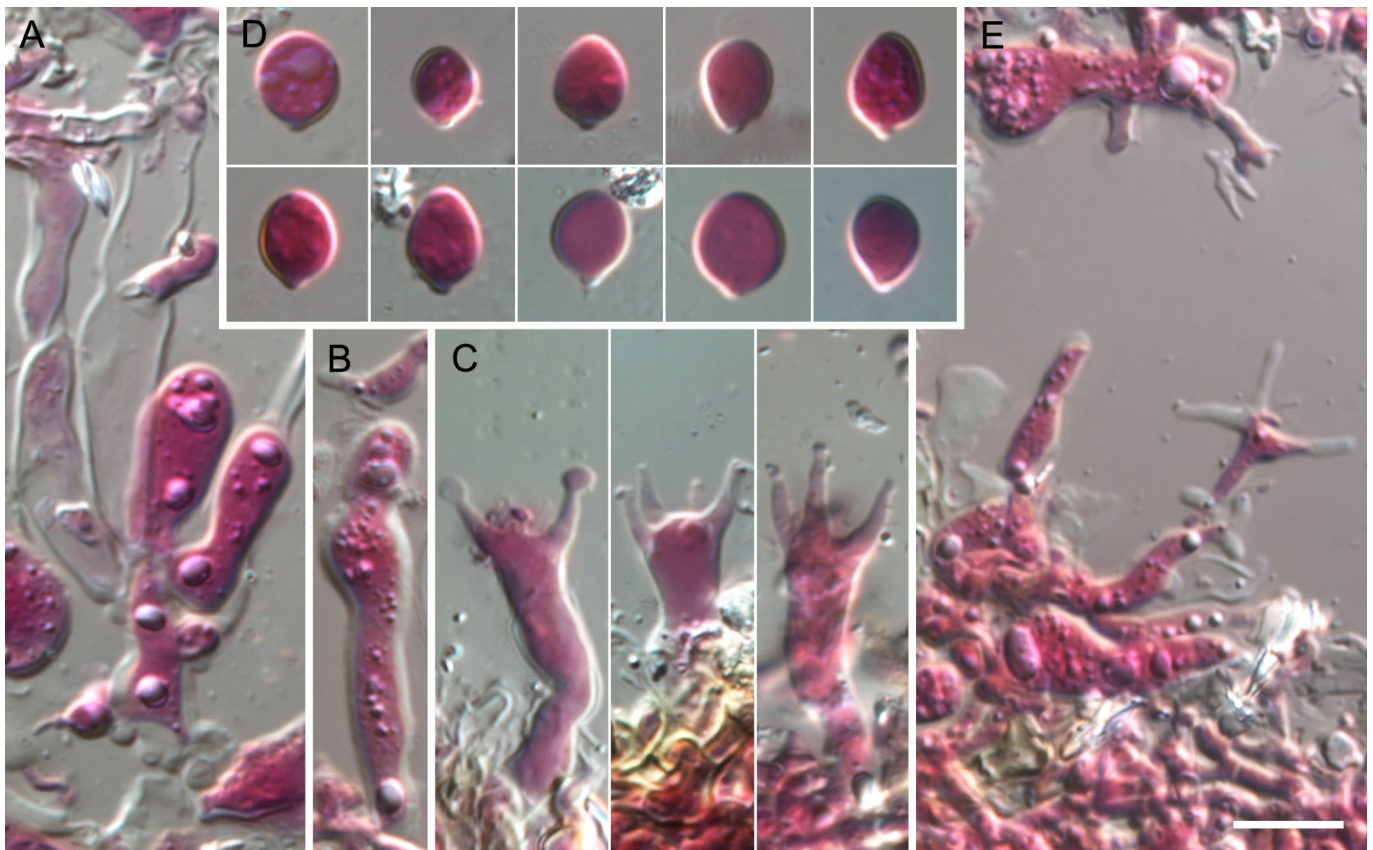
Additional specimens examined (*specimens seen by Diederich 1996, not re-examined in 2022). **France:** *Alpes-de-Haute-Provence:* Forcalquier, on *P. grisea*, 1996, Diederich 12952 (BR). *Bouches-du-Rhône:* Le Grand Caunet, Font Blanche, 400 m, on *P. grisea*, 2013, Poumarat 2013-336 (BR). Puy-de-Dôme, same locality as type, on *P. grisea*, 2020, Pinault (BR). **Italy:** *Emilia-Romagna:* Prov. Bologna, Ponticella, Parco Regionale Gessi Bolagnesi, Via Palazza, on *P. grisea*, 2019, Brackel 8100 (herb. Brackel). *Sardegna:* Prov. Oristano, Sarcidano, Borgo Pirastesa E Laconi, on *P. venusta*, 2014, Brackel 7402 (herb. Brackel). *Toscana:* Prov. Arezzo, c. 18 km SSW Arezzo, Santuario Santa Maria delle Vertighe, 43.3296°N, 11.7514°E, 280 m, on *P. grisea*, 2020, Diederich 19579 (BR); Livorno, Allee von Bolgheri, on *P. grisea*, 2013, Brackel 6882 (herb. Brackel); prov. Pistoia, Pracchia, on *P. grisea*, 2018, Brackel 8062 (herb. Brackel); prov. Siena, Colle Val d'Elsa, on *P. grisea*, 2012, Brackel 6579 (herb. Brackel). **Netherlands:** *Limburg:* ESE of Maastricht, W of Wittem, castle, on *P. grisea*, 2021, van den Boom 60228 (herb. van den Boom); *Noord-Holland:* Castricum, on *P. grisea*, 1986, Apt-



Zyzygomyces physconiae, France, holotype. Basidiomatal galls on the thallus of *Physconia grisea*. Scale bar: 500 μm .



Zyzygomyces physconiae, France, holotype. Pruinoso basidiomatal galls on the thallus of *Physconia grisea*. Scale bar: 500 μm .



Zyzygomyces physconiae. A, Italy, Brackel 8062, B–E, France, holotype. A, Fertile hypha with clamped haustorium, clamped probasidia and old collapsed basidia. B, Immature basidium. C, Mature basidia. D, Basidiospores. E, Asteroconidia-producing conidiogenous cells with one asteroconidium. In phloxine. Scale bar: 10 μ m.

root 17032 (BR)*; Hoorn, harbour, on brick of wall, on *P. grisea*, 1997, Aptroot 40187, 40188 (BR). **Spain:** *Navarra*: Pamplona, parque de la Taconera, on *P. grisea*, 1993, Etayo (herb. Etayo)*. **USA:** *California*: Lake Co., Clear Lake State Park, on Soda Bay on S side of Clear Lake, on Soda Bay Rd E of Finley near Lakeport, on *P. sp.*, 1992, Tucker 31710A (SBBG); Madera Co., Bass Lake, North Fork road, Sierra National Forest, on *P. deterosa*, 1985, Bratt 4794 (IMI 298272)*; Mariposa Co., Yosemite National Park, near Old El Portal, Merced River Bridge on CA140, 37.6720°N, 119.7924°W, 653 m, on *P. sp.*, 2009, Lendemer 19666 (NY); Riverside Co., Peninsular Range, San Bernardino National Forest, San Jacinti Mountains, vicinity of Boxwood Spring (Halfway Spring), N facing slope above North Fork San Jacinto River, Blackburn Canyon Quad, 33°44'31"N, 116°47'11"W, 3796 ft,



Zyzygomyces physconiae

on *P. californica*, 2008, Lendemer 11498 (NY); San Diego Co., Cleveland National Forest, S of Paloma Ravine, along the S side of Sunrise Road, 32°51'09"N, 116°27'09"W, 6000 ft, on *P. fallax*, 2004, Lendemer 2724 (BR, NY); San Luis Obispo Co., along Lopez Canyon Road, N of Lopez Lake, on *P. enteroxantha*, 1986, Bratt 5061 (SBBG); San Luis Obispo Co., on side road to Cerro Alto campground off Cal. State Hwy 41, 6.9 mi NE from junction with State Hwy 1 N of Morro Bay, on *Quercus*, on *P. sp.*, 1996, Tucker 34623 (SBBG); Santa Barbara Co., Davey Brown trailhead on road 7NO7, Figueroa Mountain, Los Padres National Forest, San Rafael Range, 34°43'47"N, 119°58'14"W, 4000 ft, on *P. americana*, 1998, Tucker 35934 (SBBG); Santa Barbara Co., Sierra Madre Mts, Hwy 166 near Tepusquet Rd, on *P. sp.*, 2010, Hollinger 1305 (UBC); Tuolumne Co., Riverside Park, on N Fork of Tuolumne River, Buchanan Mine Rd, E of Sonora, on *P. californica*, 2005, Tucker 38630 (SBBG). *Washington*: Columbia River Gorge, Klickitat River, 20 km N of the Dalles on Hwy 142, 45°50'N, 121°10'W, on *P. distorta*, 1990, Goward 90-462A (BR, UBC).

References (all as *Syzygospora/Heterocephalacria physciacearum* on *Physconia*). Diederich 1996 [Brackel 2015, Brackel & Berger 2019, Diederich 2003, Etayo 2010, Kocourková et al. 2012, Tucker 2014].

Zyzygomyces polyblastidii Diederich, Flakus, Etayo & Rodr. Flakus, sp. nov.

Diagnosis: Characterized by the waxy-gelatinous, uniformly orange to dark brown basidiomata on *Polyblastidium japonicum*, 0.3–1.5 mm diam., the (2–)3-sterigmate basidia, $35\text{--}54 \times 3.5\text{--}7.5 \mu\text{m}$, and the ellipsoid basidiospores, $6.5\text{--}8.5 \times 4.5\text{--}5.5 \mu\text{m}$.

Etymology: From *Polyblastidium*, the host lichen.

Type: Bolivia, Dept. Tarija, Prov. Burnet O'Connor, close to Soledad, old road between Entre Ríos and Chuquisaca, $21^{\circ}39'45''\text{S}$, $64^{\circ}07'22''\text{W}$, 1750 m, Bolivian-Tucuman forest with shrubs and *Alnus acuminata*, on *Polyblastidium japonicum* 31 July 2015, A. Flakus 27763 (KRAM – holotype; LPB – isotype).

MycoBank: MB844625

Basidiomata waxy-gelatinous, uniformly medium orange to dark brown, convex, with a slightly constricted base, not tuberculate, inducing gall formation, 0.3–1.5 mm diam. **Subbasidial hyphae** thick-walled, $2.5\text{--}3.5 \mu\text{m}$ diam., clamp connections not observed; haustoria frequent, with a basal clamp. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, $35\text{--}54 \times 3.5\text{--}7.5 \mu\text{m}$, with (2–)3 sterigmata, $1.5\text{--}2.5 \mu\text{m}$ diam., $5\text{--}7.5 \mu\text{m}$ long. **Basidiospores** ellipsoid or ovoid to almost limoniform, $6.5\text{--}8.5 \times 4.5\text{--}5.5 \mu\text{m}$. **Asexual stage** not observed.

Notes. This species resembles *Zyzygomyces physconiae* by the brown, non-tuberculate basidiomata, but is distinguished

by the narrower basidiospores, $4.5\text{--}5.5 \mu\text{m}$ vs $6\text{--}8 \mu\text{m}$ wide. *Zyzygomyces mobergii*, also growing on *Polyblastidium* cf. *japonicum*, is distinguished by the smaller, agglomerate to almost tuberculate basidiomata, basidia that are basally much broader, $8\text{--}11.5 \mu\text{m}$, and much larger basidiospores, $9\text{--}12.5 \times 5\text{--}7.5 \mu\text{m}$. Both species are also phylogenetically distinct.

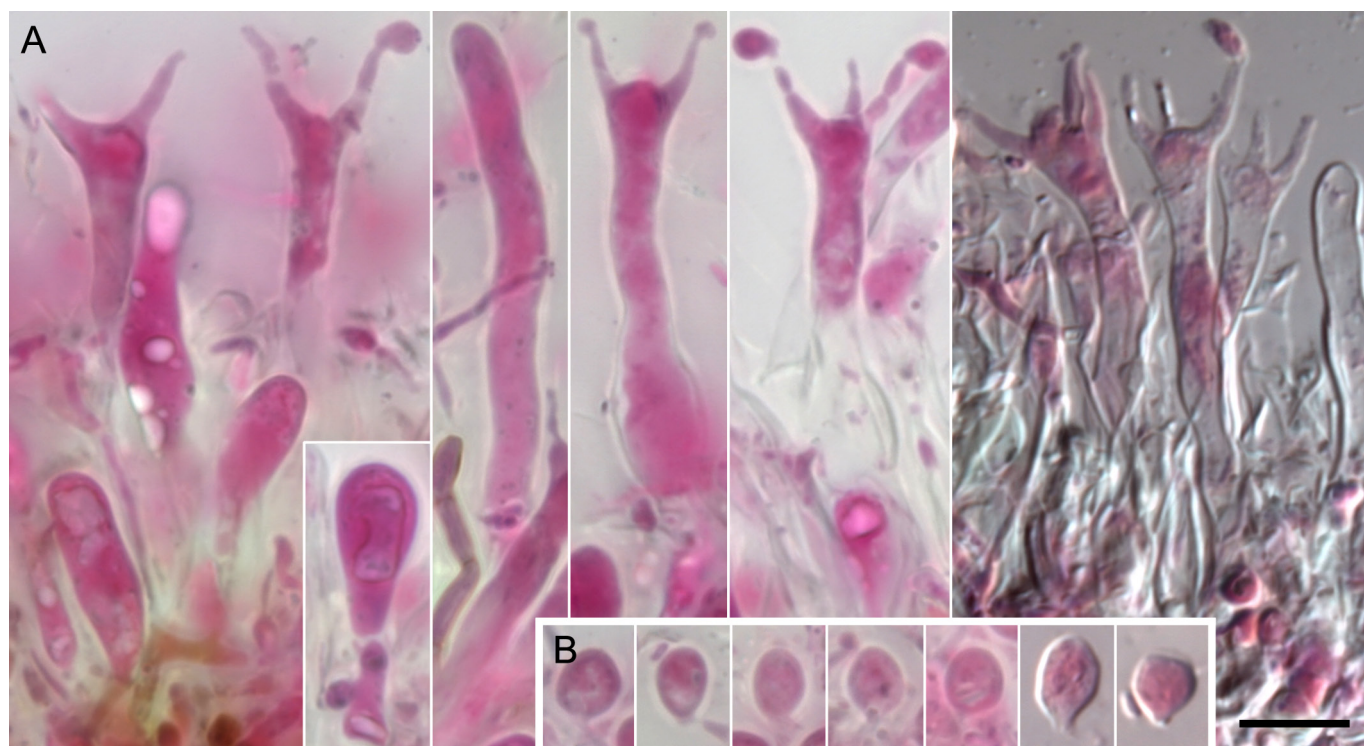
Ecology and host. On the thallus of *Polyblastidium japonicum*.

Distribution. South America (Bolivia).

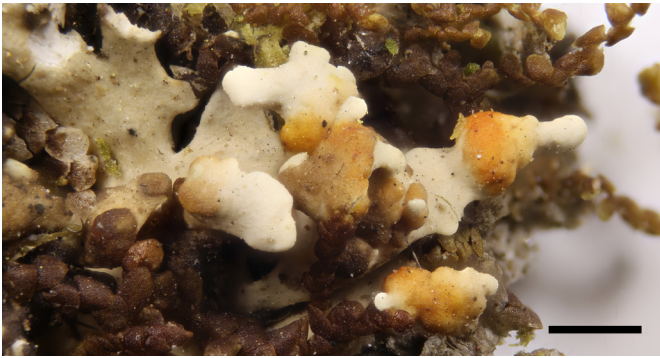
Additional specimen examined. **Bolivia:** Same locality as type, Etayo 30521 (LPB). Dept. Tarija, Prov. Burnet O'Connor, 60 km from Tarija, new road between Tarija and Entrer Ríos, $21^{\circ}28'52''\text{S}$, $64^{\circ}17'41''\text{W}$, 1837 m, on *Polyblastidium japonicum*, 2015, Etayo 30678 (LPB, herb. Etayo).



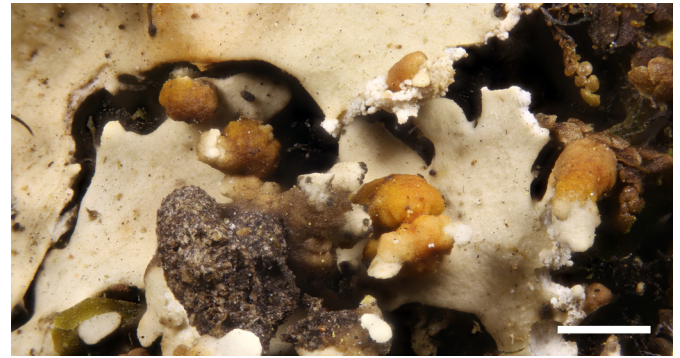
Zyzygomyces polyblastidii s. str.



Zyzygomyces polyblastidii s. str., Bolivia, holotype. A, Basidia in various stages of development. B, Basidiospores. In phloxine. Scale bar: 10 μm .



Zyzygomycetes polyblastidii s. str., Bolivia, holotype. Basidiomatal galls on the thallus of *Polyblastidium japonicum*. Scale bar: 1 mm.



Zyzygomycetes polyblastidii s. str., Bolivia, holotype. Basidiomatal galls on the thallus of *Polyblastidium japonicum*. Scale bar: 1 mm.

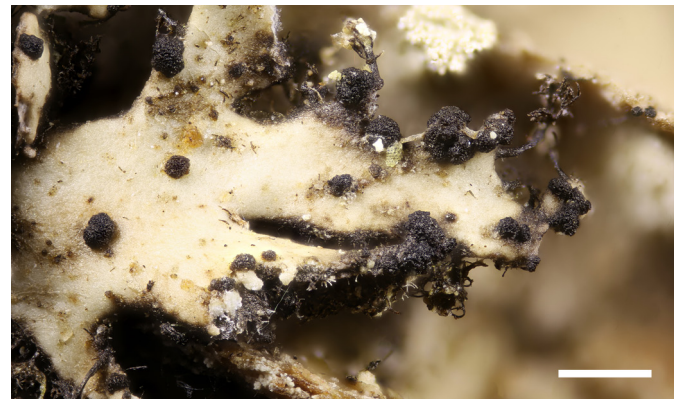
Zyzygomycetes polyblastidii Diederich, Flakus, Etayo & Rodr. Flakus, s. lat.

Several *Polyblastidium*-inhabiting *Zyzygomycetes* specimens are phylogenetically only distantly related to *Z. polyblastidii* s. str. or have not been sequenced and need further study, and may provisionally be called *Z. polyblastidii* s. lat.

Distribution. North America (USA: North Carolina), South America (Bolivia; Colombia; Ecuador), Africa (Ethiopia) and Oceania (Papua New Guinea).

Specimens examined (on *Polyblastidium* cf. *japonicum*). **Bolivia:** Dept Chuquisaca, Prov. Hernando Siles, 15 km W of Monte Agudo, 19°48'57"S, 64°05'60"W, 1815 m, 2015, Flakus 26844 (KRAM, LPB). Dept. Cochabamba, Prov. Carrasco, Parque Nacional Carrasco, near Río Lopez Mendoza, 17°30'25"S, 65°16'51"W, 2248 m, 2014, Flakus 25681 (KRAM, LPB). Dept. Tarija, Prov. Burnet O'Connor, between Tarija and Entre Ríos, 21°27'50"S, 64°12'51"W, 1924 m, 2015, Etayo 29935 (LPB, herb. Etayo). Dept. Tarija, Prov. O'Connor, 26 km from Entre Ríos, near Soledad, 21°39'52"S, 64°07'22"W, 1700 m, 2012, Etayo 28780 (herb. Etayo). Dept. La Paz, Prov. Saavedra, km 202 on road from Apolo to Charazani villages, 20 km from Charazani, 15°12'35"S, 68°51'30"W, 2259 m, 2011, Etayo 27414 (LPB). **Colombia:** Nariño, Municipio Pasto, Corregimiento El Encano, Res. Nat. Tunguragua, SE Lake La Cocha (Guamués), 2700 m,

1998, Etayo 15854 (herb. Etayo). **Ecuador:** Prov. Loja, Sierra Sur, Loja, Cajanuma, Parque Nac. Podocarpus, 2750-3000 m, 1999, Etayo 20137 (herb. Etayo). **Ethiopia:** Prov. Godjam, Insel Entons im Tana-See, 1966, Sebald (STU). **Papua New Guinea:** Simbu prov., Mount Wilhelm, Pindaunde valley, near lake Piunde, 1992, Diederich 10209 (BR). **USA:** *North Carolina:* Graham Co., Nantahala National Forest, Tsali Recreation Area, S shore of Fonatana Lake, Mouse Branch Loop between Murphy Gap and jct of FSR1286 and FSR2550, 35°24'26"N,



Zyzygomycetes polyblastidii s. lat., Bolivia, Flakus 25681. Blackish basidiomatal galls on the thallus of *Polyblastidium* cf. *japonicum*. Scale bar: 500 µm.



Zyzygomycetes polyblastidii s. lat., Papua New Guinea, Diederich 10209. Basidiomatal galls on the thallus of *Polyblastidium* sp. Scale bar: 1 mm.



Zyzygomycetes polyblastidii s. lat., USA, North Carolina, Lendemer 46912. Basidiomatal galls on the thallus of *Polyblastidium* sp. Scale bar: 500 µm.

83°35'35"W, 1830 ft, 2016, Lendemer 46912 (NY); Swain Co., Great Smoky Mountains National Park, terminus of Lakeshore Drive to jct of Lakeshore Trail and White Oak Branch Trail, 35°28'N, 83°33'W, 2010, Lendemer 23503 (NY).

Zyzygomyces* sp. 1 on *Heterodermia isidiophora

Basidiomata waxy-gelatinous, medium to dark reddish brown, applanate to convex, not tuberculate, often irregular in outline, inducing gall formation, 0.2–0.6 mm diam. *Hymenium* examined overmature, with only a few remnants of old basidia observed.

Notes. The specimen is very much overmature, and only a few remnants of old basidia were seen. Phylogenetically, it is distinct from all other sequences and thus represents an undescribed *Zyzygomyces* species possibly confined to *Heterodermia* s. str.

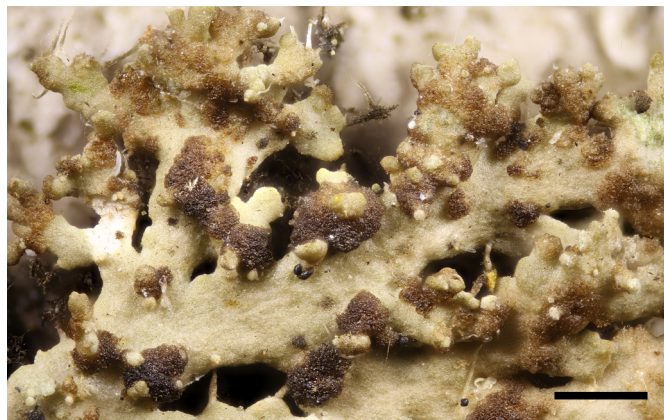
Ecology and host. On the thallus of *Heterodermia isidiophora*.

Distribution. Asia (Japan).

Specimen examined. **Japan:** Honshu, Tochigi Prefecture, Shimotsuke Province, Nikko City administrative region, Nikko National Park, 2.2 km NNE of Yumoto village (Yumoto Onsen), western shore of lake Karikomi, 36°49'27"N, 139°25'52"E, 1618 m, on *Heterodermia isidiophora*, 2019, Ertz 24665 (BR).



Zyzygomyces sp. 1 on *Heterodermia isidiophora*



Zyzygomyces sp. 1, Japan, Ertz 24665. Basidiomatal galls on the thallus of *Heterodermia isidiophora*. Scale bar: 500 µm.

Zyzygomyces* sp. 2 on *Heterodermia* gr. *comosa

Basidiomata waxy-gelatinous, whitish, convex, tuberculate, inducing gall formation, 0.2–0.7 mm diam. *Haustoria* frequent, with a basal clamp. *Hymenium* containing ellipsoid probasidia, basal clamp not observed. *Basidia*, when overmature, c. 36 µm long, with 3 sterigmata ($n = 1$), c. 5–5.5 µm long. *Basidiospores* ovoid, 8×6 µm ($n = 1$). *Asexual morph:* asteroconidia present in specimen Tucker 6269.

Notes. The recently examined specimen contains probasidia and few overmature basidia, thus not suitable for a formal description. The material differs from the other *Zyzygomyces* species by the whitish tuberculate basidiomatal galls.

Ecology and hosts. On the thallus of *Heterodermia* gr. *comosa*, incl. *H. erinacea*.

Distribution. North America (USA: California) and Oceania (Papua New Guinea).

Specimens examined. **Papua New Guinea:** Northern Province: Owen Stanley Range, Myola, 9°09'S, 147°46'E, 2100 m, small shrubs in grassland, on *Heterodermia* gr. *comosa*, 1995, Sérusiaux (LG). **USA:** California: Santa Cruz County, Summit Ridge Road, on *H. erinacea*, 1966, Tucker 6269 (SBBG) [specimen seen by Diederich 1996, not re-examined in 2022].

Reference. [Diederich 1996 as *Syzygospora physciacearum*].



Zyzygomyces sp. 2 on *Heterodermia* gr. *comosa*



Zyzygomyces sp. 2, Papua New Guinea, Sérusiaux s. n. Basidiomatal galls on the thallus of *Heterodermia* gr. *comosa*. Scale bar: 1 mm.

Zyzygomyces* sp. 3 on *Physcia albinea

Basidiomata waxy-gelatinous, medium to dark reddish brown, convex, not tuberculate, inducing gall formation, 0.15–0.7 mm diam. *Haustoria* frequent, with a basal clamp. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, $65\text{--}90 \times 5\text{--}7.5\ \mu\text{m}$, with at least 2 sterigmata ($n = 1$), c. $5.5\ \mu\text{m}$ long. *Basidiospores* not seen. *Asexual morph* not observed.

Notes. Amongst the *Zyzygomyces* species confined to *Physcia* s. str., basidiomata in this species clearly differ from *Z. physciacearum* by the red-brown colour, and from *Z. aipoliae* by the more delimited galls on the apothecial margin and thallus. Further, basidia are much longer than in these three species. It resembles other species with reddish brown basidiomata on *Heterodermia* s. lat., but the assumed host specificity of all these taxa suggests a different, yet undescribed species.

Ecology and host. On the thallus and apothecia of *Physcia albinea*.

Distribution. North America (USA: California).

Specimen examined. USA: California: Santa Ynez Mtns, top of Refugio Pass, on *Quercus*, on *Physcia albinea*, 1981, Bratt 2262 (BR, SBBG).



Zyzygomyces sp. 3 on *Physcia albinea*



Zyzygomyces sp. 3, USA, California, Bratt 2262. Basidiomata on the thallus and apothecia of *Physcia albinea*. Scale bar: 500 μm .

Zyzygomyces* sp. 4 on *Pyxine

Basidiomata waxy-gelatinous, medium to dark brown, convex, often with a constricted base, not tuberculate, inducing gall formation, 0.2–0.5 mm diam. *Hymenium* examined overmature. *Basidia* when overmature, c. $32\ \mu\text{m}$ long, with 3 sterigmata ($n = 2$), c. $5\text{--}7\ \mu\text{m}$ long. *Basidiospores* not seen. *Asexual morph* not observed.

Notes. As the specimen is overmature and in a poor condition, only an incomplete description can be provided. The host choice suggests a distinct, undescribed species.

Ecology and host. On the thallus of an unidentified, corticolous *Pyxine* species with a UV– thallus devoid of vegetative propagules and apothecia.

Distribution. North America (Mexico: Baja California Sur).

Specimen examined. Mexico: Baja California Sur: Sierra de la Laguna, western slopes ESE above Todos Santos, $23^{\circ}29'N$, $109^{\circ}59'W$, 1500 m, on *Pyxine*, 1993, Hafellner 40302 (GZU).

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Zyzygomyces sp. 4 on *Pyxine*



Zyzygomyces sp. 4, Mexico, Baja California Sur, Hafellner 40302. Basidiomatal galls on the thallus of *Pyxine* sp. Scale bar: 500 μm .

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *TREMELLOMYCETES*

Order *TREMELLALES*

by P. Diederich, A. M. Millanes & M. Wedin

Diederich, P., A. M. Millanes & M. Wedin. 2022. Class *Tremellomycetes*, order *Tremellales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 105–282.

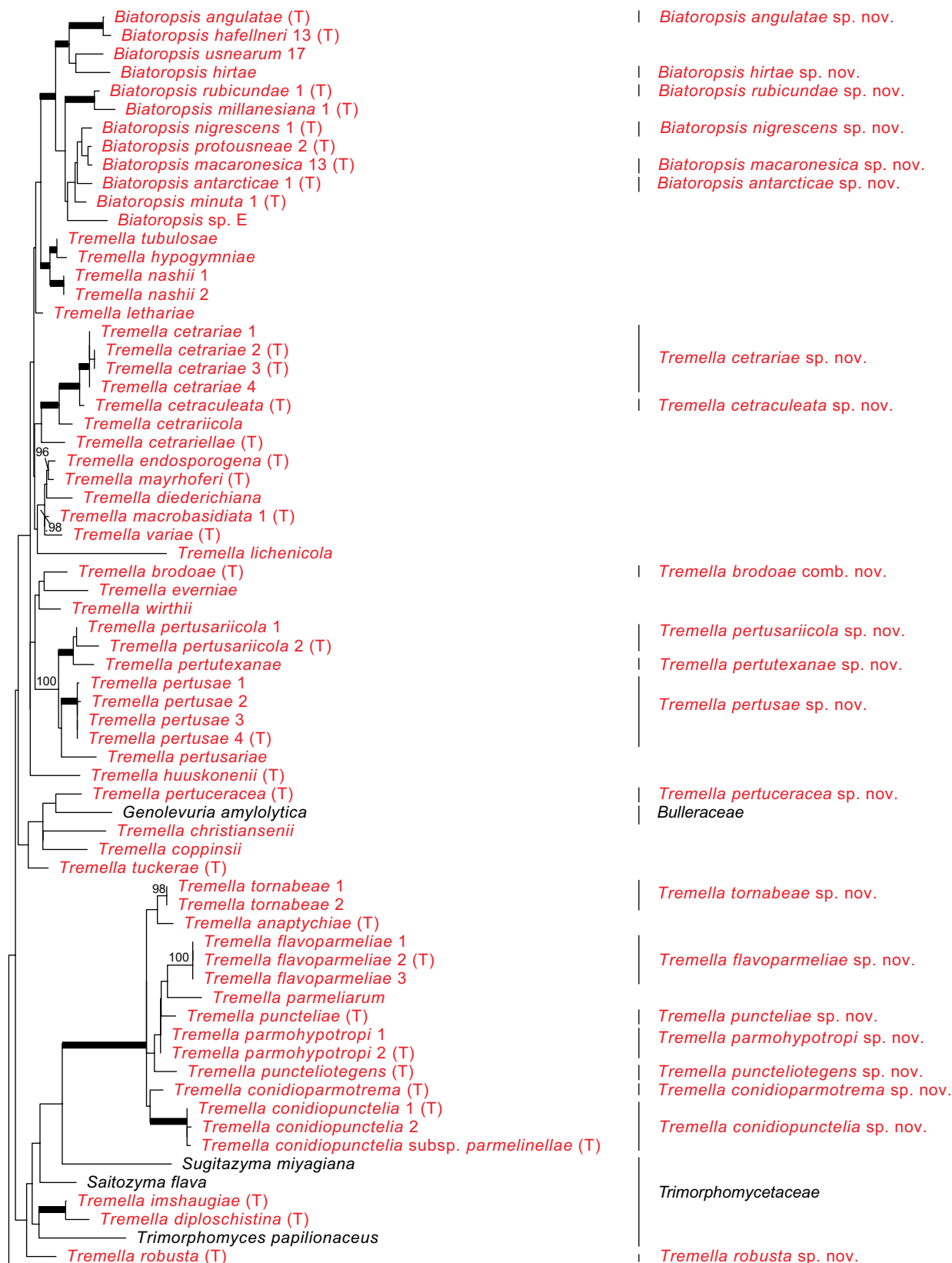
Introduction and phylogeny

The *Tremellales* is a large group of the so-called jelly-fungi, initially circumscribed based on the presence of gelatinous basidiocarps, cruciate septate basidia, and spores germinating by repetition (Martin 1945). Some years later, Bandoni (1984, 1987) achieved detailed studies using both light and transmission electron microscopy, and emended the order *Tremellales* to include taxa with dolipore septa (i. e., septa with a small hole of a particular morphology that allows exchange of cellular contents between adjacent cells) and *Tremella*-type parenthesomes (i. e., cap shaped membranous structures that cover the dolipores), tremelloid basidia, haploid yeast states, and a predominantly mycoparasitic habit. The *Tremellales* currently include 33 genera distributed in 11 families: *Bulleraceae*, *Bulleribasidiaceae*, *Carcinomyetaceae*, *Cryptococcaceae*, *Cuniculitremaceae*, *Naemateliaceae*, *Phaeotremellaceae*, *Rhynchogastremaceae*, *Sirobasidiaceae*, *Tremellaceae* and *Trimorphomycetaceae*. The monophyly of these families have been confirmed by multigene phylogenies (Liu et al. 2015a). However, the phylogeny presented in this Flora is based only on ITS and nuSLU, because these are the molecular markers available for most lichenicolous taxa. Therefore, several of the currently accepted families are recovered as polyphyletic in our phylogeny. *Tremella* was earlier the most heterogeneous genus in the *Tremellales* and repeatedly also proved to be strongly polyphyletic. Chen (1998) divided the genus in different subgroups that later adopted the category of genera (Liu et al. 2015b), and *Tremella* s. str. (the only genus currently included in the *Tremellaceae*) is now restricted to the former *Mesenterica* and *Fuciformis* groups. A large number of species are, however, still temporarily named ‘*Tremella*’ although they do not belong in *Tremella* s. str. or in the family *Tremellaceae*. That applies, for instance, to all lichenicolous species in the genus, but also to many other non-lichenicolous species. We anticipate that the generic and family delimitation in the *Tremellales* will suffer from severe rearrangements in the near future. Our taxon sampling for the phylogeny of the *Tre-*

mellales is clearly biased towards lichenicolous species, and we have only included a few representatives of each of the currently accepted families in the group. All sequenced species of lichenicolous *Tremellales* are, however, included in this tree. The aim of our phylogeny is not to deal with family assignments of the lichenicolous taxa but rather to place the sequenced lichenicolous species, which means 27 of the 58 newly described species – plus one subspecies – in a general phylogenetic framework of the *Tremellales*. For larger and more evenly sampled phylogenies of the *Tremellales*, see Liu et al. (2015a, 2015b) and Millanes et al. (2011), but sound phylogenetic hypotheses that include lichenicolous taxa are still missing.

Regarding their life cycle, as it is the case in many heterobasidiomycetes, most species in the *Tremellales* are dimorphic, switching between a haploid unicellular yeast phase and a dikaryotic filamentous phase (Bandoni 1995). One characteristic of the dikaryotic mycelium is that, in nature, it must grow associated with another fungus. As examples of two well-known non-lichenicolous taxa, *Tremella mesenterica* grows associated with corticioid fungi of the genus *Peniophora*, and *Naematelia aurantia* grows associated with *Stereum* species. A number of microscopic taxa, however, grow only as unicellular yeasts in nature and are predominantly saprotrophs, as *Bullera unica*, or animal parasites, as *Cryptococcus neoformans* and *Cryptococcus gattii*, causing the life-threatening human disease cryptococcosis in immunosuppressed patients (Waters & Nelson 2005). Traditionally, yeast and filamentous taxa have been studied by different groups of researchers and therefore the characters selected as traits of taxonomic value have also been completely different: mainly biochemical characters in yeasts, and macro- and micromorphological characters in filamentous species. The desirable trend would be to standardise diagnostic characters as much as possible in all representatives, although this is still a complicated task (Liu et al. 2015). The works by

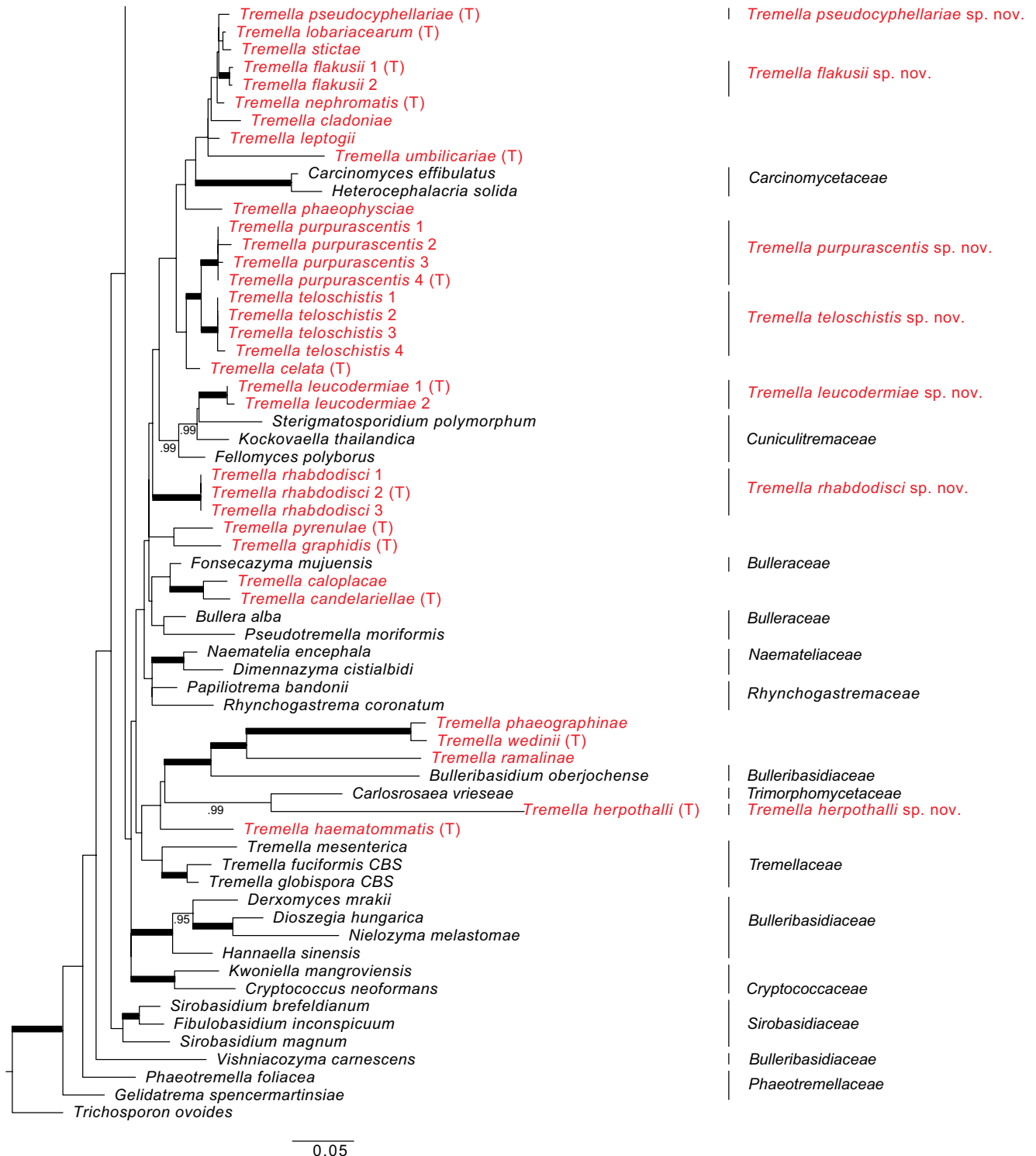
Maximum likelihood phylogeny based on ITS and nuLSU sequences, representing the *Tremellales*. Branches in boldface indicate nodes supported by both Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . When nodes received support only from one of the two methods, ML-BS values ≥ 70 are indicated below branches and Bayesian posterior probabilities values ≥ 0.95 , over branches. Branch lengths are scaled to the expected number of substitutions per site. Red font indicates lichenicolous species. Family assignments of non-lichenicolous taxa, and names of newly described – or newly sequenced – lichenicolous species are indicated in the right margin. Type specimen of lichenicolous species are indicated with ‘(T)’. See tree on pages 108–109 for a larger taxon sampling within *Biatoropsis*. [See tree on pages 106–107.]



Phylogeny of Tremellales. [Caption on page 105; continues on next page.]

Diederich in the mid 1990s revealed for the first time the diversity of lichenicolous species in the group, that had been totally neglected until then. Later, its phylogenetic placement in the *Tremellales* was confirmed by molecular methods (Millanes et al. 2011). The microscopic structures of the lichenicolous taxa are often smaller compared to other more conspicuous tremel-

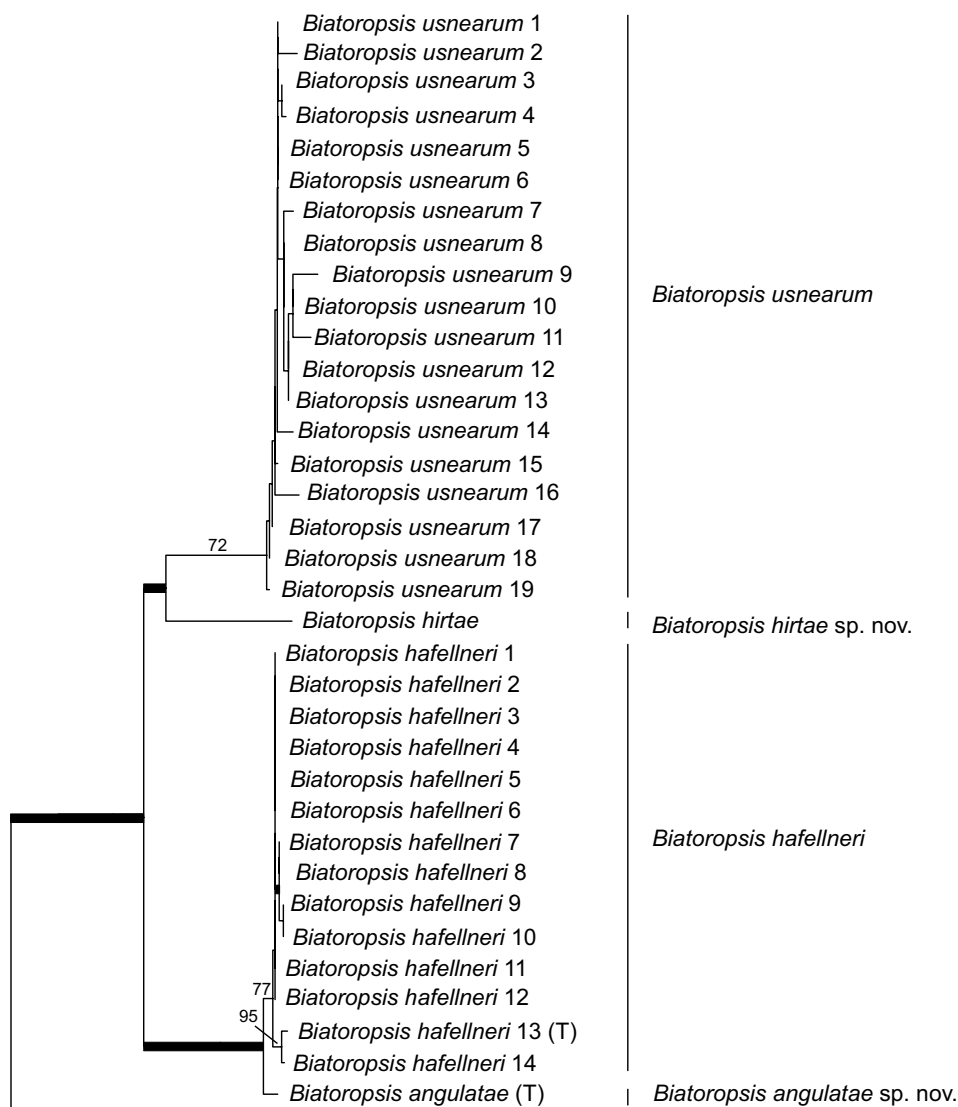
lanean species, and host selection is often a great aid to identify species. The lichenicolous *Tremellales* are in general widespread and follow the geographical distribution of their lichen hosts. Evidence suggests that speciation is driven by host selection rather than by geographical isolation (Werth et al. 2013, Millanes et al. 2014b, 2015, 2016, Diederich & Ertz 2020). Af-



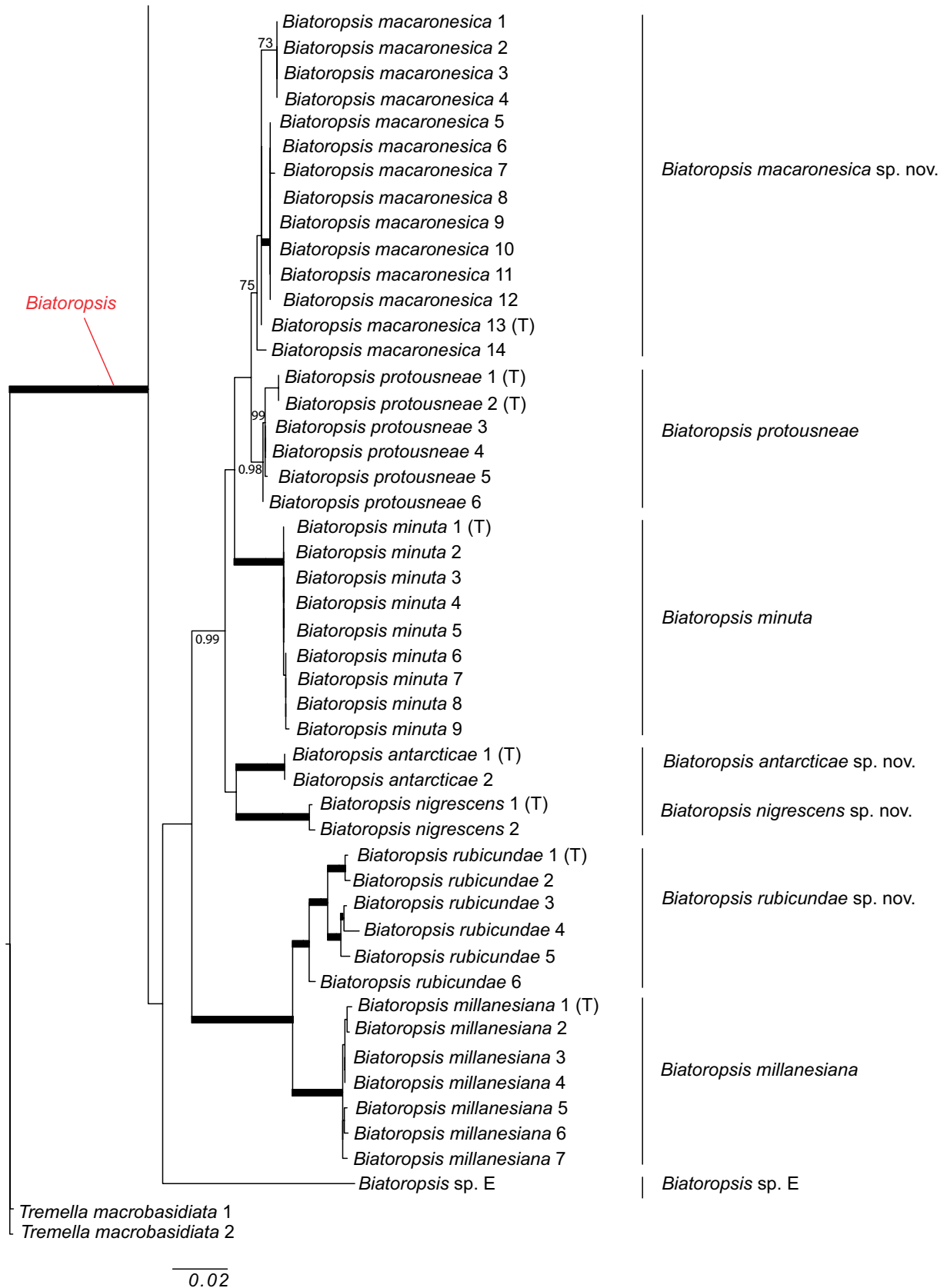
Phylogeny of *Tremellales*. [Caption on page 105; continued from previous page.]

ter Diederich's revision in 1996, numerous lichenicolous species have been discovered and described on new hosts, and this Flora is the most representative example in the past 25 years. In addition, a large amount of overlooked diversity is probably also hidden in several species complexes. One of these is *Biatoropsis*, on which we have made substantial progress during the preparation of this volume, but several other complexes are still under study. *Biatoropsis* is a common and widespread lichenicolous taxon, growing on different hosts of the genera *Usnea* and *Protousnea*. It was first described as an ascomycete by Räsänen (1934), while Diederich (1990), Diederich & Christiansen (1994) later understood that it was a heterobasidiomycete. Millanes et al. (2011) confirmed its placement

within the *Tremellales* using molecular methods, and that it included several independent lineages. Some of these were later described as species based on molecular and morphological evidence (Millanes et al. 2016, Diederich & Ertz 2020), whereas other lineages remained undescribed awaiting more thorough morphological studies. Here, we formally describe two of these so far unnamed lineages as *Biatoropsis macaronesica* and *B. rubicundae*. But four other new species on new hosts, unknown to date, are also described, based on morphological and molecular methods: *B. angulatae*, *B. antarcticae*, *B. hirtae* and *B. nigrescens*. However, despite these recent advances, we expect that the understanding and knowledge of the diversity within *Biatoropsis* will still increase in the coming years.



Maximum likelihood phylogeny based on ITS and nuLSU sequences, with an enlarged taxon sampling focusing on *Biatoropsis*. Branches in bold-face indicate nodes supported by both Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . When nodes received support only from one of the two methods, ML-BS values ≥ 70 are indicated over branches, and Bayesian posterior probabilities values ≥ 0.95 , below branches. Species names are indicated in the right margin. Type specimen are indicated with '(T)'. Red font for *Biatoropsis* indicates that all species in this genus are lichenicolous. Branch lengths are scaled to the expected number of substitutions per site. [Continues on next page.]



Key to the species of *Biatoropsis*

Many *Biatoropsis* specimens, especially those on unusual hosts, can only be identified with certainty using DNA sequences. The following practical key allows identifying a considerable number of specimens using a combination of morphological characters, host selection and geographical distribution.

- 1 On *Protousnea* in South America
 - 2 On *P. dusenii*; basidiomatal galls pale to dark brown or black *Biatoropsis protousneae* (125)
 - 2' On *P. magellanica*; basidiomatal galls pale to medium brown *Biatoropsis* sp. E (130)
- 1' On *Usnea*
 - 2 Epibasidia absent; basidia producing minuscule, hyaline, aseptate conidia, 3–5(–6) × 2–3 µm; basidiomatal galls dark brown to black, pustular, surface gelatinous, with irregular openings to release conidia; on *U. antarctica* and *U. aurantiaco-atra* *Biatoropsis antarcticae* (114)
 - 2' Epibasidia present when mature; basidia producing subspherical to ellipsoid basidiospores with a lateral apiculus; basidiomatal galls not pustular, closed, in most species not blackish, waxy-gelatinous
 - 3 Basidia 1-septate, the two cells elongating laterally before the formation of epibasidia; basidiomatal galls regularly convex to subglobose, pale to medium orange, occasionally brown, 0.1–1.3 mm diam.; on the *U. fragiles-cens* aggr., mainly *U. cornuta* *Biatoropsis hafellneri* (115)
 - 3' Basidia 1–3-septate
 - 4 Basidiomatal galls broad, with a flat or slightly convex surface and a strongly constricted base, resembling apothecia with a flat disk, pale to medium brown or orange (two morphologically similar, but phylogenetically distinct species; specimens of *B. usnearum* s. str. may also key out here, but typically have basidiomata with a pinkish tinge)
 - 5 On *Usnea hirta* *Biatoropsis hirtae* (117)
 - 5' On *Usnea angulata* *Biatoropsis angulatae* (112)
 - 4' Basidiomatal galls with a strongly convex surface, subspherical to applanate
 - 5 Basidiomatal galls relatively small, 0.1–0.8 mm diam., rarely over 1 mm diam. when old
 - 6 Basidiomatal galls basally distinctly constricted, with a smooth and slightly shiny surface, blackish brown to black from the beginning, rarely medium brown, 0.3–1 mm diam., dispersed over the thallus of *U. capillacea*, *U. inermis*, *U. nidifica*, *U. subalpina* and *U. torulosa* *Biatoropsis nigrescens* (123)
 - 6 Basidiomatal galls subspherical, basally only slightly constricted, except when old, with a slightly rough and matt surface, pale to dark brown, never blackish
 - 7 Basidiomatal galls constantly medium to dark brown, 0.1–0.8 mm diam., abundant and often touching each other; on *U. perplexans*, more rarely on *U. barbata* *Biatoropsis minuta* (122)
 - 7' Basidiomatal galls variable in colour, pale to dark brown, 0.1–0.6(–1) mm diam., more applanate when old, dispersed or rarely agglomerated; on *U. esperantiana*, *U. flavocardia*, *U. fragiles-cens*, *U. glabrata*, *U. cf. krogiana* and *U. macaronesica* *Biatoropsis macaronesica* (118)
 - 5' Basidiomatal galls frequently over 1 mm diam. when old
 - 6 Basidiomata typically pale pinkish brown, even when old, rarely medium to dark brown, becoming very large and flattened when old, up to 2.5 mm diam., often with a depressed centre, margin sometimes almost lobate; on *U. barbata*, *U. cavernosa*, *U. florida*, *U. glabrescens*, *U. intermedia* and *U. subfloridana* *Biatoropsis usnearum* (128)
 - 6' Basidiomata medium to dark brown, rarely exceeding 1.5 mm diam.
 - 7 Basidial cells elongating laterally at maturity; on *U. exasperata* s. lat. in the isles of the South Western Indian Ocean *Biatoropsis millanesiana* (121)
 - 7' Basidial cells not elongating at maturity; on *U. ceratina*, *U. erinacea* and *U. rubicunda* *Biatoropsis rubicundae* (126)

Key to the lichenicolous species of *Tremella*

As lichenicolous species of *Tremella* are very poor in taxonomically useful microscopical characters, and because of the continuously increasing number of species, an identification key based on morphology alone would be near to impossible. We abandoned therefore the idea of presenting such a key, and instead gave a host-based key in the introductory part of this volume. Two smaller keys are nevertheless given, one for the conidial species and one for the species with aseptate basidia.

Key to the lichenicolous species of *Tremellales* mainly reproducing by conidia

This key allows identifying species that mainly or exclusively reproduce by hyaline, aseptate conidia. Species with a hymenium producing asteroconidia, lunate conidia or catenulate conidia are not considered here.

- 1 Hymenium containing numerous basidia with reduced or missing epibasidia, producing conidia instead of basidiospores
 - 2 Basidia transversely 3-septate, $19\text{--}25 \times 4.5\text{--}7.5\ \mu\text{m}$; conidia $3\text{--}5(-6) \times 2\text{--}3\ \mu\text{m}$; on *U. antarctica* and *U. aurantiaco-atra*..... ***Biatoropsis antarcticae*** (114)
 - 2 Basidia longitudinally septate
 - 3 Basidia subspherical, not constricted at the septa, producing apically 4 conidia
 - 4 Conidia $4.5\text{--}5.5 \times (3.5\text{--})4\text{--}4.5\ \mu\text{m}$, with a hyaline basal appendage; basidiomata pale orange-brown, 0.25–0.6 mm diam.; on the lower surface of *Xanthoria parietina* ***Tremella occultixanthoriae*** (206)
 - 4' Conidia narrower, without a basal appendage
 - 5 Conidia $2.5\text{--}4 \times 2\text{--}3\ \mu\text{m}$; on *Cetraria aculeata*..... ***Tremella cetraculeata*** (146)
 - 5' Conidia $5.5\text{--}7.5 \times 2\text{--}3\ \mu\text{m}$; on *Cetraria islandica*..... ***Tremella cetrariae*** (147)
 - 3 Basidia made of 2–4 cells connected only at the base, each cell producing apically conidia, often with annellides
 - 4 Conidia $12.5\text{--}15.5 \times 2.5\text{--}3.5\ \mu\text{m}$; basidia $14.5\text{--}26.5 \times 4\text{--}6\ \mu\text{m}$; basidiomatal galls 0.5–4.5 mm diam.; on *Brodoa intestiniformis* ***Tremella brodoae*** (140)
 - 4' Conidia $4\text{--}9.5 \times 2.5\text{--}3.5\ \mu\text{m}$; basidia $13\text{--}18.5 \times 3.5\text{--}6.5\ \mu\text{m}$; basidiomatal galls 1–2 mm diam.; on *Cetraria ericetorum*..... ***Tremella cervina*** (145)
 - 3' Basidia with short deciduous epibasidia not producing basidiospores, but acting as diaspores resembling conidia, $9\text{--}17 \times 1.8\text{--}2.5\ \mu\text{m}$; on *Aspicilia* ***Tremella aspiciliae*** (138)
 - 1' Hymenium made of conidiophores abundantly producing basally clamped conidia
 - 2 Conidiomata pale to dark reddish brown; conidia $5\text{--}6.5 \times 4\text{--}5\ \mu\text{m}$; on *Parmotrema* ***Tremella conidioparmotrema*** (155)
 - 2' Conidiomata medium to dark brown, rapidly turning black
 - 3 Conidiomata superficial, subspherical, 0.15–0.5 mm diam.; conidia $5.5\text{--}8 \times 4\text{--}5.5\ \mu\text{m}$; on *Usnea longissima* ***Tremella confluens*** (154)
 - 3' Conidiomata immersed in the host thallus, erumpent, flat or sometimes becoming convex, 0.4–1.8 mm diam.
 - 4 Conidia $5\text{--}7 \times 4\text{--}5\ \mu\text{m}$; on *Punctelia*..... ***Tremella conidiopunctelia*** subsp. ***conidiopunctelia*** (157)
 - 4' Conidia $4.5\text{--}5.5 \times 3.5\text{--}4.5\ \mu\text{m}$; on *Parmelinella amazonica* ***Tremella conidiopunctelia*** subsp. ***parmelinellae*** (159)

Key to the lichenicolous species of *Tremellales* with aseptate basidia

- 1 Basidia stalked, stalk $(5\text{--})8\text{--}14(-17)\ \mu\text{m}$ long; basidiospores $5\text{--}7 \times 4.5\text{--}6\ \mu\text{m}$; on the thallus of *Leptogium* .. ***T. monospora*** (200)
- 1' Basidia not stalked, or stalk $1\text{--}7(-11)\ \mu\text{m}$ long; basidiospores over $10\ \mu\text{m}$ long; in apothecia and surrounding thallus of *Lecanora carpinea*
 - 2 Basidia smooth-walled, $17\text{--}40 \times 9.5\text{--}17\ \mu\text{m}$; old basidia filled with thick-walled conidial 'endospores'; basidiospores globose to subglobose, $Q = 0.8\text{--}1.1$; apiculus lateral ***T. endosporogena*** (168)
 - 2' Basidia acanthoid, surface varying from smooth to echinate or tuberculate, $10\text{--}15 \times 7.5\text{--}12\ \mu\text{m}$; old basidia without 'endospores'; basidiospores ellipsoid, $Q = 1.3\text{--}1.6$; apiculus at proximal end..... ***Heteroacanthella ellipsospora*** (130)

TREMELLOMYCETES Doweld

Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001). Type: Tremella Pers.

TREMELLALES Fr.

as ‘*Tremellinae*’, *Systema Mycologicum* 1: 2 (1821). Type: *Tremella* Pers.

BIATOROPSIS Räsänen

Ann. bot. Soc. Zool.-bot. fenn. ‘Vanamo’ 5: 8 (1934). Type: *B. usnearum* Räsänen

Molecular data: yes (T, L). *Number of species:* 11[1]–0–0.

Basidiomata variable in form and colour, waxy-gelatinous. *Context hyphae* without clamps; haustoria tremelloid. *Hymenium* containing numerous probasidia; probasidial initials clavate, without or with basal clamp; hyphidia and cystidia absent. *Basidia*, when mature, clavate to subcylindrical, transversely septate; epibasidia subcylindrical. *Basidiospores* subglobose to ellipsoid, with a distinct lateral apiculus, germinating with a germ tube. *Asexual stage:* catenulate conidia are common; lunate conidia have been observed once; in one species, basidia act as conidiogenous cells producing aseptate, hyaline conidia.

Notes. This genus was described for an unusual ascomycete resembling a small *Biatora*, but was later recognized as representing a species of basidiomycetes belonging to the *Tremellales* (Diederich & Christiansen 1994, Millanes et al. 2014b, 2016). While Diederich & Christiansen (1994) regarded *B. usnearum* as a single variable species, phylogenetic results by Millanes et al. (2014) suggested a species complex confined to *Usnea* and *Protousnea* hosts, comprising many species having similar macro- and micromorphological characters, but phylogenetically distinct. We describe here six new species, but still are not able to identify many specimens, either as these are morphologically intermediate between several known species, or as they do not fully agree with any of these.

Ecology. All species are lichenicolous, inducing galls on *Usnea* and *Protousnea* thalli.

Biatoropsis angulatae Diederich & Millanes, sp. nov.

Diagnosis: Characterized by the broad, applanate, medium brown basidiomata, 0.7–1.8 mm diam., developing on the thallus of *Usnea angulata*, the subcylindrical, 1–3-transseptate basidia, $23\text{--}30 \times 3\text{--}5\ \mu\text{m}$, with individual cells strongly elongating at maturity, $30\text{--}50 \times 4\text{--}8\ \mu\text{m}$ (poorly distinct epibasidia included), and the shortly ellipsoid basidiospores, $7\text{--}9 \times 5.5\text{--}7.5\ \mu\text{m}$.



Biatoropsis angulatae, USA, Minnesota, holotype. Basidiomata on the thallus of *Usnea angulata*. Scale bar: 1 mm.



Biatoropsis angulatae, USA, Minnesota, holotype. Basidioma on the thallus of *Usnea angulata*. Scale bar: 1 mm.



Biatoropsis angulatae, Australia, Queensland, Stevens 7299. Basidioma on the thallus of *Usnea angulata*. Scale bar: 1 mm.



Biatoropsis angulatae, Australia, Queensland, Stevens 7223. Basidiomata on the thallus of *Usnea angulata*. Scale bar: 1 mm.

Etymology: From *Usnea angulata*, the host lichen.

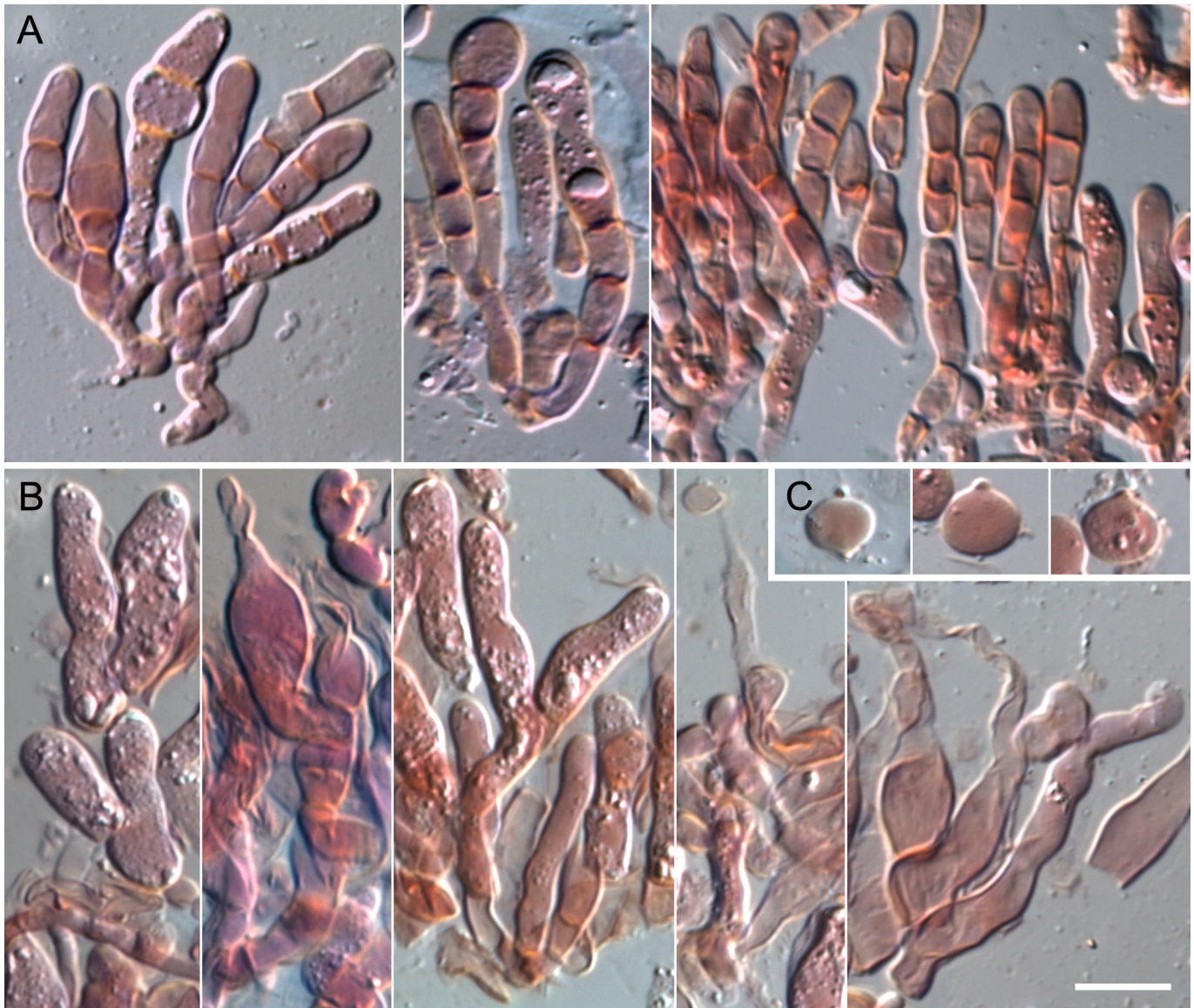
Type: USA, Minnesota, Cass Co., Leech Lake, Oak Point, 47°13'09"N, 94°30'41"W, on branches and trunk of *Abies balsamea* in an old growth community of *Thuja occidentalis* and *A. balsamea*, on *Usnea angulata*, 25 May 2016, B. Henderson 59 & L. Becker (BR – holotype).

Mycobank: MB844636

Basidiomata broad and strongly applanate, surface flat to convex, inducing basally strongly constricted galls, margin when young bordered by a narrow host thallus margin, waxy-gelatinous, medium brown, 0.7–1.8 mm diam. *Context hyphae* and subbasidial hyphae thick-walled, 3–4.5 µm diam., without clamps; haustoria not observed. *Hymenium* hyaline, containing numerous subcylindrical proba-

sidia, basal clamp not observed. *Basidia*, when mature, 2–4-celled, with three transverse septa, not constricted at the septa, the lower cell basally slightly attenuated, usually longer than the upper cells, 23–30 × 3–5 µm; the individual cells laterally much elongate at maturity, 4–8 µm thick; epibasidia poorly distinct from the elongate basidial cells, both together 30–50 µm long. *Basidiospores* shortly ellipsoid, 7–9 × 5.5–7.5 µm. *Asexual stage* unknown.

Notes. This species is distinguished by the broad and flattened basidiomata on the thallus of *Usnea angulata*. Phylogenetically, it is closely related to *Biatoropsis hafellneri*, with which it shares the basidial cells that strongly elongate at maturity. That species is distinguished, however, by the subglobose basidiomata and the constantly 2-celled basidia.



Biatoropsis angulatae, A, USA, Minnesota, holotype, B–C, Australia, Stevens 7299. A, Mature basidia before spore production. B, Basidia with laterally elongated cells, one producing a young spore. C, Basidiospores. In ammoniacal Congo red pre-stained with phloxine. Scale bar: 10 µm.



Biatoropsis angulatae

Ecology and host. On the thallus of *Usnea angulata*.

Distribution. North America (USA: Minnesota) and Oceania (Australia: Queensland).

Additional specimens examined (both on *Usnea angulata*). **Australia:** Queensland: S. loc., 28°07'S, 152°30'E, 900 m, in rain-forest, s. d., Stevens 7223 (BR); Blackbutt, 26°52'S, 152°11'E, 350 m, Stevens 7299 (BR).

MycoBank: MB844637

Basidiomata breaking through the host cortex and becoming superficial, pustular, with a large apical opening, exposed parts with a very rough surface when dry, gelatinous, dark brown to black, 0.3–1.6 mm diam. *Context hyphae* and subbasidial hyphae thick-walled, 3.5–5.5 µm diam., without clamps, mostly hyaline to pale brown, some dark brown; haustoria present but not abundant. *Hymenium* mostly hyaline, partly brown, containing numerous subcylindrical probasidia without a basal clamp. *Basidia*, when mature, 4-celled, thick-walled, with three transverse septa, hardly constricted at the septa, the lower cell basally slightly attenuated, usually not longer than the other cells, 19–25 × 4.5–7.5 µm; epibasidia reduced, hardly visible, functioning as conidiogenous cells. *Basidiospores* unknown. *Conidia* hyaline, aseptate, ellipsoid, base slightly attenuated and truncate, 3–5(–6) × 2–3 µm; conidiogenesis not sure, probably holoblastic; leaving scars after conidial production.

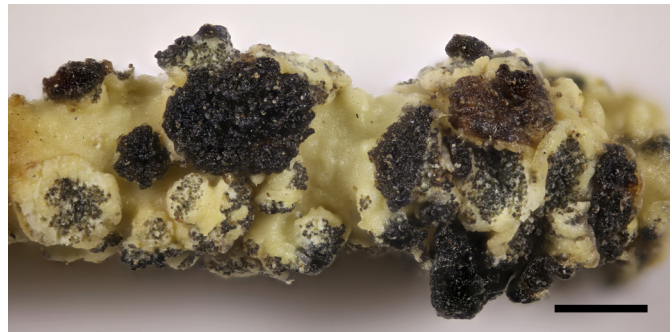
Notes. This species is remarkable by the basidia with reduced epibasidia, acting as conidiogenous cells, the absence of basidiospores, the small, hyaline conidia, and the strongly gelatinous blackish basidiomata with a rough open surface.

***Biatoropsis antarcticae* Diederich, Etayo & Millanes, sp. nov.**

Diagnosis: Characterized by the pustular, dark brown to black basidiomata, 0.3–1.6 mm diam., with a rough, strongly gelatinous surface, developing on the thallus of *Usnea antarctica* and *U. aurantiaco-atra*, the short subcylindrical, 3-transseptate basidia, 19–25 × 4.5–7.5 µm, the reduced epibasidia acting as conidiogenous cells, the missing basidiospores, and the hyaline, aseptate, basally slightly truncate conidia, 3–5(–6) × 2–3 µm.

Etymology: From *Usnea antarctica*, the host lichen of the type.

Type: Antarctica, South Shetland Islands, Livingston Island, Caleta Alemana, piedras cercana al oeste de la playa, 62°40'02"S, 60°24'07"W, 15 m, on *Usnea antarctica*, 23 Febr. 2018, J. Etayo 31265 (MAF-Lich – holotype; BR, herb. Etayo – isotypes).



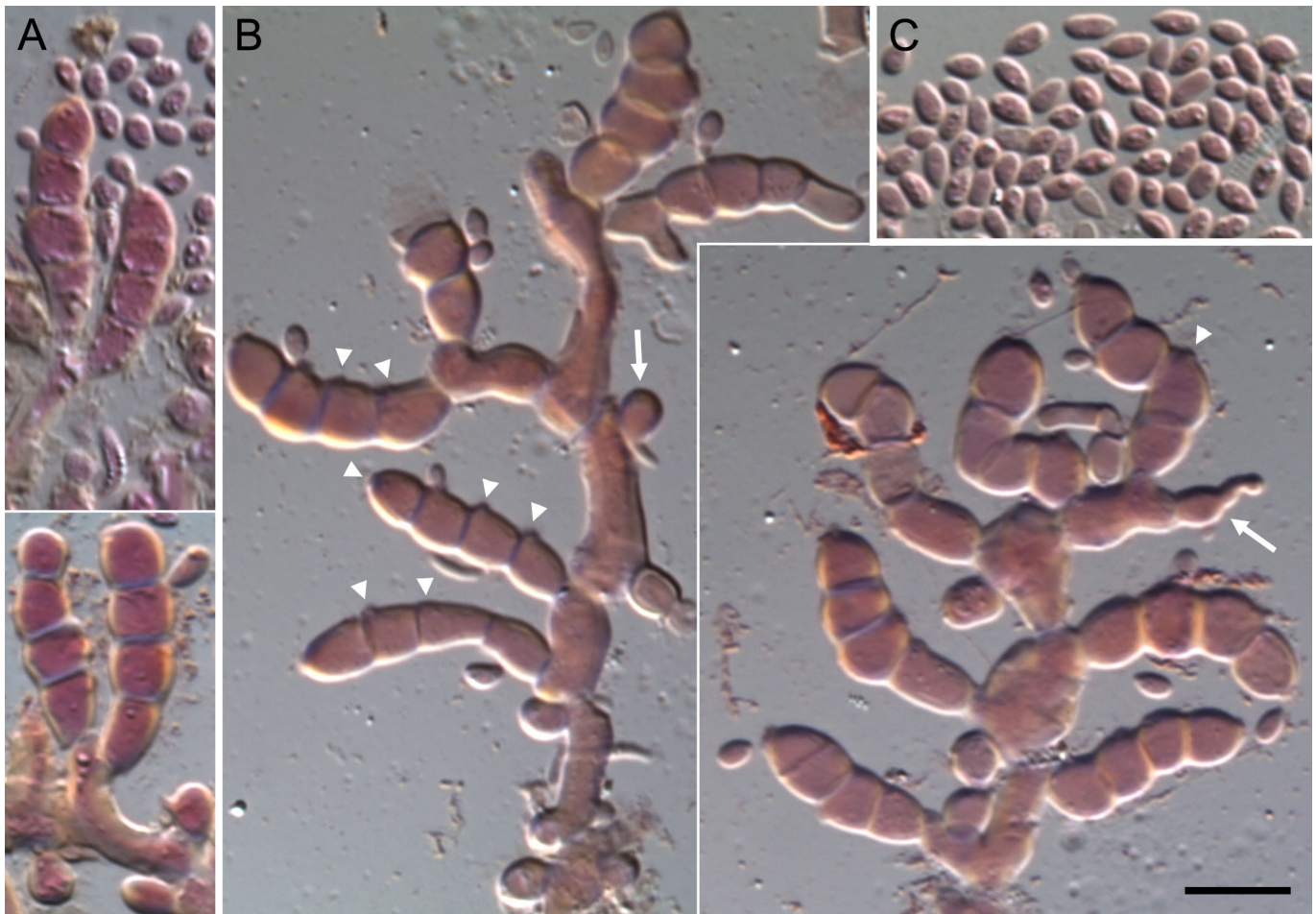
Biatoropsis antarcticae, Antarctica, South Shetland Islands, holotype. Basidiomata on the thallus of *Usnea antarctica*. Scale bar: 500 µm.



Biatoropsis antarcticae, Antarctica, South Shetland Islands, holotype. Basidiomata on the thallus of *Usnea antarctica*. Scale bar: 500 µm.



Biatoropsis antarcticae, Antarctica, South Shetland Islands, Etayo 31457. Basidiomata on the thallus of *Usnea antarctica*. Scale bar: 500 µm.



Biatoropsis antarctica, Antarctica, South Shetland Islands, holotype. A, Mature basidia producing conidia. B, Hyphae with mature basidia and haustoria (arrows); arrow heads point at scars after conidial production. C, Conidia. In ammoniacal Congo red pre-stained with phloxine. Scale bar: 10 μ m.

It is interesting to note a remarkable similarity with the phylogenetically unrelated *Tremella cetraculeata* and *T. cetrariae*, which have very similar, blackish, strongly gelatinous, pustular basidiomata, and basidia producing hyaline conidia instead of epibasidia and basidiospores.

Ecology and hosts. On the thallus of *Usnea antarctica* and *U. aurantiaco-atra*.

Distribution. Antarctica (South Shetland Islands: Livingston Island).

Additional specimens examined. **Antarctica:** South Shetland Islands, Livingston Island, 2018: Sally Rocks, mountain slope with many large stones between soil ledges, 62°42'04"S, 60°24'59"W, 60–70 m, on *Usnea antarctica*, Etayo 31457 (herb. Etayo); Pico Radio just over the base española, on *U. aurantiaco-atra*, 130 m, 62°39'55"S, 60°23'51"W, Etayo 31662 (herb. Etayo); Base Española Juan Carlos I, cliffs behind zodiak's hangar, 62°39'40"S, 60°22'57"W, 13–20 m, on *U. antarctica*, Etayo 31681 (MAF-Lich, herb. Etayo); Punta Barnard, boulders near a great beach and in a promontory near it, 62°45'07"S, 60°19'43"W, 0–5 m, on *U. antarctica*, Etayo 31711 (MAF-Lich).



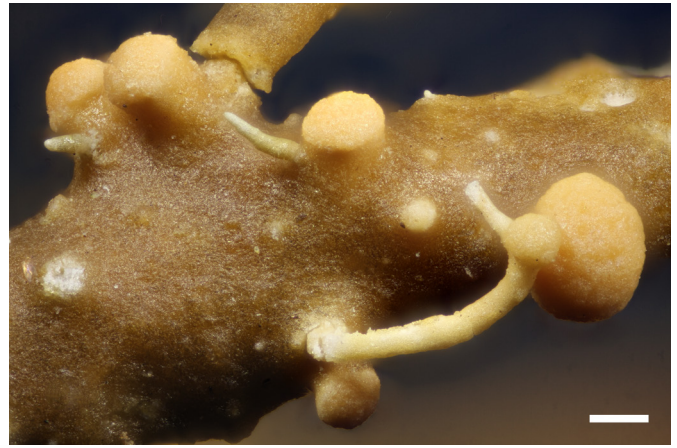
Biatoropsis antarctica

***Biatoropsis hafellneri* Millanes, Diederich, M. Westb. & Wedin**

Herzogia 29: 341 (2016). **Type:** UK, Cornwall, Lamorna Cove, Lamorna Valley, 50°03'N, 05°32'E, on *Usnea cornuta*, 11 Apr. 2004, M. Wedin 7308 (UPS F766824 – holotype; GZU, S F102403 – isotypes).



Biatoropsis hafellneri, Azores, Diederich 17087b. Basidiomata on *Usnea cornuta*. Scale bar: 1 mm.



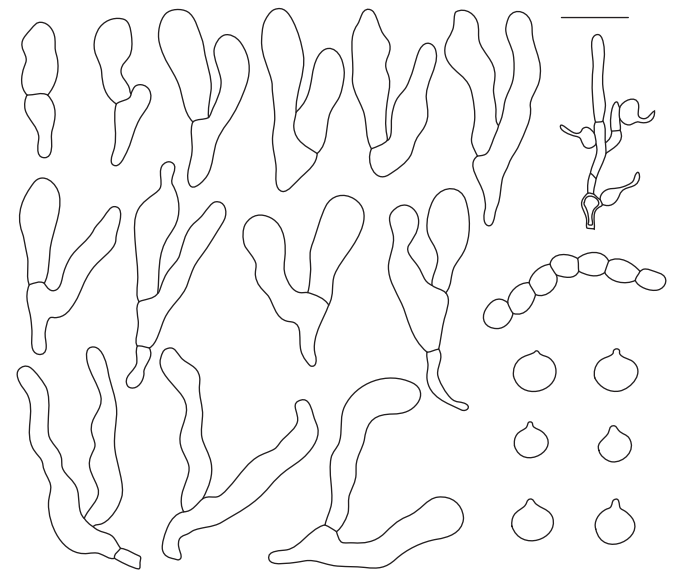
Biatoropsis hafellneri, France, Diederich 14614. Basidiomata on *Usnea cornuta*. Scale bar: 200 μ m.

Basidiomatal galls initially regularly convex to subglobose, later constricted at the base, sometimes with a central depression and/or tuberculate when mature, very pale to orangish, occasionally brown, waxy-gelatinous when wet 0.1–1.3 mm diam., often developing on broken fibrils. *Context hyphae* thin-walled, 2–3 μ m diam., clamps occasionally present; haustoria frequent. *Hymenium* hyaline, containing numerous clavate probasidia, often developing from a basal clamp (not visible in mature basidia). *Basidia*, when mature, 2-celled (exceptionally 3-celled), with one transverse septum, 20–46 \times 4–8 μ m, the two cells laterally much elongate at maturity, sometimes giving the appearance of two immature independent basidia, individual basidial cells up to 40 μ m long, 4–8 μ m wide; epibasidia elongate, often not clearly distinguishable from the elongate basidial cells. *Basidiospores* globose to subglobose, 5–8.5 \times 5–9 μ m. *Asexual stage*: hyaline catenulate conidia have been observed, cells 3–8 \times 3–5 μ m.

Notes. *Biatoropsis hafellneri* is distinguished by basidia consisting of two cells that elongate laterally before the formation of epibasidia. Similar basidia are found in *Tremella christiansenii*, *T. diderichiana* and *T. hypocenomyces*, although none of these species grow on *Usnea*. Phylogenetically, *B. hafellneri* is closely related to *B. usnearum*, a species with 4-celled basidia.



Biatoropsis hafellneri



Biatoropsis hafellneri, UK, holotype (modified from Millanes et al. 2016). Basidia, basidiospores, catenulate conidia and haustorial branches. Scale bar: 10 μ m.

Ecology and hosts. On the thallus of *Usnea cornuta* and other species in the *U. fragilesce* aggregate, often on decorticated areas remaining after fibrils of the host thallus have broken away.

Distribution. Europe (France; Norway; Spain; UK: England, Scotland, Wales) and Macaronesia (Azores; Canary Islands; Madeira).

Additional specimens examined. **Canary Islands:** La Palma: Barlovento, 28.8083°N, 17.8052°W, 735 m, on *Usnea cornuta*, 2016, Wagner 16-13, 16-14 (BR).

References. Millanes et al. 2014b, 2016 [Roux 2020].

Biatoropsis hirtae Diederich & Millanes, sp. nov.

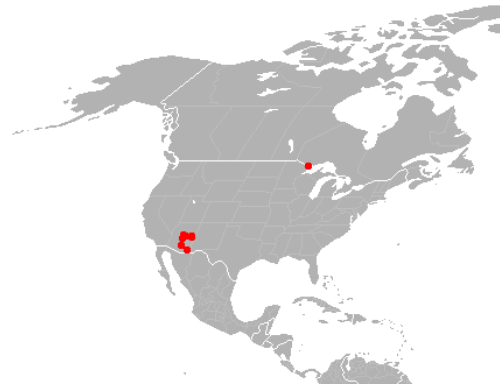
Diagnosis: Characterized by the broad, applanate, pale to medium brown basidiomata, 0.3–1.4 mm diam., 0.1–0.4 mm tall, developing on the thallus of *Usnea hirta*, the clavate to subcylindrical, 3-transseptate basidia, $24\text{--}45 \times 4.5\text{--}6.5\ \mu\text{m}$, and the ellipsoid basidiospores, $5.5\text{--}8.5 \times 4.5\text{--}7.5\ \mu\text{m}$.

Etymology: From *Usnea hirta*, the host lichen.

Type: USA, Arizona, Gila Co., Tonto National Forest, Col. Devin Trail no 290, above Washington Park, along Mail Creek, $34^{\circ}26'N$, $110^{\circ}16.33'W$, on *Usnea hirta*, 11 July 1997, T. Nash 39494 (ASU – holotype; BR, S F102404 – isotypes).

MycoBank: MB844638

Basidiomata broad and strongly applanate, surface flat to convex, often centrally depressed when old or saddle shaped, basally often strongly constricted and sometimes almost stipitate when old, margin when young bordered by a narrow host thallus margin, occasionally bent downwards when old, waxy-gelatinous, pale to medium brown, rarely dark brown, 0.3–1.4 mm diam., 0.1–0.4 mm tall. **Context hyphae** and subbasidial hyphae thick-walled, 2–4 μm diam.; haustoria present, basal clamp not observed. **Hymenium** hyaline, containing numerous clavate to subcylindrical probasidia, basal clamp not observed. **Basidia**, when mature, 4-celled, with three transverse septa, not or slightly constricted at the septa, the lower cell usually not attenuated at the base and not longer than the upper cells, $24\text{--}45 \times 4.5\text{--}6.5\ \mu\text{m}$; the three lower cells laterally much elongate at maturity, 4–6 μm thick; epibasidia poorly distinct from the elongate basidial cells, both together up to at



Biatoropsis hirtae

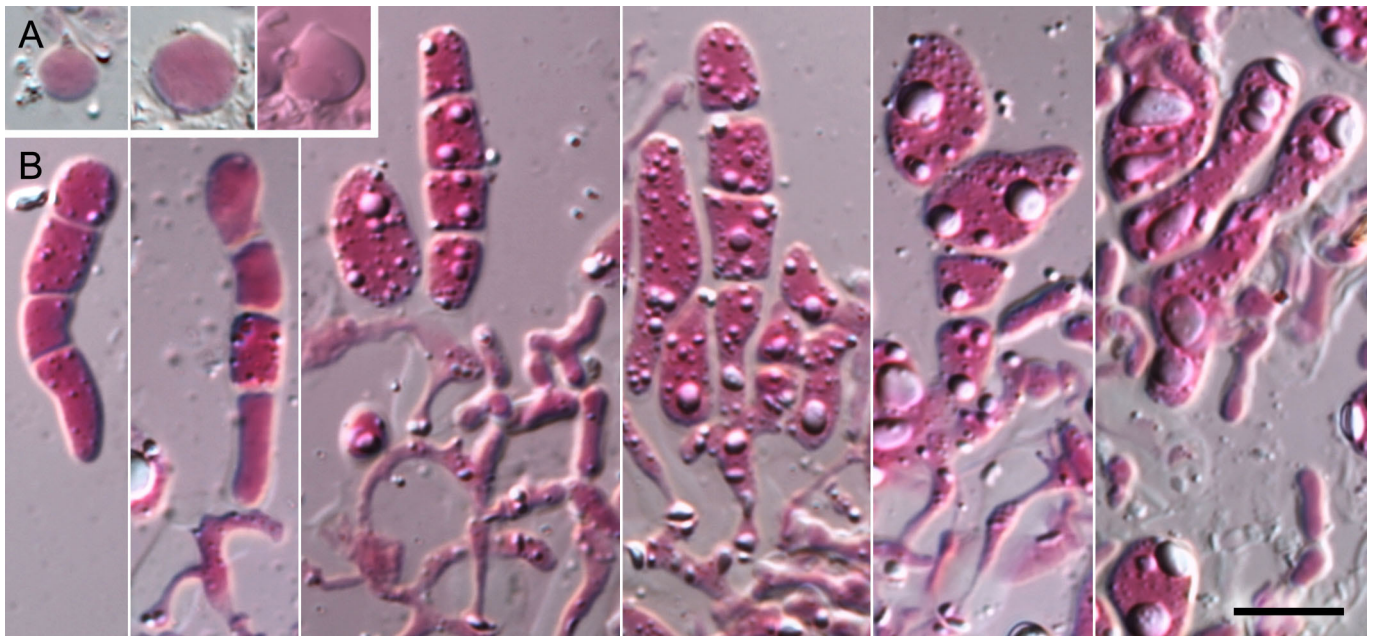
least 30 μm long. **Basidiospores** shortly ellipsoid, $5.5\text{--}8.5 \times 4.5\text{--}7.5\ \mu\text{m}$. **Asexual stage** unknown.

Notes. This taxon is distinguished from the other *Biatoropsis* species by the broad, applanate basidiomata developing on the thallus of *Usnea hirta*. It appears to be very common in USA, Arizona, but should be searched for in the entire distribution area of the host. It frequently grows together with *Tremella nashii*, distinguished by the basidiomata inducing swollen concolorous galls and the longitudinally septate tremelloid basidia.

Ecology and host. On the thallus of *Usnea hirta*.

Distribution. North America (USA: Arizona, Minnesota).

Additional specimens examined (all on *Usnea hirta*). **USA:** Arizona: Apache Co., Mount Baldy Wilderness, first drainage W of the Little Colorado River Valley, $33^{\circ}58'N$, $109^{\circ}32'W$, 2900 m,



Biatoropsis hirtae, USA, Arizona, holotype. A, Basidiospores. B, Basidia in different stages of development, the right ones with laterally enlarged cells. In phloxine. Scale bar: 10 μm .



Biatoropsis hirtae, USA, Arizona, holotype. Basidiomata on the thallus of *Usnea hirta*. Note the thin host thallus margin (left and middle), and thallus fragments covering young ascomata. Scale bar: 500 μ m.



Biatoropsis hirtae, USA, Arizona, holotype. Basidiomata on the thallus of *Usnea hirta*. The smaller ones still with a thin host thallus margin, the large one saddle-shaped. Scale bar: 500 μ m.



Biatoropsis hirtae, USA, Arizona, Walden 9. Three basidiomata on the thallus of *Usnea hirta* (arrows point at intermixed basidiomata of *Tremella nashii*) Scale bar: 500 μ m.



Biatoropsis hirtae, USA, Arizona, Thayer 34. Stipitate basidioma on the thallus of *Usnea hirta*. Scale bar: 500 μ m.



Biatoropsis hirtae, USA, Arizona, Nash 20992. Basidioma on the thallus of *Usnea hirta*. Scale bar: 500 μ m.

1994, Nash 34751 (ASU); Cochise Co., Chiricahua Mountains, lower portion of Morse Canyon, 31°51'N, 109°19.5'W, 3 Sept. 1983, Nash 20992 (ASU, BR); Coconino Co., Coconino National Forest, c. 3.58 km SW Crystal Springs and 4.81 km N Meyers, 34.5015°N, 111.3661°W, 2018, Thayer 34 (BR); Gila Co., 16

ENE of Payson, 34°17'N, 111°07'W, 1700 m, 1995, Kantrud 245 (ASU). Greenlee Co., Apache-Sitgreaves National Forest, c. 36.4 km S Alpine and 10.1 km W of New Mexico border, 33.6104°N, 109.1554°W, 2019, Walden 9 (BR); Pima Co., road to Mount Lemon, NE of Tucson, 32°25'N, 110°43'W, March 1985, Ryan 12533 (ASU, BR). *Minnesota*: Cook Co., Superior National Forest, c. 4.87 km W Lutsen and 11.08 km NE Tofte, 47.6491°N, 90.7396°W, 2016, Gockman 5545b (BR).

Biatoropsis macaronesica Diederich & Millanes, sp. nov.

Diagnosis: Characterized by the relatively small, convex, basally slightly constricted, pale to dark brown basidiomata, 0.1–0.6 mm diam., when old up to 1(–1.3) mm, developing on the thallus of *Usnea* species, the clavate to subcylindrical, 3-transseptate basidia (rarely with one longitudinal apical septum), 24–45 \times 4–10 μ m, and the ellipsoid basidiospores, 6.5–8.5 \times 5–7.5 μ m.

Etymology: From *Macaronesia*, where the species is particularly common and abundant.

Type: Canary Island, La Palma, Barlovento, am Ende der befestigten Zuwegung zum Kratersee südlich des Ortes, 28.8083°N, 17.8052°W, 735 m, on *Erica arborescens*, on *Usnea esperantiana*, 8 May 2016, H.-G. Wagner 16-10 (BR – holotype).

Mycobank: MB844639

Basidiomata relatively small, subspherical, basally slightly constricted, waxy-gelatinous, pale to medium or dark brown, 0.1–0.6 mm diam.; when old, medium to dark brown, becoming applanate with an uneven surface, up to 1(–1.3) mm diam. *Context hyphae* and subbasidial hyphae thick-walled, 1.5–4.5 µm diam.; haustoria present, without basal clamp. *Hymenium* hyaline, containing numerous clavate to subcylindrical probasidia without basal clamp. *Basidia*, when mature, 4-celled, usually with three transverse septa, rarely with two transverse septa and one longitudinal septum in the upper segment, not or slightly constricted at the septa, $24\text{--}45 \times 4\text{--}10$ µm, the lower cell usually attenuated at the base, often longer than the other cells, the upper cell often broader than the other cells, up to 12 µm diam.; individual cells not elongating laterally at maturity; epibasidia 3–6 µm diam., 20–40(–55) µm long. *Basidiospores* ellipsoid, $6.5\text{--}8.5 \times 5\text{--}7.5$ µm. *Asexual stage* unknown.

Notes. This species was called ‘lineage A1’ in Millanes et al. (2014), then ‘*Biatoropsis* sp. A1’ in Millanes et al. (2016). It represents the sister clade of *B. protousneae* and was tentatively considered as an assemblage of several species in Millanes et al. (2016). We exclude here the subclade with mainly Chilean specimens and consider the remaining material as representing a single species that is particularly common in Macaronesia. *Biatoropsis usnearum* s. str. is distinguished by the larger basidiomata that are frequently

flattened, and are typically pinkish brown, even when old. Morphologically intermediate specimens cannot be identified with certainty without molecular data.

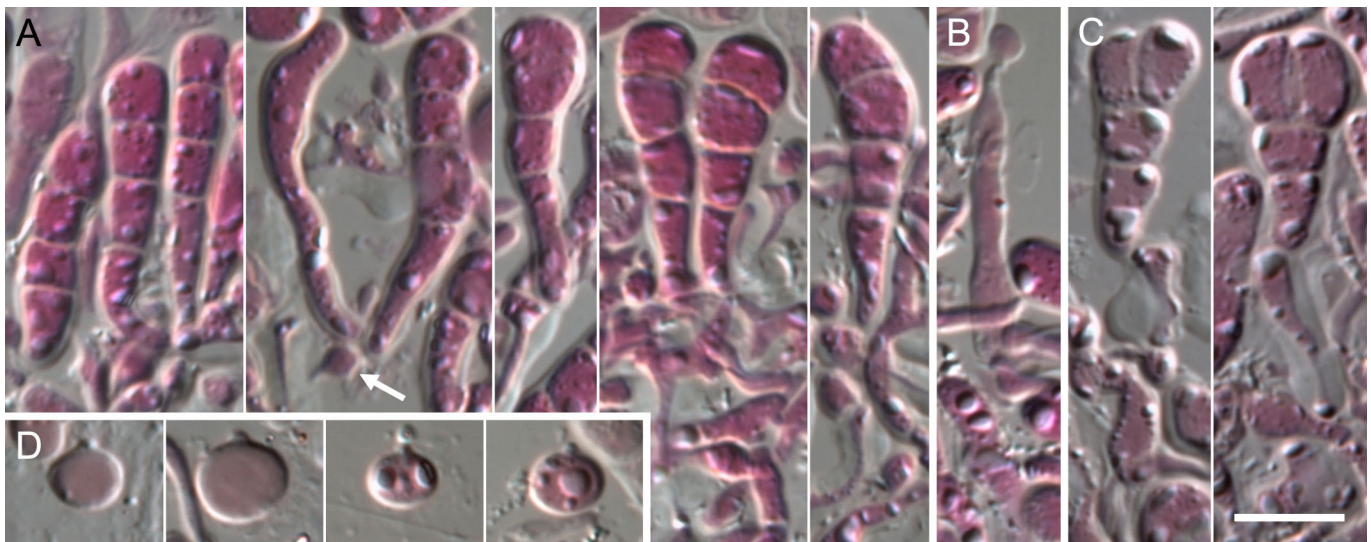
Ecology and host. On the thallus of *Usnea esperantiana*, *U. flavocardia*, *U. fragilescens*, *U. glabrata*, *U. cf. krogiana* and *U. macaronesica*.

Distribution. Europe (Spain), Macaronesia (Azores: Pico; **Canary Islands: La Palma**; Madeira) and Oceania (New Zealand).

Additional specimens examined. **Azores:** Pico: S of Sao Roque do Pico, forest remnants on the shore of Lagoa Capita, 38.4858°N, 28.3161°W, 780 m, *Usnea macaronesica*, 2010, Diederich 17058 (BR). **Canary Islands:** *La Palma:* Same locality as type, Wagner 16-9 (BR); Villa de Mazo, 28.6134°N, 17.8034°W, 975 m, on *U. cf. flavocardia*, 2016, Wagner 16-21 (BR); W Villa de Mazo, 28.6205°N, 17.8130°W, 1046 m, on *U. flavocardia*, 2016, Wagner 16-2 (BR); El



Biatoropsis millanesiana



Biatoropsis macaronesica, Canary Islands, La Palma, holotype. A, Basidia and haustorium (arrow). B, Epibasidium with young basidiospores. C, Basidia with 1 apical longitudinal septum. D, Basidiospores. In phloxine. Scale bar: 10 µm.



Biatoropsis macaronesica, Canary Islands, La Palma, holotype. Basidiomata on the thallus of *Usnea esperantiana*. Scale bar: 1 mm.



Biatoropsis macaronesica, Madeira, Diederich 17774. Old basidioma on the thallus of *Usnea esperantiana*. Scale bar: 1 mm.



Biatoropsis macaronesica, Azores, Pico, Diederich 17058. Basidiomata on the thallus of *Usnea macaronesica*. Scale bar: 1 mm.



Biatoropsis macaronesica, Madeira, Diederich 17778. Old basidiomata on the thallus of *Usnea* cf. *krogiana*. Scale bar: 1 mm.



Biatoropsis macaronesica, Canary Islands, Amo de Paz. Basidiomata on *Usnea flavocardia*. Scale bar: 500 μ m.



Biatoropsis macaronesica, Madeira, Diederich 17792. Basidiomata on the thallus of *Usnea flavocardia*. Scale bar: 1 mm.

Paso, Refugio El Pilar, 28°36'N, 17°50'W, 1452 m, on *U. flavocardia*, 2009, Amo de Paz (MAF-Lich). **Madeira:** Between Camacha and Paso de Poiso, along road ER 203, 32.6817°N, 16.8713°W, 800–1000 m, on *U. esperantiana*, 2014, Diederich 17772, 17774 (BR), 17773 (S F291464); S of Santana, W of Casa de Abrigo das Queima-

das, along Levada do Caldeirão Verde, 32.7848°N, 16.9082°W, 910 m, on *U. flavocardia*, 2014, Diederich 17779, 17780 (BR), 17782 (S); ibid., on *Usnea* cf. *krogiana*, Diederich 17778 (BR); S of Santana, Queimadas, 900 m, on *Usnea*, 1992, Diederich 4855 (BR); Ra-
baçal, along Levada das 25 Fontes, between forestry house and 25

fountains, 32.7635°N, 17.1338°W, 830–1050 m, on *U. flavocardia*, 2014, Diederich 17792, 17797 (BR); E of Ribeiro Frio, along Levada do Furado, 32.7377°N, 16.8842°W, 860 m, on *U. flavocardia*, 2014, Diederich 17770 (BR); road between Ribeira Brava and S Vicente, 2 km N of Encumeada, 800 m, on *Usnea*, 1992, Diederich 4871 (BR). **New Zealand:** *North Island:* Wellington, Waikanae, Lake Papaitonga, 40°38'38"S, 175°13'45"E, 20 m, on *U. flavocardia*, 2009, Myles (S F-186043, dupl. ex OTA 060693). **Spain:** León, La Bañeza, Herreros de Jamuz, 20 km from La Bañeza, road towards Castrocontrigo, 42°12'03"N, 6°6'12"W, on *U. glabrata*, 2008, Pérez-Ortega (MAF).

Biatoropsis millanesiana Diederich & Wedin

in Diederich & Ertz, *Plant and Fungal Systematics* 65: 25 (2020).
Type: Mauritius, Rivière Noire, Chamarel, Ebony Forest, around the viewpoint, 20°25'49" S, 57°22'27" E, 350 m, on branches of trees, on *Usnea exasperata* s. lat., 8 Aug. 2016, P. Diederich 18524 (MAU – holotype; BR, MAF-Lich, S – isotypes).

Basidiomata convex, basally constricted, sometimes slightly tuberculate when mature, waxy-gelatinous when wet, pale brown to more frequently dark brown or blackish, (0.3–)0.6–1.5(–2.5) mm diam. *Context hyphae* thin-walled, 2–3 µm diam., clamps not observed; haustoria frequent. *Hymenium* hyaline, containing numerous clavate to subcylindrical probasidia, basal clamp not observed. *Basidia*, when mature, 4-celled, with three transverse septa, not or slightly constricted at the septa, the lower cell with an attenuated stalk-like base and often longer than the upper cells, 21–72 × 4–10 µm (incl. stalk-like base, excl. epibasidia), lower part of the stalk-like base 2–4 µm diam.;

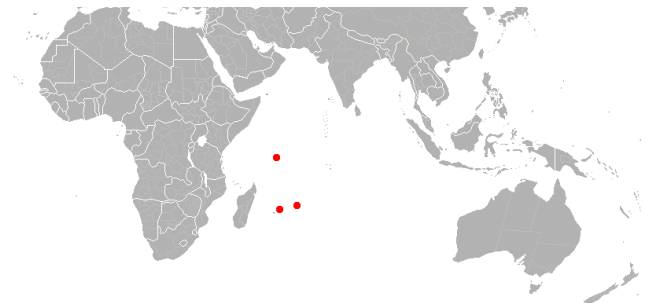
the three lower cells laterally much elongate at maturity, sometimes giving the appearance of immature independent basidia, 4–6 µm thick; epibasidia up to 50 µm long. *Basidiospores* globose to ellipsoid, (4–)5–8 × (5.5–)6–9(–11) µm. *Asexual stage* not observed.

Notes. This species has been described for a phylogenetically distinct lineage confined to *Usnea exasperata* s. lat. in the south-western Indian Ocean. It is characterized by the medium sized, mostly dark brown basidiomata and the 3-septate basidia, in which the three lower cells elongate laterally at maturity, giving the appearance of several individual, aseptate basidia.

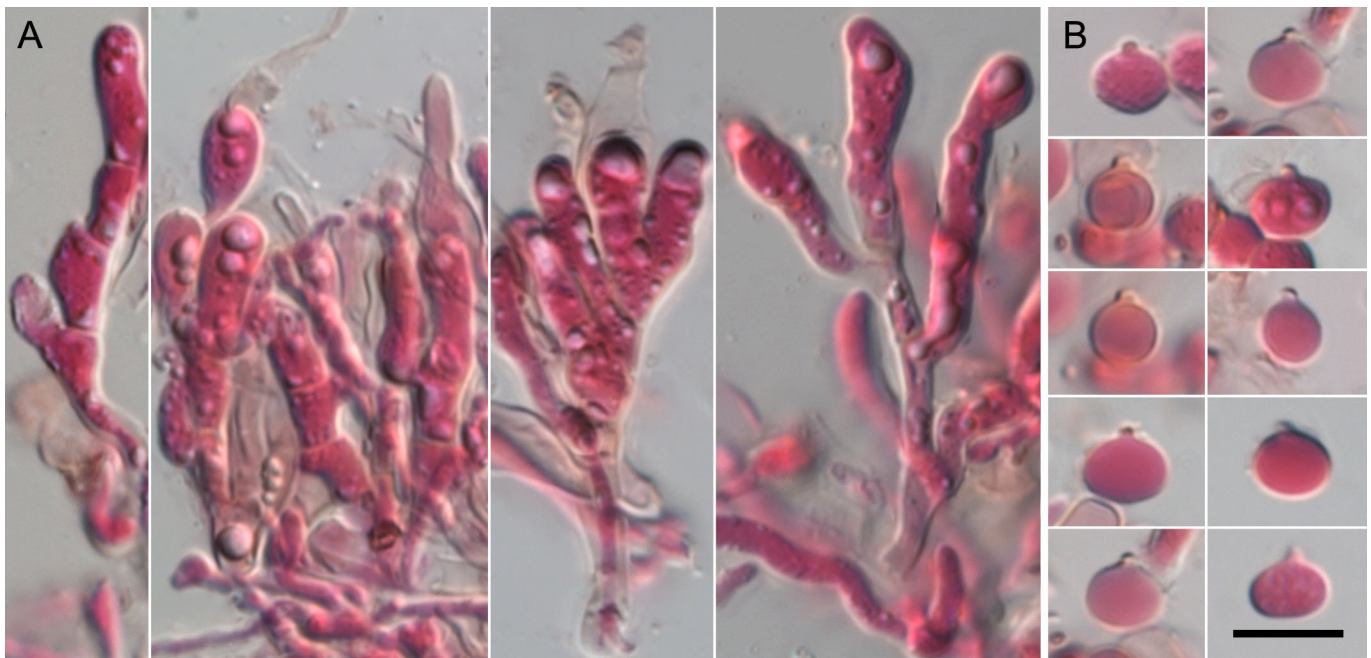
Ecology and host. On the thallus of *U. exasperata* s. lat.

Distribution. Indian Ocean (**Mauritius:** Mauritius, Rodrigues; Seychelles).

Reference. Diederich & Ertz 2020.



Biatoropsis millanesiana



Biatoropsis millanesiana, Mauritius, holotype. A, Basidia in different stages of development, showing the individual cells elongating laterally at maturity. B, Basidiospores. In a mixture of phloxine and Congo red. Scale bar: 10 µm.



Biatoropsis millanesiana, Mauritius, holotype. Basidiomata on *Usnea exasperata*. Scale bar: 500 μ m.



Biatoropsis millanesiana, Seychelles, Diederich 18087b. Basidiomata on *Usnea exasperata*. Scale bar: 500 μ m.

Biatoropsis minuta Millanes, Diederich, M. Westb. & Wedin

Herzogia 29: 345 (2016). *Type*: Spain, Palencia, Piedrasluengas, Piedrasluengas mountain pass, 43°2.95'N, 4°27.19'W, on *Usnea barbata*, 5 Apr. 2010, G. Aragón s.n. (S F102398 – holotype; BR, UPS F766826 – isotypes).

Basidiomata convex, basally slightly constricted, sometimes with a central depression when mature, waxy-gelatinous when wet, brown to dark brown or black, 0.1–0.8 mm diam. *Context hyphae* thin-walled, 2–3 μ m diam., clamps not observed; haustoria frequent. *Hymenium* hyaline, containing numerous clavate probasidia, basal clamps not observed. *Basidia*, when mature, 4-celled, with three transverse septa, often constricted at the septa, the lower cell with an attenuated stalk-like base, often longer than the upper cells, 20–46(–50) \times 4–10 μ m (incl. stalk-like base, excl. epibasidia), lower part of the stalk-like base 2–4 μ m diam.; epibasidia elongate. *Basidio-*

spores globose to subglobose, 5–9.5 \times 5–8 μ m. *Asexual stage*: hyaline catenulate conidia have been observed, cells 2–6 \times 2–4 μ m.

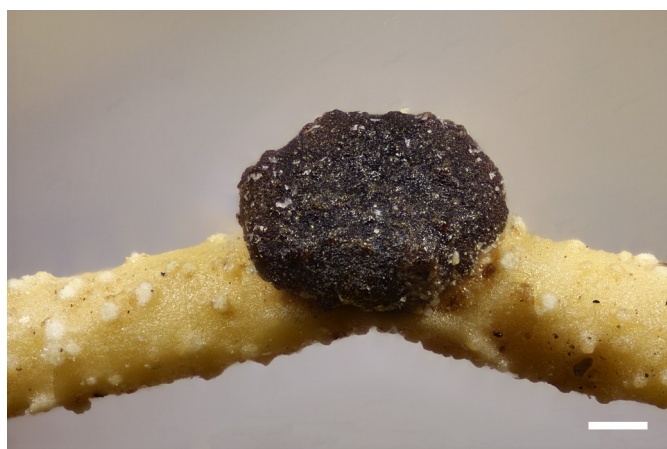
Notes. This is a widespread taxon, distinguished from other *Biatoropsis* species by the medium to dark brown basidiomatal galls that are always smaller than 1 mm.

Ecology and hosts. On the thallus of *Usnea barbata* and *U. perplexans* (= *U. lapponica*).

Distribution. Europe (Norway; Spain; Sweden; Switzerland), North America (Canada: British Columbia; USA: Arizona) and Asia (India).

Additional specimen examined. **Switzerland**: Valais: SE of Les Haudères, forêt de Tauge, 46.0784°N, 7.5193°E, 1500–1600 m, on *Larix*, on *Usnea perplexans*, 2012, Diederich 17333 (BR).

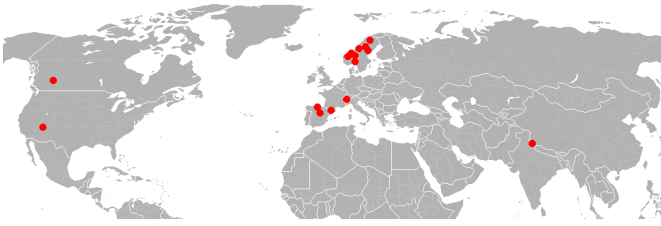
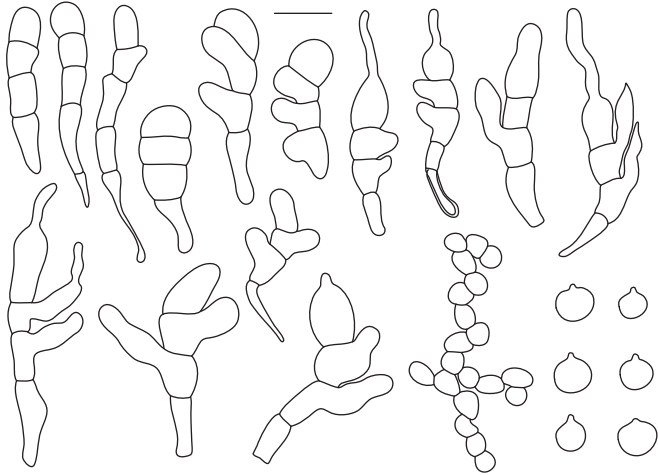
References. Millanes et al. 2014b, 2016.



Biatoropsis minuta, Spain, holotype. Basidioma on *Usnea barbata*. Scale bar: 200 μ m.



Biatoropsis minuta, Canada, Goward 91-13. Basidiomata on *Usnea perplexans*. Scale bar: 500 μ m.

*Biatoropsis minuta**Biatoropsis minuta*, Spain, holotype (modified from Millanes et al. 2016). Basidia, basidiospores and catenulate conidia. Scale bar: 10 µm.***Biatoropsis nigrescens* Diederich, Millanes & F. Berger, sp. nov.**

Diagnosis: Characterized by the relatively small, convex, basally constricted, blackish brown to black, rarely medium brown basidiomata, 0.3–1 mm diam., developing on the thallus of *Usnea* species, the clavate to subcylindrical, 3-transseptate basidia, $22\text{--}36 \times 3.5\text{--}9.5$ µm, and the small, ellipsoid basidiospores, $5.5\text{--}6.5 \times 3.5\text{--}4.5$ µm.

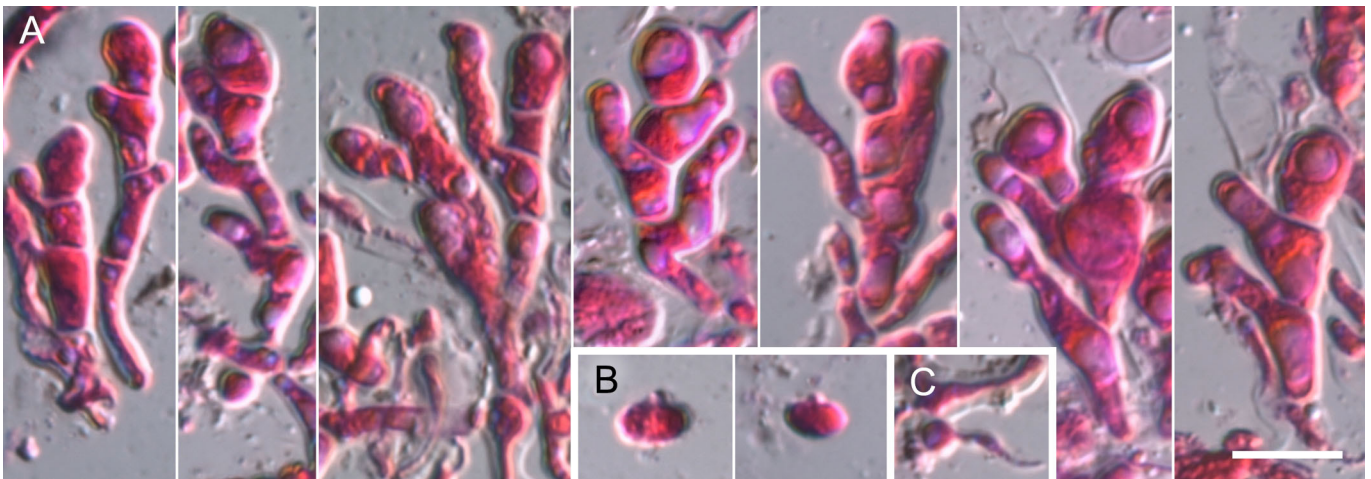
Etymology: From *nigrescens*, becoming black, in reference to the basidiomata that are mostly black when mature.

Type: Australia, Tasmania, Hobart, Mt Wellington, $42^\circ 53' 42''\text{S}$, $147^\circ 14' 14''\text{E}$, 1260 m, alpine Gipfelvegetation, on *Usnea capillacea*, 13 Nov. 2017, F. Berger 32655 (BR – holotype).

MycoBank: MB844640

Basidiomata convex, basally constricted, with a smooth surface, waxy-gelatinous, usually blackish brown to black from the beginning, rarely medium brown, 0.3–1 mm diam. **Context hyphae** and subbasidial hyphae thick-walled, 2–4 µm diam.; haustoria present, without basal clamp. **Hymenium** hyaline, containing numerous clavate to subcylindrical probasidia without basal clamp. **Basidia**, when mature, 4-celled, with three transverse septa, not or slightly constricted at the septa, the lower cell usually attenuated at the base, often longer than the other cells, $22\text{--}36 \times 3.5\text{--}9.5$ µm; the three lower cells elongating laterally at maturity; epibasidia poorly distinct from the elongate basidial cells, both together $3.5\text{--}4.5$ µm diam., up to at least 40 µm long. **Basidiospores** ellipsoid, $5.5\text{--}6.5 \times 3.5\text{--}4.5$ µm. **Asexual stage** unknown.

Notes. The type specimen from Tasmania is distinguished by small, almost black basidiomata with a smooth surface, dispersed over the host thallus. This specimen, and a second one from New Zealand (Berger 31714), have been

*Biatoropsis nigrescens**Biatoropsis nigrescens*, Australia, Tasmania, holotype. A, Basidia in various stages of development. B, Basidiospores. C, Haustorium. In phloxine. Scale bar: 10 µm.



Biatoropsis nigrescens, Australia, Tasmania, holotype, sequenced specimen. Basidiomata on the thallus of *Usnea capillacea*. Scale bar: 500 µm.



Biatoropsis nigrescens, Australia, Queensland, Stevens 7297. Basidioma on the thallus of *Usnea nidifica*. Scale bar: 500 µm.



Biatoropsis nigrescens, Australia, Victoria, Stevens 7201. Basidiomata on the thallus of *Usnea inermis*. Scale bar: 500 µm.



Biatoropsis nigrescens, Australia, New South Wales, Rambold 3771. Basidiomata on the thallus of *Usnea subalpina*. Scale bar: 500 µm.



Biatoropsis nigrescens, Australia, Victoria, Stevens 4606. Basidiomata on the thallus of *Usnea inermis*. Scale bar: 500 µm.



Biatoropsis nigrescens, New Zealand, Berger 31714, sequenced specimen. Basidiomata on the thallus of *Usnea* sp. Scale bar: 500 µm.

included in our phylogenetic analysis, and both obviously represent a same new species. The New Zealand specimen, however, has mainly pale brown basidiomata, only some becoming blackish. We consider the new *Biatoropsis nigrescens* therefore as a species with basidiomata that are either black from the beginning, or that turn black with age.

We have examined a number of additional specimens from Oceania that agree morphologically, although their identification, without molecular data, can only be tentative. All these specimens are here provisionally accepted as belonging to the new species. Microscopically, this species is similar to most other species with 3-septate basidia. The few

basidiospores observed are smaller than in other species, but that needs to be confirmed from additional specimens. Basidiomata of *Biatoropsis minuta* are similar in size, 0.1–0.8 mm diam., but they are typically medium to dark brown, with a rougher surface, and are usually much more abundant, often touching each other. *Biatoropsis hafellneri* also has relatively small basidiomata, but they are pale to orange-brown, and basidia are 2-celled.

Ecology and host. On the thallus of *Usnea capillacea*, *U. inermis*, *U. nidifica*, *U. subalpina*, *U. torulosa* and *Usnea* sp.

Distribution. Oceania (**Australia:** New South Wales, Queensland, **Tasmania**, Victoria, Western Australia; New Zealand; Papua New Guinea).

Additional specimens examined. **Australia:** New South Wales: Bungonia Caves, rim above Shoalhaven River, on *Usnea inermis*, 1968, Weber *Lich. Exs.* 328 [as *U. poliotrix*] (BR); near Taralga, 34°27'S, 149°48'E, 1140 m, on *U. subalpina*, 1991, Stevens (BR); Kosciuszko Nat. Park, Yarrangobilly Caves, 35°43'S, 148°29'E, 1060 m, on *U. subalpina*, 1986, Rambold 3771 (BR). **Queensland:** Atherton Tableland, Danbulla Drive, 17°13'S, 145°40'E, 900 m, on *U. nidifica*, Stevens 5406 (BR); Mary River Heads, 25°28'S, 152°52'E, 0 m, on mangroves, on *U. nidifica*, Stevens 7297 (BR); Swan Bay Stradbroke Island, 27°45'S, 153°26'E, 0 m, on *Cerlops tagal* in a mangrove, on *U. nidifica*, Stevens 3071 (BR). **Tasmania:** Poatina Rd, 41°29'S, 147°53'E, on *U. cf. inermis*, Bratt & Cashin (BR [ex HO 40081]); Brady's Sugarloaf, 42°16'S, 146°32'E, 980 m, on *U. torulosa*, 1992, Kantvilas 90/92 (BR, HO). **Victoria:** Sassafras Gap, 36°37'S, 147°45'E, 1216 m, on *Eucalyptus*, on *U. inermis*, Stevens 4606 (BR); Mt Buffalo, The Hump, 36°47'S, 146°46'E, 1700 m, on *U. inermis*, Stevens 7195a (BR); *ibid.*, 1400 m, on *U. subalpina*, Stevens 7195b (BR); Lake Mountain, Echo Flat Area, 37°30'S, 145°53'E, 1200 m, on *U. inermis*, Stevens 5070 (BR); Mt Beauty to Bright road, 36°44'S, 147°05'E, > 500 m, on *U. inermis*, Stevens 7201 (BR). **Western Australia:** Tone River Bridge, Muir Highway, on *U. cf. subalpina*, 1980, s. coll. (BR [ex PERTH 001632]). **New Zealand:** South Island: Hamner Springs, Molesworth road, mountain N Acheron Roadhouse, 42°23'23"S,

172°56'37"E, 750–1200 m, on *Usnea*, 2017, Berger 31714 (herb. Berger). **Papua New Guinea:** Madang Prov.: Near Bogia, along road Bogia-Josephstaal, near Tanggu church, 4°27'S, 144°56'E, 330 m, on *Usnea*, 1992, Diederich 11529 (BR).

***Biatoropsis protousneae* Millanes, Diederich, M. Westb. & Wedin**

Herzogia 29: 347 (2016). **Type:** Chile, XII Region of Magallanes and Chilean Antarctica, Puerto Natales, along the road to Lake Balmaceda, 51°56.48'S, 72°23.28'W, on *Protousnea dusenii*, 14 Jan. 2008, S. Pérez-Ortega 207 (S F291460 – holotype; BR, MAF-Lich – isotypes).

Basidiomata convex, basally constricted, tuberculate and often with a central depression when mature, waxy-gelatinous when wet, pale to light brown, dark brown, or black, 0.1–2.4 mm diam. **Context hyphae** thin-walled, 2–3 µm diam., clamps not observed; haustoria frequent. **Hymenium** hyaline, containing numerous clavate probasidia, basal clamp not observed. **Basidia**, when mature, 4-celled, with three transverse septa, often constricted at the septa, the lower cell with an attenuated stalk-like base, often longer than the upper cells, 22–60 × 4–10 µm (incl. stalk-like base, excl. epibasidia), lower part of the stalk-like base 2–4 µm diam.; epibasidia 2–4 µm wide, up to 45 µm long. **Basidiospores** globose to subglobose, 5–8 × 5–9 µm. **Asexual stage:** hyaline catenulate conidia have been observed, cells 3–7 × 3–6 µm.

Notes. This species is similar to specimens belonging to the phylogenetically closely related clade A1 (Millanes et al. 2014b). That taxon is distinguished, however, by its host selection, growing on several *Usnea* species.

Ecology and host. On the thallus of *Protousnea dusenii*.

Distribution. South America (Argentina; **Chile**).

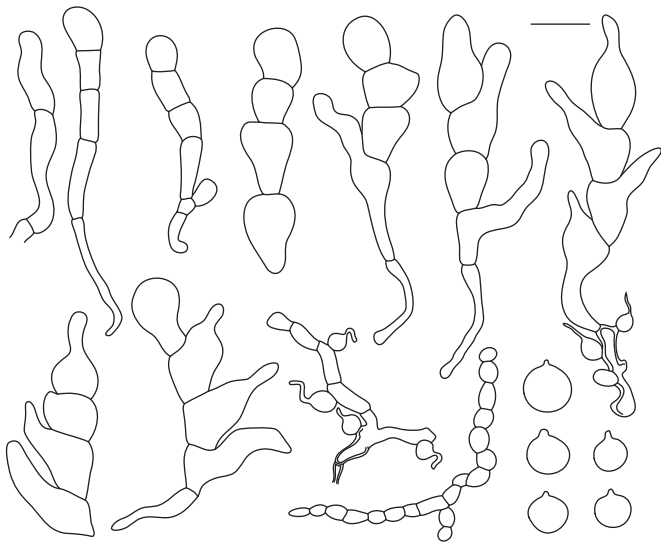
References. Millanes et al. 2014b, 2016.



Biatoropsis protousneae, Chile, holotype. Basidiomata on *Protousnea dusenii*. Scale bar: 500 µm.



Biatoropsis protousneae, Chile, holotype. Basidiomata on *Protousnea dusenii*. Scale bar: 500 µm.



Biatoropsis protousneae, Chile, holotype (modified from Millanes et al. 2016). Basidia, basidiospores, catenulate conidia and haustorial branches. Scale bar: 10 μ m.



Biatoropsis protousneae

***Biatoropsis rubicundae* Diederich & Millanes, sp. nov.**

Diagnosis: Characterized by the convex, medium to dark brown or blackish basidiomatal galls, often with an orange or reddish tinge, 0.5–1.6 mm diam., developing on the thallus of *Usnea* species, the clavate to subcylindrical, 1–3-transseptate basidia, 28–35 \times 3.5–6.5 μ m, and the subglobose to ellipsoid basidiospores, 5.5–9 \times 4–7 μ m.

Etymology: From *Usnea rubicunda*, the host lichen of the type.

Type: France, Pyrénées-Atlantiques, 15 km SSE of Saint-Jean-de-Luz, S of Sare, forêt communale de Sare, along road D306 to col de Lizarieta, on *Quercus*, on *Usnea rubicunda*, 26 Aug. 2015, P. Diederich 18149 (BR – holotype).

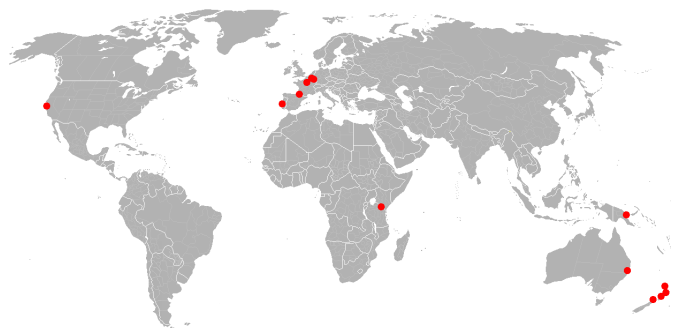
MycoBank MB844641

Basidiomatal galls convex, subspherical or sometimes slightly applanate, soon with a constricted base, when old often flattened, sometimes with an irregular surface,

smooth, cartilaginous, medium brown when young, often with an orange or reddish tinge, soon dark reddish brown to blackish, 0.5–1.6 mm diam. *Context hyphae* thin-walled, 1.5–2 μ m thick, clamps absent; haustoria not seen. *Hymenium* containing numerous clavate probasidia, basal clamp not observed. *Basidia*, when mature, clavate to subcylindrical, with 1–3 transverse septa, 28–35(–53) \times 3.5–6.5 μ m, the lower cell attenuated; epibasidia cylindrical, 4–7 μ m thick, up to 35–45 μ m long. *Basidiospores* subglobose to ellipsoid, 5.5–9 \times 4–7 μ m. *Asexual stage* unknown.

Notes. This species is part of ‘lineage F’, as defined by Millanes et al. (2014b) and referring to specimens inhabiting *Usnea ceratina*, *U. hirta* and *U. rubicunda*. Millanes et al. (2016) added to this lineage a specimen on *U. exasperata*. Diederich & Ertz (2020) regarded this lineage as a species complex, and they described the new *B. millanesiana* for specimens from the South-West Indian Ocean inhabiting *Usnea exasperata*. The North American material on *U. hirta* is described as the new *B. hirtae* (see above), while the remaining specimens on *U. ceratina*, *U. rubicunda* and the closely related *U. erinacea* are here described as the new *B. rubicundae*. Macroscopically, *B. hirtae* is distinguished by the particularly broad and flattened basidiomata that are constantly pale to medium brown. Basidiomata of both *B. millanesiana* and *B. rubicundae* are typically subglobose or slightly applanate and much darker. Microscopically, basidial cells in *B. millanesiana* often elongate laterally before the formation of epibasidia, while this has not been observed in the two other species. Although these species may be regarded as semi-cryptic, their hypothetical host-specificity would easily allow identifying the majority of specimens. We have seen several morphologically similar, yet unidentified specimens on other *Usnea* species, for which molecular data would be indispensable for a correct identification.

Ecology and host. On the thallus of *Usnea rubicunda*, *U. ceratina* and *U. erinacea*.



Biatoropsis rubicundae



Biatoropsis rubicundae, France, holotype. Basidiomata on the thallus of *Usnea rubicunda*. Scale bar: 500 μ m.



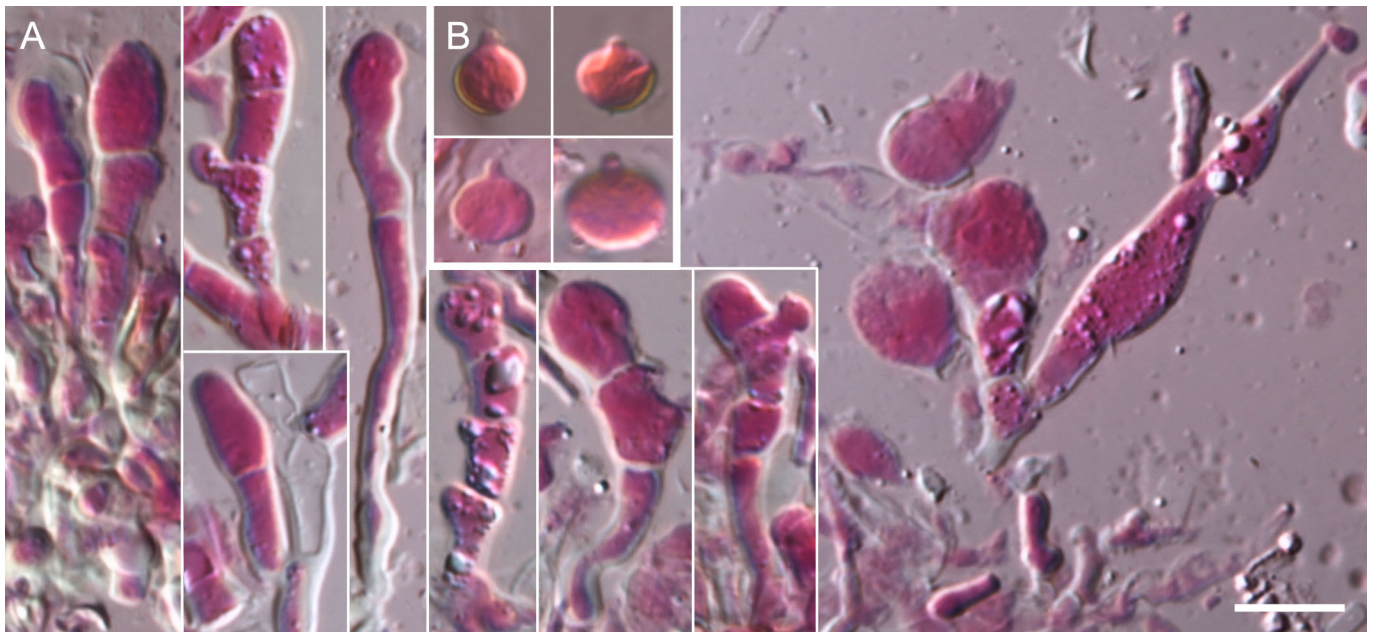
Biatoropsis rubicundae, New Zealand, Berger 16609. Basidioma on the thallus of *Usnea rubicunda*. Scale bar: 500 μ m.

Distribution. Europe (Belgium; France; Luxembourg; Portugal), Africa (Tanzania) and Oceania (Australia: Queensland; New Zealand; Papua New Guinea).

Additional specimens examined. **Australia:** *Queensland:* Bunya Mt. National Park, 26.83°S, 151.67°E, 900 m, on *Usnea rubicunda*, no collector ('8118 RR') (BR). **Belgium:** 3 km E of Chiny, near barrage de la Vierre, on *U. ceratina*, 2003, Diederich 15789 (BR). **France:** *Seine-et-Marne:* Forêt de Fontainebleau, vallée de la Solle, 90 m, on *U. ceratina*, 1991, Diederich 9477 (BR). **Luxembourg:** S. loc., on *U. ceratina*, c. 1840, Tinant 600, 601a (LUX). **New Zealand:** *North Island:* Rotorua, Lake Tarawera, N coast, 1 km E of Humphreys Bay, on *U. rubicunda*, 2001, Berger 16609 (BR, S F92784, herb. Berger); Wellington, c. 25 km N of Masterton, 40°43.23'S, 175°38.4'E, on *U. rubicunda*,

2010, Wedin 9429 (S F181399). *South Island:* Hwy 6 Nelson, direction Picton, Pelorus Bridge, 4°18'04"S, 173°34'12"E, 30 m, on *U. rubicunda*, 2017, Berger 31715 (S, herb. Berger). **Papua New Guinea:** *Madang Province:* Huon Peninsula, Finisterre range, Yupna valley, Teptep village, 5°57'S, 146°33'E, on *U. rubicunda*, 1992, Diederich 10800 (BR). **Tanzania:** Arusha region, Arusha National Park, Mount Meru, around 3 km from the trekking starting point on Momela road in direction to Miriakamba huts, 3°13'58"S, 36°49'26"E, 1943 m, on *U. erinacea*, 2016, Galán Boluda 4 (G). **USA:** *California:* Marin Co., Sky Trail, on *U. ceratina*, 11 July 2008, Kocourková s.n. (S F264679).

References (as *Biatoropsis* sp. F). Diederich & Ertz 2020, Millanes et al. 2014b, 2016.



Biatoropsis rubicundae, France, holotype. A, Basidia in different stages of development. On the right, the lower basidial cell has a large epibasidium carrying a young basidiospore. B, Basidiospores. In phloxine. Scale bar: 10 μ m.

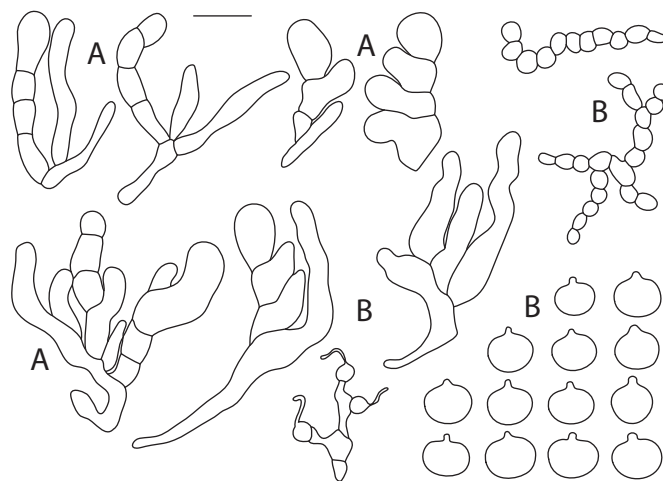
***Biatoropsis usnearum* Räsänen**

Ann. bot. Soc. Zool.-bot. fenn. 'Vanamo' 5(9): 8 (1934). *Type*: Finland, Ostrobothnia borealis, Simo Kuusella, on '*Usnea comosa*', 1 July 1915, V. Räsänen (H – lectotype).

Basidiomata extremely variable in form, size and colour, generally subspherical and convex with a constricted base, often with lobate margins, sometimes flattened or with a concave central part, rarely effuse and covering larger areas around the branches of the host, surface smooth, rarely tuberculate, cartilaginous, pale pinkish, reddish brown, dark brown or black, 0.2–2.5 mm diam. *Context hyphae* thin-walled, 2–3 µm thick, clamps absent; haustoria frequent. *Hymenium* containing numerous clavate probasidia, basal clamp not observed. *Basidia*, when mature, clavate to subcylindrical, with 1–3 transverse septa, 20–44 × 3–6.5 µm; epibasidia 2–3 µm thick, up to 85 µm long. *Basidiospores* subglobose to ellipsoid, 4.5–8 × 4–7.5 µm. *Asexual stage*: hyaline catenulate conidia often present, cells 3–5 × 2–3.5 µm.

Notes. *Biatoropsis usnearum* was considered as a common, widespread fungus inhabiting *Usnea* species (Diederich & Christiansen 1994), but later proved to represent a complex of many morphologically often only slightly distinct species. The global distribution and host range of *B. usnearum* s. str. are therefore yet poorly known, and many specimens originally identified as that species must now be considered as doubtfully unidentified. The species is rather well characterized by the large, pale pinkish brown basidiomata that may in some specimens become darker, sometimes through the presence of parasitic fungi. Our current circumscription of the species is rather conservative by including only specimens that have either been sequenced or that present the very typical, large, pinkish brown basidiomata.

Ecology and hosts. On the thallus of *Usnea subfloridana*, *U. barbata*, *U. cavernosa*, *U. florida*, *U. glabrescens* and *U. intermedia*.



Biatoropsis usnearum s. str. A, Scotland, Millanes 507; B, Canada, Björk 14689 (modified from Millanes et al. 2016). Basidia, basidiospores, catenulate conidia and haustorial branches. Scale bar: 10 µm.

Distribution. Europe (Austria; Finland; Poland; Sweden; UK: Scotland) and North America (Canada: Alberta, British Columbia; USA: Minnesota), surely much more common and widespread. No map is given.

Additional specimens examined. **Canada:** Alberta: Boreal Plains, on *U. glabrescens*, 2012, Golder (UBC). **British Columbia:** Robson Valley, near Driscoll Creek, on *Usnea barbata*, 2011, Björk 22557 (UBC); *ibid.*, W of Slim Creek, on *U. glabrescens*, 2011, Björk 22523 (UBC); Homathko Valley Sandbar, 51°2'N, 124°58'W, on *Usnea* sp., 2007, Björk 14689 (UBC). **Poland:** Wybrzeże Słowinkie coast, vicinity of Białogóra village, 54°49'N, 17°56'E, on *U. subfloridana*, 2000, Kowalewska (BR, UGDA-L). **Sweden:** Uppland, Älvkarleby, S of Island Tjäder-Holmen, 0°26'N, 17°19'E, 45 m, 2006, Millanes 005 (S-F102399). **UK:** Scotland: Isle of Skye, S Kyle of Lochalsh, S Loch Na Béiste, on *U. subfloridana*, 1987, Diederich 8844 (BR); Isle of Raasay (E Isale of Skye), South Fearn, on *U. subfloridana*, 1987, Diederich 8768 (BR); NW Fort Augustus, Ceannacroc Forest, Torgyle



Biatoropsis usnearum s. str., UK, Millanes 507. Basidiomata on the thallus of *Usnea subfloridana*. Scale bar: 1 mm.



Biatoropsis usnearum s. str., Canada, Björk 14689. Basidiomata on the thallus of *Usnea* sp. Scale bar: 500 µm.



Biatoropsis usnearum s. str., Poland, Kowalewska. Basidiomata on the thallus of *Usnea subfloridana*. Scale bar: 1 mm.



Biatoropsis usnearum s. str., UK, Scotland, Diederich 8844. Basidiomata on the thallus of *Usnea subfloridana*. Scale bar: 1 mm.



Biatoropsis usnearum s. str., USA, Minnesota, Gockman 5554b. Basidiomata on the thallus of *Usnea* cf. *subfloridana*. Scale bar: 1 mm.



Biatoropsis usnearum s. str., Canada, British Columbia, Bjork 22569. Basidiomata on the thallus of *Usnea barbata*. Scale bar: 1 mm.



Biatoropsis usnearum s. str., Canada, British Columbia, Bjork 22523. Basidiomata on the thallus of *Usnea glabrescens*. Scale bar: 1 mm.



Biatoropsis usnearum s. str., USA, Minnesota, Gockman 5556. Basidiomata on the thallus of *Usnea cavernosa*. Scale bar: 1 mm.

Bridge, on *U. subfloridana*, 1987, Diederich 8867 (BR); West Ross, Duirinish, west side of Port Bàn, on *Usnea subfloridana*, 2010, Millanes 507 (S F291462). USA: Minnesota: Cook Co., Superior National Forest (SNF), 8.3 km N Tofte and 13 km W

Lutsen, 47.6477°N, 90.8480°W, on *U. cavernosa*, 2018, Gockman 5556 (BR); Cook Co., SNF, 14.3 km W Grand Marais and 15.7 km NE Lutsen, 47.7454°N, 90.5253°W, on *U. cavernosa*, 2018, Gockman 5583 (BR); Cook Co., SNF, on Artist's Point in Grand

Marais, 47.7455°N, 90.3303°W, on *U. cavernosa*, 2018, Gockman 5796 (BR); Cook Co., 8.3 km SW Hovland and 20.5 km E of Grand Marais, 47.8100°N, 90.0751°W, on *U. cavernosa*, 2018, Gockman 5797 (BR); Lake Co., SNF, 13 km NW Taconite Harbor and 16–20 km N Little Marais, 47.58°N, 91.08°W, on *U. cavernosa*, 2018, Gockman 5546 (BR); *ibid.*, on *U. cf. subfloridana*, 2018, Gockman 5547, 5549, 5550, 5554, 5598, 5600 (BR).

References. Diederich 1996, Diederich & Christiansen 1994, Millanes et al. 2014b, 2016. Reports of *B. usnearum* s. lat. are not considered here.

Biatoropsis sp. E

Basidiomata pale to dark brown, convex, subspherical, basally constricted, with a smooth surface, rarely tuberculate or with a central depression when mature, 0.2–0.85 mm diam. **Hymenium** containing numerous clavate probasidia, basal clamp not observed; haustoria frequent. **Basidia** transversely 1–2-septate (immature?), 21–33 × 4–7 µm, basal clamps not observed; immature epibasidia up to 10 µm long. **Basidiospores** subspherical, 5–8 × 5–7 µm. **Asexual stage:** lunate conidia have been observed.

Notes. Millanes et al. (2014b) reported an Argentinian specimen on *Protousnea magellanica* representing a distinct lineage, called ‘lineage E’. More specimens would be useful for a formal description.

Ecology and host. On the thallus of *Protousnea magellanica*.

Distribution. South America (Argentina), known from one locality.

Specimen examined. **Argentina:** Rio Negro, Parque Nacional Nahuel Huapi, Lago Guiterrez, along the stream Arroyo Negro, mixed *Nothofagus dombeii*-*N. pumilio* forest, on *Austrocedrus*, on *Protousnea dusenii*, 41°21'44"S, 71°29'45"W, 890 m, 2010, Wedin 8742 (S F264824).

Reference. Millanes et al. 2014b.

Heteroacanthella Oberw.

in Oberwinkler et al., *Transactions of the Mycological Society of Japan* 31: 208 (1990). **Type:** *H. variabilis* Oberw. & Langer

Molecular data: yes. **Number of species:** 1–0–0 (3).

Basidiomata resupinate, effused, ceraceous, in lichenicolous species often reduced and inconspicuous. **Hymenium** hyaline, comprising numerous probasidia, basidia and clavate, acanthoid hyphidia. **Basidia** aseptate, with an acanthoid ornamentation, epibasidia elongate with 1 or 2 sterigmata. **Basidiospores** ellipsoid, self-replicating.

Notes. Species of *Heteroacanthella* are characterized by the aseptate basidia and the clavate hyphidia, both with an acanthoid ornamentation. They have very rarely been collected, and no sequences are currently available from the generic type.

Ecology. Two species are saprotrophic and one lichenicolous.

Heteroacanthella ellipsospora J. C. Zamora, Pérez-Ortega & V. J. Rico

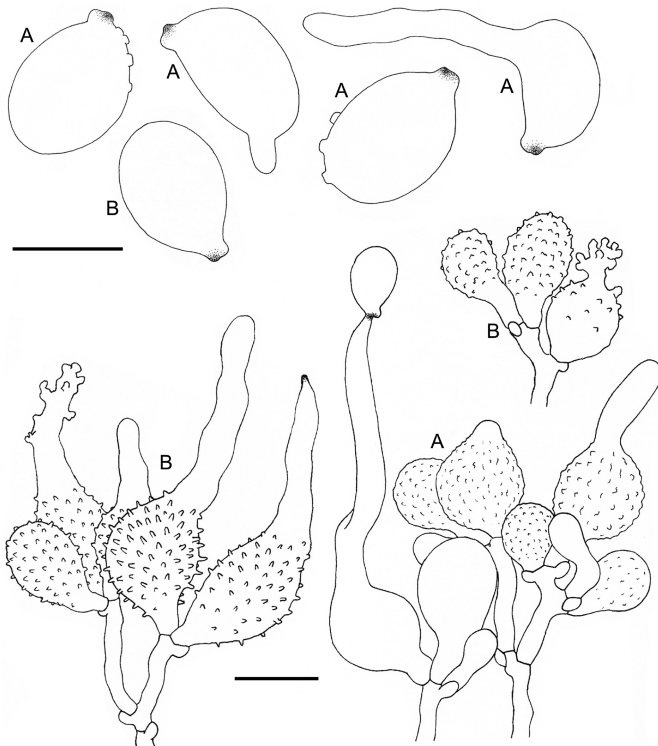
Lichenologist 46 (1): 18 (2014). **Type:** Spain, Comunidad de Madrid, Madrid, Collado-Villalba, near Urbanización La Chopera, in *Lecanora carpinea* (also parasitized by *Taeniolella delicata*) on *Prunus* sp. branches, 40°39'12"N, 4°00'01"W, 890 m, 29 Dec. 2010, J. C. Zamora, A. González & F. Prieto (MAF-Lich 18273 – holotype).

Basidiomata reduced, intrahymenial or in the host thallus surrounding apothecia, not visible or inducing pale brown swellings, 0.1–0.8 mm diam. **Context hyphae** smooth, hyaline, thin to slightly thick-walled, 1.5–4.5 µm diam., with clamp connections; haustoria unclear, mother cell 5–10.5 × 3–4 µm, haustorial filament 0.5–1.5 µm thick. **Hymenium** hyaline, containing probasidia, basidia and hyphidia-like cells, often reduced; acanthoid hyphidia-like cells 8–23 × 5–12 µm, with spine-like protuberances, 1–7 µm long, in the upper part; probasidia thin-walled, subspherical to pyriform, often stalked. **Basidia** aseptate, 1-celled, thin- to thick-walled, mostly stalked, subspherical, pyriform to broadly clavate, (9–)10–15(–16) × 7.5–12 µm (stalk not included), acanthoid, surface smooth to echinate or tuberculate (ornamentation up to 3 µm high), stalk 1–7(–11) µm long; epibasidia subcylindrical, (2–)3–5.5(–6) µm thick, (8–)17–64(–77) µm long, smooth or with few spiny processes, with one or rarely two or more refractive sterigmata. **Basidiospores** broadly ellipsoid to ellipsoid, with a refractive apiculus at the proximal end, (9–)10–14(–14.5) × (6–)6.5–9.5(–10) µm. **Asexual stage:** basidiospores sometimes germinating by formation of blastic conidia, 3.5–5.5 × 2.5–4 µm. [Modified from Zamora et al. 2014.]

Notes. When basidia are almost smooth, this species may be confused with *Tremella endosporogena*, also confined to *Lecanora carpinea*, but differing by the larger, always smooth-walled basidia, 17–40 × 9.5–17 µm, old basidia



Heteroacanthella ellipsospora, Spain, Villaviciosa de Odón, Zamora. Basidiomata on the apothecia of *Lecanora carpinea*. Scale bar: 500 µm.



Heteroacanthella ellipsospora, Spain, A, MAF-Lich 18275, B, MAF-Lich 18274 (modified from Zamora et al. 2014). Basidia, basidiospores and acanthoid hyphidia. Scale bars: 10 μ m.

occasionally filled with thick-walled ‘endospores’ and globose to subglobose basidiospores with a lateral apiculus.

Ecology and host. In the hymenium and surrounding thallus of *Lecanora carpinea*, sometimes resulting in pale coloured gall-like areas.

Distribution. Europe (Spain; Sweden).

Specimen examined. **Spain:** Madrid, Villaviciosa de Odón, área recreativa ‘El Sotillo’, 40.3693°N, 3.9458°W, 580 m, on *Lecanora carpinea*, Zamora (BR).

References. Zamora et al. 2014 [Ekman et al. 2019].



Heteroacanthella ellipsospora

TREMELLA Pers.

Neues Mag. Bot. 1: 111 (1794), nom. cons. Type: *T. mesenterica* (Schaeff.) Retz.

Molecular data: yes (T, L). **Number of species:** 117[6]–0–0 (300). At least 200 non-lichenicolous species of *Tremella* are known, but many additional doubtful species have been described.

Basidiomata often cerebriform to foliose, ranging from 0.2 mm to as much as 8 cm; distinct basidiomata lacking in species that are endoparasitic in other basidiomycetes or intrahymenial in apothecia of discomycetes; lichenicolous taxa often induce galls on the host thallus, or have waxy-gelatinous, typically pulvinate, frequently very small basidiomata. **Context hyphae** thin- to thick-walled; clamp connections are characteristic of most species in the genus, but are lacking in some lichenicolous species; haustoria frequent, usually with a basal clamp. **Hymenium** hyaline, containing numerous probasidia that are sometimes intermixed with conidiogenous cells; probasidial initials subspherical, ellipsoid or clavate, sometimes with an attenuated base, the mature structures globose to ellipsoid, pyriform, clavate, sometimes stalked; in most species, proliferations occur through a basal clamp; hyphidia absent or reduced; cystidia absent. **Basidia**, when mature, (1–)2–4-celled, with longitudinal, oblique or transverse septa; epibasidia subcylindrical, elongate. **Basidiospores** hyaline, subspherical to ellipsoid, with a distinct, mostly lateral apiculus, exceptionally almost limoniform (*T. cetrariicola*) or gasteroid. **Asexual stage** often present: either conidiogenous cells producing single conidia (many species), catenulate conidia or asteroconidia.

Notes. The genus *Tremella* in its current circumscription is heterogeneous, as shown by our phylogenetic tree on pages 106–107.

Ecology. Most species are fungicolous, incl. lichenicolous.

Tremella abrothalli Diederich & Goward, sp. nov.

Diagnosis: Characterized by the intrahymenial growth in apothecia of *Abrothallus parmeliarum* that may become swollen, the transversely 1-septate basidia, $17\text{--}21 \times 7\text{--}8 \mu\text{m}$, and the ellipsoid basidiospores, $5.5\text{--}8 \times 5\text{--}6.5 \mu\text{m}$.

Etymology: From *Abrothallus*, the host fungus.

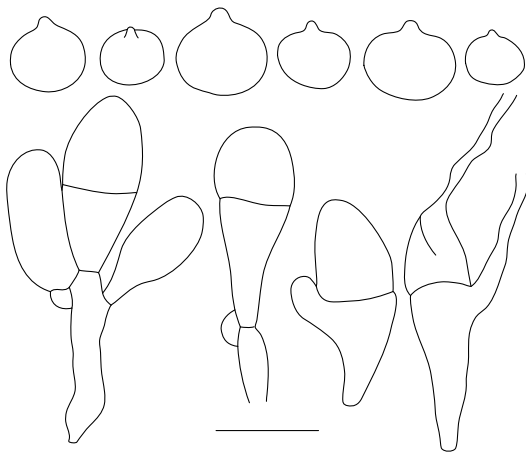
Type: Canada, British Columbia, 10 km N of Boswell on Hwy 3A, above Kootenay lake, 49°27'N, 116°45'W, 570 m, boulder bed and bluff partially treed with Douglas-fir and lodgepole pine, rather mossy, in apothecia of *Abrothallus parmeliarum*, 30 July 1981, T. Goward 81-1669 (UBC – holotype; BR – isotype).

Mycobank: MB844642

Basidiomata developing in the hymenium of the host, macroscopically visible as swellings of the host apothecia. **Context hyphae** not observed; subbasidial hyphae 2–3(–5) μm diam.; haustoria not observed. **Hymenium** reduced,



Tremella abrothalli, Canada, British Columbia, holotype. Swollen apothecia of *Abrothallus parmeliarum* with intrahymenial basidia. Scale bar: 500 μ m.



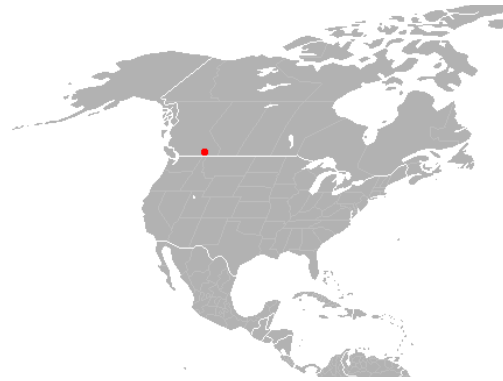
Tremella abrothalli, Canada, British Columbia, holotype. Basidia and basidiospores. Scale bar: 10 μ m.

probasidia intermixed with asci and paraphysoids of the host; probasidial initials ellipsoid, with a basal clamp. *Basidia*, when mature, elongate ellipsoid, transversely 1-septate, not or slightly constricted at septum, $17\text{--}21 \times 7\text{--}8 \mu\text{m}$, lower cell basally or slightly attenuated; epibasidia cylindrical, up to $3 \mu\text{m}$ diam., at least $30 \mu\text{m}$ long. *Basidiospores* ellipsoid, $5.5\text{--}8 \times 5\text{--}6.5 \mu\text{m}$. *Asexual stage* unknown.

Notes. Although this species is not really lichenicolous, but fungicolous on a lichenicolous host, it may nevertheless be treated amongst the lichenicolous *Tremella* species. It is distinguished from other intrahymenial species with transversely 1-septate basidia by the shorter basidia.

Ecology and host. Hyperparasitic in the hymenium of *Abrothallus parmeliarum* growing on galls induced by *Nesolechia oxyspora* on the thallus of *Parmelia saxatilis*.

Distribution. North America (Canada: British Columbia), known only from the type locality.



Tremella abrothalli

Tremella acarosporae Diederich & Hollinger, sp. nov.

Diagnosis: Characterized by the intrahymenial growth in the apothecia of *Acarospora* sp. that become swollen and strongly convex, waxy-gelatinous, dark brown, $0.3\text{--}0.8 \text{ mm}$ diam., and the transversely 1-septate basidia, $16\text{--}29 \times 5.5\text{--}8.5 \mu\text{m}$.

Etymology: From *Acarospora*, the host lichen.

Type: USA, Nevada, Lincoln Co., Terry Benches (c. 20 km N of Mesquite), 36.9895°N , 114.0865°W , 800 m, N facing limestone (caliche clifflet at top of loose open slope), on *Acarospora* sp., 18 April 2017, J. Hollinger 16600 & N. Noell (BRY-C – holotype).

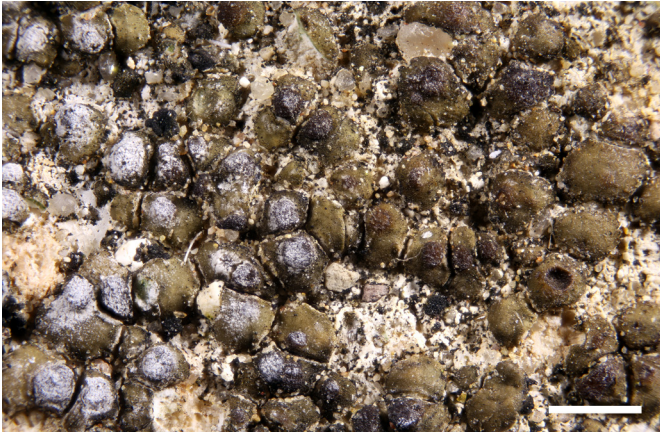
Mycobank: MB844643

Basidiomata reduced, intrahymenial, soon becoming strongly swollen, then almost superficial, pulvinate, subspherical or slightly elongate, strongly convex, waxy-gelatinous, dark brown, often covered by a white pruina, $0.3\text{--}0.8 \text{ mm}$ diam. **Context hyphae** not observed; subbasidial hyphae $1.5\text{--}2 \mu\text{m}$ diam.; haustoria not observed. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, elongate ellipsoid to clavate, 2-celled, transversely septate, $16\text{--}29 \times 5.5\text{--}8.5 \mu\text{m}$, cells more or less equal in length; epibasidia cylindrical, at least $28 \mu\text{m}$ long. **Basidiospores** not observed. **Asexual stage** unknown.

Notes. The new species can be detected by the swollen host apothecia that otherwise resemble healthy apothecia, have the same dark brown colour and the same white pruina. The apothecia examined were still young, without asci and ascospores, but instead filled with elongate, transversely 1-septate basidia.

Ecology and host. On an unidentified species of *Acarospora* over limestone. The host apothecia are young and immature, immersed, with a flat or concave disk.

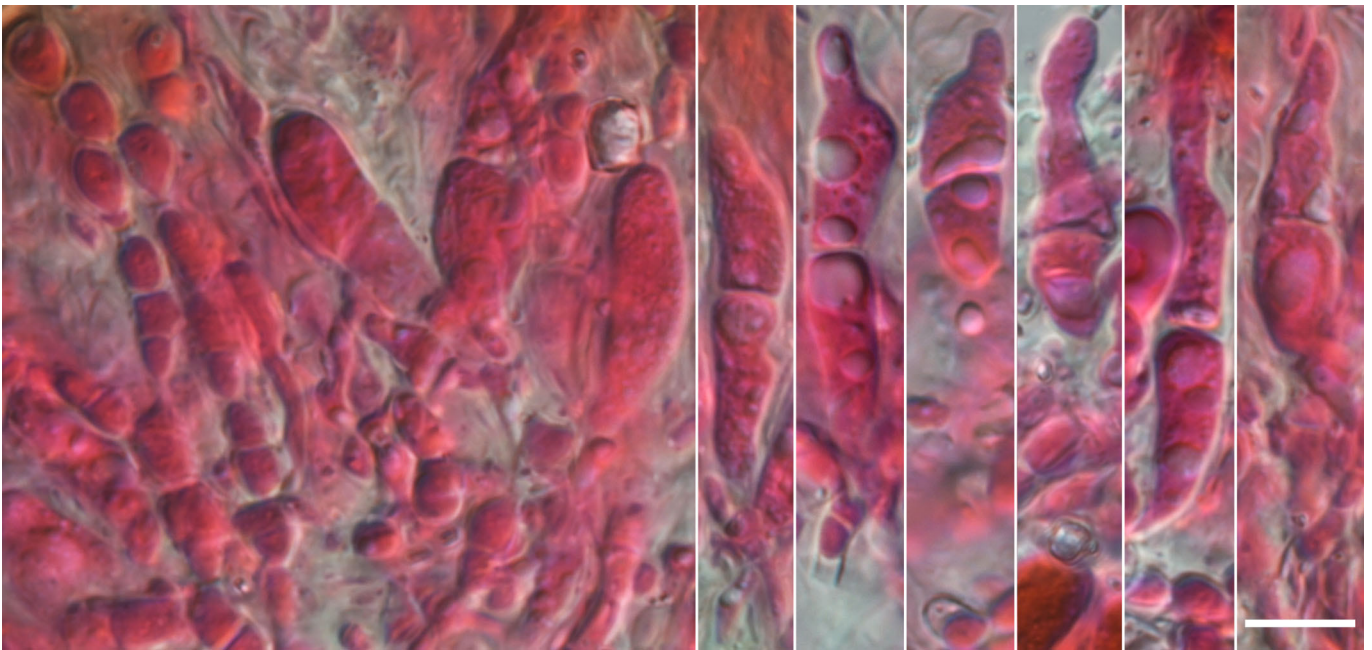
Distribution. North America (USA: Nevada), known only from the type locality.



Tremella acarosporae, USA, Nevada, holotype. Fertile thallus of the host *Acarospora* sp. (left), and developing basidiomata (right). Scale bar: 1 mm.



Tremella acarosporae, USA, Nevada, holotype. Strongly convex, pruinose basidiomata over the apothecia of *Acarospora* sp. Scale bar: 500 μ m.



Tremella acarosporae, USA, Nevada, holotype. Hymenium with 1-septate basidia and moniliform host hyphae. In phloxine. Scale bar: 10 μ m.



Tremella acarosporae

Tremella alectoriae Diederich & Holien, sp. nov.

Diagnosis: Characterized by the large and abundant, mostly concolorous galls appearing as swellings of the thallus of *Alectoria sarmentosa*, up to 1.5 mm long, the subspherical longitudinally 1-septate basidia, $7.5\text{--}14.5(-18) \times 7\text{--}11 \mu\text{m}$, and the ellipsoid basidiospores, $6\text{--}6.5 \times 5\text{--}5.5 \mu\text{m}$.

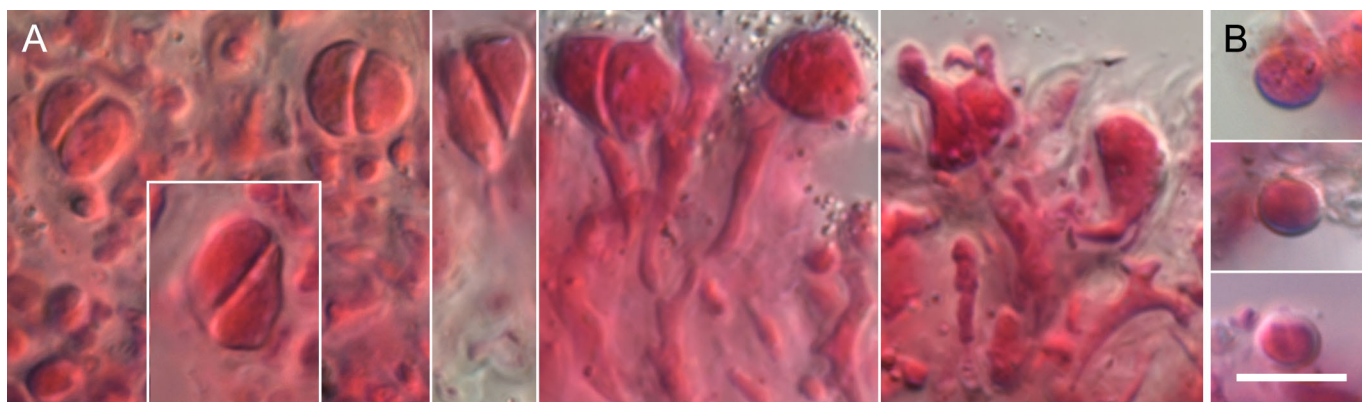
Etymology: From *Alectoria*, the host lichen.

Type: Norway, S-Trøndelag, Trondheim, Bymarka, W end of lakelet lille Leirsjøen, 200 m, on *Picea abies*, on *Alectoria sarmentosa*, 3 Oct. 1999, H. Holien 7934 (TRH – holotype; BR – isotype).

MycoBank: MB844644



Tremella alectoriae, Norway, holotype. Basidiomatal galls on the thallus of *Alectoria sarmentosa*. Scale bar: 500 μm .



Tremella alectoriae, Norway, holotype. A, 1-septate basidia. B, Basidiospores. In phloxine. Scale bar: 10 μm .

Basidiomata gall-inducing, resulting in numerous swellings of the host thallus branches, concolorous to the thallus or sometimes darker brown, 0.3–1.5 mm diam. *Context hyphae* thick-walled, 3.5–5 μm , clamps not observed; subbasidial hyphae thick-walled, 2–4.5 μm diam.; haustoria present, with a basal clamp. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid, 2-celled, with a longitudinal or rarely oblique septum, 7.5–14.5(–18) \times 7–11 μm ; epibasidia cylindrical, at least 15 μm long. *Basidiospores* ellipsoid, 6–6.5 \times 5–5.5 μm . *Asexual stage* unknown.

Notes. This is a very conspicuous species inducing the formation of large and very abundant galls on the host thallus, in some parts occupying over 50% of the thallus surface. It is therefore astonishing that the species is just known from a single specimen.

It is interesting to note that Tagirdzhanova et al. (2021) obtained sequences of a *Tremella* and a *Cyphobasidium* from the cortex of *Alectoria sarmentosa* in Canada (British Columbia) and the USA (Idaho).

Ecology and host. On the thallus of *Alectoria sarmentosa*.

Distribution. Europe (Norway), known only from the type locality.

*Tremella alectoriae**Tremella anaptychiae****Tremella anaptychiae* J. C. Zamora & Diederich**

in Zamora et al., *Phytotaxa* 307: 257 (2017). *Type*: Spain, Castilla-La Mancha, Guadalajara, El Cardoso de la Sierra, near Jarama river, 41°6'15" N, 3°29'20" W, 1260 m, on *Anaptychia ciliaris* thallus, on *Crataegus monogyna*, 16 Apr. 2011, J. C. Zamora & B. Zamora s.n. (MAF-Lich 21306 – holotype; AH, BR, MA-Fungi, S – isotypes).

= *Tremella* sp. 5, in Diederich, *Bibl. Lichenol.* 61: 174 (1996).

Basidiomata subglobose to somewhat tuberculate when old, with a frequently constricted base, waxy-gelatinous, cream-coloured, pinkish, brownish or blackish, 0.2–2 mm diam. *Context hyphae* and subbasidial hyphae thick-walled, 3–5.5 µm diam., usually without clamp; haustoria abundant. *Hymenium* containing numerous claviform to narrowly ellipsoid probasidia, basal clamps not observed. *Basidia*, when mature, longitudinally, obliquely or transversely 1-septate, often with a distinct stalk; upper part (without stalk) ellipsoid, claviform or subglobose, 15–20 × 10–15 µm; stalk 2–21(–24) µm long; epibasidia subcylindrical, 3–4 µm thick, 10–30(–60) µm long. *Basidiospores* subspherical to broadly ellipsoid, 5.5–9 × 5–9 µm. *Asexual stage*: asteroconidia sometimes present, 10–15 µm diam., individual arms 3.5–8 µm long; conidiogenous cells 17–26 × 1.5–4 µm diam. [Modified from Zamora et al. 2017.]



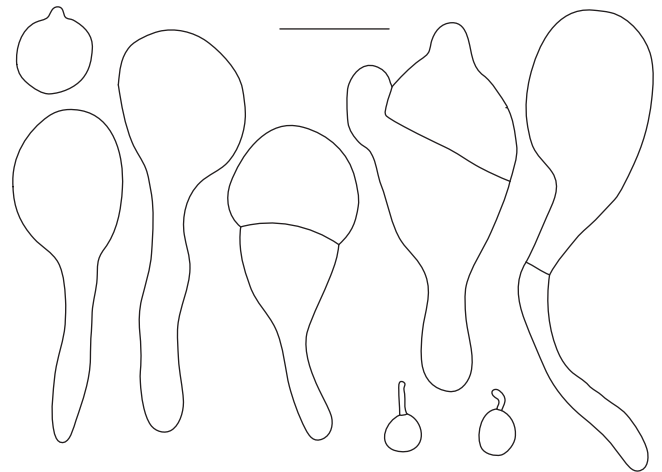
Tremella anaptychiae, Spain, isotype. Basidiomata on *Anaptychia ciliaris*. Scale bar: 500 µm.

Notes. *Tremella anaptychiae* is characterized by the convex brownish basidiomata on the thallus of *Anaptychia ciliaris*, the 1-septate stalked basidia, and the medium sized basidiospores. A specimen on *A. setifera* from the Canary Islands, La Gomera (Hafellner 33596, GZU) has much darker, almost black basidiomata, but is immature; more material on that host is needed to assess its identity.

Ecology and host. On the thallus (including lower surface and cilia) of *Anaptychia ciliaris*.

Distribution. Europe (France; Greece; Italy; North Macedonia; **Spain**; Sweden) and Macaronesia (Canary Islands: Gran Canaria, La Palma).

References. Diederich 1996 as *Tremella* sp. 5, Zamora et al. 2017 [Brackel & Berger 2019, Brackel & Döbbeler 2020, Roux 2020].



Tremella anaptychiae, North Macedonia, Hafellner 3906 (modified from Diederich 1996). Basidia, basidiospore and haustorial branches. Scale bar: 10 µm.

***Tremella aptrootii* Diederich & Common, sp. nov.**

Diagnosis: Characterized by the large, subglobose, often applanate, centrally depressed, lobate or tuberculate, waxy-gelatinous basidiomata on the thallus of *Astrothelium* spp., 0.1–1.5(–5) mm diam., the frequently stalked basidia with a subspherical, pyriform or ellipsoid, obliquely 2–4-celled upper part, 13–20 × 9–18 µm, and the subspherical to ellipsoid or limoniform basidiospores, 4.5–9.5 × 5.5–8.5 µm.

Etymology: Named after André Aptroot, lichenologist.

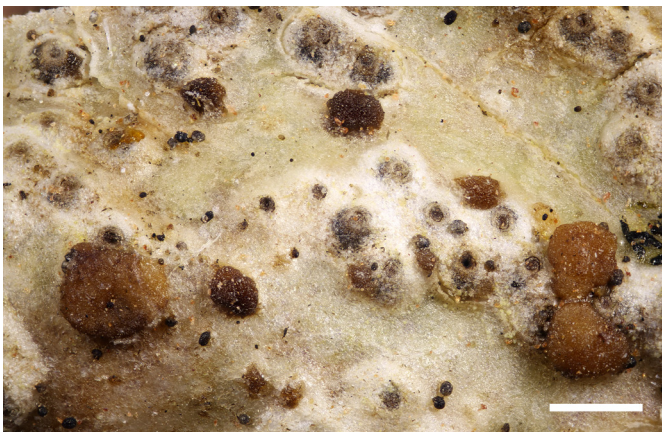
Type: USA, Florida, Hillsborough Co., Hillsborough River State Park, Florida Trail, 28.149°N, 82.235°W, on *Astrothelium* sp., 15 Sept. 2011, R. Common 9474E (BR – holotype).

Mycobank: MB844645

Basidiomata superficial, subglobose when young, soon becoming slightly applanate, often centrally slightly depressed, marginally lobed to almost tuberculate when old, pale to dark reddish brown or blackish, waxy-gelatinous, 0.1–1.5(–4) mm diam. *Context hyphae* and subbasidial hyphae thick-walled, 2.5–3 µm diam., with clamp connections; haustoria frequent, with clamp connections. *Hymenium* containing numerous clavate to subspherical probasidia with a basal clamp. *Basidia*, when mature, often distinctly stalked, stalk 3–25 µm long, upper part (without stalk) subspherical, pyriform or ellipsoid, 2–4-celled, septa mainly oblique, 13–20 × 9–18 µm; epibasidia subcylindrical, 2.5–4.5 µm diam., at least 25 µm long. *Basidiospores* subspherical with a lateral apiculus to ellipsoid or limoni-

form with a basal apiculus, 4.5–9.5 × 5.5–8.5 µm. *Asexual stage* unknown.

Notes. Material of this species was included in *Tremella harrisii* by Diederich (1996). The hosts of many specimens are either sterile or immature and can hardly be identified. However, with the kind help of André Aptroot, it was possible to identify most hosts at generic level, and it appeared that they all belong to either *Astrothelium* or *Polymeridium*. Specimens on these two host genera differ by several characters: (1) basidiomata on *Polymeridium* are always subspherical and medium to dark brown; those on *Astrothelium* may be subspherical when young, but soon become slightly applanate or centrally depressed, often marginally lobate or almost tuberculate, and their colour is variable, from pale or medium brown to frequently dark brown or blackish; (2) basidiomata on *Polymeridium* are relatively small, 0.15–0.3 mm diam., rarely up to 0.7 mm, while those on *Astrothelium* are typically at least 0.5 mm when mature, some even much larger; (3) basidia on *Polymeridium* are rarely stalked, while



Tremella aptrootii, Brazil, Aptroot 84067. Basidiomata on the thallus of *Astrothelium* sp. Scale bar: 500 µm.



Tremella aptrootii, Brazil, Aptroot 84067. Basidiomata on the thallus of *Astrothelium* sp. Scale bar: 500 µm.



Tremella aptrootii, USA, Florida, Harris 37710B. Basidiomata on the thallus of *Astrothelium variolosum*. Scale bar: 500 µm.



Tremella aptrootii, Brazil, Cáceres 27769. Basidiomata on the thallus of *Astrothelium* cf. *bicolor*. Scale bar: 500 µm.



Tremella aptrootii, USA, Florida, holotype. Basidiomata on the thallus of *Astrothelium variolosum* s. lat. Scale bar: 500 µm.



Tremella aptrootii, USA, Florida, Common 10296B. Basidiomata on the thallus of *Astrothelium* sp. Scale bar: 500 µm.



Tremella aptrootii, USA, Florida, Common 9204B. Basidiomata on the thallus of *Astrothelium* sp. Scale bar: 500 µm.



Tremella aptrootii, USA, Florida, Common 9204B. Basidiomata on the thallus of *Astrothelium* sp. Scale bar: 500 µm.

many basidia on *Astrothelium* have a long and narrow stalk, abruptly enlarging in a subspherical upper basidial part. Consequently, we consider the material on *Astrothelium* as a new species that we dedicate to our friend André Aptroot, expert of the host family *Trypetheliaceae* and collector of the new species. Unfortunately, no sequences could be obtained from neither *T. aptrootii* nor *T. harrisii*.

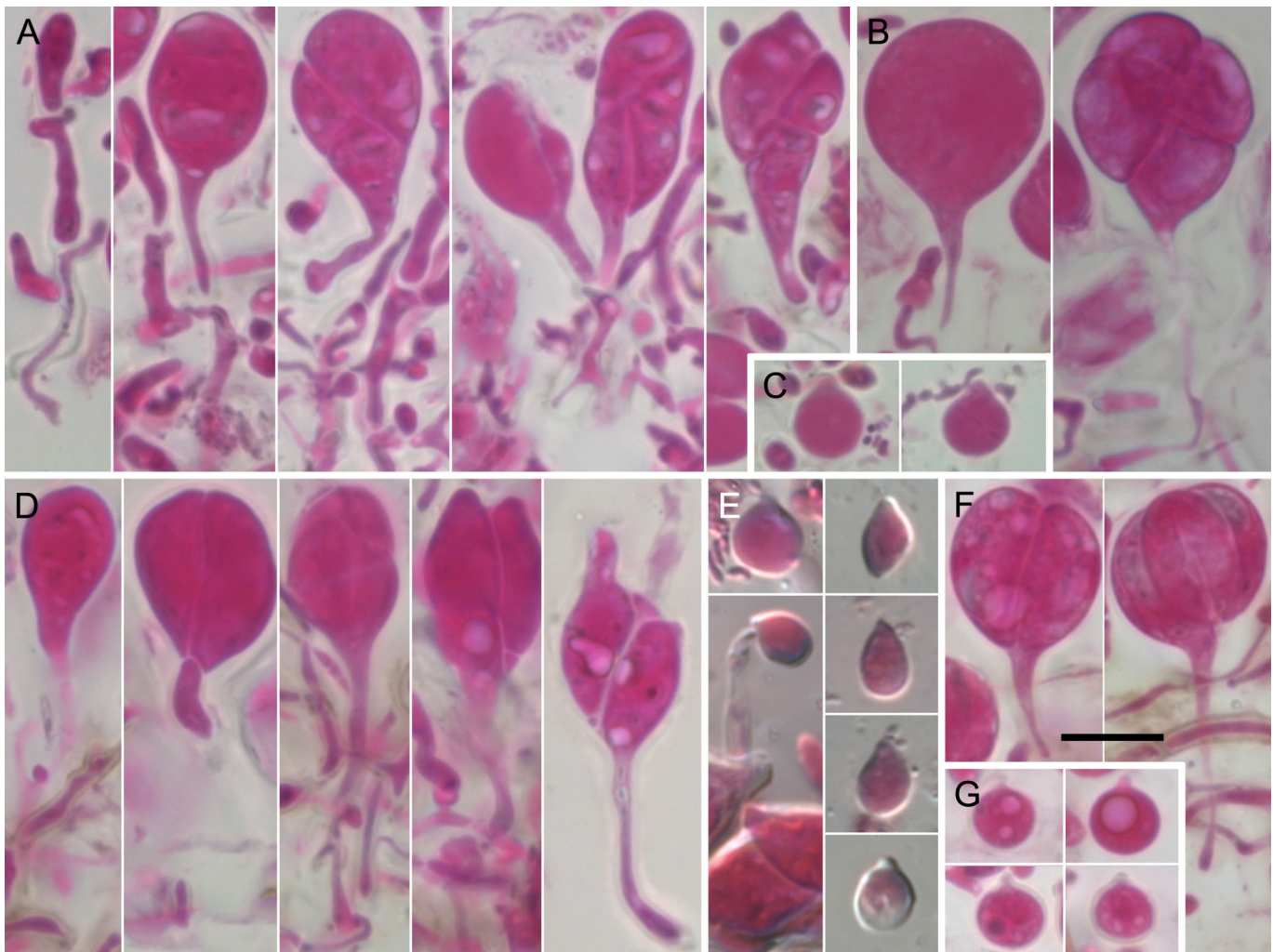
Ecology and hosts. On the thallus of corticolous species of *Astrothelium*.

Distribution. North America (USA: Florida), Caribbean (Dominican Republic; Puerto Rico) and South America (Brazil; Ecuador).

Additional specimens examined (all on *Astrothelium* sp.). **Brazil:** Santa Catarina, São Francisco do Sul, Parque Estadual do Acaraí, 26°17'20"S, 48°32'35"W, 10 m, in restinga vegetation on tree, 2015, Cáceres & Aptroot (ISE 27769). Estado do Rio Grande do Sul, Santana do Livramento, APA do Ibirapuitã, Estância São Maurício, 2012, Kässer 807 (HAS 89246); Mato Grosso Alta Floresta, RPPN Cristalino, 9.9167°S, 55.9167°W, 250–300 m, 2021, Aptroot



Tremella aptrootii



Tremella aptrootii. A, USA, Florida, holotype, B–C, Brazil, Aptroot 84067, D–E, USA, Florida, Harris 37710B, F–G, USA, Florida, Common 102963. A, B, D, F, Basidia in different stages of development, most with a long stalk-like base, some with a basal clamp. C, E, G, Basidiospores. In phloxine. Scale bar: 10 μ m.

84067 (CGMS; BR). **Dominican Republic:** San Cristobal, Cordillera Central, sobre Loma Resoli, Najayo Arriba de San Cristobal, 18°24'N, 70°12'W, 650 m, 1987, Zanoni & Jimenez 39097E (NY). **Puerto Rico:** Mun. Maricao, along the Río Lajas at the termination of Hwy 425, 18°11'N, 66°58'W, 400 m, 1992, Harris 27684A (BR, NY). **USA:** *Florida:* Hillsborough Co., Hillsborough River State Park, 28.1434°N, 82.2297°W, 2011, Common 9204B (BR); *ibid.*, Florida Trail, 28.149°N, 82.235°W, 2011, Common 9242B (BR), 9474E (BR); Hillsborough Co., near Morris Bridge Rd, 28.115°N, 82.301°W, 2016, Common 10104D (BR); Pasco Co., Zephyrhills, Woodfern Ave., 28.246°N, 82.192°W, 35 m, 2019, Common 10351C p. p. (BR); Seminole Co., along Econlockhatchee River at Little-Big Econlockhatchee Canoe Launch, on Co. Rd 419, 28°39'N, 81°10'W, 1996, Harris 37710B (NY); Sumter Co., Richloam Wildlife Management Area, 28.44°N, 82.084°W, 35 m, 2019, Common 10296B (BR); Volusia Co., Orange City, Blue Spring State Park, 1988, Harris 23804 (NY). *Texas:* Houston Co., Along White Rock Creek, 10 mi SE of Crocket, 1965, Johnson (BR, NY).

References. Diederich 1996 as *Tremella harrisii* [Etayo 2017].

***Tremella aspiciliae* Diederich, Coppins & A. Fletcher, sp. nov.**

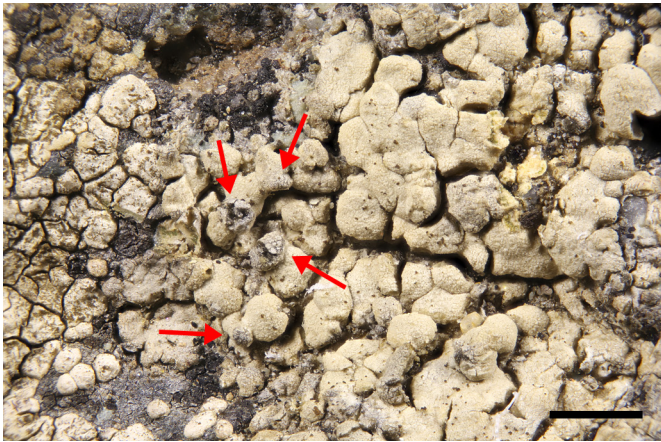
Diagnosis: Characterized by pustular basidiomatal galls on the thallus of *Aspicilia*, 0.2–0.45 mm diam., ellipsoid, 4-celled, longitudinally septate basidia, 9–14 \times 6–9 μ m, deciduous epibasidia, 9–17 \times 1.8–2.5 μ m, and the absence of basidiospores.

Etymology: From *Aspicilia*, the host lichen.

Type: UK, Wales, Gwynedd, Bardsey Island, summit, on exposed rocks, 160 m, on *Aspicilia caesiocinerea*, 10 Sept. 2003, A. Fletcher (LSR – holotype).

Mycobank: MB844646

Basidiomata superficial, inducing pustular galls, sub-spherical, not gelatinous, concolorous to the thallus, but apical opening darker, 0.2–0.45 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3.5–7 μ m diam.; haustoria not observed. *Hymenium* containing numerous ellipsoid probasidia, basal clamps indistinct. *Ba-*



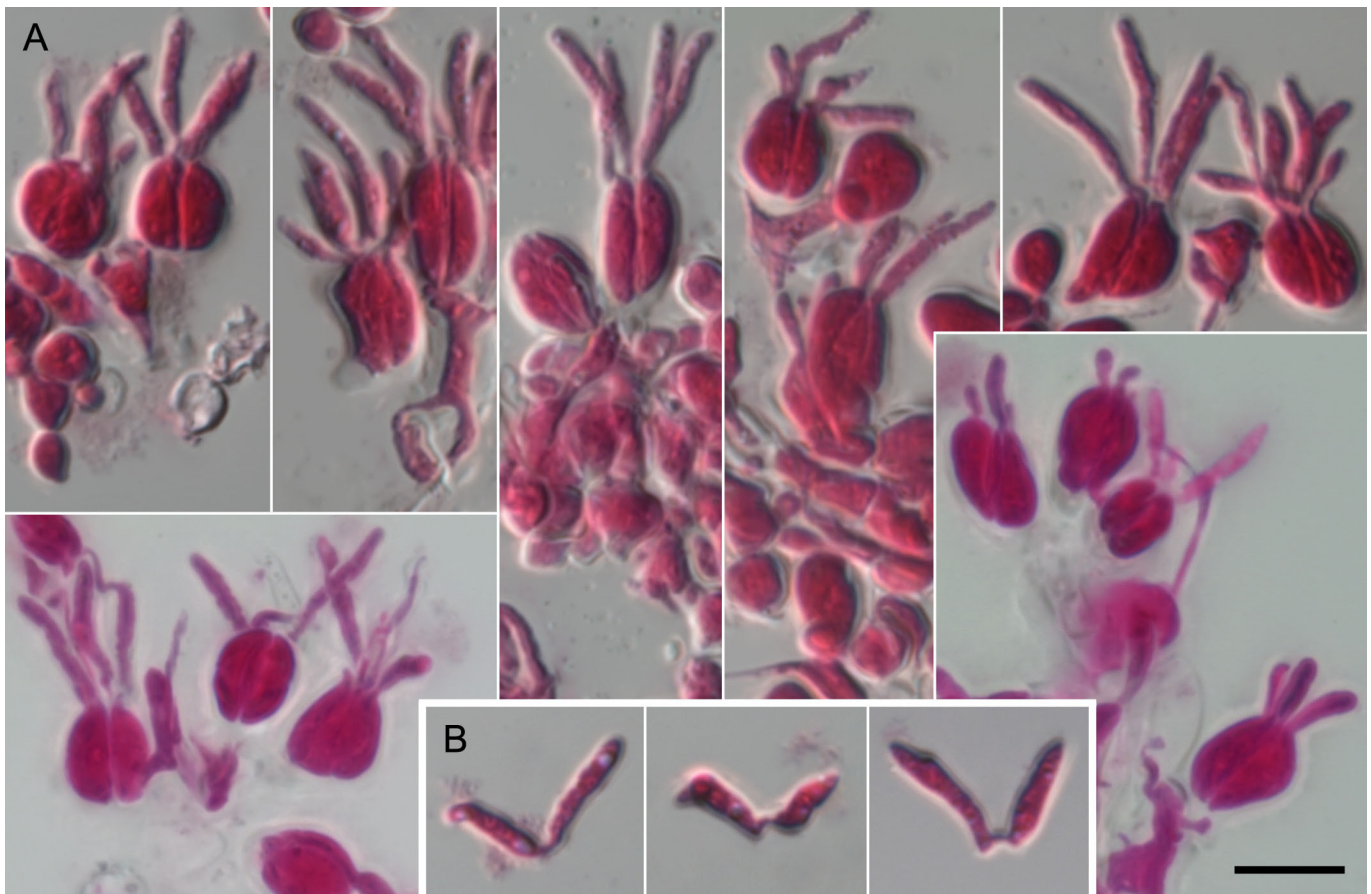
Tremella aspiciliae, UK, Wales, holotype. Sterile thallus of *Aspicilia caesiocinerea* (left), modified, bullate thallus with larger convex areoles (centre and right) and pustular basidiomatal galls (arrows). Scale bar: 1 mm.

sidia, when mature, ellipsoid, 4-celled, with longitudinal or very rarely oblique septa, never catenulate, $9\text{--}14 \times 6\text{--}9 \mu\text{m}$, wall $0.5\text{--}1 \mu\text{m}$ thick; epibasidia cylindrical, deciduous, separating from the basidia at maturity and acting as

diaspores, $9\text{--}17 \times 1.8\text{--}2.5 \mu\text{m}$. *Basidiospores* not observed. *Asexual stage* unknown.

Notes. This species is remarkable by the very regular ellipsoid, cruciately septate, 4-celled basidia producing deciduous epibasidia that obviously act as diaspores, while basidiospore production has not been observed. As no sequence data are available, the species is included in *Tremella* s. lat. Within *Tremella*, at least two non-lichenicolous species with deciduous epibasidia are known, both producing basidiospores: *T. brasiliensis* (A. Möller) Lloyd, distinguished by cartilaginous-gelatinous basidiomata up to 3 cm, very large basidia, $25\text{--}40 \times 20\text{--}28 \mu\text{m}$, and larger epibasidia, up to $150 \times 6 \mu\text{m}$, and *T. mayorgae* Lowy, distinguished by gelatinous basidiomata, up to 1 cm high, larger basidia, $23\text{--}26 \times 8.5\text{--}10.5 \mu\text{m}$, and larger epibasidia, $22\text{--}30.5 \times 5\text{--}7.5 \mu\text{m}$, with acicular sterigmata (Lowy 1971, 1977).

Deciduous epibasidia are also known from other tremellalean fungi, especially in the genera *Fibulobasidium* Bandoni and *Sirobasidium* Lagerh. & Pat. (Bandoni 1979). *Sirobasidium* differs from *Tremella aspiciliae* by the production of catenulate basidia. In *Filobasidium*, basal basidial clamps eventually enlarge to become additional basidia,



Tremella aspiciliae, UK, Wales, holotype. A, Basidia with epibasidia in different stages of development. B, Deciduous epibasidia acting as diaspores. In phloxine. Scale bar: $10 \mu\text{m}$.



Tremella aspiciliae

resulting as well in a kind of basidial chains. Additionally, in both genera, detached epibasidia may still produce ballistospores (homologous to basidiospores in *Tremella*).

Ecology and host. On *Aspicilia caesiocincerea*, inducing the formation of pustular galls over a modified, bullate thallus. Collected at the summit of an island, on rocks, with peat soil dominated by *Calluna vulgaris* and *Ulex europaeus*. The site is very exposed to sea winds from all directions, but is not densely bird-perched.

Distribution. Europe (UK: Wales), known only from the type locality.

Tremella brodoae (P. Pinault & Cl. Roux) Diederich, Millanes & Hafellner, comb. nov.

Epicladonia brodoae P. Pinault & Cl. Roux, *Bull. Soc. linn. Provence* 71: 67 (2020). *Type*: France, Massif central, Auvergne, département du Puy-de-Dôme, puy du Sancy, commune de Chambon-sur-Lac, col de la croix Saint-Robert, versant E de la coulée de trachyandésite (plateau de la Durbise), au pied de la coulée, 1500 m, sur les gros blocs, on *Brodoa*

intestiniiformis, 29 July 2018, P. Pinault (MARSSJ [in herb. Roux, n° 26995] – holotype; BR – isotype).

Mycobank: MB844647

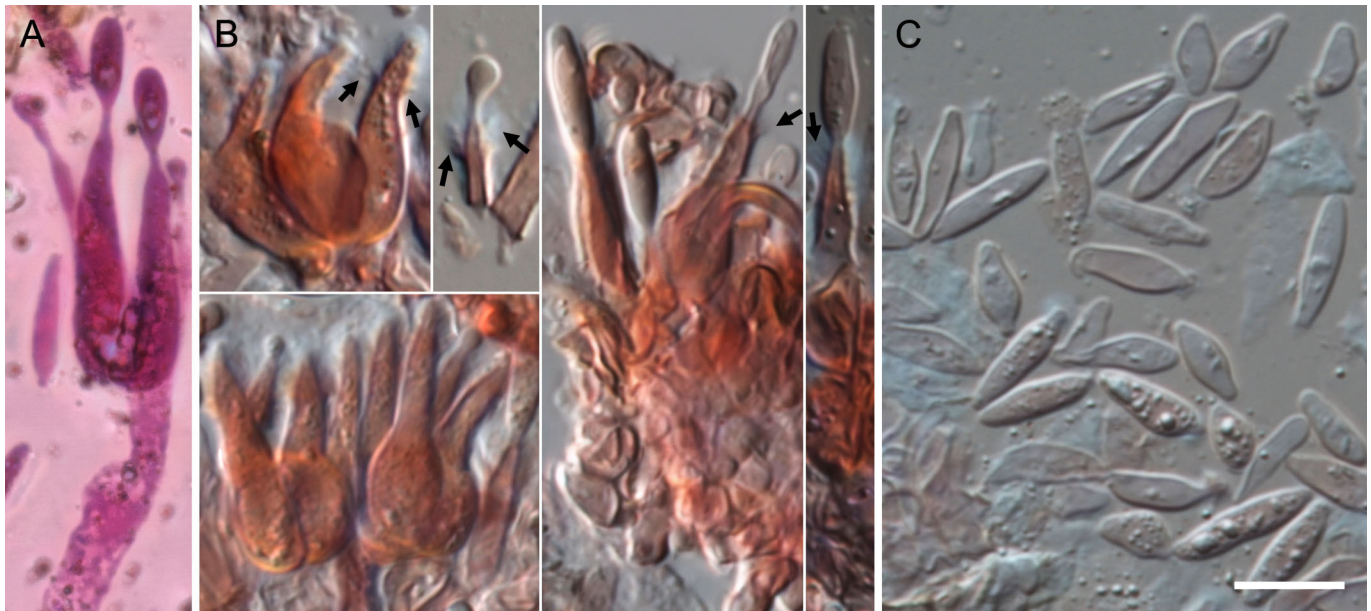
Basidiomata inducing the formation of large bullate galls, initially concolorous to the host thallus, eventually dark brown to almost black, shiny, 0.5–4.5 mm diam. *Context hyphae* not observed; subbasidial hyphae 3.5–5.5 µm diam.; haustoria not observed. *Hymenium* containing numerous ellipsoid probasidia, basal clamps not observed. *Basidia*, when mature, hyaline, longitudinally septate, 2–4-celled, cells elongating at maturity, only fixed together at the base, individual cells narrowly ellipsoid to ampulliform, with a strongly attenuated apex, 14.5–26.5 × 4–6 µm (incl. the narrow apex); epibasidia reduced, functioning as conidiogenous cells. *Basidiospores* unknown. *Conidiogenesis* holoblastic, conidiogenous cells percurrent, with up to 3 annellations. *Conidia*



Tremella brodoae, Austria, Hafellner 41863. Galls on the thallus of *Brodoa intestiniiformis*. Scale bar: 500 µm.



Tremella brodoae, Austria, Hafellner 57108. Galls on the thallus of *Brodoa intestiniiformis*. Scale bar: 500 µm.



Tremella brodoae, Austria, Hafellner 57108. A–B, Mature basidia with reduced epibasidia functioning as conidiogenous cells (arrows point at annellations). C, Conidia. A, in phloxine, B–C, in ammoniacal Congo red. Scale bar: 10 µm.

hyaline, aseptate, narrowly ellipsoid to fusiform, 12.5–15.5 × 2.5–3.5 µm, basally slightly truncate.

Notes. This species was originally described in the genus *Epicladonia*, as the conidiogenesis formally agrees with that of this genus, while the fertile loci within the galls were regarded as pycnidia with a poorly distinct, colourless wall. The conidiogenous cells always arising by 2–4 suggested, however, that they represent basidia with reduced epibasidia, producing conidia instead of basidiospores, and this has been confirmed in our phylogeny. Such a conidiogenesis was previously unknown, but is also found in three newly described *Tremella* species growing on *Cetraria* hosts, and in the new *T. occultixanthoriae*. Amongst these, *Tremella cervina*, found on *Cetraria ericetorum*, has similar basidiomatal galls, basidia with individual cells fixed together only at the base, and reduced epibasidia functioning as conidiogenous cells. The differences between both are explained under *T. cervina*.

Ecology and host. On the thallus of *Brodoa intestiniformis*, inducing the formation of large, bullate galls.

Distribution. Europe (Austria; France).

Additional specimens examined (all on *Brodoa intestiniformis*). **Austria:** Kärnten: Zentralalpen, Saualpe W von Wolfsberg, Bergrücken zwischen Ladinger Spitz und Speikkogel, W-exponierte Hänge, kurz E vom Sandofen, N über der Steiner Hütte, 46°50'25"N, 14°38'10"E, 1860 m, Felsburg knapp über der aktuellen Waldgrenze, Eklogit, auf Neigungsflächen großer Blöcke, 2011, Hafellner 41863 (GZU). **Tirol:** Osttirol, Nationalpark Hohe Tauern, Venediger-Gruppe, Innergschlöß NW von Matrei, kurz E vom Venedigerhaus, am orographisch linken Ufer des Gschlöß Baches, 47°07'35"N, 12°27'40"E, 1690 m, Blöcke in einer subalpinen Weide, auf Neigungsflächen von Glimmerschieferblöcken, 1998, Hafellner 57108 (BR, GZU). **France:** Same locality as type, 2021, Pinault (BR).

Reference. Pinault & Roux 2020.



Tremella brodoae

Tremella caloplacae (Zahlbr.) Diederich s. lat.

in Sérusiaux et al., *Lejeunia* n. S. 173: 31 (2003); *Lindaupsis caloplacae* Zahlbr., *Ber. Deutsch. Bot. Ges.* 24: 145 (1906). **Type:** Crete, 'an Kalkfelsen bei Kristallenia', 1904, R. Sturany (W 11196, lichenicolous fungus in apothecia of *Vario- spora aurantia*: lectotype, designated by Sérusiaux et al. 2003).

= *Tremella* sp. 1, in Diederich, *Bibl. Lichenol.* 61: 167 (1996)

Basidiomata either on the host thallus or intrahymenial, often gall-inducing. **Context hyphae** thin-walled, 1.5–3 µm diam., with clamp connections; haustoria present. **Hymenium** containing numerous ellipsoid or elongate probasidia



Tremella caloplacae s. str., Greece, Crete, lectotype. Basidiomatal galls on the apothecia of *Variospora aurantia*. Scale bar: 1 mm.



Tremella caloplacae s. lat., Luxembourg, Diederich 17473. Basidiomatal galls on the apothecia of *Xanthoria parietina*. Scale bar: 1 mm.

with a basal clamp, reduced when intrahymenial. *Basidia*, when mature, with one transverse, more rarely oblique or longitudinal septum, the lower cell often with an attenuated, stalk-like base, $16\text{--}25 \times 7\text{--}10\ \mu\text{m}$; epibasidia $2.5\text{--}3.5\ \mu\text{m}$ diam., at least $45\ \mu\text{m}$ long. *Basidiospores* ellipsoid to subspherical, $7\text{--}8 \times 6\text{--}6.5\ \mu\text{m}$. *Asexual stage*: ellipsoid blastoconidia have been observed. [Modified from Diederich 1996.]

Notes. *Tremella caloplacae* s. lat. represents a species complex, comprising numerous species, all confined to a particular *Teloschistaceae* host genus. As they are currently being studied and will be formally described elsewhere, we treat the species here in a large sense.

Ecology and hosts. *Tremella caloplacae* s. str. is known from the thallus of *Variospora aurantia*, *V. dolomitica*, *V. flavescens* and *V. thallincola*. Other species from this complex are known or have been reported from many *Teloschistaceae* hosts, including *Athallia*, *Calogaya*, *Caloplaca* s. str., *Leproplaca*, *Pisutiella* (described below as *Tremella pisutiellae*), *Pyrenodesmia*, *Rufoplaca*, *Rusavskia*, *Teloschistes* (described below as *T. teloschistis*), *Usnochroma*, *Xanthocarpia*, *Xanthomendoza* (described below as *T. xanthomendozae*) and *Xanthoria parietina*.

Distribution. *Tremella caloplacae* s. str. has been described from Europe (Greece: Crete). The detailed distribution of this and related species will be published elsewhere.

References. Diederich 1996 as *Tremella* sp. 1, Sérusiaux et al. 2003.

Tremella candelariellae Diederich & Etayo

in Diederich, *Bibl. Lichenol.* 61: 52 (1996). Type: Luxembourg, Oesling, 1 km E of Esch-sur-Sûre, near tunnel and road N15, alt. 300 m, on *Candelariella vitellina*, 2 May 1992, P. Diederich 4836 (LG – holotype; BR – isotype).

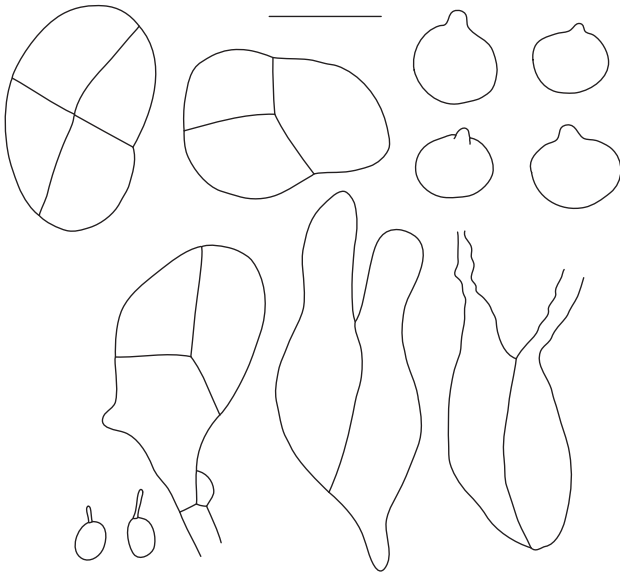
Basidiomata inducing the formation of superficial, convex, bright yellow galls on the host thallus, often with a constricted base, with a granular, pruinose surface, not gelatinous, $0.1\text{--}0.8\ \text{mm}$ diam., or intrahymenial *Context hyphae* thin-walled, $1.5\text{--}2.5\ \mu\text{m}$ diam., clamps not observed; haustoria frequent. *Hymenium* containing numerous ellipsoid probasidia, often with an attenuated base, with a basal clamp. *Basidia*, when mature, ellipsoid, 2–4-celled, septa longitudinal or oblique, rarely transverse, $18\text{--}23 \times 10\text{--}12\text{--}(14.5)\ \mu\text{m}$; epibasidia elongate, cylindrical, $3.5\text{--}4\ \mu\text{m}$ diam., at least $25\text{--}30\ \mu\text{m}$ long. *Basidiospores* ellipsoid, $6.5\text{--}8 \times 5\text{--}6\ \mu\text{m}$. *Asexual stage*: asteroconidia observed in one specimen.

Notes. This species is easily recognized by the swollen thallus granules or apothecia of *Candelariella* species, these often with a rough or pruinose surface.

Ecology and hosts. On the thallus and apothecia of *Candelariella vitellina*, *C. aurella*, *C. efflorescens* and *C. xanthostigma*.



Tremella candelariellae, Luxembourg, isotype. Basidiomatal galls on the thallus of *Candelariella vitellina*. Scale bar: 500 μm .



Tremella candeleriellae, Luxembourg, holotype (modified from Diederich 1996). Basidia, basidiospores and haustoria. Scale bar: 10 µm.



Tremella candeleriellae

Distribution. Europe (Austria; Belgium; Czech Republic; Estonia; Finland; [Luxembourg](#); Poland; Russia; Spain; Sweden; UK: England), North America (Canada: Ontario; USA: Missouri, New York, Ohio, Pennsylvania, Tennessee) and Asia (Türkiye).

References. Diederich 1996 [Hafellner 2009, Kocakaya et al. 2020, Kukwa & Jabłońska 2008, Sérusiaux et al. 2003, Suija et al. 2010, Svensson & Westberg 2010, Urbanavichus 2016, Vondrak et al. 2022, Westberg et al. 2008].

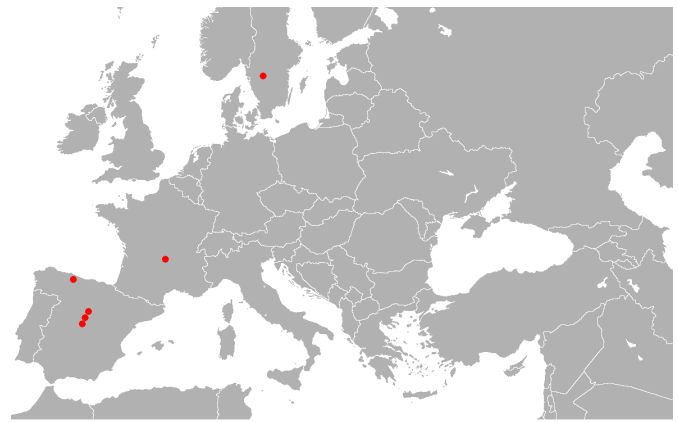
***Tremella celata* J. C. Zamora, Millanes, V. J. Rico & Pérez-Ortega**

in Zamora et al., *Mycologia* 108: 383 (2016). *Type:* Spain, Comunidad de Madrid, Madrid, San Lorenzo de El Escorial, La Herrería forest, near Ermita de la Virgen de Gracia, 40°34'24" N, 4°09'18" W, 973 m, in the thallus of *Ramalina fraxinea*, on bark of *Quercus pyrenaica*, 18 Nov. 2011, M. Vivas, B. Zamora & J. C. Zamora (MAF-Lich 19726 – holotype; AH, UPS – isotypes).

Basidiomata resupinate, inducing the formation of diffuse and often inconspicuous, waxy, 0.5–4 mm long, cream-colored galls visible on the thallus surface of host, be-



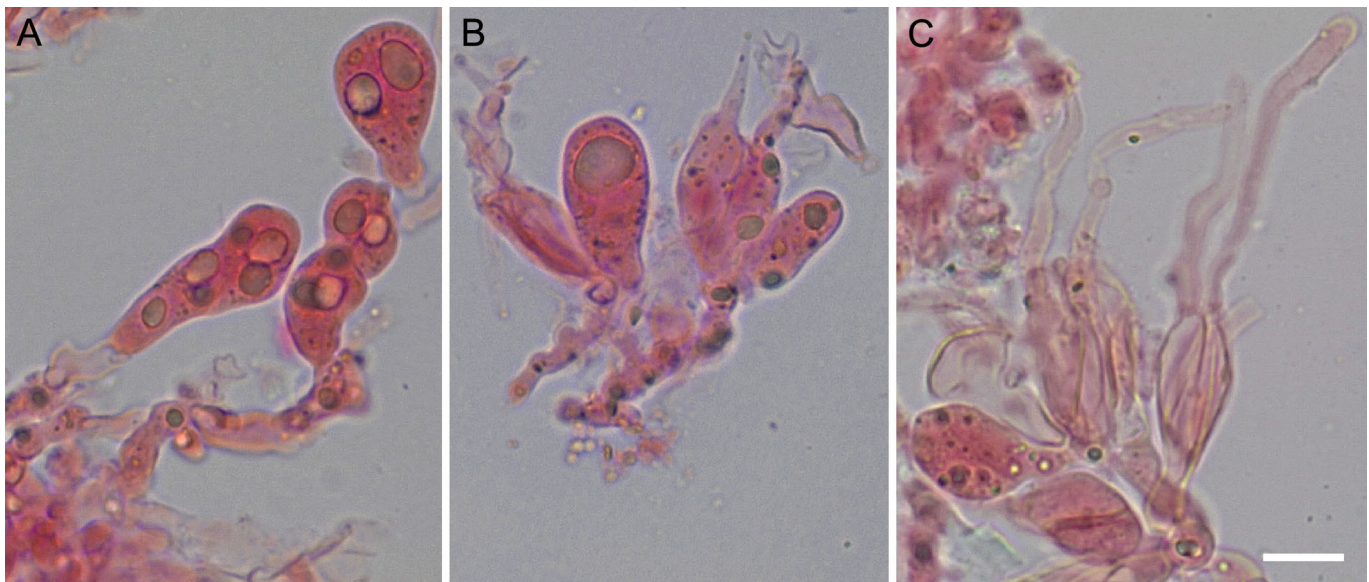
Tremella celata, France, Pinault 555. Resupinate basidioma on the thallus of *Ramalina fraxinea*. Scale bar: 1 mm.



Tremella celata

coming dark when old, sometimes coalescent. *Context hyphae* and subbasidial hyphae thick-walled, 2.5–4 µm diam., without distinct clamps; haustoria frequent. *Hymenium* with numerous subglobose to cylindrical probasidia, without basal clamps, but occasionally with obscure spur-like pseudoclamps. *Basidia*, when mature, 2(–4)-celled, often with an attenuated or stalk-like base but sometimes sessile, with a longitudinal or oblique septum, 9–18 × 7.5–11.5 µm (including the attenuated base but not the stalk, when present), stalk 1–8 × 1.5–3 µm; epibasidia subcylindrical to narrowly fusiform, 2–4 µm thick, up to 40 µm long. *Basidiospores* subspherical, 5.5–7 × 5.5–7(–8) µm. *Asexual stage* unknown. [Modified from Zamora et al. 2016.]

Notes. *Tremella celata* is an inconspicuous but probably common species growing on the thallus of *Ramalina fraxinea*. It is characterized by the almost resupinate galls and the longitudinally or obliquely 1(–3)-septate basidia that occasionally have a short stalk-like base. *Tremella ramalinae* is distinguished by the (3)–4-celled basidia with two transverse septa and one apical longitudinal septum. *Tre-*



Tremella celata, France, Pinault 55. A, Probasidia. B, Mature basidia. C, Mature basidia with elongate epibasidia. In ammoniacal Congo red. Photos: P. Pinault. Scale bar: 10 μm .

mella tuckerae is macroscopically similar to *T. celata*, but is distinguished by the larger basidia with individual cells that elongate at maturity.

Ecology and host. On the thallus of *Ramalina fraxinea*.

Distribution. Europe (France; [Spain](#); Sweden).

Specimens examined. **France:** Puy-de-Dôme, s. loc., on *Ramalina fraxinea*, 2015, Pinault 55, 555 (BR).

Reference. Zamora et al. 2016.

Ecology and host. On the cephalodia of *Pannaria papuana*.

Distribution. Oceania ([Papua New Guinea](#)), known only from the type locality.

Reference. Diederich 1996.



Tremella cephalodiicola

Tremella cephalodiicola Diederich

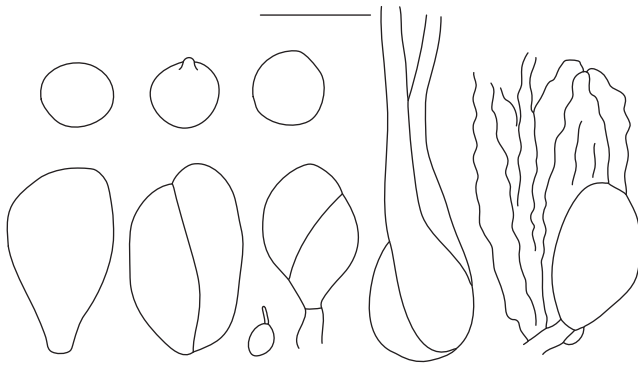
Bibl. Lichenol. 61: 55 (1996). **Type:** Papua New Guinea, Simbu Province, Mount Wilhelm area, Bundi Gap, on road Keglsugl-Bundi, alt. 2800 m, 5.8°S, 145.1°E, in subalpine forest remnants, on *Pannaria papuana*, 4 Aug. 1992, P. Diederich 11040 (LG – holotype; BR – isotype).

Basidiomata medium brown, strongly convex, subspherical, often elongate, never tuberculate, inducing gall formation, firm gelatinous, a little waxy, 0.25–0.5(–1) mm diam. **Context hyphae** not observed; haustoria rare. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, 2–4-celled, with longitudinal or slightly oblique septa, 13–17 \times 8–12 μm ; epibasidia subcylindrical, 2–3.5 μm diam., at least 20 μm long. **Basidiospores** subspherical, 6.5–7.5 \times 5.5–6.5 μm . **Asexual stage** unknown.

Notes. This is a poorly known species, described from a single specimen on a host endemic to Papua New Guinea. Hyphidia reported by Diederich (1996) are here interpreted as host hyphae.



Tremella cephalodiicola, Papua New Guinea, isotype. Basidiomata on *Pannaria papuana*. Scale bar: 500 μm .



Tremella cephalodiicola, Papua New Guinea, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorium. Scale bar: 10 μ m.

***Tremella cervina* Diederich & Millanes, sp. nov.**

Diagnosis: Characterized by the dark brown to black, convex, basally constricted basidiomatal galls on the thallus of *Cetraria ericetorum*, 1–2 mm diam., with a shiny and smooth surface, the 2–4-celled, longitudinally septate basidia with cells only fixed together at the base, individual cells 13–18.5 \times 3.5–6.5 μ m, and epibasidia acting as conidiogenous cells, producing hyaline, aseptate conidia, 4–9.5 \times 2.5–3.5 μ m.

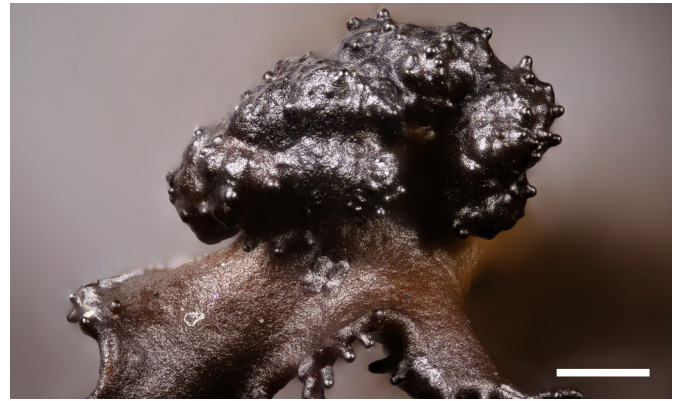
Etymology: From *cervinus*, deer coloured, referring to the brown basidiomatal galls, and at the same time an allusion to the collecting locality, an excellent viewpoint of Matterhorn (Italian: *Cervino*).

Type: Switzerland, Valais, Zermatt, between Riffelgrat and Gornergrat, 2600 m, on *Cetraria ericetorum*, Aug. 2000, D. Chevalier (BR – holotype).

Mycobank: MB844648

Basidiomatal galls strongly convex, basally constricted, surface smooth, often uneven to almost tuberculate, shiny, dark brown to black, 1–2 mm diam. **Context hyphae** and subbasidial hyphae thick-walled, hyaline, 2.5–3.5 μ m diam.; haustoria frequent, with a basal clamp. **Hymenium** containing numerous ellipsoid probasidia, proliferations occurring through the basal clamp. **Basidia**, when mature, hyaline, longitudinally septate, 2–4-celled, cells elongating at maturity, only fixed together at the base, individual cells narrowly ellipsoid to ampulliform, with a strongly attenuated apex, 13–18.5 \times 3.5–6.5 μ m; epibasidia reduced, functioning as conidiogenous cells. **Basidiospores** unknown. **Conidiogenesis** holoblastic. **Conidia** hyaline, aseptate, narrowly ellipsoid to subcylindrical, 4–9.5 \times 2.5–3.5 μ m, basally slightly truncate.

Notes. This species is remarkable in having basidia with reduced epibasidia that do not produce basidiospores, but function as conidiogenous cells producing conidia. A similar conidiogenesis is also known from *Tremella brodoae* that differs by the often larger basidiomatal galls, reaching 4.5 mm in diam., slightly longer basidia, 14.5–26.5 \times 4–6 μ m, and much longer conidia, 12.5–15.5 \times 2.5–3.5 μ m.



Tremella cervina, Switzerland, holotype. Basidiomatal gall on the thallus of *Cetraria ericetorum*. Scale bar: 500 μ m.



Tremella cervina, Switzerland, holotype. Basidiomatal gall on the thallus of *Cetraria ericetorum*. Scale bar: 500 μ m.

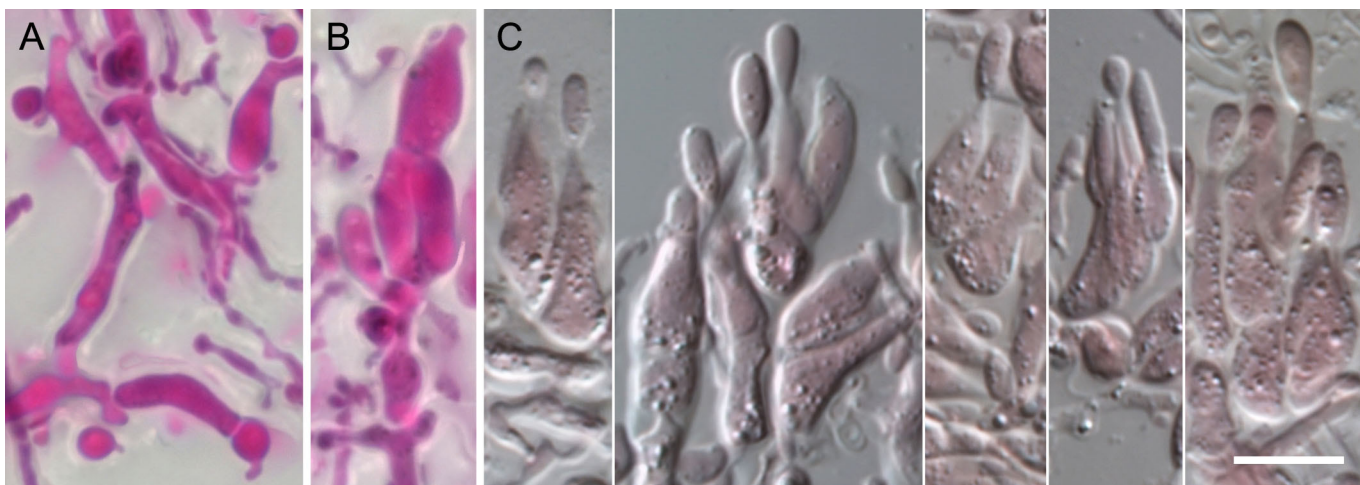
Tremella cetraculeata and *T. cetrariae* also have basidia producing conidia instead of basidiospores, but they differ in having pustular basidiomata with a large apical opening and a rough surface becoming gelatinous when wet, and the subspherical basidia with cells apically not separating.

Ecology and host. Gall-inducing on the thallus of *Cetraria ericetorum*.

Distribution. Europe ([Switzerland](#)), known only from the type locality.



Tremella cervina



Tremella cervina, Switzerland, holotype. A, Context hyphae with clamped haustoria. B, Fertile hyphae producing basidia. C, Mature basidia with conidia. In phloxine. Scale bar: 10 μ m.

***Tremella cetraculeata* Diederich, Millanes & Hollinger, sp. nov.**

Diagnosis: Characterized by the dark brown to black, pustular basidiomata on the thallus of *Cetraria aculeata*, when open with a rough, gelatinous surface, 0.4–1.3 mm diam., the subspherical, (2–)4-celled, longitudinally septate basidia, $8.5\text{--}12 \times 7\text{--}9.5 \mu\text{m}$, and the reduced epibasidia acting as conidiogenous cells, producing hyaline, aseptate conidia, $2.5\text{--}4 \times 2\text{--}3 \mu\text{m}$.

Etymology: A noun in apposition, being a contraction of the noun phrase ‘*Cetraria aculeata*’, the host lichen.

Type: Canada, British Columbia, Marble Range, Porcupine Mountain (c. 1.5 km W of peak), 51.120°N , 121.842°W , 2150 m, on alpine turf, on *Cetraria aculeata*, 25 July 2016, J. Hollinger 14274 & C. Björk (UBC – holotype).

Mycobank: MB844650

Basidiomata breaking through the host cortex and becoming superficial, pustular, with a large apical opening, exposed

parts with a very rough surface when dry, gelatinous, dark brown to black, 0.4–1.3 mm diam. **Context hyphae** and sub-basidial hyphae thick-walled, hyaline to brown, $2\text{--}5 \mu\text{m}$ diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous probasidia; probasidial initials subspherical to ellipsoid, proliferations occurring through the basal clamp. **Basidia**, when mature, hyaline to dark brown, subspherical to shortly ellipsoid, cruciately (2–)4-celled, with longitudinal septa, $8.5\text{--}12 \times 7\text{--}9.5 \mu\text{m}$; epibasidia reduced, functioning as conidiogenous cells, with conidia appearing as produced directly from the basidia. **Basidiospores** unknown. **Conidiogenesis** probably holoblastic. **Conidia** hyaline, ellipsoid, $2.5\text{--}4 \times 2\text{--}3 \mu\text{m}$, basally slightly truncate.

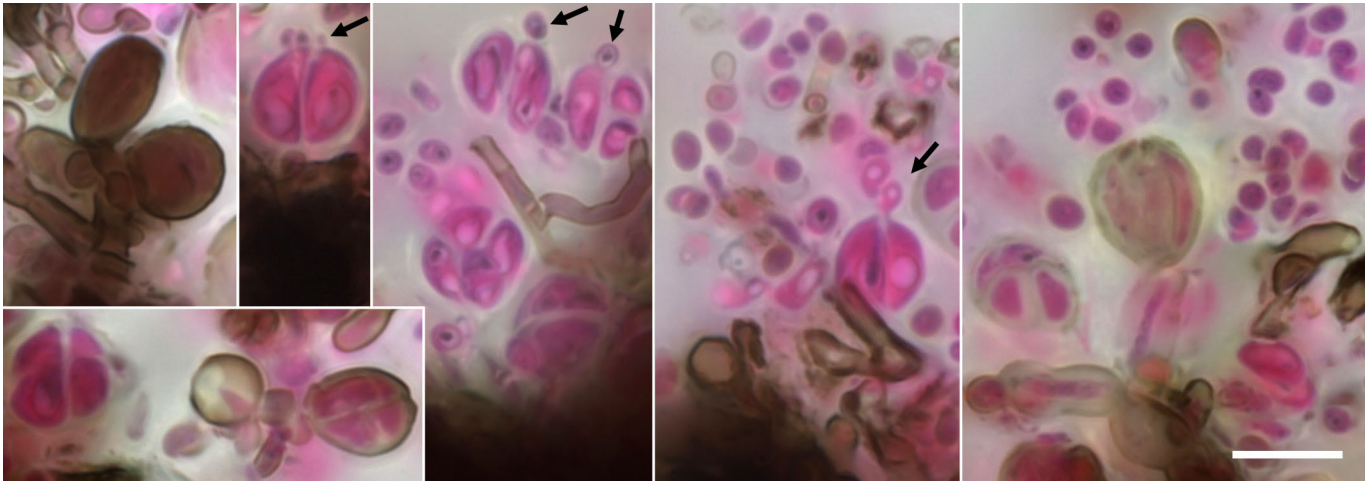
Notes. This species is remarkable by having subspherical basidia with reduced epibasidia producing aseptate, hyaline conidia. The similar *Tremella cetrariae* differs by the much larger conidia, $5.5\text{--}7.5 \times 2\text{--}3 \mu\text{m}$, and *T. occultixanthoriae* by the pale brown, waxy-gelatinous basidiomata and conidia



Tremella cetraculeata, Canada, British Columbia, holotype. Basidiomata on *Cetraria aculeata*. Scale bar: 1 mm.



Tremella cetraculeata, Canada, British Columbia, holotype. Basidioma on *Cetraria aculeata*. Scale bar: 500 μ m.



Tremella cetraculeata, Canada, British Columbia, holotype. Fertile hyphae, immature and mature basidia, some with a brown wall (e. g., upper left), and conidia. Arrows point to the formation of young conidia from reduced epibasidia. In phloxine. Scale bar: 10 μ m.

with a basal appendage. Both *T. brodoae* and *T. cervina* differ by basidial cells attached to each other only at the base.

Ecology and host. Gall-inducing on the thallus of *Cetraria aculeata*.

Distribution. North America (Canada: British Columbia), known only from the type locality.



Tremella cetraculeata

Tremella cetrariae Diederich, Millanes, F. Berger & Zamora, sp. nov.

Diagnosis: Characterized by the dark brown to black, pustular basidiomata on the thallus of *Cetraria islandica*, when open with a rough, gelatinous surface, up to 2(–3) mm diam., the subspherical, 2–4-celled, longitudinally septate basidia, 9–11.5 \times 7–10 μ m, and the reduced epibasidia acting as conidiogenous cells, producing hyaline, aseptate conidia, 5.5–7.5 \times 2–3 μ m.

Etymology: From *Cetraria*, the host lichen.

Type: Austria, Tirol, Osttirol, Defereggental, Stallersattel, Zwergstrauchheide am Weg vom Stallersee zum Halssattel, 46°53'16"N, 12°12'13"E, 2050 m, on *Cetraria islandica*, 12 July 2020, F. Berger 34958, E. Zimmermann & S. Feusi (BR – holotype).

Mycobank: MB844651

Basidiomata breaking through the host cortex and becoming superficial, pustular, with a large apical opening and divergent margins, exposed parts with a very rough surface when dry, gelatinous, dark brown to black, up to 2 mm diam., or elongate and up to 3 mm. *Context hyphae* not observed; sub-basidial hyphae thick-walled, 2.5–4 μ m diam.; haustoria present, with a basal clamp. *Hymenium* containing numerous probasidia; probasidial initials subspherical to ellipsoid, proliferations occurring through the basal clamp. *Basidia*, when mature, hyaline to brownish, subspherical to shortly ellipsoid, cruciately 2–4-celled, with longitudinal septa, 9–11.5 \times 7–10 μ m; epibasidia reduced, functioning as conidiogenous cells, with conidia appearing as produced directly from the basidia. *Basidiospores* unknown. *Conidiogenesis* probably holoblastic. *Conidia* hyaline, narrowly ellipsoid, subcylindrical, sometimes slightly bent, apically sometimes narrower, 5.5–7.5 \times 2–3 μ m, basally slightly truncate.

Notes. This species has particular basidia with reduced epibasidia producing conidia. The similar *Tremella cetraculeata* differs by the much smaller conidia, 2.5–4 \times 2–3 μ m. *T. brodoae* and *T. cervina* differ by basidial cells attached to each other only at the base. *T. occultixanthoriae* differs by pale brown, waxy-gelatinous basidiomata.

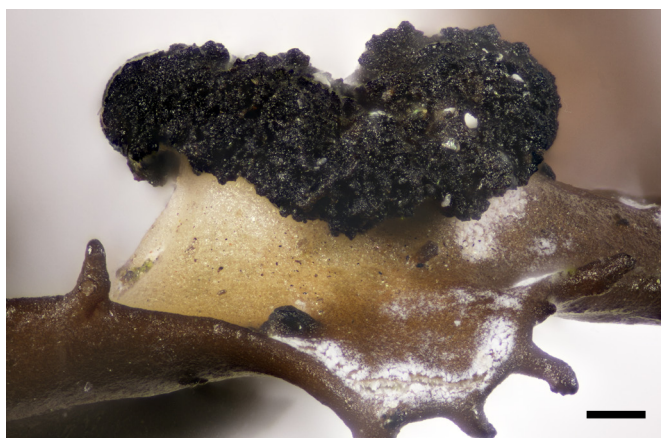
Ecology and host. Gall-inducing on the thallus of *Cetraria islandica*.

Distribution. Europe (Austria; Spain).

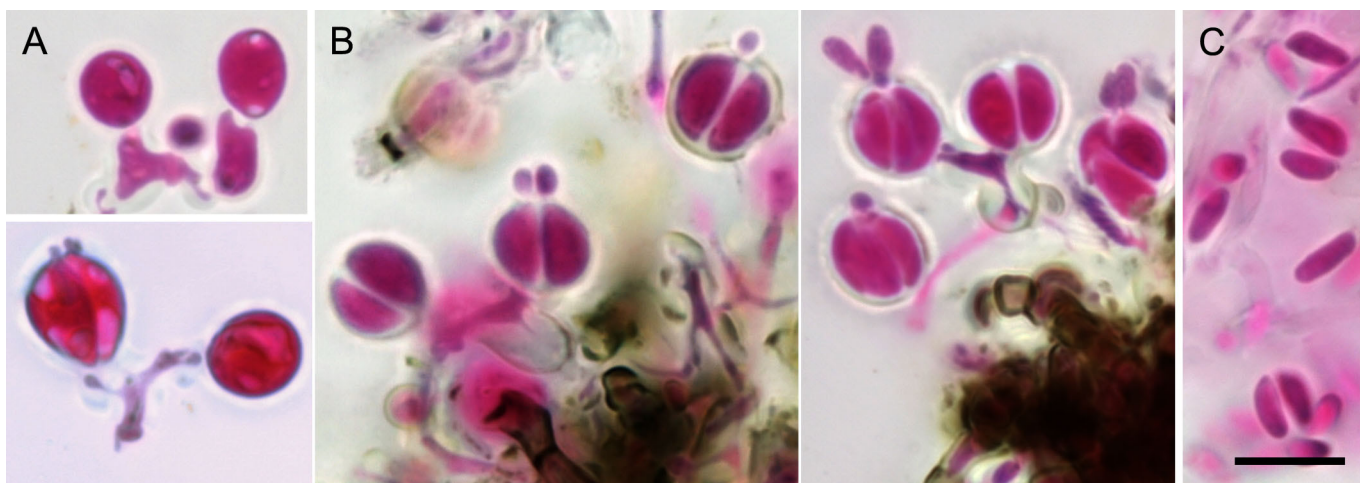
Additional specimens examined (all on *Cetraria islandica*). **Austria:** Salzburg: Hohe Tauern, Glocknergruppe, Umgebung der Rudolfshütte, 2280 m, 1988, Türk 12531 (GZU 3-2014). **Tirol:** Zillertal, Tuxertal, Weg zur Höllensteinhütte, 47°08'16"N, 11°43'11"E, 1550 m, bewaldete Blockhalde, Berger 33594 (herb. Berger). **Spain:** Asturias, Caso, Lago Ubales, 43°6'12"N, 5°21'12"W, 1720 m, 2012, Zamora (G). Zaragoza, Tarazona, Moncayo, peñas alrededor del Santuario, 1997, Etayo 14155 (MA-Fungi 98692).



Tremella cetrariae, Austria, holotype. Basidiomata on *Cetraria islandica*. Scale bar: 200 μ m.



Tremella cetrariae, Austria, Berger 33594. Basidiomata on *Cetraria islandica*. Scale bar: 200 μ m.



Tremella cetrariae, Austria, holotype. A, Fertile hyphae with clamped probasidia. B, Mature basidia producing conidia on reduced epibasidia. C, Conidia. In phloxine. Scale bar: 10 μ m.



Tremella cetrariae

Tremella cetrariellae Millanes, Diederich, M. Westb., Pippola & Wedin

Lichenologist 47: 362 (2015). *Type*: Norway, Finnmark, Sør Varanger, Balgami, area with siliceous rocks, *Empetrum* and *Betula nana*, next to the sea and to a small lake, 69°58.75'

N, 29°34.883' E, 21 m, on *Cetrariella delisei*, 4 July 2014, A. Millanes 1130 (S F264653 – holotype).

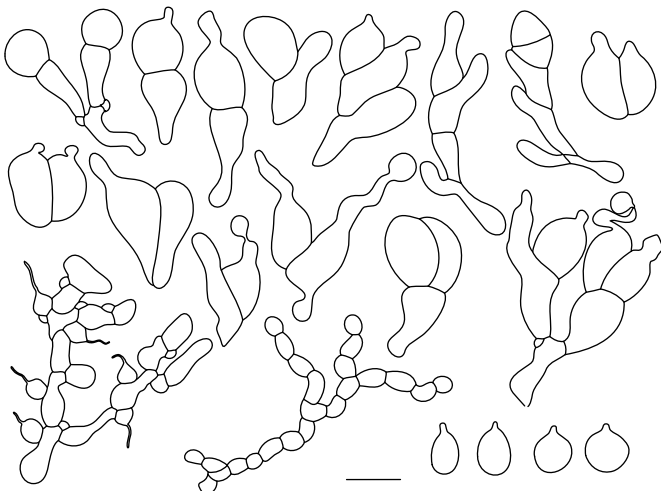
Basidiomata superficial, waxy-gelatinous, inducing the formation of pale to dark brown or black, convex to subglobose, often tuberculate galls, 0.1–1.5 mm diam., very rarely with a central depression. *Context hyphae* thin- to thick-walled, often with clamp connections, 1.5–4 μ m diam.; haustoria frequent. *Hymenium* containing numerous clavate probasidia with a basal clamp. *Basidia*, when mature, 2–4-celled, with transverse, longitudinal, or oblique septa; when transversely septate, the lower cell with an attenuated stalk-like base, 10–31 \times 4–11 μ m; when longitudinally or obliquely septate, 9–13 \times 11–18 μ m; epibasidia subcylindrical, (1–)2–5 μ m diam., up to 28 μ m long. *Basidiospores* subspherical to shortly ellipsoid, 4–8 \times 4–8 μ m. *Asexual stage*: catenulate, hyaline to brownish conidia, (2–)3–8 \times 3–10 μ m.



Tremella cetrariellae, Finland, Halonen 43. Basidiomata on the thallus of *Cetrariella delisei*. Scale bar: 200 µm.



Tremella cetrariellae, Finland, Halonen 43. Basidiomata on the thallus of *Cetrariella delisei*. Scale bar: 200 µm.



Tremella cetrariellae, Finland, Norway and Sweden, holotype, Huuskonen 692, Millanes 874 and Westberg s.n. (modified from Millanes et al. 2015). Basidia, basidiospores, catenulate conidia and haustorial branches. Scale bar: 10 µm.

Notes. This species was included by Diederich (1996) in *Tremella cetrariicola*, a taxon confined to *Tuckermannopsis* hosts. It is distinguished by basidiomatal galls that frequently become tuberculate when mature, while the central depression often present in *T. cetrariicola* is usually missing, and 2–4-celled basidia (those in *T. cetrariicola* are predominantly 2-celled). Phylogenetically, it comprises two distinct subclades, the two together being sister to the *T. cetrariicola* clade.

Ecology and host. On the thallus of *Cetrariella delisei*.

Distribution. Europe (Finland; Norway; Russia; Svalbard; Sweden) and North America (Greenland).

References. Millanes et al. 2015 [Suija & Jüriado 2020, Zhurbenko & Zhdanov 2013 as *Tremella cetrariicola*].



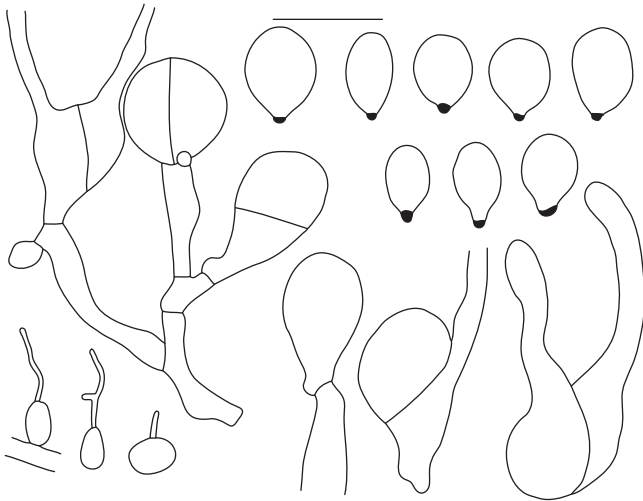
Tremella cetrariellae

Tremella cetrariicola Diederich & Coppins

in Diederich, *Bibl. Lichenol.* 61: 57 (1996). *Type:* UK, Scotland, VC 96, Easternness, NW of Fort Augustus, Ceannacroc Forest, Torgyle Bridge (28/31.13), on *Pinus sylvestris*, on *Tuckermannopsis chlorophylla*, 1 June 1987, P. Diederich 8864 & B. Coppins [11654] (E – holotype; BR, LG – isotypes).

Basidiomata superficial, waxy-gelatinous, reddish or greyish brown, sometimes dark brown to black, pale brown when young, convex, often with a constricted base, generally with a typical central depression, old basidiomata sometimes tuberculate, 0.4–1.8 mm diam. **Context hyphae** thick-walled, 2–4 µm diam., clamps not observed; haustoria frequent. **Hymenium** containing numerous ellipsoid probasidia, some with an attenuated base, with a basal clamp. **Basidia**, when mature, ellipsoid, 2- or 4-celled, septum longitudinal or oblique, rarely transverse, 10–18(–23) × 6.5–12 µm; epibasidia elongate, cylindrical, 1.5–4 µm diam., 25–40 µm long. **Basidiospores** ellipsoid to almost limoniform, 5.5–9.5 × 4–8 µm, with a distinct refractive apiculus at the lower end. **Asexual stage** unknown.

Notes. This species is distinguished by the brown basidiomata typically with a central depression and the unusual basidiospores with a refractive apiculus situated at the lower end. Basidia are all 2-celled in some specimens, in-



Tremella cetrariicola, Scotland, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.



Tremella cetrariicola, Scotland, holotype. Basidiomata on the thallus of *Tuckermannopsis chlorophylla*. Scale bar: 200 µm.

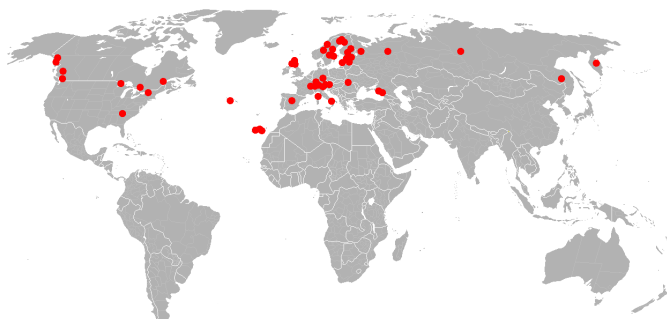
cluding the type, but are mostly 4-celled in Vězda Lichenes Selecti Exsiccati 342.

Ecology and hosts. On the thallus of *Tuckermannopsis chlorophylla*, *T. americana* and *T. ciliaris*.

Distribution. Europe (Austria; Estonia; Finland; France; Germany; Italy; Latvia; Russia; Sweden; Switzerland; **UK: Scotland**, Ukraine), Macaronesia (Azores; Canary Islands), North America (Canada: British Columbia, Ontario, Quebec; USA: Alaska, Georgia, Michigan, New York) and Asia (Russia).

Additional specimens examined (all on *Platismatia glauca*). **Azores:** Pico, S of Sao Roque do Pico, 2010, Diederich 17038 (BR). **Switzerland:** Berner Oberland, woodland near Brienz, 1996, van den Boom 17746 (herb. van den Boom).

References. Diederich 1996, 2003, Pippola & Kotiranta 2008 [Alstrup 2014, Brackel 2014, Brackel & Puntillo 2016, Brinker 2020, Darmostuk et al. 2020, Diederich 2003, Etayo 1996, Hafellner et al. 2004, Himelbrant et al. 2017, Kocourková & Brackel 2005, Millanes et al. 2014a, Roux 2020, Spribille et al. 2010, 2020, Suija 2005, Thor 1992, Urbanavichus & Urbanavichene 2014, Urbanavichus et al. 2020, Zhurbenko 2014, Zhurbenko & Kobzeva 2014, Zhurbenko & Zhdanov 2013, Zhurbenko et al. 2012, Zimmermann & Berger 2018].

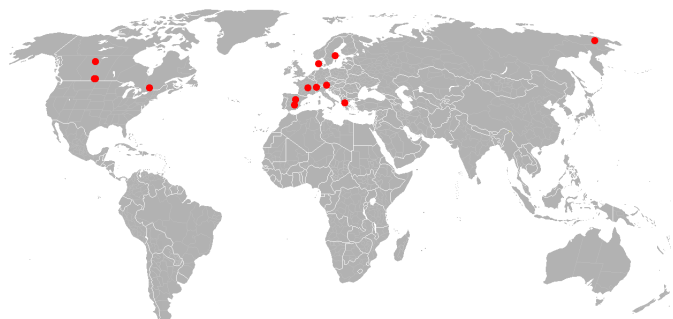


Tremella cetrariicola

Tremella christiansenii Diederich

Bibl. Lichenol. 61: 60 (1996). **Type:** Denmark, West Jutland, Ho, Skallingen, in the dunes called 'Høje Knolde', on *Salix repens*, on *Physcia tenella*, 20 July 1941, M. S. Christiansen 607 (C – holotype; BR – isotype).

Basidiomata inducing the formation of convex, irregular, often tuberculate or cerebriform galls on the host thallus, brown to dark brown, waxy-gelatinous, 0.4–2 mm diam., or developing on host apothecia, resulting in deformations resembling an agglomeration of numerous small apothecia. **Context hyphae** thin-walled, 1.5–2.5 µm diam.; subbasidial hyphae thick-walled, 2–4 µm diam., clamp connections not observed; haustoria present. **Hymenium** containing numerous subspherical or rarely ellipsoid probasidia, 9–14 µm diam., with a basal clamp. **Basidia**, when mature, 2-celled, with one longitudinal (exceptionally transverse) septum, 10–18 µm diam., near the septum 10–17 µm long, individual cells elongating and growing separately, each cell up to 30 µm long (epibasidium not included), in the upper part 4–11 µm diam.; epibasidia subulate to subcylindrical, sometimes not clearly distinct from the elongate part of the basidial cells, 3–5 µm diam., at least 50 µm long. **Basidiospores** subspherical, 9–12 × 8.5–10.5 µm. **Asexual stage** unknown.



Tremella christiansenii



Tremella christiansenii, Denmark, isotype. Basidiomata on *Physcia tenella*. Scale bar: 500 µm.



Tremella christiansenii, Spain, Zamora s. n. Basidiomata causing a deformation of *Physcia leptalea* apothecia (top left). Scale bar: 2 mm.

Notes. When this species induces the formation of galls on the host thallus, it might be mistaken for basidiomata of *Zygomycetes physciacearum*, easily distinguished by the elongate, aseptate basidia. When host apothecia are

infected, the resulting galls resemble an agglomeration of numerous small apothecia. Microscopically, the species is characterized by the unusual basidia in which individual cells elongate separately before the formation of the epiba-



Tremella christiansenii, Denmark, holotype (modified from Diederich 1996). Fertile hyphae, basidia, basidiospores and haustoria. Scale bar: 10 µm.

sidium. Similar basidia are known in several other lichenicolous *Tremella* species, such as *T. hypocenomycis*.

Ecology and hosts. On the thallus of *Physcia tenella*, *P. aipolia*, *P. dubia*, *P. leptalea* and *P. stellaris*, gall-inducing.

Distribution. Europe (Austria; [Denmark](#); France; Greece; Sweden; Switzerland), North America (Canada: Alberta, Quebec, Saskatchewan) and Asia (Russia).

Additional specimens examined. **Canada:** Alberta: Boreal Plains, NE regions of Alberta, on *P. stellaris*, 2007, Golden & Ass. (BR). **France:** Puy-de-Dôme: Châteaugay, on *Physcia adscendens* and *P. stellaris*, 2020, Pinault (BR). **Spain:** Guadalajara, Tamajón, 41.0006°N, 3.2492°W, s. d., Zamora (BR).

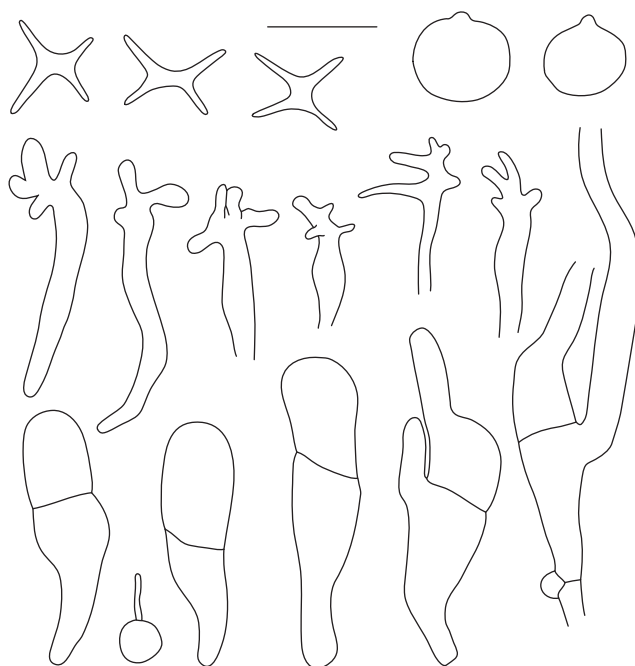
References. Diederich 1996 [Berger & Zimmermann 2021, Brodo et al. 2021, Ekman et al. 2019, Freebury 2014, Hafellner 2018, Roux 2020, Zhurbenko 2009].

Tremella cladoniae Diederich & M. S. Christ.

in Diederich, *Bibl. Lichenol.* 61: 65 (1996). *Type:* Germany, Schwarzwald, Bernau, Spiesshorn, on *Cladonia* sp., 13 Aug. 1916, G. Lettau s. n. (B 93630 – holotype; BR – isotype).

Basidiomatal galls inducing pinkish brown convex galls on the host thallus, later reddish brown, subspherical, tuberculate or irregular, 0.1–2.2 mm diam. **Context hyphae** thin-walled, 1.5–2.5 µm diam., clamp connections not observed; haustoria frequent. **Hymenium** containing numerous claviform probasidia with a basal clamp, often mixed with conidiogenous cells. **Basidia**, when mature, with one transverse septum in the upper third or quarter, 20–36 × 4.5–8 µm; epibasidia cylindrical, 2.5–4 µm diam., at least 30 µm long. **Basidiospores** subspherical, 7–10 × 6–8 µm. **Asexual stage:** asteroconidia present in older basidiomata, 9–11 µm diam., arms 2.5–5 µm long; conidiogenous cells 21–27 × 1.5–2.5 µm.

Notes. This is a common species inducing pinkish brown galls on *Cladonia* thalli. Contrary to common belief, mac-



Tremella cladoniae, Germany, holotype, except right basidium and haustorial branch: Luxembourg, Diederich 3640 (modified from Diederich 1996). Basidia, basidiospores, conidiogenous cells and asteroconidia. Scale bar: 10 µm.

roscopically this species cannot be distinguished with certainty from *Zyzygomyces bachmanii*, and a microscopical examination of basidia is always necessary for a correct identification.

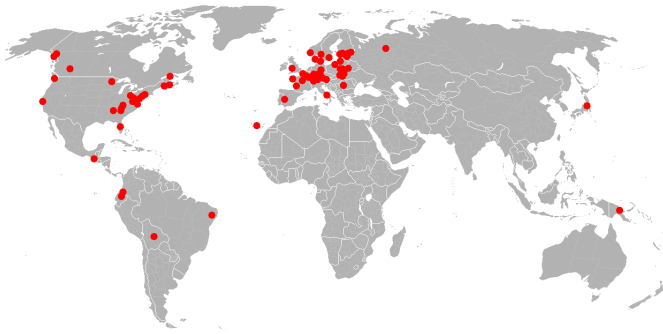
Ecology and hosts. On the squamules of the primary thallus, rarely on podetia of *Cladonia* sp., *C. chlorophaea*, *C. coniocraea*, *C. fimbriata*, *C. foliacea*, *C. furcata*, *C. grayi*, *C. macilenta*, *C. ochrochlora*, *C. pachycladodes*, *C. pyxidata* and others.

Distribution. Europe (Belarus; Belgium; Denmark; Estonia; France; [Germany](#); Italy; Lithuania; Luxembourg; Poland; Romania; Russia; Spain; Sweden; Switzerland; UK: Wales; Ukraine), Macaronesia (Canary Islands: Tenerife), North America (Canada: British Columbia, New Brunswick; USA: Alabama, Alaska, California, Florida, Georgia, Maine, Maryland, Minnesota, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Virginia, Washington, West Virginia), Central America (Guatemala), South America (Bolivia; Brazil; Colombia, Ecuador), Asia (Japan) and Oceania (Papua New Guinea).

Additional specimens examined (all on *Cladonia*). **Bolivia:** Cerca de Siberia, km 232, 17°48'13"S, 64°40'45"W, 2550 m, 2012, Etayo 28107 (LPB, herb. Etayo). **Guatemala:** Dept. de Quetzaltenango, Municipio de Zunil, Volcan Zunil, 14°44'32"N, 91°28'03"W, 2905 m, 2004, Quedensley 1052 (NY). **Japan:** Honshu, Tochigi Prefecture, Shimotsuke Province, Nikko City administrative region, Nikko National Park, 5.3 km ESE of Yumoto village (Yumoto Onsen), the Utsunomiya University for-



Tremella cladoniae, Germany, isotype. Basidiomata on *Cladonia* sp. Scale bar: 500 µm.

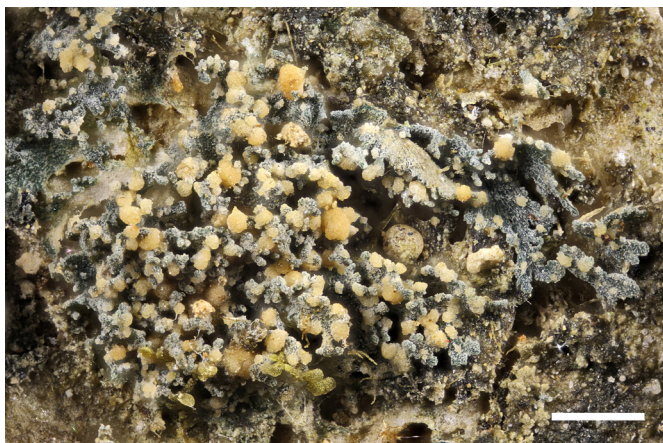
*Tremella cladoniae*

est on the S slope of Mt. Taro, NE of where dirt road ends, 36°47'59"N, 139°28'59"E, 1656 m, 2019, Ertz 24593 (BR). **USA:** *Alaska:* City and Borough of Juneau, mainland NW of Juneau, along Glacier Hwy, just N of Herbert River, 58°31.5'N, 134°47.8'W, 10 m, 1999, Tønsberg 27635 (BG L-71780). *California:* Sonoma Co., Goat Rock on peninsula W of Jenner, 2002, Tucker 37807 (SBBG). *Minnesota:* Aitkin Co., c. 14.37 km SE Jacobsen and 19.16 km S of Wawina, 46.8858°N, 93.1808°W, 2018, Gockman 5754 (BR).

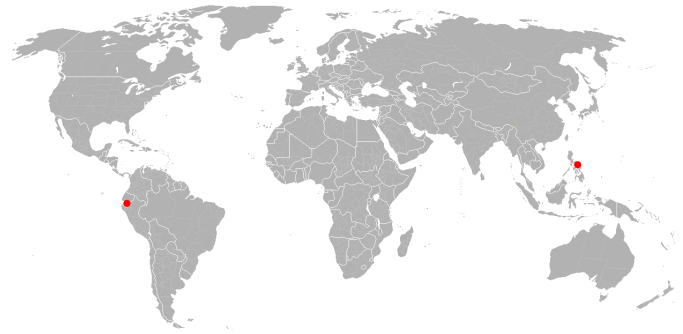
References. Diederich 1996 [Alstrup 2014, Bachmann 1927, Brackel 2014, 2020, Brackel et al. 2018, Diederich 2003, Etayo 2002, 2017, Etayo et al. 2020, Gockman et al. 2020, Hafellner 2002, 2016, Himelbrant et al. 2013, Kocourková & Brackel 2005, Kukwa 2005, Kukwa & Flakus 2009, Kukwa & Kowalewska 2007, Kukwa et al. 2010, 2013, Millanes et al. 2014a, Motiejūnaitė 2000, 2007, Pippola & Kotiranta 2008, Roux 2020, Spribille et al. 2010, 2020, Stepanchikova et al. 2020, Stordeur et al. 2018, Suija 2005, Teuber et al. 2021, Tsurykau 2017, Zhurbenko 2009].

Tremella coccocarpiae Diederich

Bibl. *Lichenol.* 61: 69 (1996). *Type:* Philippines, Sorsogon Province, between Irosin and Bulusan, Bulusan Volcano National Park, around the crater lake, alt. 320 m, 12°46' N, 124°04' E, in a virgin forest, on *Coccocarpia rottleri*, 20



Tremella coccocarpiae, Philippines, isotype. Basidiomata on the thallus of *Coccocarpia rottleri*. Scale bar: 500 µm.

*Tremella coccocarpiae*

July 1994, P. Diederich 13105 (CAHUP – holotype; BR, LG – isotypes).

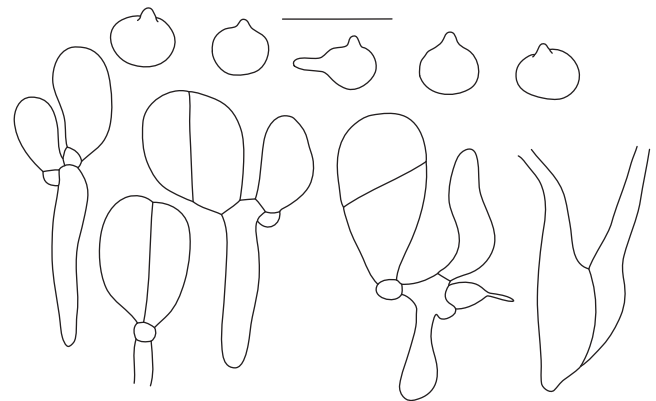
Basidiomata superficial, pulvinate, subspherical, waxy-gelatinous, pale brown, 0.05–0.2 mm diam. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2.5–4 µm diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid, 2-celled, with longitudinal or rarely oblique septa, 11–15 × 6.5–9 µm; epibasidia cylindrical, at least 20 µm long. **Basidiospores** ellipsoid, 5.5 × 4–4.5 µm. **Asexual stage** unknown.

Notes. This species strongly resembles *T. microcarpa* in its extremely small, pale brownish basidiomata; that species differs by larger basidiospores, 5.5–8.5 × 4.5–7 µm, and slightly shorter and broader basidia, 9.5–12.5 × 7–11 µm.

Ecology and hosts. On the thallus of *Coccocarpia rottleri* and *C. sp.*

Distribution. South America (Ecuador) and Asia (Philippines).

References. Diederich 1996 [Etayo 2017].



Tremella coccocarpiae, Philippines, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branch. Scale bar: 10 µm.

Tremella confluens Pippola, Diederich & Goward, sp. nov.

Diagnosis: Characterized by the black, strongly convex, gelatinous conidiomata, 0.15–0.5 mm diam., a hymenium made of thick-walled, hyaline to brown conidiophores and conidiogenous cells, ellipsoid conidia, $5.3\text{--}8 \times 4.1\text{--}5.7\ \mu\text{m}$, with an apically very thick wall, and the host choice, *Usnea longissima*.

Etymology: From *confluens*, confluent, referring to the confluent basidiomata.

Type: Canada, British Columbia, Haida Gwaii, Bag Inlet, $52^{\circ}21'\text{N}$, $131^{\circ}21'\text{W}$, outcrop above high tide line, on branch of *Pyrus fusca*, on *Usnea longissima*, 28 July 2003, T. Goward 03-223 (BR – holotype).

Mycobank: MB844652

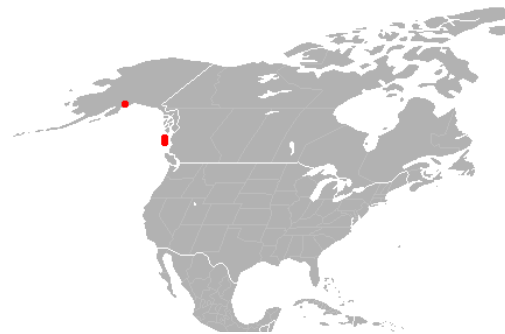
Basidiomata absent. **Conidiomata** superficial, pulvinate, subspherical, gelatinous, black, 0.15–0.5 mm diam., dispersed over thin host branches, often confluent on older branches. **Context hyphae** $2.5\text{--}4.5\ \mu\text{m}$ diam., thick-walled, hyaline to brown, without clamps; fertile hyphae (conidiophores) thick-walled, $3\text{--}5.5\ \mu\text{m}$ diam., hyaline or brown; haustoria present, with a basal clamp, large, mother cell $5.5\text{--}6.5 \times 3.5\text{--}4.5\ \mu\text{m}$, filament $1\text{--}2\ \mu\text{m}$ thick, wall thick, hyaline to brownish. **Hymenium** containing numerous conidiogenous cells, proliferations occurring through the basal clamp. **Conidiogenous cells** subcylindrical, determinate, discrete, polyblastic, producing apically one or several conidia, $6.5\text{--}11.5 \times 2.5\text{--}4.5\ \mu\text{m}$, each conidium with a basal clamp. **Conidia** ellipsoid, base rounded, aseptate, $(4.3\text{--})5.3\text{--}8.0(10.0) \times (3.6\text{--})4.1\text{--}5.7(6.9)\ \mu\text{m}$ ($n = 50$, measured in KOH + phloxine); wall hyaline to brownish, basally very thin, laterally gradually becoming thicker, apically $1\text{--}4\ \mu\text{m}$ thick; when mature, conidia may act in turn as conidiogenous cells and produce new conidia with a basal clamp.

Notes. This species is distinguished from the other asexual lichenicolous *Tremella* species by the relatively small, strongly convex, black conidiomata, the conidiophores, conidiogenous cells, conidia and haustoria with a thick wall that often becomes brownish, and the large haustoria. No basidia have been observed while preparing this description, although a single, longitudinally 1-septate basidium, $c. 9 \times 8\ \mu\text{m}$, may have been observed by one of us (E. P.) during an earlier examination.

Ecology and host. On the thallus of *Usnea longissima*.

Distribution. North America (**Canada:** **British Columbia:** **Haida Gwaii** [= Queen Charlotte Islands]; **USA:** **Alaska**).

Additional specimens examined (all on *Usnea longissima*). **Canada:** **British Columbia, Haida Gwaii:** Same locality as type, on *Pyrus fusca*, 2003, Goward 03-220 (BR); Burnaby Island, section cove, $52^{\circ}25'\text{N}$, $131^{\circ}21'\text{W}$, *Tsuga-Alnus* forest along shore of protected cove, 1971, Brodo (BR); Graham Island, Kumdis Bay, 2 mi NE of Port Clements, $53^{\circ}42'\text{N}$, $132^{\circ}08'\text{W}$, *P. fusca* grove with scattered *Picea sitchensis* at the edge of a broad salt marsh, 1971, Brodo (BR); Ellen Island, shoreline, old village site, on *Alnus rubra*, 2003, Goward 03-175 (UBC). **USA:** **Alaska:** Rocky Bay, Montague Island, Prince William Sound, $60^{\circ}30'\text{N}$, $147^{\circ}00'\text{W}$, on *P. sitchensis*, Wright 2005-40 (BR).



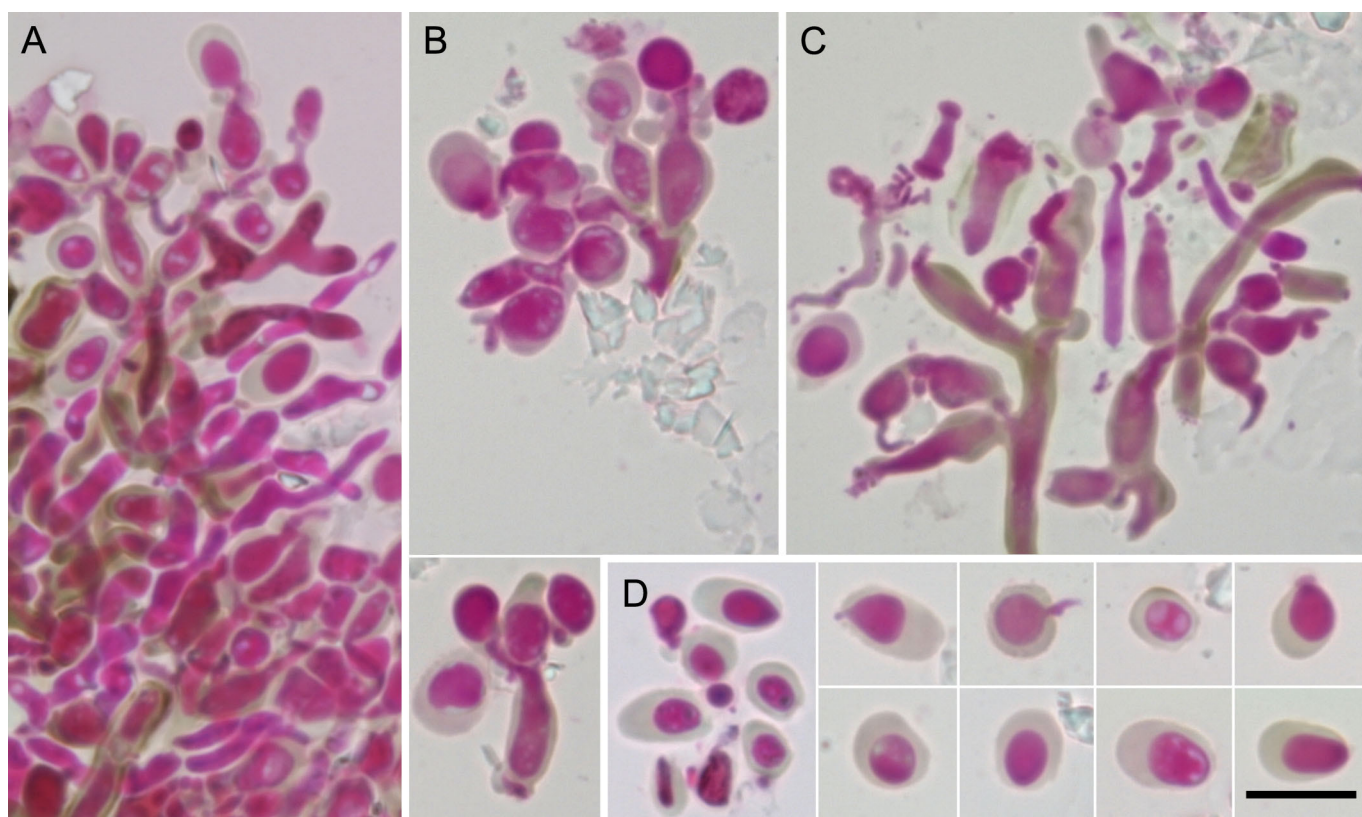
Tremella confluens



Tremella confluens, Canada, British Columbia, holotype. Conidiomata on the thallus of *Usnea longissima*. Scale bar: 500 μm .



Tremella confluens, USA, Alaska, Wright 2005-40. Conidiomata on the thallus of *Usnea longissima*. Scale bar: 500 μm .



Tremella confluens, Canada, British Columbia, holotype. A–B, Conidiophores, conidiogenous cells and conidia. C, Fertile hyphae with clamp connections, haustoria and one conidium (left). D, Mature conidia. In phloxine. Scale bar: 10 µm.

***Tremella conidioparmotrema* Diederich, Etayo & Milanes, sp. nov.**

Diagnosis: Characterized by the pale to dark reddish brown, slightly to strongly convex, strongly gelatinous and slightly translucent basidiomata/conidiomata, 0.15–0.5 mm diam., a hymenium containing regions with basidia and others with conidiophores and conidiogenous cells, cruciately septate (2–)4-celled basidia, 17–25 × 11–18 µm, large basidiospores, 6.5–9.5 × 6–8.5 µm, and ellipsoid conidia, 5.1–6.4 × 4.3–5.0 µm, and the host choice, *Parmotrema* sp.

Etymology: A noun in apposition, from *conidium*, as the species is known from the conidial stage (in addition to the sexual stage), and *Parmotrema*, the host lichen.

Type: Ecuador, Prov. Pichincha, entre Cumbayá y cerro de la Virgen, taludes y bosque de *Polylepis* cerca ‘casa de las truchas’, 3650–3800 m, on corticolous *Parmotrema* sp., 26 July 1999, J. Etayo 19911 (BR – holotype).

Mycobank: MB844653

Basidiomata/conidiomata superficial, strongly gelatinous and slightly translucent, very pale yellowish brown to medium or sometimes dark reddish brown, slightly to strongly convex and then almost subspherical, basally not or slightly constricted, 0.15–0.5 mm diam., sometimes fusing and then up to 1 mm diam. *Context hyphae* not observed; subbasidial

hyphae below basidia and conidiophores thick-walled, 2.5–5 µm diam.; haustoria not observed. *Hymenium* containing regions with basidia and adjacent regions with occasionally branched conidiophores; probasidial initials subspherical to ellipsoid; proliferations of basidia and of conidiogenous cells occurring through the basal clamp. *Basidia*, when mature, ellipsoid, sometimes with a narrow, almost stalk-like base, (2–)4-celled, cruciately longitudinally septate, 17–25 × 11–18 µm; epibasidia cylindrical, 28–40 µm long, 3–6 µm thick. *Basidiospores* subspherical to shortly ellipsoid, 6.5–9.5 × 6–8.5 µm. *Conidiogenous cells* elongate ellipsoid to subcylindrical, with a rounded base, determinate, discrete, polyblastic, producing apically one to several conidia, 7–15 × 2.5–5 µm, each conidium with a basal clamp. *Conidia* ellipsoid, base slightly truncate, aseptate, (4.9–)5.1–6.4(–7.8) × (3.9–)4.3–5.0(–5.5) µm (n = 50), wall 0.5–0.8 µm thick; when mature, conidia act in turn as conidiogenous cells, and produce a new conidium with a basal clamp.

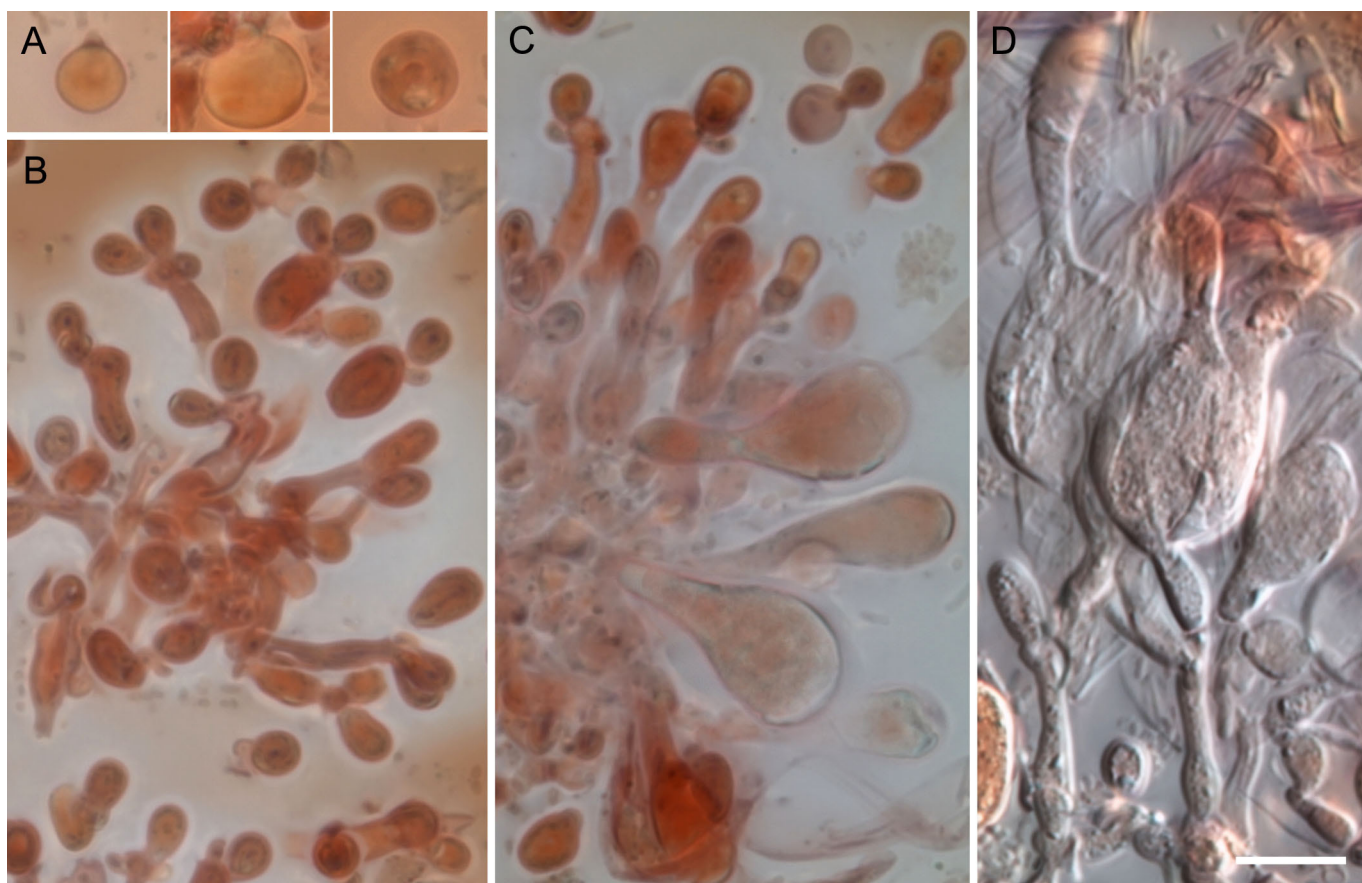
Notes. This is one of the rare lichenicolous *Tremella* species having a hymenium made of conidiophores producing clamped conidia. Contrarily to *T. confluens* and *T. conidiopunctelia*, this species also presents the sexual stage. It is further distinguished from *C. conidiopunctelia* by the basidiomata that are superficial from the beginning, are pale to dark reddish brown, and never



Tremella conidioparmotrema, Ecuador, holotype. One mature and many yellowish young basidiomata on the thallus of *Parmotrema* sp. Scale bar: 500 μ m.



Tremella conidioparmotrema, Ecuador, holotype. Young basidiomata on soralia (left) and mature basidiomata on the thallus (right) of *Parmotrema* sp. Scale bar: 500 μ m.



Tremella conidioparmotrema, Ecuador, holotype. A, Basidiospores. B, Conidiophores, conidiogenous cells and conidia. C, Conidiophores mixed with probasidia. D, Mature basidia. In ammoniacal Congo red. Scale bar: 10 μ m.

turn blackish when old. *Tremella parmotrema*, also growing on *Parmotrema* hosts, is distinguished by the very large and convex basidiomatal galls, up to 4 mm diam., that are never gelatinous and translucent, and the missing asexual stage.

Ecology and host. On the corticolous thallus of an unidentified species of *Parmotrema*.

Distribution. South America (Ecuador), known only from the type locality.



Tremella conidioparmotrema, Ecuador, holotype. Basidiomata on soralia of *Parmotrema* sp. Scale bar: 500 µm.



Tremella conidioparmotrema, Ecuador, holotype. Basidiomata on soralia of *Parmotrema* sp. Scale bar: 500 µm.



Tremella conidioparmotrema

Tremella conidiopunctelia Diederich, Millanes, Lendemer, D. P. Waters & Giavarini, sp. nov.

Diagnosis: Characterized by the pale to dark brown or blackish, strongly gelatinous conidiomata, the absence of basidia and basidiospores, the presence of conidiophores, conidiogenous cells and clamped, sometimes catenulate conidia, $5.1\text{--}6.8 \times 3.9\text{--}4.9 \mu\text{m}$, and the host choice, *Punctelia caseana*.

Etymology: A noun in apposition, from *conidium*, as the species is known only from the conidial stage, and *Punctelia*, the host lichen.

Type: USA, New Jersey, Hunterdon Co., Lebanon Township, Crystal Springs Preserve, Headwaters of Spruce Run, 40.7630°N , 74.8576°W , mixed hardwood forest (maple/birch) along stream with ponds, on *Acer*, on *Punctelia caseana*, 23 Sept. 2020, D. P. Waters 5448 (NY – holotype).

Mycobank: MB844654

Basidiomata absent. **Conidiomata** initially immersed and covered by a thin cortical layer of the host that soon breaks to expose the fertile layer, gelatinous, dark brown to black, flat to slightly convex, rarely becoming strongly convex when old, $0.4\text{--}1.8 \text{ mm}$ diam. **Context hyphae** $2\text{--}2.5 \mu\text{m}$ diam., thick-walled; fertile hyphae (conidiophores) thick-walled, $2\text{--}3.5 \mu\text{m}$ diam.; haustoria present, basal clamp not observed, $3.5\text{--}5 \times 2.5\text{--}3.5 \mu\text{m}$. **Hymenium** containing numerous conidiogenous cells, proliferations occurring through the basal clamp. **Conidiogenous cells** elongate ellipsoid to

subcylindrical, with a rounded base, determinate, discrete, polyblastic, producing apically one to several conidia, $8\text{--}21 \times 2.5\text{--}4.5 \mu\text{m}$, each conidium with a basal clamp. **Conidia** ellipsoid, base slightly truncate, aseptate, thin-walled, $(4.4\text{--})5.1\text{--}6.8(-9.3) \times (3.3\text{--})3.9\text{--}4.9(-6.2) \mu\text{m}$ ($n = 214$); when mature, conidia act in turn as conidiogenous cells, become thick-walled, and produce a new conidium with a basal clamp, sometimes becoming shortly catenulate.

Notes. This is a remarkable *Tremella* species in which basidia and basidiospores are absent, while the hymenium entirely consists of conidiophores, conidiogenous cells and conidia. Conidia all have a distinct basal clamp. Mature conidia may become slightly elongated and more thick-walled, then act as conidiogenous cells and in turn produce conidia, always with a basal clamp. This suggests that conidia are most probably dikaryotic.

Catenulate-clamped conidia have also been observed in different non-lichenicolous *Tremella* species, such as *T. mesenterica* or *T. mellea*, but in these species, the basidial stages are also known (e.g., Bandoni 1958, 1987, Wong et al. 1985).

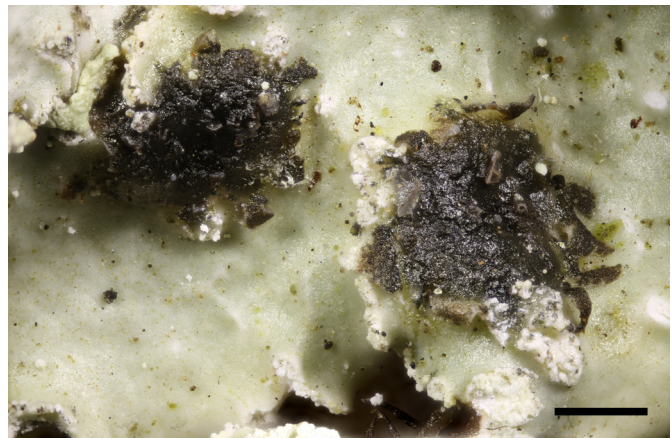
Ecology and host. On corticolous thalli of *Punctelia caseana* and *P. subrudecta*, often in forests. Lendemer & Hodgkinson (2010) have distinguished two morphotypes of *P. caseana*, the first one with mainly marginal soralia, and the second with mainly laminal soralia. The new *Tremella* is known only from the second morphotype.

Distribution. Europe (UK: England) and North America (USA: New Jersey, Ohio, Pennsylvania, West Virginia). The examination of hundreds of specimens of *Punctelia caseana* has revealed that the *Tremella* does not occur in its entire range, but instead seems to be concentrated in southern New Jersey and adjacent areas. The species had already been reported from New Jersey and Pennsylvania as an unidentified *Tremella* species by Harris & Lendemer (2005) and Lendemer (2006).

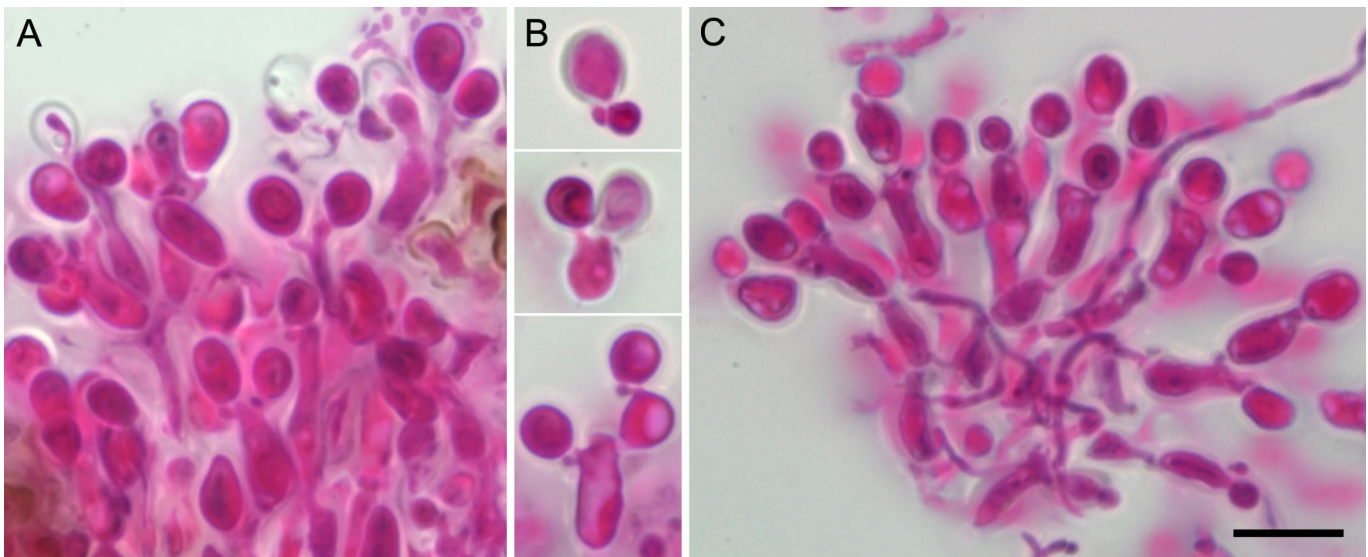
Additional specimens examined. UK (all on *Punctelia subrudecta*): England: South Hampshire, New Forest National Park, Amie's Wood, Linwood, 2020, Giavarini 229a (herb. Giavarini); ibid., Mark Ash Wood, 2022, Giavarini 229b, 229c (herb. Giavarini). USA (all on



Tremella conidiopunctelia s. str., USA, New Jersey, holotype. Conidiomata on *Punctelia caseana*. Scale bar: 500 μ m.



Tremella conidiopunctelia s. str., USA, New Jersey, holotype. Conidiomata on *Punctelia caseana*. Scale bar: 500 μ m.



Tremella conidiopunctelia s. str., USA, New Jersey. A–B, holotype, C, Lendemer 3492. Conidiophores, conidiogenous cells and clamped conidia, in phloxine. Scale bar: 10 μ m.

P. caseana): New Jersey: Atlantic Co., Pleasant Mills Cemetery, W of Batsto, Batsto Natural Area, Wharton State Forest, 39°38'30"N, 74°39'40"W, 3 m, on *Pinus*, 2004, Lendemer 3153 (NY); Burlington Co., along the W shore of the Skit Branch of the Batsto River, S of an unnamed pavel road, N of Carranza Memorial, N of Friendsip, 2.5 mi NE of Hampton Furnace, Wharton State Forest, 39°47'10"N, 74°39'34"W, 15 m, on *Quercus*, 2004, Lendemer 3492 (NY); Burlington Co., W of the shore of the Batsto River and E of the Mullica River, S of Batsto, Wharton State Forest, 39°38'28"N, 74°39'04"W, 3 m, on *Quercus*, 2004, Lendemer 3246 (NY). Ohio: Adams Co., Oliver Township, Chaparral Prairie State Nature Preserve, N of Chaparral Road, c. 3 mi NW of SR 247, 38°50'22"N, 83°34'31"W, 265 m, 2006, Harris 52804A (NY). Pennsylvania: Carbon Co., State Game Lands No. 129, E of PA 901, 1 mi W of Dilldown Creek, 2 mi N of Albrightsville, 41°01'10"N, 75°34'55"W, 2009, Lendemer 17452 (NY). Tennessee: Sevier Co., Great Smoky Mountains National Park, Foothills Parkway, Cove Mountain, W slopes of Crooked Arm Ridge, above Starkey Hollow, c. 0.5 mi NE of Rimmel Rd.,

35°43'20"N, 83°53'40"W, 630 m (2075 ft), on *Pinus rigida*, 2021, Lendemer 71184 (NY). West Virginia: Tucker Co., Monongahela National Forest, trail from Forest Service Road 75 along boundary of Dolly Sods Wilderness to confluence of Alder Run Bog and Fisher Spring Run Bog, 39°01'25"N, 79°19'33"W, 1175 m, on *Acer rubrum*, 2014, Harris 60539-A (NY).



Tremella conidiopunctelia s. str.

Tremella conidiopunctelia subsp. *parmelinellae* Diederich, Millanes, Common & Lawrey, subsp. nov.

Diagnosis: Differs from subsp. *conidiopunctelia* by the smaller conidia, $4.5\text{--}5.7 \times 3.5\text{--}4.3\ \mu\text{m}$, and the different host choice, *Parmelinella amazonica*.

Etymology: From *Parmelinella*, the host lichen.

Type: USA, Florida, Hillsborough Co., Hillsborough River State Park, Florida Trail, 28.1483°N, 82.25°W, on corticolous *Parmelinella amazonica*, 26 Oct. 2011, R. Common 9239A (BR – holotype).

Mycobank: MB844655

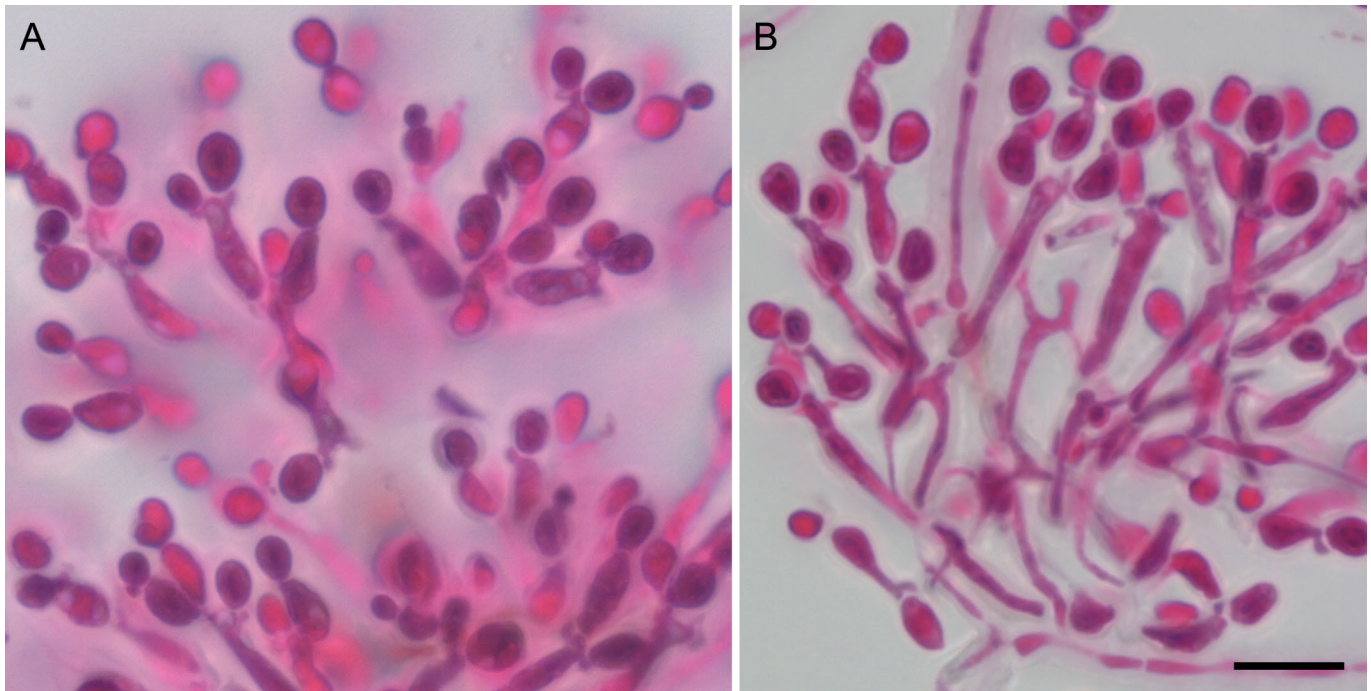
Basidiomata absent. *Conidiomata* initially immersed, breaking through the host cortex to expose the fertile layer, gelatinous, pale brown when young, rapidly dark brown to black, flat to slightly convex, 0.4–1.2 mm diam. *Context hyphae* 1.5–2.5 μm diam., thick-walled; fertile hyphae (conidiophores) thick-walled, 2–4 μm diam., septa with clamps; haustoria not observed. *Hymenium* containing numerous conidiogenous cells, proliferations occurring through the basal clamp. *Conidiogenous cells* elongate ellipsoid to subcylindrical, with a rounded base, determinate, discrete, polyblastic, producing apically one to several conidia, $10\text{--}19 \times 2.5\text{--}4\ \mu\text{m}$, each conidium with a basal clamp. *Conidia* ellipsoid, base slightly truncate, aseptate, thin-walled, $(3.7\text{--})4.5\text{--}5.7(7.3) \times (3.0\text{--})3.5\text{--}4.3(5.0)\ \mu\text{m}$ ($n = 284$); when mature, conidia act in turn as conidiogenous cells, become thick-walled, and produce a new conidium with a basal clamp.

Notes. Macroscopically and microscopically, this taxon strongly resembles *Tremella conidiopunctelia*. It differs, however, by several characters: first, the conidia are smaller, although some overlap exists, second, the host seems always to be *Parmelinella amazonica*, vs *Punctelia* species, and third, the ITS sequence differs by two nucleotide bases. These differences may be considered as minor, and therefore the recognition of two distinct species, although plausible, may be premature until more molecular data are available. As further, the two host species seem to have disjunct distribution patterns, we may anticipate that allopatric speciation occurs, as populations on both hosts became geographically and ecologically isolated from each other, preventing gene flow. *Parmelinella amazonica* is a tropical/subtropical species, while both *Punctelia* hosts are temperate species. In this situation, populations on both hosts may best be recognized as subspecies.

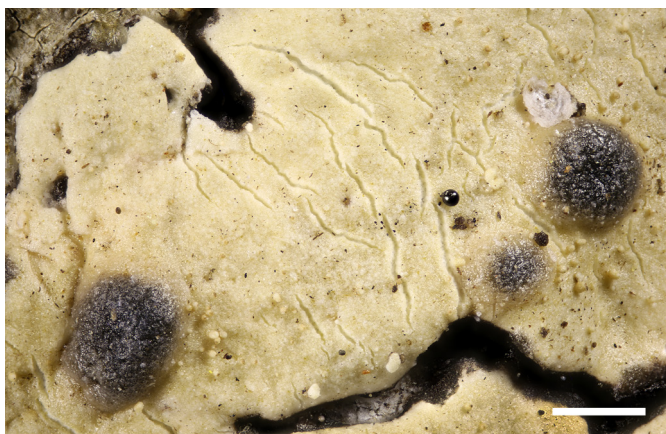
Ecology and host. On the thallus of *Parmelinella amazonica*.

Distribution. North America (USA: Florida).

Additional specimens examined (all on *Parmelinella amazonica*). USA: Florida: Clay Co., Gold Head Branch State Park, sand pine scrub at Devil's washbasin, corticolous, 1992, Platt 235 (SBBG); Marion Co., Florida Greenways along Oklawaha River at Eureka East Boat Ramp on S side of river at County Road 316, 29°22'N, 81°54'W, mixed hardwood-*Taxodium-Sabal* swamp grading into *Quercus virginiana*, on *Q. virginiana* bark, 1996, Lawrey 1591 (BR).



Tremella conidiopunctelia subsp. *parmelinellae*, USA, Florida. A, holotype, B, Lawrey 1591. Conidiophores, conidiogenous cells and clamped conidia, in phloxine. Scale bar: 10 μm .



Tremella conidiopunctelia subsp. *parmelinellae*, USA, Florida, holotype. Conidiomata on *Parmelinella amazonica*. Scale bar: 500 μ m.



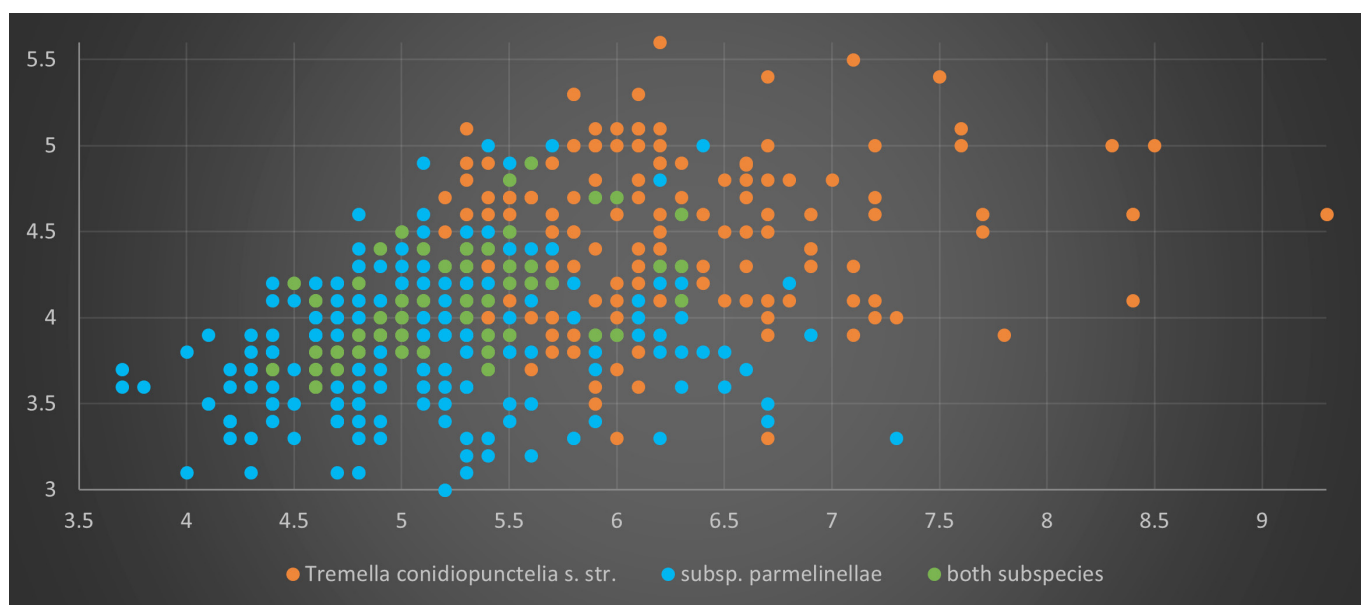
Tremella conidiopunctelia subsp. *parmelinellae*, USA, Florida, Platt 235. Conidiomata on *Parmelinella amazonica*. Scale bar: 500 μ m.



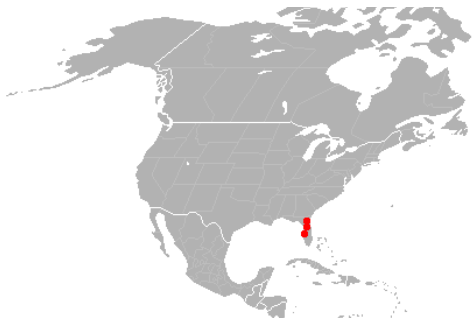
Tremella conidiopunctelia subsp. *parmelinellae*, USA, Florida, Lawrey 1591. Young conidiomata on *Parmelinella amazonica*. Scale bar: 500 μ m.



Tremella conidiopunctelia subsp. *parmelinellae*, USA, Florida, Lawrey 1591. Mature conidioma on *Parmelinella amazonica*. Scale bar: 500 μ m.



Conidial size in μ m of *Tremella conidiopunctelia* s. str. (on *Punctelia caseana*) and subsp. *parmelinellae* (on *Parmelinella amazonica*).

*Tremella conidiopunctelia* subsp. *parmelinellae**Tremella coniocarpi****Tremella coniocarpi* Diederich & Common, sp. nov.**

Diagnosis: Characterized by the convex, pale brown, gelatinous basidiomata on the thallus of *Coniocarpon cinnabarinum*, 0.2–0.45 × 0.2–0.35 mm, the 4-celled basidia with longitudinal septa, 11–20 × 8–13.5 µm, and the basidiospores 5.5–6.5 × 5–5.5 µm.

Etymology: From *Coniocarpon*, the host lichen.

Type: USA, Florida, Sumter Co., 28.5783°N, 82.0916°W, 20–40 m, on dead branches of oak, on *Coniocarpon cinnabarinum*, 30 July 2016, R. Common 10170D (BR – holotype).

Mycobank: MB844656

Basidiomata superficial, convex, roundish to elongate, gelatinous, pale brown, not gall-inducing, 0.2–0.45 × 0.2–0.35 mm. **Context hyphae** 1.5–2 µm diam.; subbasidial hyphae thick-walled, 2.5–5 µm diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, broadly ellipsoid, very rarely ellipsoid with a narrower lower cell but never stalked, 4-celled, longitudinally cruciately septate, 11–20 × 8–13.5 µm in lateral view, 12–16.5 × 9.5–15 µm from above; epibasidia cylindrical. **Basidiospores** ellipsoid, 5.5–6.5 × 5–5.5 µm. **Asexual stage** unknown.

Notes. This species differs from most other known lichenicolous *Tremella* species by the 4-celled basidia and the relatively small, pale brown, not gall-inducing, gelatinous basidiomata. *Tremella haematommatis* and *T. wirthii* dif-

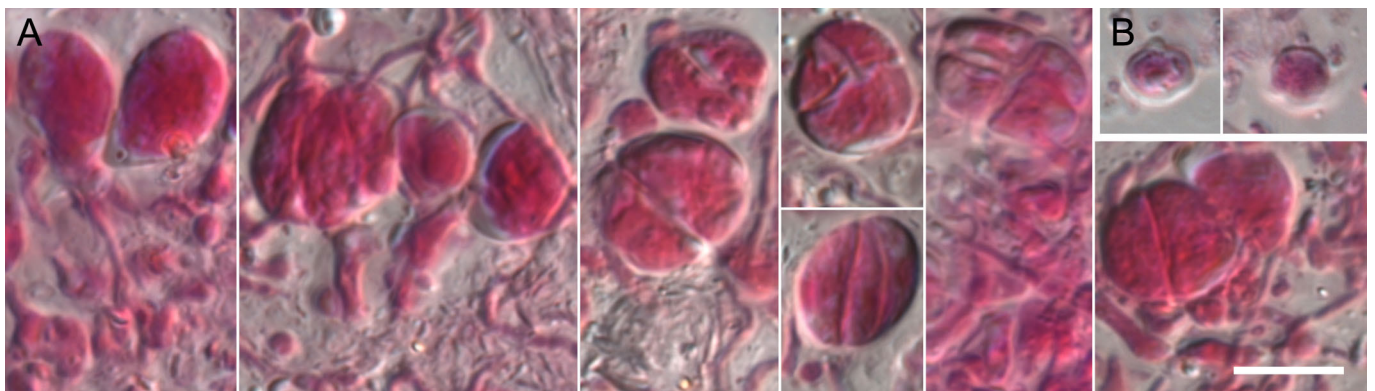
fer by the larger basidiospores, over 7 × 6.5 µm. *Tremella graphidastrae* is microscopically similar, but differs by the more orange-brown basidiomata. *Tremella synarthoniae*, a species growing on a related host, differs by orange-brown basidiomata and constantly 1-septate basidia.

Ecology and host. On the thallus of corticolous *Coniocarpon cinnabarinum*.

Distribution. North America (USA: Florida), known only from the type locality.



Tremella coniocarpi, USA, Florida, holotype. Basidiomata on an almost sterile thallus of *Coniocarpon cinnabarinum*. Scale bar: 500 µm.



Tremella coniocarpi, USA, Florida, holotype. A, Basidia. B, Basidiospores. In phloxine. Scale bar: 10 µm.

***Tremella coppinsii* Diederich & G. Marson**

Notes RBG Edinb. 45: 175 (1988). *Type*: Malaysia, Sarawak, Gunong Mulu National Park, 4th Division, Baram District, Gunong Mulu, summit, on *Platismatia regenerans*, 27 Apr. 1978, B. Coppins 5011 (E – holotype; BR – isotype).

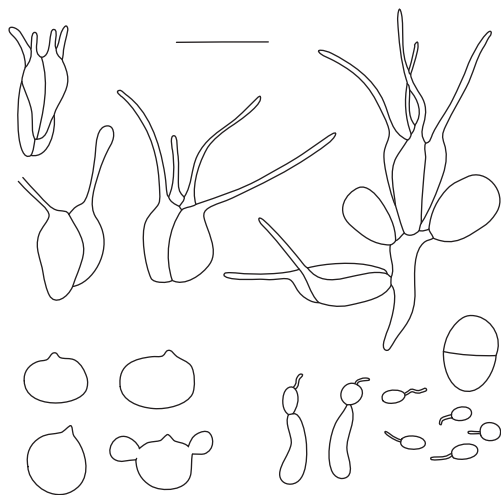
Basidiomata growing on the thallus of the host, pinkish to reddish orange, waxy to firm gelatinous, applanate or pulvinate, 0.3–0.7 mm diam. *Context hyphae* thick-walled, 2–3.5 µm diam., clamp connections not observed; haustoria present. *Hymenium* containing numerous conidiogenous cells intermixed with subspherical or ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid, 2–4-celled by longitudinal septa, 8–13 × 5–12 µm; epibasidia subcylindrical, at least 25 µm long, 2–3 µm diam. *Basidiospores* ellipsoid, rarely subspherical, 6–10 × 4–6.5 µm. *Asexual stage*: asteroconidia present, 9–20 µm diam., individual arms 3–12 µm long; conidiogenous cells 16–26 µm long, 3–6 µm diam.

Notes. This species is well characterized by the basidiomata that always have a reddish tinge on the thallus of *Platismatia* species.

Ecology and hosts. On the thallus of *Platismatia regenerans*, *P. glauca* and *P. interrupta*.

Distribution. Europe (Austria; Belgium; Estonia; France; Germany; Ireland; Lithuania; Norway; Poland; Sweden; UK: England, Northern Ireland, Scotland, Wales), Macaronesia (Azores; Canary Islands; Madeira), North America (Canada: New Brunswick, Quebec; USA: Maine) and Asia (Japan; [Malaysia](#); [Sarawak](#)).

Additional specimen examined. **Japan**: Honshu, Gunma Prefecture, Katashina-mura, Nillo National Park, 4.7 km E of Marunuma Kogen Ski Resort, 36°48'56"N, 139°22'41"E, 1818 m, on *Platismatia interrupta*, 2019, Ertz 24849 (BR).



Tremella coppinsii, Malaysia, holotype (modified from Diederich & Marson 1988). Probasidia, basidia, basidiospores and haustorial branches. Scale bar: 10 µm.



Tremella coppinsii, Malaysia, isotype. Basidiomata on the thallus of *Platismatia regenerans*. Scale bar: 500 µm.

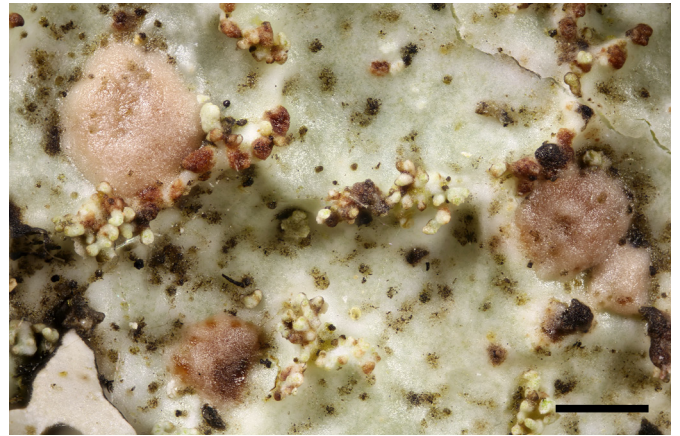
References. Berger & Zimmermann 2016, Diederich 1996, Diederich & Marson 1988 [Brackel 2014, Etayo 1996, Gorczak et al. 2021, Himmelbrant et al. 2013, Holien & Tønsberg 1994, Millanes et al. 2014a, Roux 2020, Suija 2005, Zimmermann & Berger 2018].



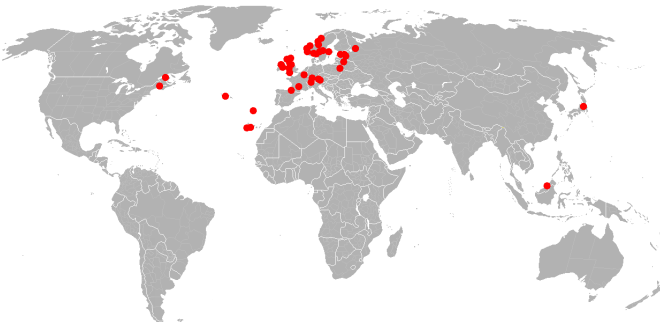
Tremella coppinsii, Sweden, Fries s. n. (modified from Diederich 1996). Basidia, basidiospores, conidiogenous cell, asteroconidia, hypha with clamp connection and haustorial branches. Scale bar: 10 µm.



Tremella coppinsii, Scotland, Diederich 15268. Basidiomata on the thallus of *Platismatia glauca*. Scale bar: 500 µm.



Tremella coppinsii, Japan, Ertz 24849. Basidiomata on the thallus of *Platismatia interrupta*. Scale bar: 500 µm.



Tremella coppinsii



Tremella dendrographae

Tremella dendrographae Diederich & Tehler

in Diederich, *Bibl. Lichenol.* 61: 74 (1996). Type: USA, California, San Luis Obispo County, along beachfront north of Museum, Morso Bay State Park, on *Dendrographa minor*, 20 Nov. 1988, C. Bratt 5863 (S – holotype; BR – isotype).

Basidiomata absent; fungus inducing the formation of convex galls concolorous with or paler than the host thallus, cerebriform when old, with a matt, non-corticated surface, 0.5–4 mm diam. *Context hyphae* 1.5–2 µm diam., clamp connections not observed; subbasidial hyphae thick-walled, 2–3 µm diam.; haustoria present but rare. *Hymenium* poorly developed, basidia situated in the outer layer of the galls; probasidial initials subspherical or ellipsoid with a basal clamp. *Basidia*, when mature, 2–4-celled, subspherical, with longitudinal septa, 17–24 × 14–23 µm, rarely elongate, with an attenuated base, with oblique or transverse septa, 25–31 × 12–14 µm; epibasidia subcylindrical, 3.5–5.5 µm diam., 40–50 µm long. *Basidiospores* subspherical, 7–9 × 7–8 µm. *Asexual stage* unknown.

Notes. This species is characterized by the particularly large, concolorous, non-corticated galls on the host thallus, containing in the outer layer numerous 4-celled basidia.

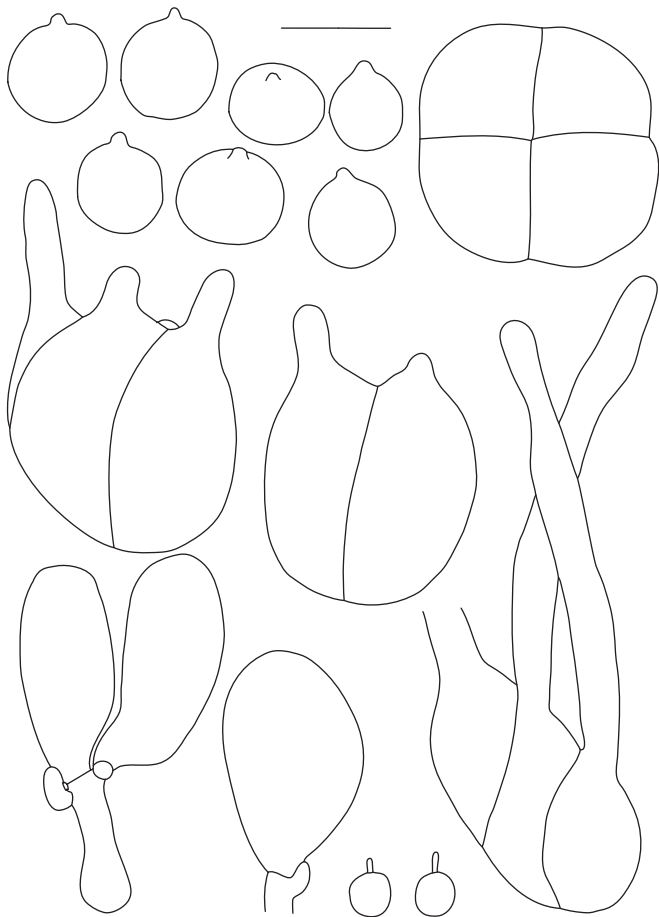
Ecology and hosts. Extremely common on the thallus of *Dendrographa minor*, *D. leucophaea* and *D. sp.*, infecting two thirds of the thalli.

Distribution. North America (Mexico; USA: California).

References. Diederich 1996 [Diederich 2003].



Tremella dendrographae, USA, California, isotype. Basidiomatal gall on the thallus of *Dendrographa minor*. Scale bar: 500 µm.

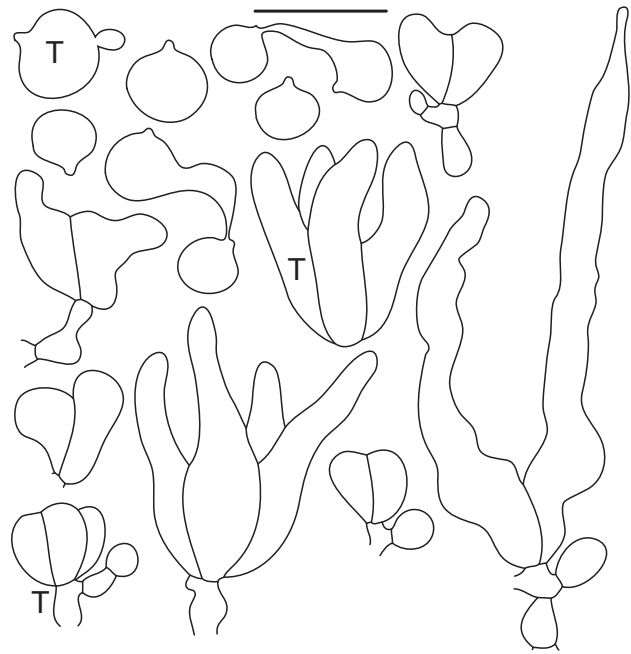


Tremella dendrographae, USA, California, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 μ m.

***Tremella diderichiana* Pérez-Ortega, Millanes, Wedin, V. J. Rico & J. C. Zamora**

in Zamora et al., *Mycologia* 108: 388 (2016). *Type*: Spain, Comunidad de Madrid, Madrid, Villanueva de la Cañada, Guadamounte residential, 40°24'49"N, 3°57'47"W, 630 m, on *Lecidea* aff. *erythrophaea* apothecia and thalli, on *Cistus ladanifer*, 7 Febr. 2015, J. C. Zamora & B. Zamora (MAF-Lich 19735 – holotype; AH, UPS – isotypes).

Basidiomata inducing the formation of convex to bullate, rounded, waxy, pale cream to pale brown, rarely brown or greenish galls in the host apothecia and thallus, 0.05–0.5(–0.7) mm diam. *Context hyphae* and subbasidial hyphae thick-walled, 3.5–8 μ m diam., clamps absent or inconspicuous; haustoria frequent. *Hymenium* with numerous subglobose to ellipsoid probasidia; basal clamps indistinct. *Basidia*, when mature, 2–4-celled, with longitudinal, exceptionally oblique septa; basidial cells elongating and growing separately, 14.5–34(–38) \times 6–13 μ m; epibasidia subcylindrical, sometimes not clearly differentiated, 20–50 \times 3.5–7.5 μ m. *Basidiospores* subspherical, rarely broadly ellipsoid, (7–)10–12.5(–13.5) \times



Tremella diderichiana, Spain, holotype (T) and MAF-Lich 19737 (modified from Zamora et al. 2016). Basidia and basidiospores, some producing secondary spores. Scale bar: 10 μ m.

(8.5–)10–14(–16) μ m, able to germinate by producing a sterigma and a secondary ballistospore, similar to a basidiospore but only 9–10 μ m diam. *Asexual stage*: ovoid to broadly ellipsoidal blastic conidia. 5–7.5 \times 4–6 μ m have been observed. [Modified from Zamora et al. 2016.]

Notes. *Tremella diderichiana* is characterized by minuscule galls on the thallus and apothecia of the host, and 2–4-celled basidia in which individual cells elongate and grow independently before forming the epibasidia and basidiospores. This basidial type is known in just a few lichenicolous *Tremella* species, such as *T. christiansenii*, *T. hypocenomycis* or *T. tuckerae*.

Ecology and host. On the thallus and apothecia of corticolous *Lecidea* aff. *erythrophaea*.

Distribution. Europe ([Spain](#)).

Reference. Zamora et al. 2016.



Tremella diderichiana



Tremella diderichiana, Spain, Los Navalucillos, MAF-Lich 19737. Basidiomata on the thallus of *Lecidea* aff. *erythrophaea*. Photo: J. C. Zamora. Scale bar: 1 mm.

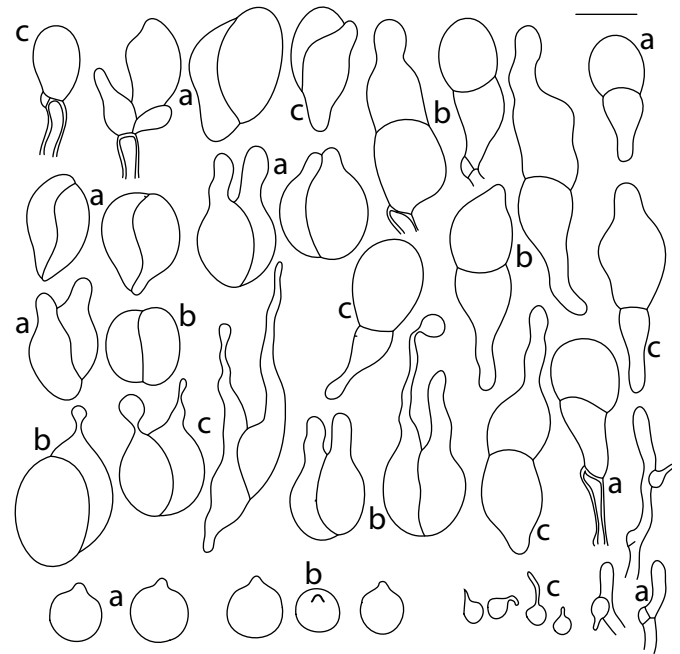


Tremella diderichiana, Spain, Villalba, MAF-Lich 19739. Basidiomata on the thallus of *Lecidea* aff. *erythrophaea*. Photo: J. C. Zamora. Scale bar: 1 mm.

***Tremella diploschistina* Millanes, M. Westb., Wedin & Diederich**

Lichenologist 44: 324 (2012). *Type*: Sweden, Uppland, Djurö par., Runmarö, Norestranden NE of Nore, 59°16'43"N, 18°47'47"E, on *Diploschistes scruposus*, 30 June 2009, M. Westberg & T. Berglund 09–400 (S – holotype).

Basidiomata waxy, inducing the formation of pale yellowish brown, dark brown or black, convex to subglobose galls on the host thallus, 0.3–0.9 mm diam., often forming groups up to 3 mm diam. *Context hyphae* thin-walled, often with clamp connections, 1.5–2.5 µm diam.; haustoria frequent. *Hymenium* containing numerous clavate probasidia, with basal clamps. *Basidia*, when mature, 2-celled, with one transverse, oblique or longitudinal septum; when transverse, the lower cell with an attenuated stalk-like



Tremella diploschistina, Sweden, holotype (a), and USA, Westberg 09-452 (b) and Rosentreter 6836 (c) (modified from Millanes et al. 2012). Basidia, basidiospores, haustorial branches and hyphae with clamps. Scale bar: 10 µm.

base, often longer than the upper cell, 14–30 × 8–14 µm (incl. stalk-like base); epibasidia 2–4 µm diam., at least 30 µm long. *Basidiospores* ellipsoid to subspherical, c. 7–9 × (5–)6–9 µm. *Asexual stage* unknown.

Notes. This species induces the formation of pale to dark brown or blackish, convex galls on the host thallus. Macroscopically, it resembles infections by other fungi, and therefore a microscopical examination is always necessary.

Ecology and hosts. On the thallus of *Diploschistes scruposus* and *D. muscorum*.



Tremella diploschistina, Sweden, holotype. Basidiomata on *Diploschistes scruposus*. Scale bar: 500 µm.



Tremella diploschistina

Distribution. Europe (Belgium; Czech Republic; Germany; [Sweden](#)) and North America (USA: Idaho, Washington).

Additional specimens examined (both on *Diploschistes scruposus*). **Belgium:** Buret, carrière au S de l'entrée du tunnel, 50.0953°N, 5.8504°E, 455 m, 1980, Diederich 2708 (BR). **Czech Republic:** W Bohemia, Šumava Mts., Hamry, nature reserve Bílá strž, 49°11'16"N, 13°09'57"E, 1075 m, 2019, Palice 27715 (BR).

References. Millanes et al. 2012 [Brackel 2019, Millanes et al. 2014a, Schiefelbein et al. 2017, Teuber et al. 2021, Vondrak et al. 2022].

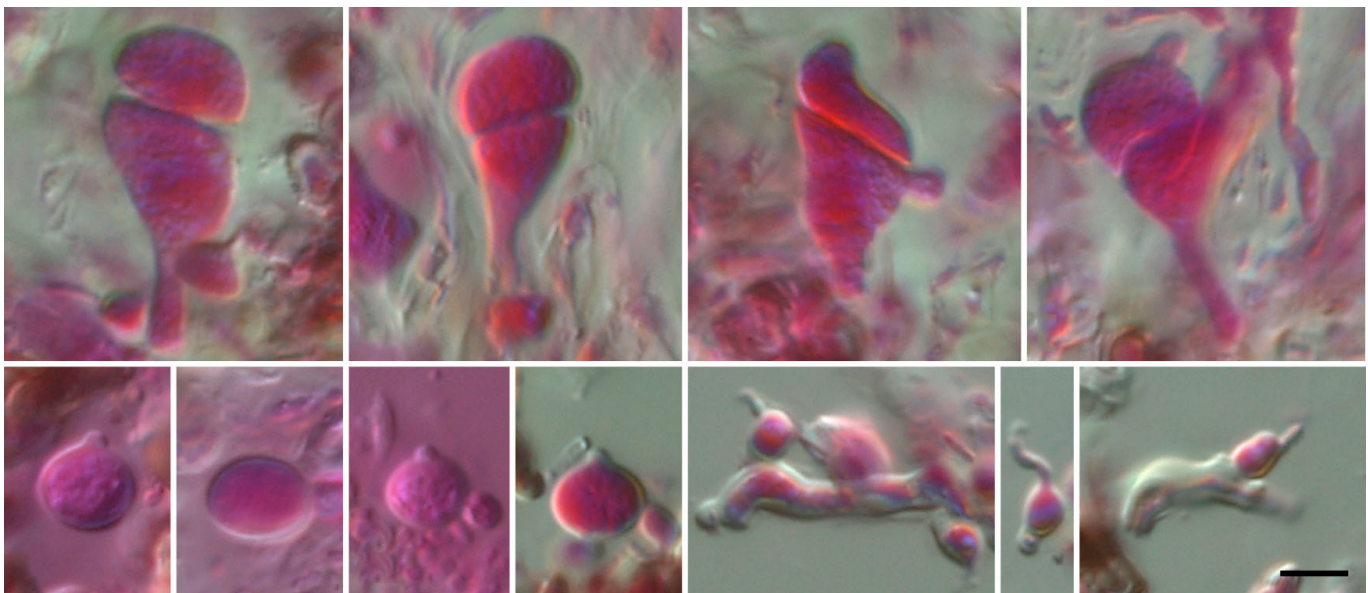
Tremella dirinariae Diederich, Millanes & Wedin

in Ariyawansa et al., *Fungal Diversity* 75: 239 (2015). **Type:** USA, Florida, Seminole Co., Little Big Econlockhatchee State Forest, along Florida Trail from entrance on Co. Rd. 426, 3.3 mi NE of Co. Rd. 419 in Oviedo, 28°41' N, 81°10' W, on *Liquidambar*, on *Dirinaria aegialita*, 10 Jan. 1996, R. C. Harris 37673 (NY – holotype; BR – isotype).

Basidiomata initially as black swellings on the host thallus, breaking through the cortex, then black, pulvinate,

often slightly taller than broad, strongly gelatinous, not gall-inducing, surface smooth to rugose, roundish to sometimes irregular in form, mainly 0.25–0.35(–1) mm diam., up to 0.3 mm tall. **Context hyphae** thick-walled, 2.2–3.5 µm diam., clamp connections not observed; haustoria present. **Hymenium** containing numerous clavate probasidia with a basal clamp. **Basidia**, when mature, 2-celled, with one transverse or oblique, exceptionally longitudinal septum, (15–)17–24 × 6.5–10(–12) µm (incl. stalk-like base), often with an attenuated stalk-like base; epibasidia 2.5–4 µm diam., up to 50 µm long. **Basidiospores** ellipsoid to subspherical, 6–8 × 5.5–6.5 µm. **Asexual stage:** ellipsoid conidia with a truncate base, 5–6.8 × 3–3.5 µm, observed in one specimen.

Notes. *Tremella purpurascens*, known from *Dirinaria purpurascens* in Florida, is distinguished by the larger, medium brown, resupinate basidiomata, 0.3–6 mm diam., c. 0.1 mm thick, the frequently longitudinally or obliquely septate, distinctly larger basidia, 16–30 × 10–17.5 µm, the much larger basidiospores, 8.5–10 × 7–9 µm, and the pres-



Tremella dirinariae, USA, Florida, holotype (modified from Ariyawansa et al. 2015). Basidia, basidiospores and haustoria. In phloxine. Scale bar: 5 µm.



Tremella dirinariae, USA, Florida, holotype. Basidiomata on the thallus of *Dirinaria aegialita*. Scale bar: 200 μ m.

ence of endospores developing in old basidia and basidiospores.

Ecology and host. On the thallus of *Dirinaria aegialita*.

Distribution. North America (USA: Florida), known only from the type locality.

Reference. Ariyawansa et al. 2015.

***Tremella emmanueliae* Diederich & Aptroot, sp. nov.**

Diagnosis: Characterized by the small, subspherical, pale brown, waxy-gelatinous basidiomata on the thallus of *Emmanuelia* species, 0.08–0.4 mm diam., or tuberculate and up to 1.2 mm diam., the elongate ellipsoid to claviform, mainly obliquely 1-septate basidia, (11.5–)14.5–26 \times 4.5–9 μ m, and the subspherical to ellipsoid basidiospores 5–6.5 \times 4.5–5.5 μ m.

Etymology: From *Emmanuelia*, the host lichen.

Type: Brazil, Minas Gerais, Catas Altas, Serra do Caraça, Parque Natural do Caraça, near Banho do Belchior, 20°06'S,

43°29'W, 1250 m, on dendriscocauloid cephalodia of corticolous *Emmanuelia ornata*, 17 Sept. 1997, A. Aptroot 41125 (BR – holotype; SP – isotype).

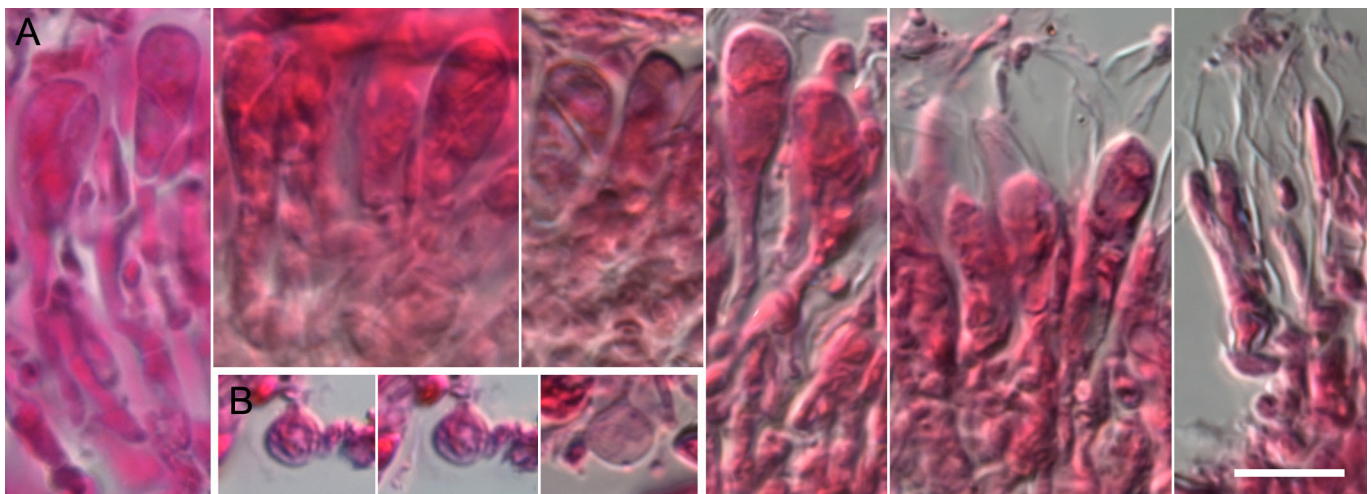
Mycobank: MB844657

Basidiomata superficial, pulvinate, subspherical, waxy-gelatinous, pale brown, 0.08–0.4 mm diam., later oft tuberculate and then up to 1.2 mm diam. **Context hyphae** thick-walled, 3–4.5 μ m diam.; subbasidial hyphae thick-walled, 2–3 μ m diam.; haustoria not observed. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, elongate ellipsoid to claviform, 2-celled, with an oblique septum, (11.5–)14.5–26 \times 4.5–9 μ m; epibasidia cylindrical, at least 20 μ m long. **Basidiospores** subspherical to ellipsoid, 5–6.5 \times 4.5–5.5 μ m. **Asexual stage** unknown.

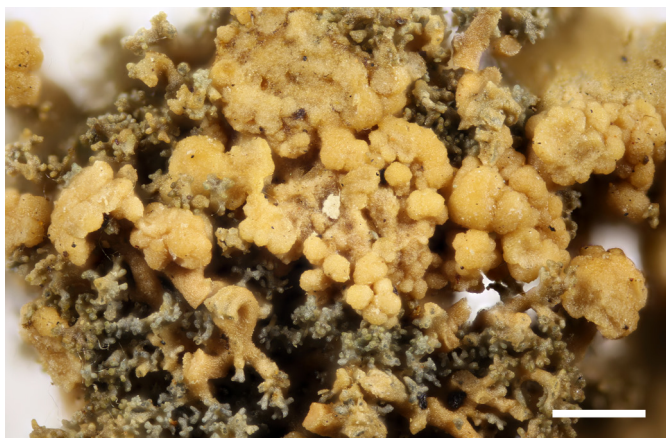
Notes. Macroscopically, this species resembles *Tremella leptogii* that differs by the 2–4-celled basidia and *T. stictae* that differs by the much shorter basidia, 10–16 \times 6–8.5 μ m. It is interesting to note that this species grows only on the dendriscocauloid cephalodia of the host, and never develops on the foliose green algal thallus. *Tremella stictae* has also been collected on independently living “*Dendriscocaulon*” thalli, but these are considered to belong to *Sticta*.

Ecology and hosts. On the dendriscocauloid cephalodia of corticolous *Emmanuelia ornata* and *E. cf. excisa*. Simon et al. (2020) reported such cephalodia from a single species, *E. ornata*. The host of Aptroot 41759 is a distinct species with much larger lobes, up to 10 mm broad, much larger cephalodia, and a medium to dark brown, well-delimited tomentum covering the lower surface, except the pale marginal zone; as it is sterile, we only tentatively attribute it to the poorly known *E. excisa*.

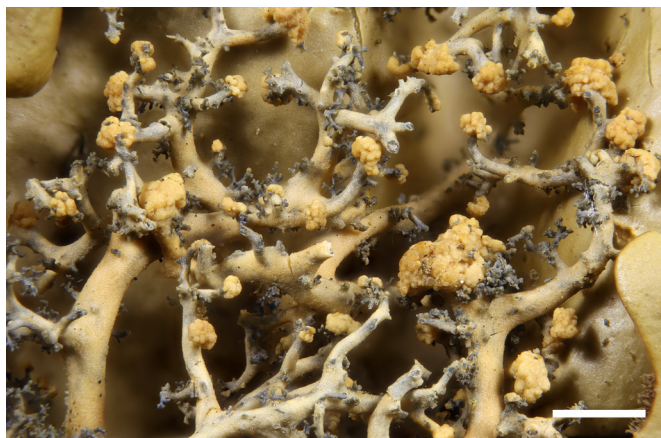
Distribution. South America (Brazil).



Tremella emmanueliae, Brazil, holotype. A, Basidia. B, Basidiospores. In phloxine. Scale bar: 10 μ m.



Tremella emmanueliae, Brazil, holotype. Basidiomata on the dendriscocauloid cephalodia of *Emmanuelia ornata*. Scale bar: 500 μ m.



Tremella emmanueliae, Brazil, Aptroot 41759. Basidiomata on the dendriscocauloid cephalodia of *Emmanuelia* cf. *excisa*. Scale bar: 1 mm.



Tremella emmanueliae

Additional specimen examined. Brazil: São Paulo, Serra da Mantiqueira, Campos do Jordão, Parque Estadual de Campos do Jordão, 22°40'S, 45°30'W, 1500 m, in *Araucaria* forest, on dendriscocauloid cephalodia of corticolous *Emmanuelia* cf. *excisa*, 1997, Aptroot 41759 (BR, SP).

***Tremella endosporogena* J. C. Zamora, Millanes, V. J. Rico & Pérez-Ortega**

in Zamora et al., *Mycologia* 108: 386 (2016). *Type*: Spain, Comunidad de Madrid, Madrid, Collado Villalba, 40°39'12"N, 4°00'01"W, 890 m, in *Lecanora carpinea* apothecia, on *Prunus* sp. branches, 31 Dec. 2010, J. C. Zamora & B. Zamora (MAF-Lich 19742 – holotype).

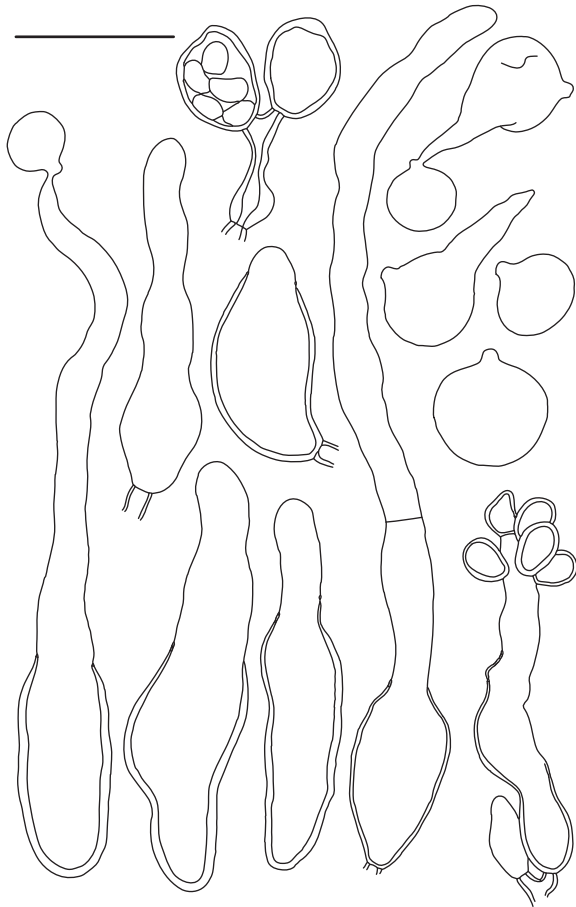
Basidiomata growing in host apothecia, first inconspicuous, soon inducing the formation of convex, waxy to gelatinous, cream-colored to yellowish or greenish galls, 0.2–1.3 mm diam. *Context hyphae* thick-walled, 2–5 μ m diam., clampless; subbasidial hyphae thick-walled; haustoria frequent. *Hymenium* a mixture of probasidia, mature basidia and conidiogenous cells; probasidia often thick-walled, claviform to pyriform. *Basidia*, when mature, 1-celled, cylindrical to claviform or broadly fusiform, sessile or with

a short stalk-like base up to 8 μ m long, (15–)17–40(–45) \times 9.5–17(–19) μ m (including stalk-like base); epibasidia subcylindrical, 70–130 \times 5–8 μ m, often poorly delimited from the basidial part. *Basidiospores* subspherical to rarely broadly ellipsoid, 9.5–15.5 \times 10–16 μ m, occasionally producing secondary ballistoconidia (similar to small basidiospores). *Asexual stage*: Thick-walled, vessel-like conidiogenous cells, 12–27(–41) \times 7–12(–17) μ m, producing thick-walled conidia by apical budding, 4–7.5 \times (2.5–)3–5 μ m; in addition, old basidia sometimes internally produce ‘endospores’, (4.5–)5–9(–10) \times (2.5–)3–6 μ m, similar to conidia from conidiogenous cells. [Modified from Zamora et al. 2016.]

Notes. This is one of the very few known heterobasidiomycetes with 1-cellular basidia. The most similar taxon, *Heteroacanthella ellipsospora*, grows on the same host species, but is distinguished by the acanthoid, stalked basidia,



Tremella endosporogena, Spain, holotype. Basidiomata in the apothecia of *Lecanora carpinea*. Photo: J. C. Zamora. Scale bar: 500 μ m.



Tremella endosporogena, Spain, holotype (modified from Zamora et al. 2016). Basidia, basidiospores, old basidium filled with endospores, and conidiogenous cell with conidia. Scale bar: 10 μ m.



Tremella endosporogena

ellipsoid basidiospores with a refractive apiculus, clamped hyphae and the absence of conidiogenous cells. *Tremella monospora*, growing on *Leptogium*, is distinguished by the smaller basidia with a long stalk and the smaller basidiospores, $5\text{--}7 \times 4.5\text{--}6 \mu\text{m}$. None of these two species produce endospores.

Ecology and host. In apothecia of corticolous *Lecanora carpinea*.

Distribution. Europe (Spain).

Reference. Zamora et al. 2016.

Tremella ertzii Diederich, sp. nov.

Diagnosis: Characterized by the subspherical, pale brown, waxy-gelatinous basidiomata on the isidia of *Pertusaria* sp., 0.25–0.55 mm diam., the very long and narrow, elongate claviform to subcylindrical, transversely 1-septate basidia, $25\text{--}45 \times 3.5\text{--}6.5 \mu\text{m}$, and the medium-sized basidiospores, $5\text{--}8.5 \times 5\text{--}6.5 \mu\text{m}$.

Etymology: Named after Damien Ertz, lichenologist in Meise Botanical Garden, Belgium.

Type: Japan, Honshu, Tochigi Prefecture, Shimotsuke Province, Nikko City administrative region, Nikko National Park, 5.3 km ESE of Yumoto village (Yumoto Onsen), the Utsunomiya University forest on the S slope of Mt. Taro, NE of where dirt road ends, $36^{\circ}47'57''\text{N}$, $139^{\circ}28'58''\text{E}$, 1620 m, oldgrowth mixed coniferous/deciduous forest, on base of a large conifer tree (cf. *Abies*), on *Pertusaria* sp., 29 Sept. 2019, D. Ertz 24543, G. Thor, M. Grube, C. Printzen & B. Kanz (BR – holotype).

Mycobank: MB844658

Basidiomata superficial, subspherical, waxy-gelatinous, pale brown, surface slightly shiny, 0.25–0.55 mm diam. **Context hyphae** not observed; subbasidial hyphae thick-walled, 3–4 μm diam.; haustoria not observed. **Hymenium** containing numerous claviform probasidia with an indistinct basal clamps. **Basidia**, when mature, elongate claviform to subcylindrical, broadest in the upper third, transversely 1-septate, upper cell shorter than lower cell, $25\text{--}45 \times 3.5\text{--}6.5 \mu\text{m}$, upper cell 9–16 μm long; epibasidia cylindrical, 2–3.5 μm thick, 25–31 μm long. **Basidiospores** shortly ellipsoid, $5\text{--}8.5 \times 5\text{--}6.5 \mu\text{m}$. **Asterosporidia** with 3–4 arms observed in specimen Scheidegger.

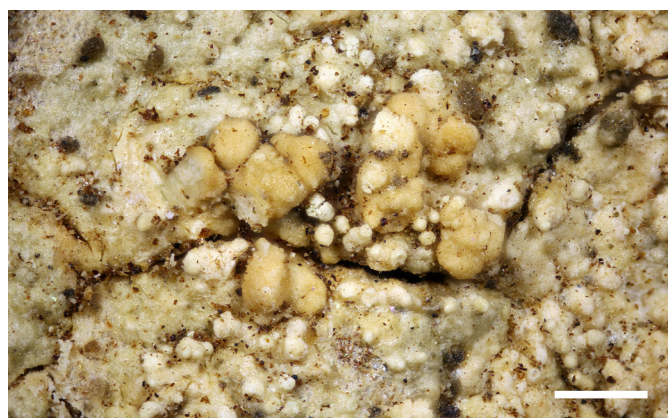
Notes. This species is remarkable by the particularly long and narrow basidia. Similar basidia are known from intrahymenial species, such as *Tremella rhizocarpicola*, as an adaptation to the development between host asci, but even then, they are usually broader. Although the holotype is beautiful and richly fertile, the subbasidial hyphae and the presence of clamp connections were difficult to examine. The new species is dedicated to my friend Damien Ertz, an outstanding lichenologist, and collector of the new species.



Tremella ertzii



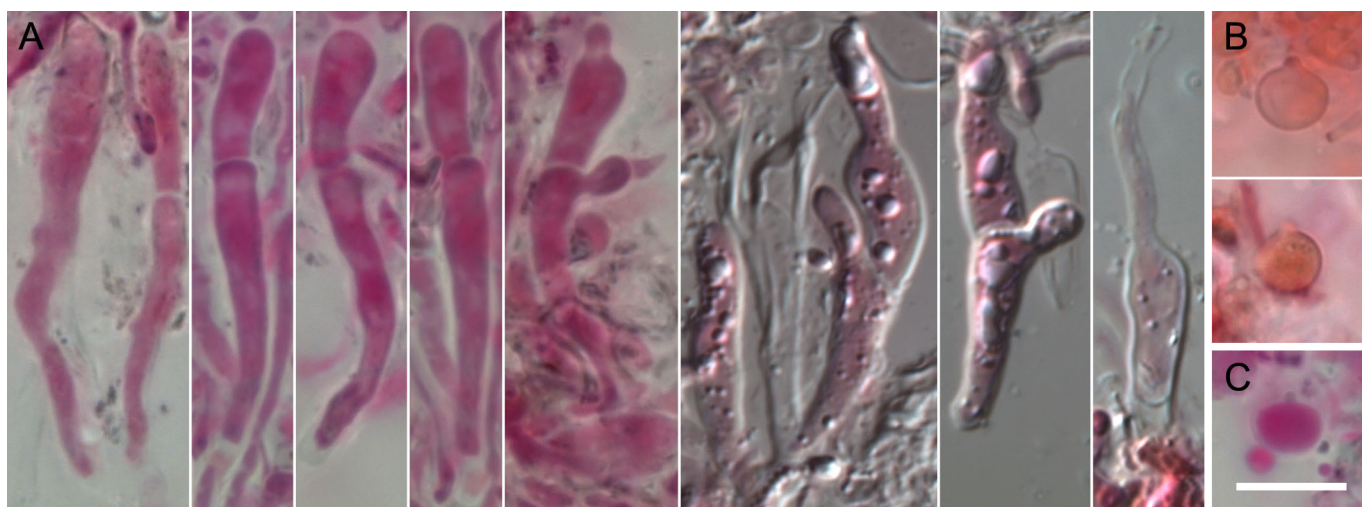
Tremella ertzii, Japan, holotype. Basidiomata on the isidia of an unidentified *Pertusaria* species. Scale bar: 500 μ m.



Tremella ertzii, Japan, Scheidegger. Basidiomata on the thallus of *Pertusaria* sp. Scale bar: 500 μ m.



Tremella ertzii, Mauritius, Diederich 18604. Basidioma on the thallus of *Pertusaria* sp. Scale bar: 500 μ m.



Tremella ertzii, Japan, holotype. A, Basidia. B–C, Basidiospores. A, C, in phloxine, B, in ammoniacal Congo red. Scale bar: 10 μ m.

Ecology and hosts. On the isidia of one or several unidentified corticolous *Pertusaria* species.

Distribution. Indian Ocean (Mauritius) and Asia (Japan).

Additional specimen examined (both on a corticolous, isidiate *Pertusaria*). **Japan:** Honchu, Mt Fuji, Mt Fuji Subaru Line, 5th station, 35°22'N, 138°44'E, 1993, Scheidegger (herb Scheidegger). **Mauritius:** Plaines Wilhems District, Black River Gorges National Park, Le Pétrin, heathland NW of Pétrin Information Centre, 20.4081°S, 57.4694°E, 675 m, 2016, Diederich 18604 (MAU).

Tremella everniae Diederich

Bibl. Lichenol. 61: 77 (1996). **Type:** China, Sichuan prov., Chengdu ['Sikang, Kangting (Tachienlu) distr., Yara], alt. 3800 m, on *Larix*, on *Evernia mesomorpha*, 18 Aug. 1934, H. Smith (UPS – holotype, BR – isotype).

Basidiomata resupinate over bullate gall-like deformations of the host reaching 15 mm diam., initially concolorous with the host thallus, becoming brown at maturity. **Context hyphae** thick-walled, 1.5–4 µm diam. or thin-walled, 1–1.5 µm diam., clamps not observed; haustoria frequent. **Hymenium** containing numerous subspherical probasidia with a basal clamp. **Basidia**, when mature, subspherical, with 1–3 longitudinal septa, 9–14 × 9–13 µm; epibasidia 1–3 µm diam., at least 40 µm long. **Basidiospores** subglobose, 5–7 × 5–6 µm. **Asexual stage** unknown.

Notes. This species is characterized by the very large bullate gall-like deformations on the host. Diederich (1996) reported a Canadian specimen from Hudson Bay, Fort George, and interpreted this as in Ontario. However, this refers to the 'Hudson's Bay Company, Fort George', located in Prince George, British Columbia.

Ecology and host. On the thallus of *Evernia mesomorpha*, gall-inducing. Reports on *Evernia prunastri* are considered as erroneous. Reports on *E. esorediosa* need verification.



Tremella everniae, China, isotype. Bullate basidiomatal gall on the thallus of *Evernia mesomorpha*. Scale bar: 2 mm.

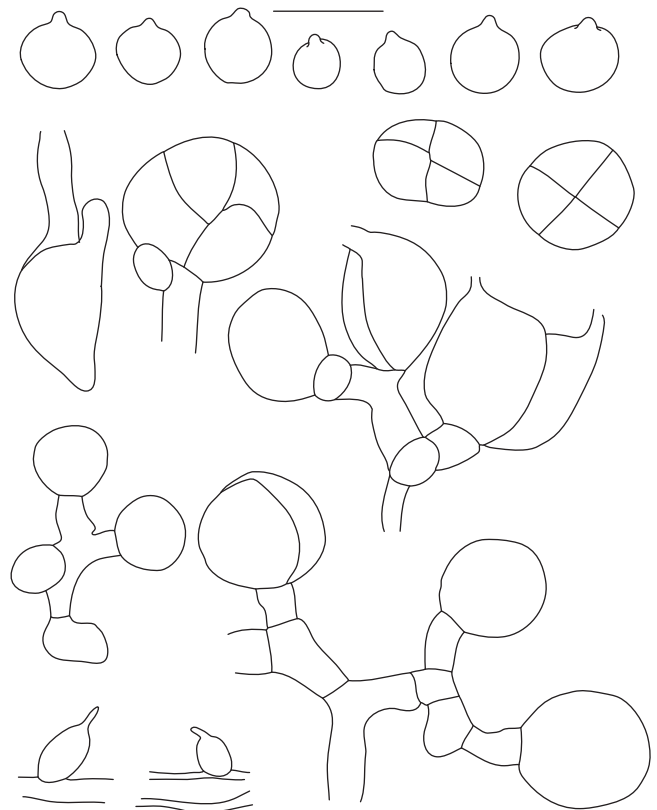


Tremella everniae

Distribution. North America (Canada: Alberta, British Columbia, New Brunswick, Ontario, Quebec; USA: Maine, Minnesota, New Hampshire, New York, Vermont) and Asia (Bhutan; China; India; Mongolia; Russia).

Additional specimen examined. USA: Minnesota: Superior National Forest, c. 12.54 km NW Taconite Harbor and 18.8 km N Little Marais, near entrance of Nine Mile Lake Campground, 47.5781°N, 91.0737°W, on *Evernia mesomorpha*, 2018, Gockman 5557 (BR).

References. Diederich 1996 [Brinker 2020, Diederich 2003, Joshi et al. 2018, Millanes et al. 2011, Zhurbenko & Ohmura 2019, Zhurbenko & Verzhinina 2014, Zhurbenko & Zhdanov 2013, Zhurbenko et al. 2019].



Tremella everniae, China, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.

Tremella flakusii Diederich, Millanes, Rodr. Flakus & Aptroot, sp. nov.

Diagnosis: Characterized by the pale to dark reddish brown, waxy-gelatinous, subspherical to rarely tuberculate basidiomata with a constricted base, 0.2–2.8 mm diam., on the thallus of *Crocodia* species, the mainly obliquely 1-septate basidia, $17\text{--}28 \times 11.5\text{--}18\ \mu\text{m}$ (without stalk), often with a stalk-like base, $8\text{--}23\ \mu\text{m}$ long, and the large, shortly ellipsoid basidiospores, $9.5\text{--}13.5 \times 7.5\text{--}11.5\ \mu\text{m}$.

Etymology: Named after Adam Flakus, collector of the type specimen.

Type: Bolivia, Dept. Cochabamba, Prov. Carrasco, Parque Nacional Carrasco, near Río Batea Mayu close to Monte Punku, $17^\circ 31' 33''\text{S}$, $65^\circ 16' 21''\text{W}$, 2430 m, lower montane Yungas forest, on *Crocodia clathrata*, 28 Nov. 2014, A. Flakus 25804 (KRAM – holotype; BR, LPB – isotypes).

Mycobank: MB844659

Basidiomata growing on the host thallus, pale brown to dark reddish brown, waxy-gelatinous, subspherical, later occasionally tuberculate, with a constricted base, 0.2–2.8 mm diam. *Context hyphae* and subbasidial hyphae thin-walled, $3\text{--}4\ \mu\text{m}$ diam., without clamps; haustoria not seen. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, ellipsoid, rarely subspherical or elongate ellipsoid, base often attenuated or with a short to long stalk-like base, 1-septate, septum oblique, rarely longitudinal or transverse, upper part (without stalk) $17\text{--}28 \times 11.5\text{--}18\ \mu\text{m}$, stalk $8\text{--}23(34)\ \mu\text{m}$ long; epibasidia subcylindrical, $35\text{--}50\ \mu\text{m}$ long. *Basidiospores* shortly ellipsoid, $9.5\text{--}13.5 \times 7.5\text{--}11.5\ \mu\text{m}$. *Asexual stage* not observed.

Notes. This fungus is distinguished from the other *Tremella* species growing on *Lobariaceae* hosts by the particularly large basidiospores and by the host choice, *Crocodia* species.

It is our pleasure to dedicate this new species to our friend Adam Flakus, Polish lichenologist, who contributed very significantly to the knowledge of lichenized and lichenicolous



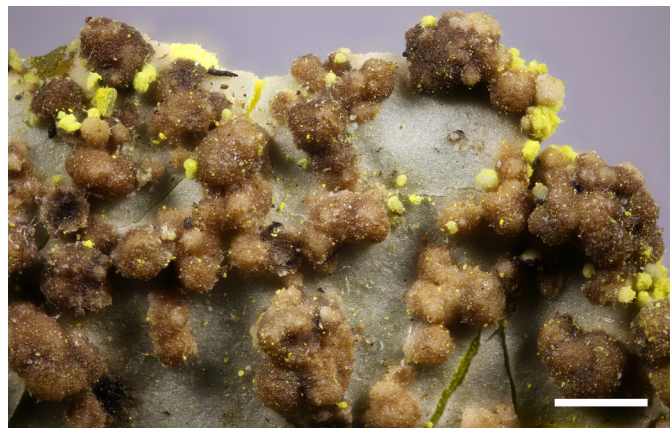
Tremella flakusii

fungi of Bolivia besides his immeasurable contribution to the foundation of the lichenological studies in this country.

Ecology and hosts. On the thallus of *Crocodia clathrata* and *C. aurata*.

Distribution. South America (Bolivia; Brazil).

Additional specimen examined. **Brazil:** Paraná, Quatro Barras, on *Crocodia aurata*, 2022, Aptroot 84597 (BR, CGMS).



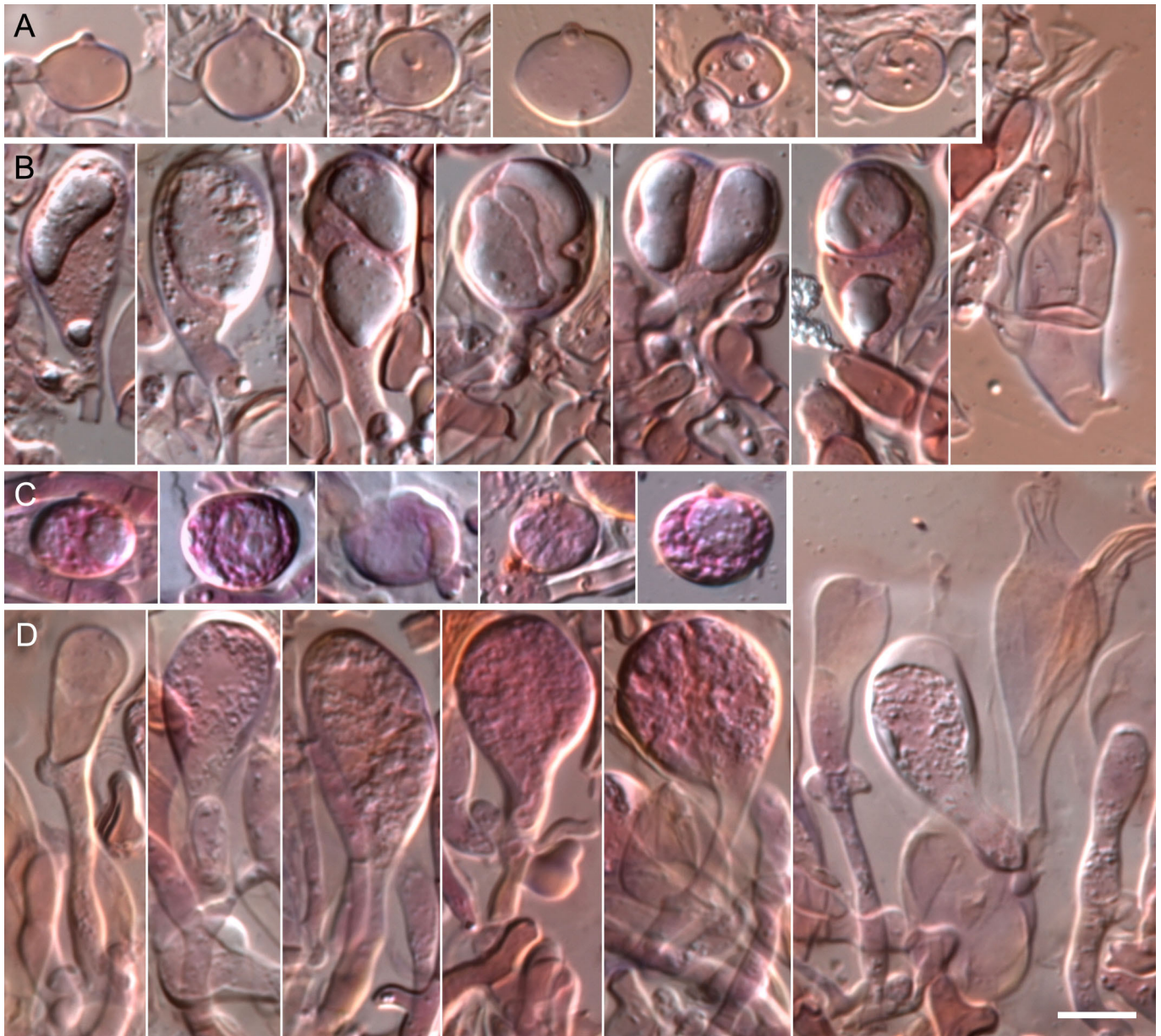
Tremella flakusii, Brazil, Aptroot 84597. Basidiomata on the thallus of *Crocodia aurata*. Scale bar: 500 μm .



Tremella flakusii, Bolivia, holotype. Pale brown basidioma on the thallus of *Crocodia clathrata*. Scale bar: 1 mm.



Tremella flakusii, Bolivia, holotype. Dark brown basidioma on the thallus of *Crocodia clathrata*. Scale bar: 1 mm.



Tremella flakusii. A–B, Bolivia, holotype, C–D, Aptroot 84597. A, C, Basidiospores. B, D, Basidia in various stages of development. In ammoniacal Congo red. Scale bar: 10 μ m.

Tremella flavoparmeliae Diederich, Hodkinson & Millanes, sp. nov.

Diagnosis: Characterized by the large, brownish, strongly convex, bullate galls up to 10 mm diam. on the thallus of *Flavoparmelia caperata*, the subspherical to ellipsoid, longitudinally 1-septate basidia, with cells longer than the septum, $16\text{--}22 \times 11\text{--}17.5 \mu\text{m}$, and the large, subspherical to shortly ellipsoid basidiospores $8.5\text{--}11.5(-13) \times 7.5\text{--}11 \mu\text{m}$.

Etymology: From *Flavoparmelia*, the host lichen.

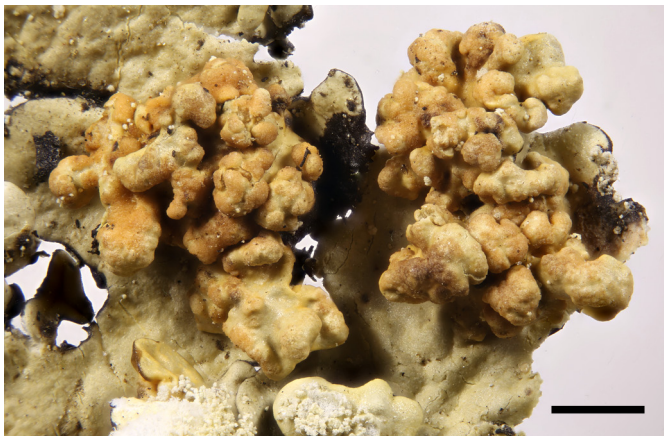
Type: USA, North Carolina, Macon Co., Highlands, Highlands Biological Station, next to New Duplex Building, $35^{\circ}03'08''\text{N}$,

$83^{\circ}11'17''\text{W}$, 1180 m, on *Flavoparmelia caperata*, 27 Sept. 2009, B. Hodkinson 11027 (NY – holotype; BR – isotype).

= *Tremella* sp. 7, in Diederich, *Op. Phil.* 4: 20 (2007).

Mycobank: MB844660

Basidiomata absent; fungus inducing the formation of brownish, strongly convex and bullate galls on the host thallus with a smooth surface, up to 10 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, $2.5\text{--}4 \mu\text{m}$ diam.; haustoria not observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to el-



Tremella flavoparmeliae, USA, North Carolina, holotype. Basidiomatal galls on the thallus of *Flavoparmelia caperata*. Scale bar: 1 mm.

lipsoïd, with 1 longitudinal septum, individual cells often longer than the septum, $16\text{--}22 \times 11\text{--}17.5\ \mu\text{m}$; epibasidia cylindrical, $20\text{--}40\ \mu\text{m}$ long. *Basidiospores* subspherical to shortly ellipsoid, $8.5\text{--}11.5\text{--}(13) \times 7.5\text{--}11\ \mu\text{m}$. *Asexual stage*: asteroconidia frequent, arms $4\text{--}7\ \mu\text{m}$; conidiogenous cells $15\text{--}10 \times 1\text{--}2.5\ \mu\text{m}$.

Notes. The galls induced by this species strongly resemble those of *Tremella everniae*, a species confined to *Evernia mesomorpha*. It differs from that species by the much larger and constantly 1-septate basidia (vs 2–4-celled basidia, $9\text{--}14 \times 9\text{--}13\ \mu\text{m}$) with cells that become longer than the septum, and from many lichenicolous species by the large basidiospores.

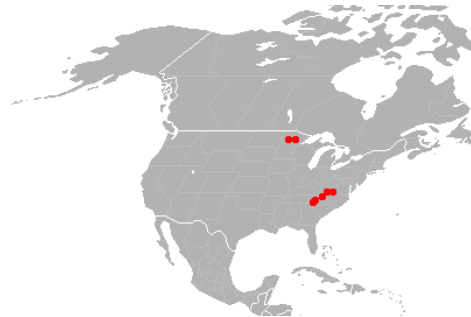
Although the host *Flavoparmelia caperata* is particularly common in Europe and other parts of the world, and the galls induced by the fungus are large and eye-catching, it is astonishing that the species is known only from the USA.

Ecology and host. On the thallus of *Flavoparmelia caperata*, gall-inducing.

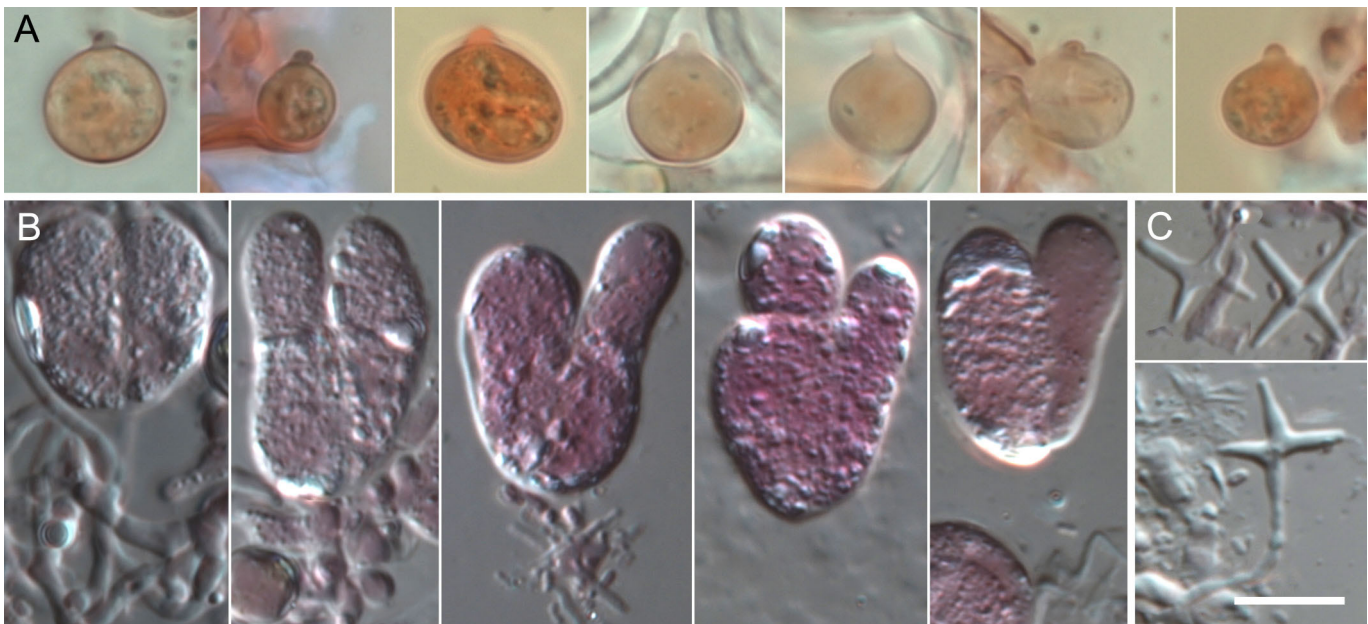
Distribution. North America (USA: Minnesota, North Carolina, Virginia).

Additional specimens examined (all on *Flavoparmelia caperata*).

USA: Minnesota: Savanna State Forest, c. 15.26 km SE of Jacobson and 16.05 km W of Floodwood, 46.9028°N , 93.1269°W , on *Larix*, 2018, Gockman 5667 (BR); Clearwater Co., 4.8 km N of Itasca State Park, $47^\circ17'30''\text{N}$, $95^\circ12'40''\text{W}$, 137 m, on *Pinus*, 1976, Wetmore 26471, *Lich. Exs.* 86 (BR). North Carolina: Ashe Co., Blue Ridge Parkway, mile 261 just N of Rte 16, Horse Gap, 1982, Reed 143781A (NY, BR); Graham Co., Nantahala National Forest, Oak Knob, c. 0.4 mi N of parking area of Huckleberry Knob Trailhead on Cheroke Skyway (NC 143), $35^\circ19'03''\text{N}$,



Tremella flavoparmeliae



Tremella flavoparmeliae, USA, North Carolina, holotype. A, Basidiospores. B, Basidia. C, Asteroconidia, one attached to conidiogenous cell. A, in ammoniacal Congo red, B–C, in phloxine. Scale bar: $10\ \mu\text{m}$.

83°59'30"W, 5400 ft, 2016, Harris 61055 (NY); Jackson Co., Nantahala National Forest, S slope of Piney Ridge Knob, along Forest Service road extension of Moses Creek Road, 11.2 mi ENE of Moses Creek Missionary Baptist Church, 35°21'N, 83°06'W, 1325 m, 1998, Buck 34936 (NY, BR); Swain Co., Nantahala National Forest, Cheoah Bald, 2.5 mi SE of Locust Cove Gap, along Appalachian Trail, c. 6.5 mi SE of NC143 at Stecoah Gap, 35°19'32"N, 83°40'50"W, 4912 ft, on *Azalea*, 2014, Lendemer 43694 (NY). *Virginia*: Grayson Co., Comer's Creek Falls, on Rte 741, 0.8 km W of Rte 16, Mount Rogers National Recreation Area, Jefferson National Forest, 36°42'41"N, 81°28'27"W, 3450 ft, mixed deciduous ravine forest, 2008, Hodkinson 9019 (DUKE); Wythe Co., 3.5 km S of intersection with Pope Rd., just SW of Collins Cover Horse Camp, near Raven Cliff Karst Area, Mount Rogers National Recreation Area, Jefferson National Forest, 36°48'26"N, 81°02'54"W, 2400 ft, 2008, Hodkinson 9209, 9227, 9248, 9257 (DUKE).

References. Diederich 2007 as *Tremella* sp. 7 [Hodkinson 2010].

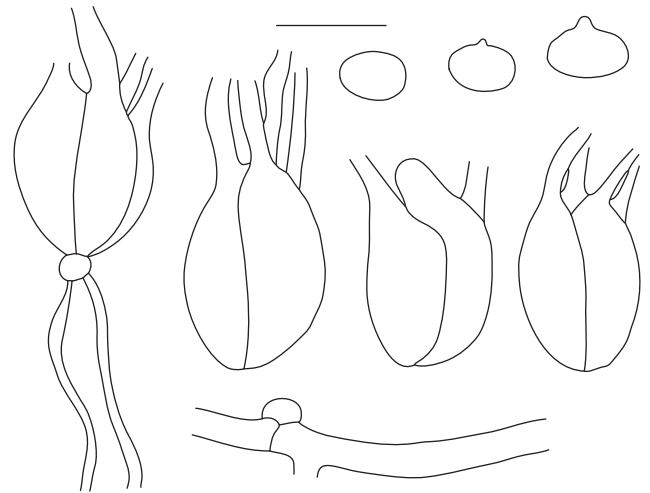
Tremella graphidastrae Diederich

Bibl. Lichenol. 61: 80 (1996). *Type:* Papua New Guinea, Madang Province, Huon Peninsula, Finisterre range, Yupna valley, Teptep village, 5°57' S, 146°33' E, alt. 2500 m, in a disturbed mountain forest, on a very old tree, on *Graphidastra multiformis*, 30 July 1992, P. Diederich 10990 (LG – holotype; BR – isotype).

Basidiomata applanate to pulvinate, immersed to superficial, discoid or irregular, often confluent, gelatinous, orange-brown, 0.1–0.5 mm diam. *Context hyphae* thin-walled, either 3–3.5 µm diam., with clamps, or 1.5–2.5 µm diam., without clamps; subbasidial hyphae thick-walled, 3–5.5 µm diam.; haustoria not observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, ellipsoid, 4-celled, with longitudinal septa, 14.5–17 × 11–12.5 µm; epibasidia at least 30 µm long. *Basidiospores* ellipsoid, 5.5–7 × 3.5–5 µm. *Asexual stage* unknown.



Tremella graphidastrae, Papua New Guinea, isotype. Basidiomata on *Graphidastra multiformis*. Scale bar: 500 µm.



Tremella graphidastrae, Papua New Guinea, holotype (modified from Diederich 1996). Basidia, basidiospores and hypha with clamp connection. Scale bar: 10 µm.



Tremella graphidastrae

Notes. *Tremella graphidastrae* is distinguished from the other species of *Tremella* with 4-celled basidia and not inducing gall formation by the small, brownish, often applanate basidiomata.

Ecology and host. On the thallus and apothecia of *Graphidastra multiformis*.

Distribution. Oceania (Papua New Guinea), known only from the type locality.

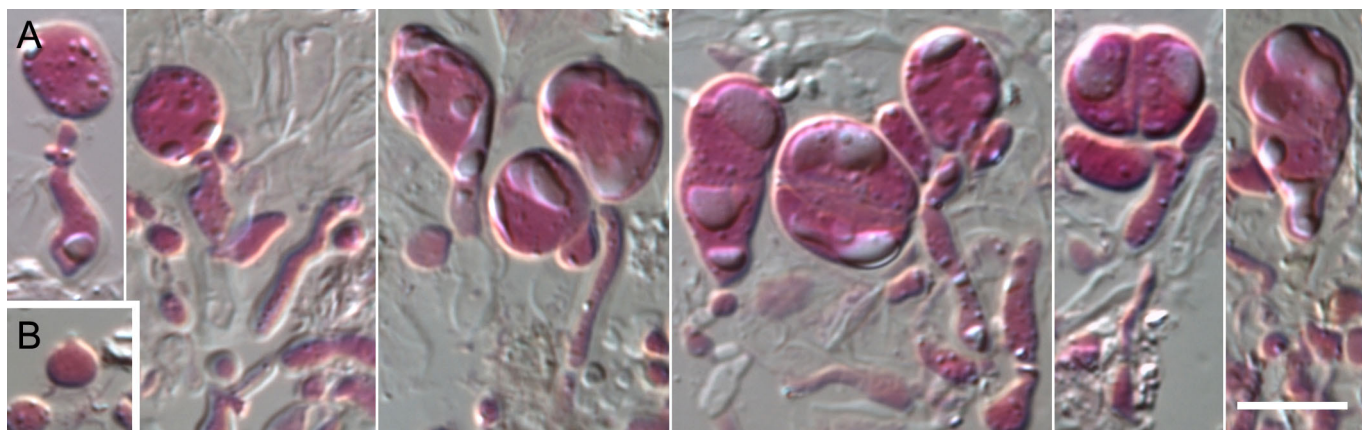
Reference. Diederich 1996.

Tremella graphidicola Diederich & Common, sp. nov.

Diagnosis: Characterized by the applanate to convex, brown, waxy-gelatinous basidiomata on the thallus of *Graphis* species, 0.1–0.5 mm diam., the relatively small, 2-celled basidia with a longitudinal, oblique or transverse septum, 8–16.5 × 5–10.5 µm, and the small basidiospores, c. 4.5–5 × 4–4.5 µm.

Etymology: From *Graphis*, the host lichen, and *incola*, dweller.

Type: USA, South Carolina, Charleston Co., Francis Marion National Forest, Little Wambaw Swamp at E end of Forest Service Road 217B, 0.9 mi NW of Forest Service Road 217 (Elden Rd), 33°04'26"N, 79°36'39"W, 25 m, swamp forest of *Taxodium*, and mixed hardwoods (*Nyssa*, *Ilex*, *Myrica*, *Quercus*), on the thallus of *Graphis* sp., 1 Dec. 2013, R. C. Harris 59456A (NY – holotype).



Tremella graphidicola, USA, South Carolina, holotype. A, Basidia. B, Basidiospore. In phloxine. Scale bar: 10 µm.

Mycobank: MB844661

Basidiomata appanate to convex, waxy-gelatinous, brown, 0.1–0.5 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2–3.5 µm diam.; haustoria present,

basal clamp not observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia, basal clamps not observed. *Basidia*, when mature, ellipsoid, 2-celled, with a longitudinal, oblique or transverse septum, 8–16.5(–19) × 5–10.5 µm; epibasidia cylindrical, 2.5–3.5 µm thick, at least 25 µm long. *Basidiospores* shortly ellipsoid, c. 4.5–5 × 4–4.5 µm. *Asexual stage* unknown.

Notes. *Tremella graphidis*, growing on the same host genus *Graphis*, is distinguished by the intrahymenial growth and



Tremella graphidicola, USA, South Carolina, holotype. Basidiomata on the thallus of *Graphis* sp. Scale bar: 500 µm.



Tremella graphidicola



Tremella graphidicola, USA, Florida, Common 9482C. Basidiomata on the thallus of *Graphis assimilis*. Scale bar: 500 µm.



Tremella graphidicola, USA, North Carolina, Harris 60318. Basidiomata on the thallus of *Graphis* sp. Scale bar: 500 µm.

the very long, transversely 1-septate, cylindrical basidia, $30\text{--}38 \times 4\text{--}5(-5.5) \mu\text{m}$. It is interesting to note that two distinct *Tremella* species are known from *Graphis* in Florida, but occupying two different ecological niches, the host thallus vs the host hymenium. Only a single, very small basidiospore has been observed in the new species.

Ecology and hosts. On the thallus of *Graphis* species, incl. *G. assimilis*.

Distribution. North America (USA: Florida, North Carolina, South Carolina).

Additional specimens examined. USA: Florida: Hillsborough Co., Hillsborough River State Park, Florida Trail, 28.149°N , 82.235°W , on *Graphis assimilis*, 2011, Common 9482C (BR). North Carolina: Hyde Co., Alligator River National Wildlife Refuge, along Chip Road 2 mi SW of jct with Whipping Creek Road, $35^{\circ}38'40''\text{N}$, $75^{\circ}58'42''\text{W}$, 1 m, on *Gordonia*, on *Graphis* sp. (TLC: traces of norstictic acid), 2014, Harris 60318 (NY).

***Tremella graphidis* Diederich, Millanes, Wedin & Common**

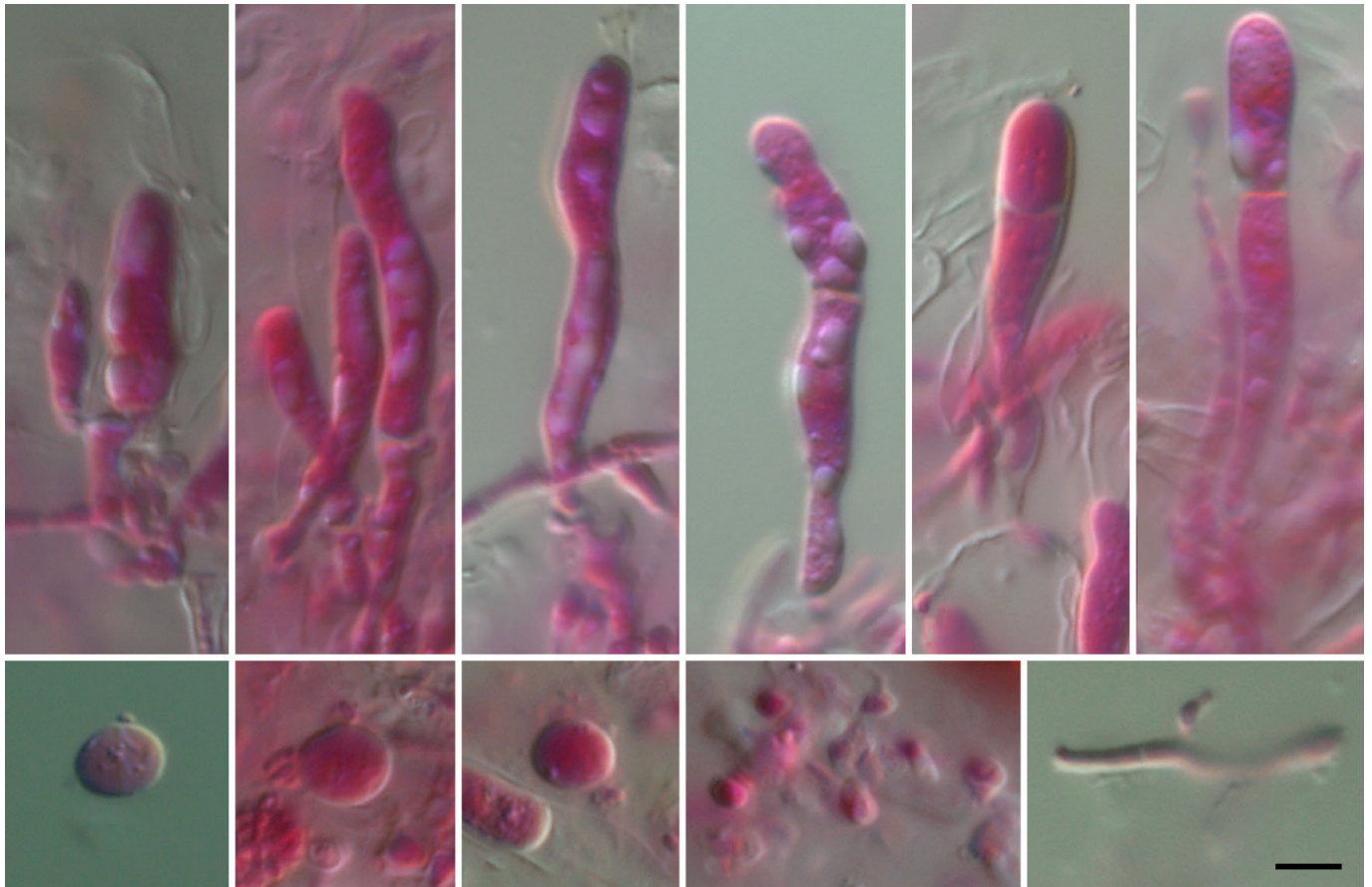
in Ariyawansa et al., *Fungal Diversity* 75: 242 (2015). *Type:* USA, Florida, Collier Co., Fakahatchee Strand State Preserve, trail N of Boardwalk, $25^{\circ}56.51' \text{N}$, $81^{\circ}28.16' \text{W}$, on *Graphis as-*



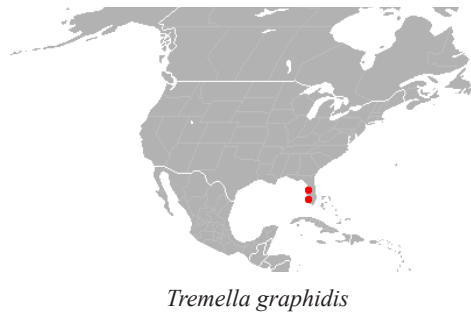
Tremella graphidis, USA, Florida, holotype. Basidioma in the hymenium of *Graphis*. Scale bar: 200 μm .

similis and *G. caesiella*, 11 Nov. 2011, R. Common 9434B (BR – holotype; S – isotype).

Basidiomata developing within the host hymenium, strongly enlarging the width of the initially narrowly lirelliform host apothecia, pale pinkish to brown, strongly gelatinous, surface rather smooth, elongate, up to $2(-3) \times 0.25 \text{ mm}$.



Tremella graphidis, USA, Florida, holotype (modified from Ariyawansa et al. 2015). Basidia, basidiospores and haustoria. In phloxine. Scale bar: 5 μm .



Context hyphae thin-walled, 1.5–2.5 µm diam., clamp connections not observed; haustoria present. Hymenium containing numerous narrowly clavate to cylindrical probasidia with a basal clamp. *Basidia*, when mature, narrowly and elongate cylindrical, 2-celled, with one transverse septum in the upper third or quarter, not or slightly constricted at the septum, 30–38 × 4–5(–5.5) µm (excl. epibasidia), without a stalk-like base; epibasidia subcylindrical, reaching at least 40 µm in length. *Basidiospores* broadly ellipsoid, 6–7 × 5–6 µm. *Asexual stage* unknown.

Notes. Contrary to *Tremella graphidicola*, this species grows intrahymenially in apothecia of several *Graphis* species. It is further distinguished from most lichenicolous species by the very long and slender basidia.

Ecology and hosts. In the hymenium of *Graphis assimilis*, *G. caesiella*, *G. cupei* and *G. cf. desquamescens*, distinctly enlarging the width of the host ascomata and gradually replacing the host hymenium.

Distribution. North America (USA: Florida).

References. Ariyawansa et al. 2015 [Diederich et al. 2019].

Tremella haematommatis Diederich

Bibl. Lichenol. 61: 82 (1996). *Type:* USA, Louisiana, Mississippi Delta, Pointe à la Hache, on *Haematomma persoonii*, 5 June 1976, E. Sérusiaux 1713 (LG – holotype; BR – isotype).

Basidiomata waxy-gelatinous, pale, amber-coloured, convex, often irregular in form, growing on the thallus, between the apothecia or on the hymenium of the host, on the hymenium appearing at first as reddish convex swellings, becoming superficial and amber-coloured, 0.1–0.8 mm diam. *Context hyphae* thin-walled, 1–2.5 µm diam., clamp connections not observed; haustoria frequent. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, 4-celled, with longitudinal or oblique septa, not or slightly stalked, 15–36 × 11–20 µm; epibasidia subcylindrical, 4–6 µm thick, 30–42 µm long. *Basidiospores* subspherical, 7–10 × 6.5–9.5 µm. *Asexual stage* unknown.

Notes. This species is rather well characterized by the amber-coloured basidiomata arising from the host apothecial

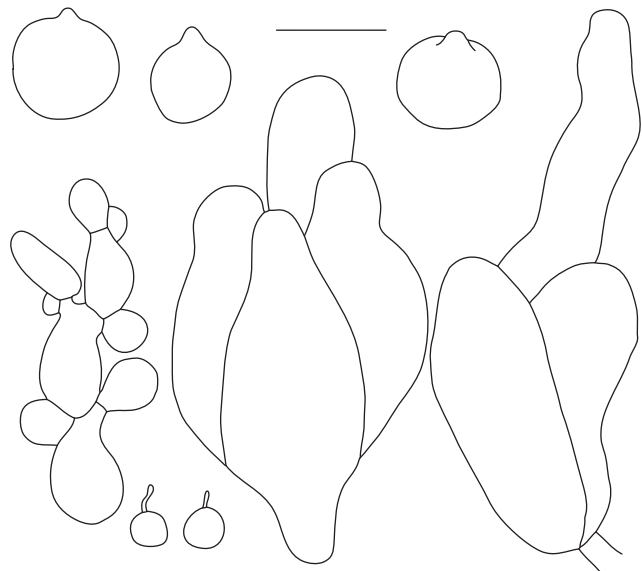


Tremella haematommatis, USA, isotype. Basidiomata on *Haematomma persoonii*. Scale bar: 500 µm.

disk or margin, eventually spreading between apothecia, the relatively large, 4-celled basidia and the large basidiospores. It may be confined to *Haematomma persoonii*. A recent record from Navarino Island in S Chile on a different host, *H. nothofagi*, with similar basidiomata but immature basidia (Etayo et al. 2021) is provisionally accepted here.

Ecology and hosts. On the corticolous thallus and apothecia of *Haematomma persoonii* (named *H. puniceum* in Diederich 1996), also reported from *H. nothofagi*.

Distribution. North America (Mexico: Baja California Sur; USA: Florida, Louisiana), also reported from South America (Chile: Navarino Island).



Tremella haematommatis, USA, holotype, except probasidia: USA, Sérusiaux 1750 (modified from Diederich 1996). Probasidia with clamp connections, mature basidia, basidiospores and haustorial branches. Scale bar: 10 µm.

*Tremella haematommatis*

Additional specimen examined. USA: Louisiana: St Tammany par., Fontainebleau State Park, Lake Pontchartrain, 30°20'N, 90°03'W, on *Nyssa*, on *Haematomma persoonii*, 1981, Tucker 21375 (SBBG).

References. Diederich 1996 [Etayo et al. 2021, Millanes et al. 2011].

Tremella harrisii Diederich

Bibl. Lichenol. 61: 85 (1996). *Type:* USA, Florida, Volusia County, Orange City, Blue Spring State Park, on *Polymeridium catapastum*, 9 Dec. 1988, R. C. Harris 23778A (NY – holotype; BR – isotype).

Basidiomata superficial, subglobose, medium to dark brown, waxy-gelatinous, 0.15–0.3(–0.7) mm diam. *Context hyphae* thick-walled, 1–1.5 µm diam., with clamp connections; haustoria frequent, with clamp connections. *Hymenium* containing numerous clavate probasidia with a basal clamp. *Basidia*, when mature, not or shortly stalked, subspherical, pyriform or ellipsoid, 2–4-celled, septa longitudinal or oblique, 15–22 × 11–16 µm; epibasidia subcylindrical, 25–35 µm long, 2.5–3 µm diam. *Basidiospores* subglobose, 6–7.5 × 5.5–6.5 µm. *Asexual stage* unknown.

Notes. *Tremella harrisii* was described by Diederich (1996) for specimens growing on *Trypetheliaceae* hosts. Here, we restrict the use of this name to populations inhabiting *Polymeridium* species, while those growing on *Astrothelium* are described above as the new *Tremella aptrootii*. The differences between both are explained under that species.

Ecology and host. On the corticolous thallus of *Polymeridium catapastum* s. lat.

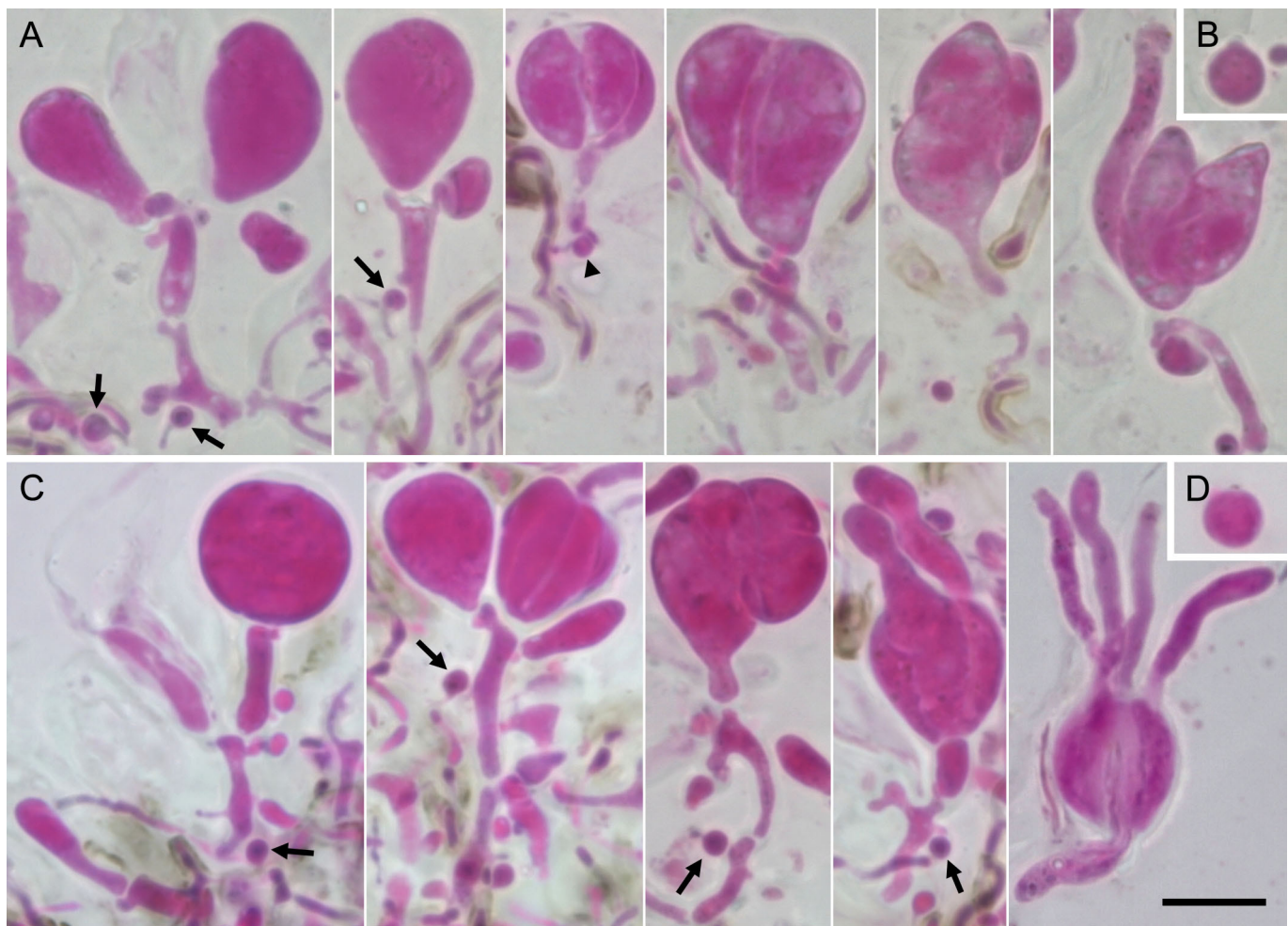
Distribution. North America (USA: Florida).



Tremella harrisii, USA, isotype. Basidiomata on the thallus of *Polymeridium catapastum*. Scale bar: 200 µm.



Tremella harrisii, USA, Ladd 12792. Basidiomata on the thallus of *Polymeridium catapastum*. Scale bar: 200 µm.



Tremella harrisii, USA, Florida. A–B, isotype, C–D, Ladd 12792. A, C, Basidia in different stages of development, fertile hyphae, haustoria (arrows), one entering a brownish host hypha (arrow head). B, D, Basidiospores. In phloxine. Scale bar: 10 μ m.

Additional specimens examined (all on *Polymeridium catapastum* s. lat.). **USA: Florida:** Liberty Co., Along Florida Hwy 65, c. 6.6 mi S of Hosford, Apalachicola National Forest, 1990, Harris 25073 (NY); Marion Co., Ocala National Forest, degraded woodland N of Hwy 42, c. 1 mi SE of Big Bass Lake, 1988, Ladd 12792 (NY); Marion Co., Ocala National Forest, along Forest Serv. Road 573 at junction of Forest Serv. Road 573A, 1989, Harris 23827 (NY); Polk Co., Saddle Blanket Lakes, SW of Lake Wales, 1992, Platt 374 (SBBG).

References. Diederich 1996 [Diederich 2003].



Tremella harrisii

Tremella herpothalli Diederich, Flakus, Rodr. Flakus, Etayo & Palice, sp. nov.

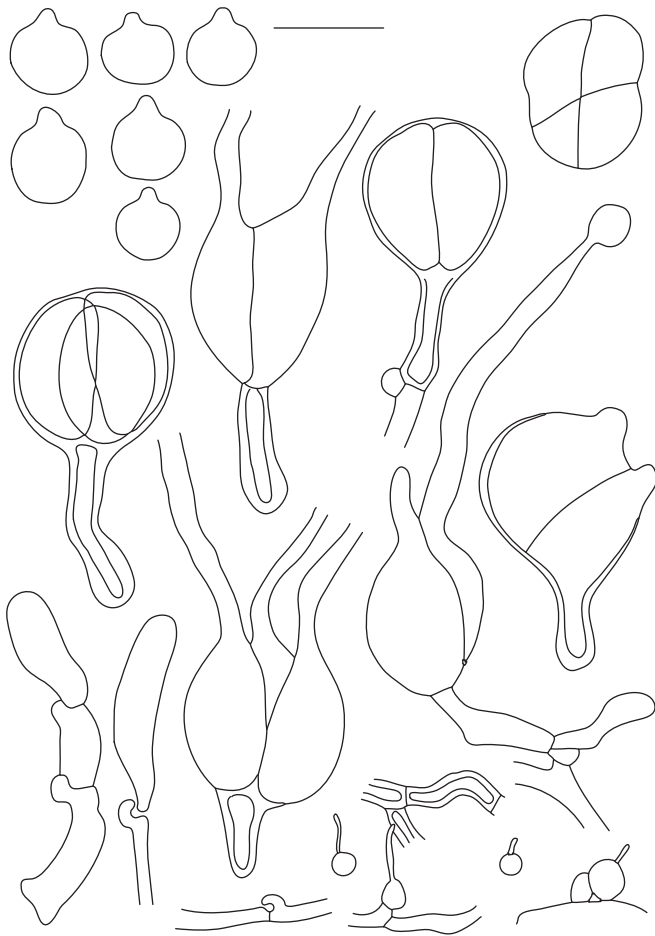
Diagnosis: Characterized by the pale yellowish brown to dark grey, non-gelatinous, matt, soft basidiomatal galls developing over the thallus of *Herpothallon*, 0.1–0.6 mm diam., the relatively small, ellipsoid, 2-celled basidia with a longitudinal, oblique or transverse septum, 12–22 \times 6.5–10 μ m, and the shortly ellipsoid basidiospores, 6–7.5 \times 4.5–7 μ m.

Etymology: From *Herpothallon*, the host lichen.

Type: Bolivia, Dept. Chuquisaca, Prov. Hernando Siles, 15 km W of Monte Agudo, 19°48'57"S, 64°05'60"W, 1815 m, disturbed Bolivian-Tucuman forest, on *Herpothallon* sp., 20 July 2015, A. Flakus 26854 (KRAM – holotype; LPB – isotype).

Mycobank: MB844662

Basidiomata superficial, pulvinate, strongly convex, roundish to shortly elongate, often agglomerating, not gelatinous, matt, soft, pale yellowish brown, 0.1–0.6 mm diam. (in specimen Palice 16071) or dark grey, 0.1–0.4 mm diam. (in the holotype), including host hyphae and thus



Tremella harrisii, USA, holotype (modified from Diederich 1996). Basidia, subbasidial hyphae, basidiospores and haustorial branches (one entering a host hypha). Scale bar: 10 μ m.

representing galls. *Context hyphae* and subbasidial hyphae not observed; haustoria present, basal clamp not observed. *Hymenium* containing numerous subspherical to ellipsoid



Tremella herpothalli, Bolivia, holotype. Basidiomata on the thallus of *Herpothallon* sp. Scale bar: 500 μ m.

probasidia, basal clamps not observed. *Basidia*, when mature, ellipsoid, 2-celled, with a longitudinal, oblique or transverse septum, 12–22 \times 6.5–10 μ m; epibasidia cylindrical, at least 40 μ m long. *Basidiospores* shortly ellipsoid, 6–7.5 \times 4.5–7 μ m. *Asexual stage* unknown.

Notes. The two known specimens are macroscopically rather different, and we hesitated to consider them as conspecific. Microscopical examination of both specimens was rather difficult, and only a small number of mature basidia could be observed. Basidiospores are very rare, with only a few observed in each specimen. As the microscopical characters are the same in both specimens, and as the hosts are both unidentified but look similar, we provisionally regard them as the same species and choose the Bolivian specimen, from which molecular data have been obtained, as the holotype. More specimens on this host genus are needed to determine whether several *Tremella* species are involved.

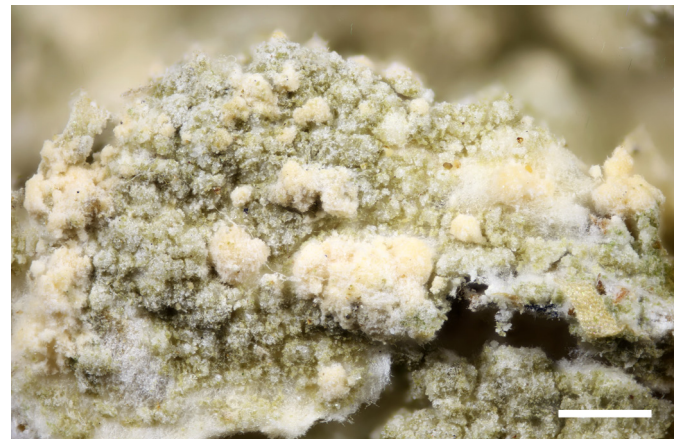
Ecology and hosts. On the thallus of unidentified sterile corticolous *Herpothallon* species.

Distribution. South America (Bolivia; Ecuador).

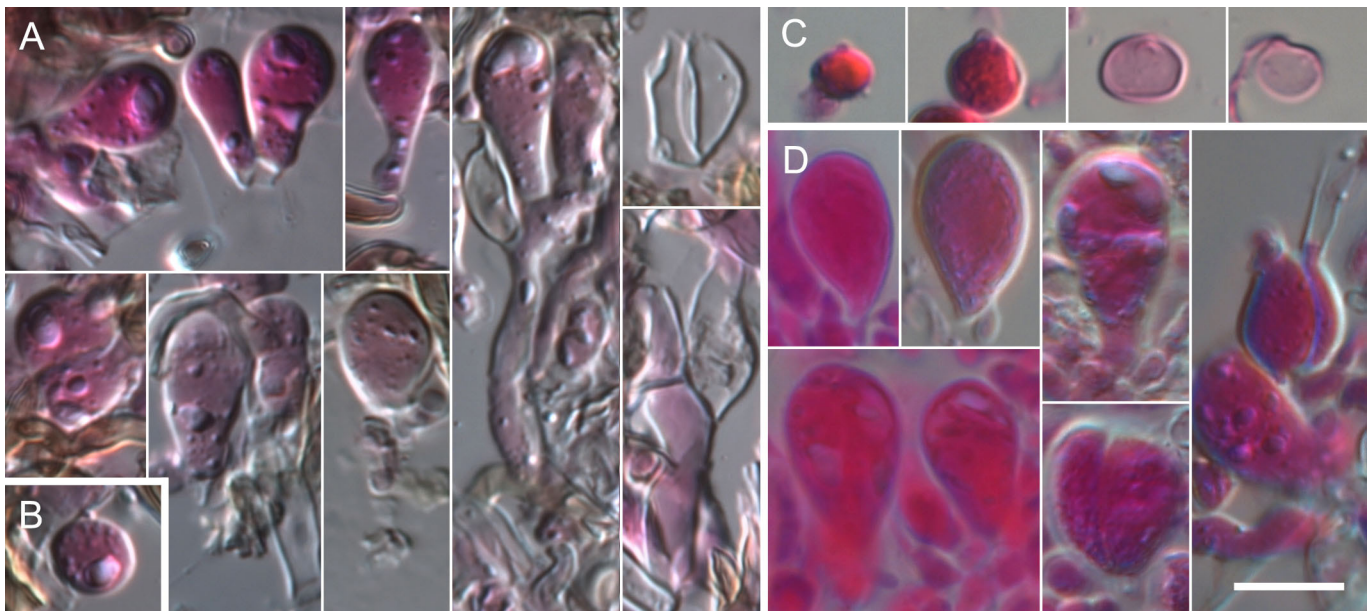
Additional specimen examined. **Ecuador:** Prov. Imbabura, Ibarra, Chachimiro, a small remnant of secondary cloud forest 1 km W of the thermal spa-centre ('las piscinas'), 0°27'40"N, 78°14'55"W, 2900 m, on *Herpothallon*, 2003, Palice 16071 & Etayo 28155 (BR, PRA, herb. Etayo).



Tremella herpothalli



Tremella herpothalli, Ecuador, Palice 16071. Basidiomata on the thallus of *Herpothallon* sp. Scale bar: 500 μ m.



Tremella herpothalli. A–B, Bolivia, holotype, C–D, Ecuador, Palice 16071. A, D, Basidia in different stages of development. B–C, Basidiospores. In phloxine. Scale bar: 10 μ m.

Tremella huuskonenii Diederich, Myllys, Goward & Lindgren

in Lindgren et al., *Fungal Biology* 119: 853 (2015). *Type*: Canada, British Columbia, Clearwater Valley, 51°51'02.45" N, 120°01'37.80" W, 715 m, over *Bryoria pikei* on branches of *Pseudotsuga menziesii*, on *Raesaenenia huuskonenii*, 9 Nov. 2011, T. Goward 11–50 (UBC – holotype; BM, BR, CANL, H – isotypes).

Basidiomata not gall-inducing, black, pulvinate, strongly gelatinous, surface smooth to rugose, elongate, up to 1.2 \times 0.5 mm (i.e., the same form and size as ascomata of the lichenicolous host, or slightly smaller), up to 0.3 mm tall. *Context hyphae* thin-walled, 1.5–2.5 μ m diam., clamp connections not observed; haustoria present. *Hymenium* con-

taining numerous clavate probasidia with a basal clamp. *Basidia*, when mature, 2-celled, with one transverse or rarely oblique septum, slightly constricted at the septum, (12–)13.5–18(–21) \times (5–)5.5–7(–8) μ m, rarely with an attenuated stalk-like base; epibasidia subcylindrical, 10–23(–29) μ m long, 2–3 μ m diam. *Basidiospores* ellipsoid to subspherical, (5.5–)6.5–8.5(–10) \times (4–)5–6.5(–7) μ m. *Asexual stage* unknown.

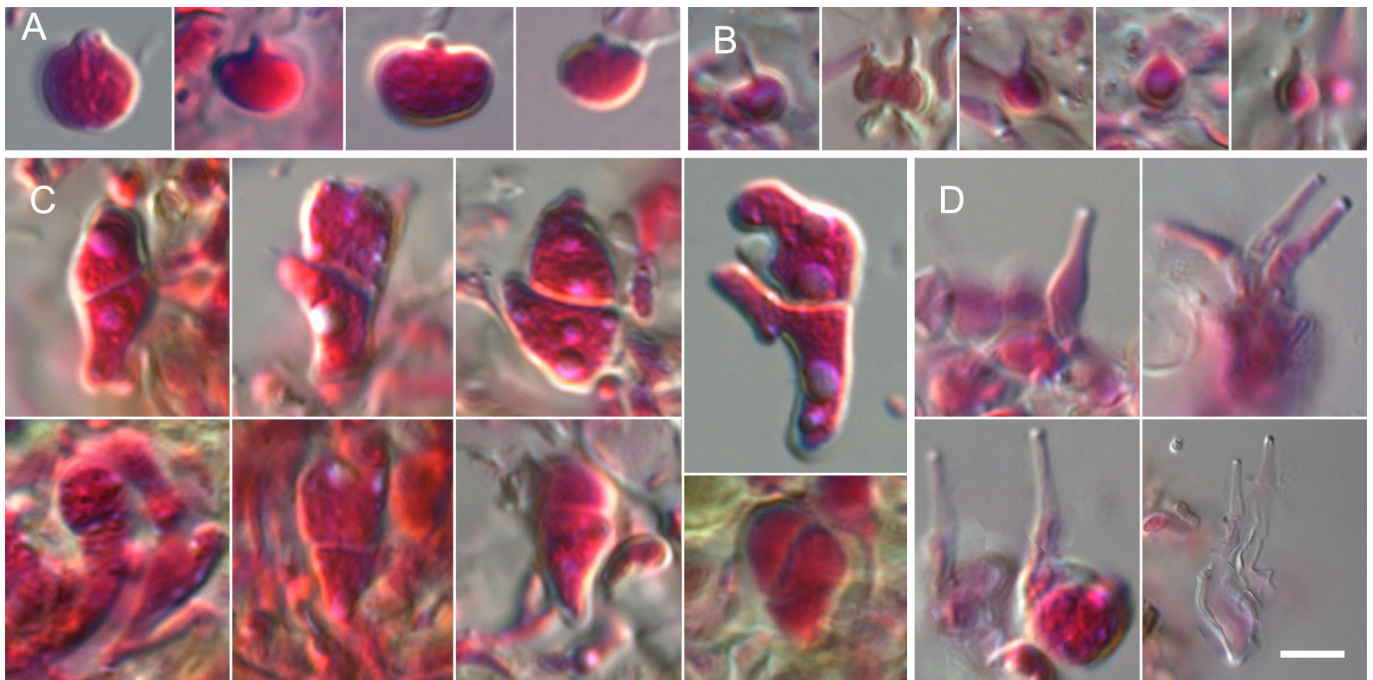
Notes. *Tremella huuskonenii* is characterized by the black basidiomata, the rather small, usually 1-transseptate basidia and the relatively short epibasidia. Although it grows on the thallus of *Bryoria* species, it develops exclusively over *Raesaenenia huuskonenii* ascomata and seems to be confined to that host.



Tremella huuskonenii, Canada, holotype. Young basidioma over *Raesaenenia huuskonenii* on *Bryoria pikei*. Scale bar: 200 μ m.



Tremella huuskonenii, Canada, Goward 12-03. Mature, swollen basidioma over *Raesaenenia huuskonenii* on *Bryoria pikei*. Scale bar: 200 μ m.



Tremella huuskonenii, Canada, British Columbia, holotype (modified from Lindgren et al. 2015). A, Basidiospores. B, Haustoria. C, Basidia. D, Epibasidia. In phloxine. Scale bars: 5 µm.



Tremella huuskonenii

Ecology and host. Hyperparasitic on *Raesaenenia huuskonenii* over *Bryoria pikei* and *B. vrangiana*.

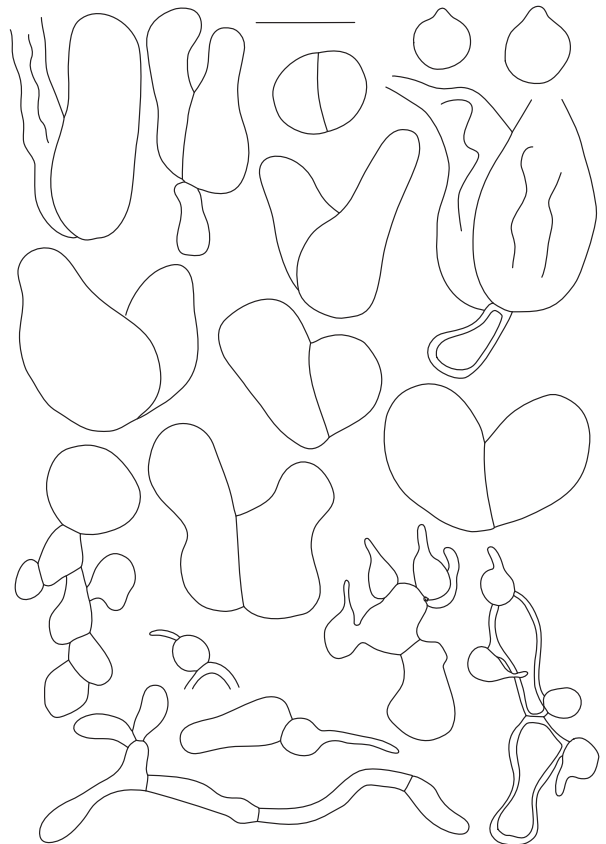
Distribution. North America (Canada: British Columbia; USA: North Carolina), Europe (Finland; Russia).

Reference. Lindgren et al. 2015.

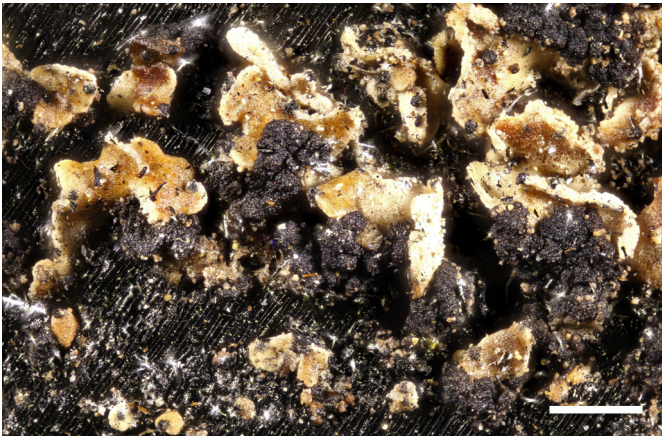
Tremella hypocenomycis Diederich

Bibl. Lichenol. 61: 87 (1996). **Type:** Finland, Ostrobothnia borealis, Pello, Turtola, on *Hypocenomyce scalaris*, 1867, J. P. Norrlin s. n. (H – holotype; BR – isotype).

Basidiomata irregular, often tuberculate or cerebriform, 0.2–2 mm diam., dark brown to black, strongly gelatinous, not inducing gall formation. **Context hyphae** thin-walled, 1.5–2.5 µm diam.; subbasidial hyphae thick-walled, 2.5–5 µm diam., 5–11 µm long; clamp connections not observed; haustoria present. **Hymenium** containing mainly subspherical or rarely ellipsoid probasidia,



Tremella hypocenomycis, Finland, holotype (modified from Diederich 1996). Basidia, basidiospores, hyphae and haustorial branches. Scale bar: 10 µm.



Tremella hypocenomycis, Finland, isotype. Black basidiomata on the thallus of *Hypocenomyce scalaris* (over carbonized wood). Scale bar: 500 μ m.



Tremella hypocenomycis, USA, Michigan, Harris 60886. Large basidiomata on the thallus of *Hypocenomyce scalaris*. Scale bar: 500 μ m.



Tremella hypocenomycis

clamp connections not observed. *Basidia*, when mature, 2(–4)-celled, with longitudinal (exceptionally transverse) septa, 10–17(–20) μ m diam., near the septa 8–14 μ m long, individual cells elongating and growing separately, each up to 24 μ m long (epibasidium not included), in the upper part 3.5–10 μ m diam.; epibasidia shrunken in herbarium material. *Basidiospores* subspherical, 5.5–7.5 μ m diam. *Asexual stage* unknown.

Notes. This taxon is distinguished from most lichenicolous *Tremella* species by the basidia with individual cells that elongate at maturity, a character otherwise also found in *T. christiansenii*, *T. tuckerae*, and other species. It is further characterized the black, gelatinous basidiomata.

Ecology and host. On the thallus of *Hypocenomyce scalaris*.

Distribution. Europe (Finland; Poland) and North America (USA: Michigan).

Additional specimen examined. USA: Michigan: Cheboygan Co., Pigeon River Country State Forest, W of Osmun Road, 6.1 mi S of MI-68, 45°17'36"N, 84°25'43"W, 860 ft, swamp forest, on *Pinus strobus*, on *Hypocenomyce scalaris*, 2015, Harris 60886 (NY).

References. Diederich 1996, Pippola & Kotiranta 2008 [Gorczak et al. 2021].

Tremella hypogymniae Diederich & M. S. Christ.

in Diederich, *Bibl. Lichenol.* 61: 90 (1996). *Type:* France, Pyrénées-Atlantiques, au sud de Arette, un peu en aval du Chalet d'Oumarre, on *Hypogymnia physodes*, 29 July 1990, P. Diederich 9145 (LG – holotype; BR – isotype).

Basidiomata often absent or inconspicuous; fungus inducing the formation of convex, pale brown, brownish orange or pinkish galls 0.1–2.5 mm diam., not constricted at the base, with a smooth surface, often dark or black due to the presence of parasitic fungi; basidiomata, when present, resupinate over the galls, often with indeterminate margins, waxy to firm gelatinous, yellowish, pinkish or pale orange. *Context hyphae* intermixed thin-walled, 1–3 μ m thick, clamps present; haustoria not observed. *Hymenium* containing a few or numerous ellipsoid probasidia with a basal clamp and conidiogenous cells. *Basidia*, when mature, 2-celled, irregular in shape and septation, with one longitudinal, oblique or transverse septum, cells often unequal in size, 11–20 \times 7–14 μ m; epibasidia subcylindrical, up to at least 30 μ m long, 2–3.5 μ m diam. *Basidiospores* subspherical to ellipsoid, 6–10 \times 5–8 μ m. *Asexual stage* poorly developed in the material examined: conidiogenous cells present, hyaline, claviform to cylindrical, 21–35 \times 5–9 μ m, immature, without apical branches, no asteronidia observed.

Notes. This species is characterized by the concolorous to pinkish basidiomatal galls on the thallus of *Hypogymnia physodes*. These often turn dark brown to black when parasitized by other lichenicolous fungi, such as *Licheniconium lecanorae*.

Ecology and host. On the thallus of *Hypogymnia physodes*, gall-inducing. Reports from other hosts are not considered here (e. g., on *H. bitteri*, Zhurbenko et al. 2019).

Distribution (only specimens on *Hypogymnia physodes*). Europe (Austria; Belarus; Belgium; Bosnia and Herzego-



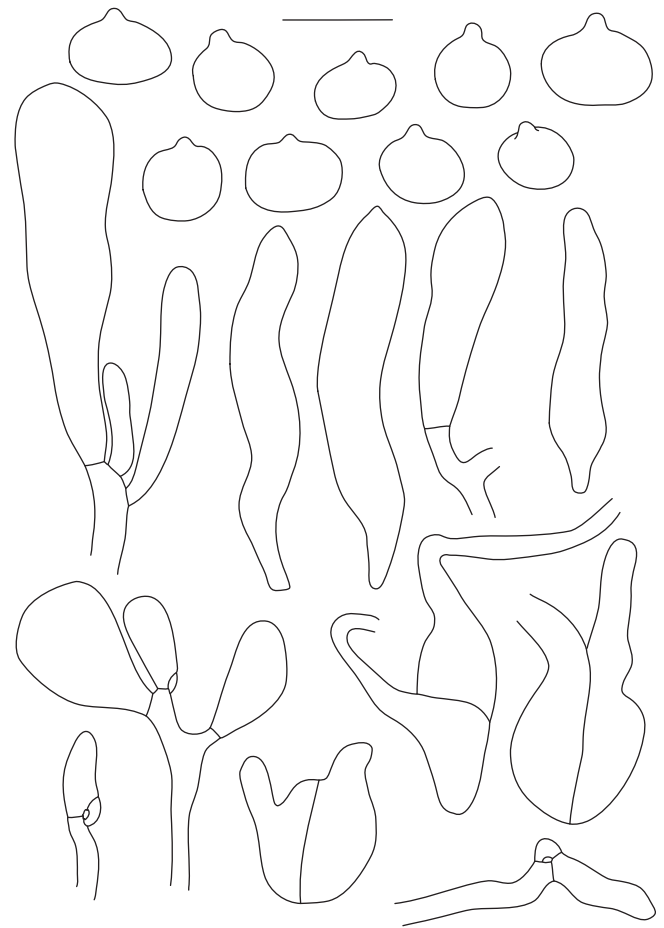
Tremella hypogymniae, France, isotype. Basidiomata on *Hypogymnia physodes*. Scale bar: 500 µm.

vina; Czech Republic; Estonia; Finland; [France](#); Germany; Ireland; Italy; Latvia; Luxembourg; Montenegro; Norway; Poland; Romania; Russia; Slovenia; Spain; Sweden; Switzerland; UK: England, Scotland), Macaronesia (Canary Islands), North America (Canada: Alberta, British Columbia, Ontario; USA: Idaho, Montana, Oregon, Washington) and Asia (Russia).

Additional specimens examined (all on *Hypogymnia physodes*).

Canada: *British Columbia:* Wells Gray Provincial Park, Helmcken Falls, 51.9569°N, 120.1819°W, 2008, 750 m, 2008, Diederich 17302 (BR); *ibid.*, 8 km N of Clearwater, Spahats Creek Falls, 51.7380°N, 120.0153°W, 740 m, 2008, Diederich 17697 (BR). **Canary Islands:** *Tenerife:* S of Los Silos, 1 km W of Erjos, Monte del Agua, 28°19'N, 16°48'W, 1140 m, 2007, Diederich 16594 (BR). **USA:** *Idaho:* Latah Co., Laird Campground, Panhandle National Forest, on Palouse River Rd., 1 mi from Sate Rte 6, 10 mi N of Harvard, 15 mi S of Emida, 1998, Tucker 36027 (SBBG). *Washington:* Island Co., Whidbey Island, along State Rd 525 1.3 km N of Greenbank, at junction Smugglers Cove Rd., 48°06.5'N, 122°35'W, 50 m, 1997, Tønssberg 24557 (BG)

References. Diederich 1996, Pippola & Kotiranta 2008 [Alstrup 2014, Alstrup et al. 2004, 2008, Bilovitz et al. 2011, Brackel 2009, 2013, 2014, 2015, Brackel & Kocourková 2006, Brackel & Puntillo 2016, Brackel et al. 2018, Diederich 2003, Etayo 1996, Hafellner 2018, Hafellner & Komposch 2007, Hafellner et al. 2004, Halonen et al. 2000, Kocourková 2000, Kukwa 2004, 2005, Kukwa &



Tremella hypogymniae, France, holotype (modified from Diederich 1996). Probasidia, basidia, basidiospores and a hypha with clamp connection. Scale bar: 10 µm.

Czarnota 2006, Kukwa & Flakus 2009, Kukwa et al. 2010, Malíček & Palice 2013, Millanes et al. 2014a, Motiejūnaitė & Grochowski 2014, Motiejūnaitė et al. 2016, Roux 2020, Schiefelbein 2013, Schiefelbein et al. 2012, Shiryayev et al. 2010, Stepanchikova et al. 2020, Strasser et al. 2015, Suija 2005, Suija et al. 2020, Tarasova et al. 2020, Tsurykau 2017, Urbanavichus et al. 2020, Zhurbenko & Davydov 2000, Zhurbenko & Kobzeva 2014, Zhurbenko & Otte 2012, Zhurbenko & Yakovchenko 2014, Zhurbenko & Zhdanov 2013, Zimmermann & Berger 2018].

Tremella imshaugiae Diederich, Coppins, R. C. Harris, Millanes & Wedin

in Diederich et al., *Bull. Soc. Nat. luxemb.* 122: 242 (2020). *Type:* UK, Scotland, VC 96, Easterness, Glen Feshie, Allt Fhearnagan, 410 m, on *Pinus* twig, on *Imshaugia aleurites*, 3 Nov. 2013, H. Paul (E 00722344 – holotype).

Basidiomata not gall-inducing, amber-coloured, convex, gelatinous, often fusing, 0.1–1 mm diam. Context hyphae thin-walled, 2–3 µm diam., often with clamps; subbasidial hyphae 2.5–5 µm thick; haustorial branches present. Hymenium hyaline, containing numerous clavate probasidia



Tremella hypogymniae



Tremella imshaugiae, Canada, Coppins 18234. Basidiomata on the thallus of *Imshaugia aleurites*. Scale bar: 200 μm .



Tremella imshaugiae

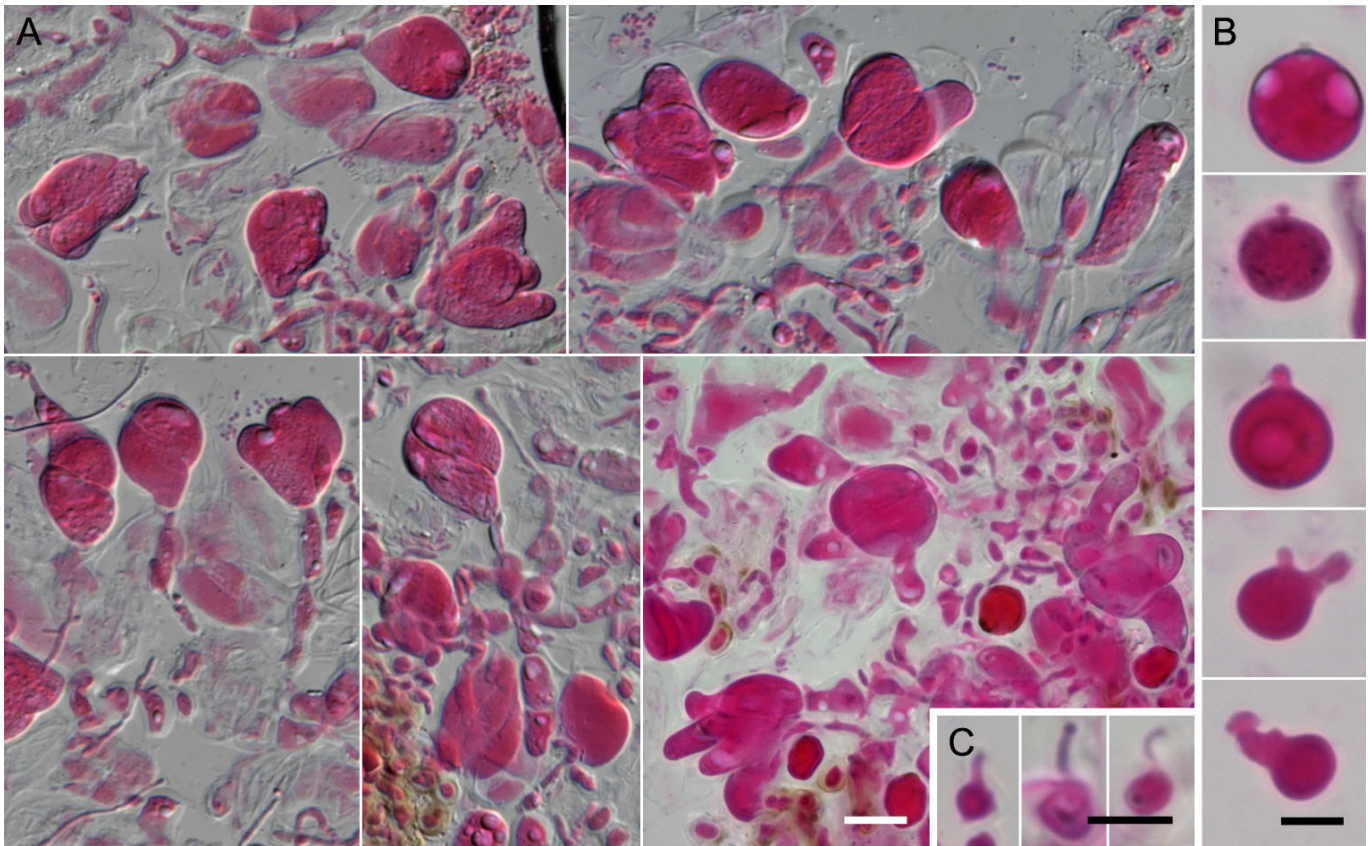
Notes. *Tremella imshaugiae* is characterized by the amber-coloured basidiomata developing over thalli of *Imshaugia aleurites*.

Ecology and host. On the thallus of corticolous *Imshaugia aleurites*.

Distribution. Europe (UK: Scotland) and North America (Canada: New Brunswick, Ontario; USA: Maine).

Additional specimen examined. **Canada:** New Brunswick: Kent Co., Kouchibouguac National Park, vicinity of parking area for Rankin Bog, along Route 117 c. 2 km NE of bridge over Kouchibouguac River, 46°48'08"N, 65°00'15"W, on *Imshaugia aleurites*, 2019, Harris 62668 (NY).

Reference. Diederich et al. 2020 [Brinker in prep.].



Tremella imshaugiae, UK, Scotland, holotype (modified from Diederich et al. 2020). A, Hymenium with basidia. B, Basidiospores. C, Haustoria. In phloxine. Scale bars: A = 10 μm , B–C = 5 μm .

***Tremella lecidellae* Diederich & Brackel, sp. nov.**

Diagnosis: Characterized by the medium yellow to orange-brown, waxy-gelatinous, not gall-inducing basidiomata, 0.1–0.4 mm diam., growing on the thallus of *Lecidella elaeochroma*, the very large, mainly longitudinally septate, 4-celled basidia, $19\text{--}32 \times 13\text{--}23\ \mu\text{m}$ and the massive epibasidia, 5–7.5 μm thick.

Etymology: From *Lecidella*, the host lichen.

Type: USA, Nebraska, Custer Co., 6 mi E, $\frac{1}{2}$ mi S of Anselmo, Victoria Springs State Recreation Area, mowed picnic and camping areas along spring-fed Victoria Creek and Lake, $41^{\circ}36.60'\text{N}$, $99^{\circ}45.06'\text{W}$, 800 m (2630 ft), on partly shaded honey locust (*Gleditsia triacanthos*) in shelterbelt, on *Lecidella elaeochroma*, 11 May 2010, M.K. Advaita 9536-B (NY – holotype).

Mycobank: MB844663

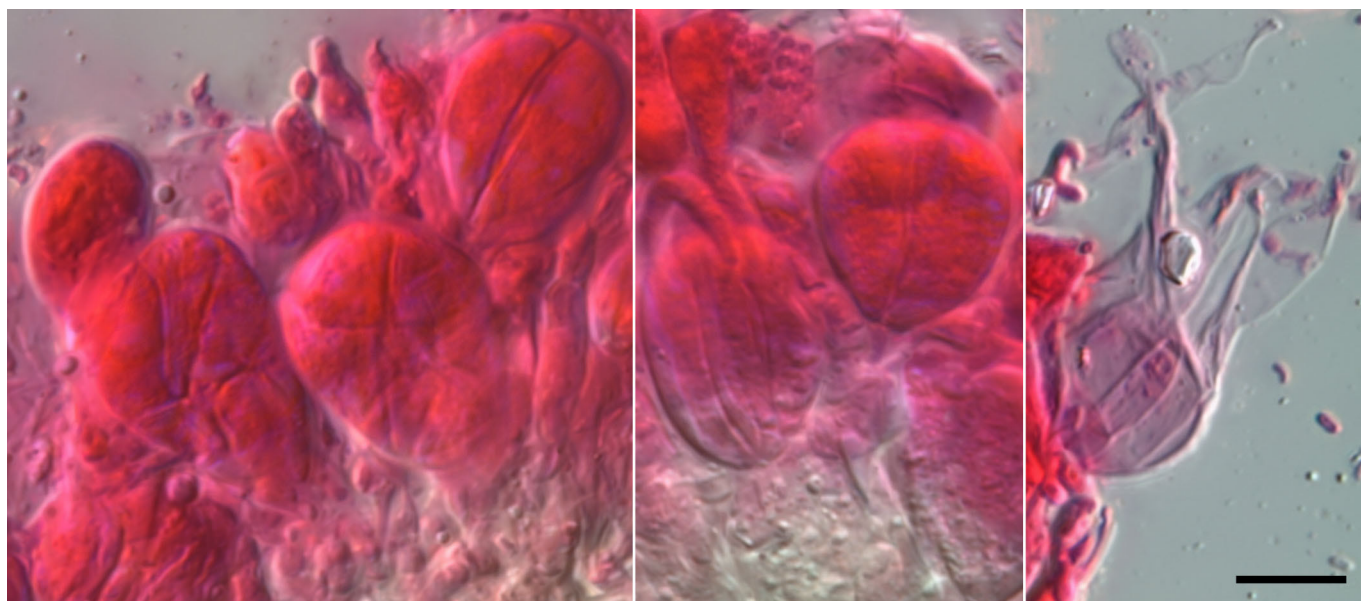
Basidiomata not gall-inducing, superficial, pulvinate, roundish or irregular in form, waxy-gelatinous, pale to medium yellow or orange-brown, basally slightly constricted, 0.1–0.4 mm diam. **Context hyphae** 2–2.5 μm diam.; subbasidial hyphae thick-walled, 3.5–4.5 μm diam.; haustoria present, but rare, basal clamp not observed. **Hymenium** containing numerous subspherical to ellipsoid probasidia, basal clamp not observed. **Basidia**, when mature, subspherical to ellipsoid, non-stalked, 4-celled, with longitudinal or rarely oblique septa, $19\text{--}32 \times 13\text{--}23\ \mu\text{m}$; epibasidia cylindrical, at least 40 μm long and 5–7.5 μm thick. **Basidiospores** not observed. **Asexual stage** unknown.



Tremella lecidellae, USA, Nebraska, holotype. Basidiomata on the thallus of *Lecidella elaeochroma*. Scale bar: 500 μm .



Tremella lecidellae, Italy, Brackel 8648. Basidiomata on the thallus of *Lecidella elaeochroma*. Scale bar: 500 μm .



Tremella lecidellae, USA, Nebraska, holotype. Mature basidia. In phloxine. Scale bar: 10 μm .



Tremella lecidellae

Notes. We formally describe this species as new, despite the absence of basidiospores in the two available specimens. The species is well characterized by the macroscopical aspect of the basidiomata, the host choice, and the large, 4-celled basidia and the thick epibasidia. Other species with similarly sized, 4-celled basidia and brownish, not gall-inducing basidiomata are *Tremella haematommatis*, a species with larger, amber-coloured basidiomata, up to 0.8 mm diam., confined to *Haematomma* species, and *T. wirthii*, with pale to dark greyish brown, gelatinous basidiomata, slightly smaller basidia, $18\text{--}24 \times 12\text{--}18\ \mu\text{m}$, and thinner epibasidia, $3.5\text{--}5.5\ \mu\text{m}$ thick, confined to *Protoparmelia* species.

Ecology and host. On the thallus of corticolous *Lecidella elaeochroma*, exceptionally spreading over the apothecial margin, not visibly damaging the host.

Distribution. Europe (Italy) and North America (USA: Nebraska).

Additional specimen examined. **Italy:** Sicily: Prov. Messina, Monti Nebrodi, an der Straße von Caronia nach Capizzi, on *Quercus cerris*, on *Lecidella elaeochroma*, 2007, Brackel 8648 (BR).

Tremella leprae Diederich & W. R. Buck, sp. nov.

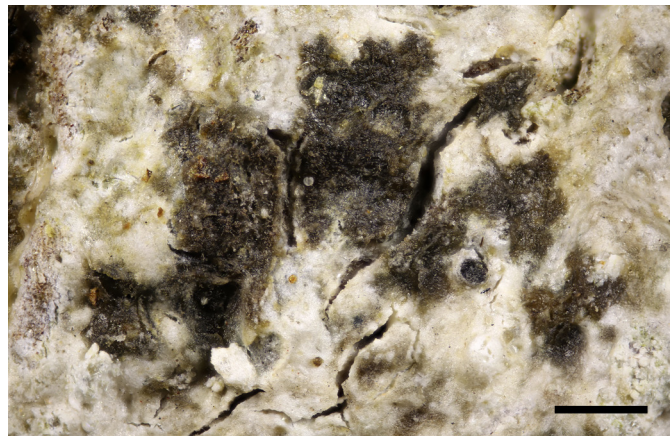
Diagnosis: Characterized by the applanate, dark brown to blackish, irregularly formed, gelatinous basidiomata on the thallus of *Lepra oahuensis*, 0.3–2 mm diam., the relatively large, 2–4-celled basidia with mainly longitudinal septa, $17\text{--}36 \times 16\text{--}25\ \mu\text{m}$, and the relatively large basidiospores $10\text{--}11.5 \times 8.5\text{--}10\ \mu\text{m}$ frequently producing yeast-like cells.

Etymology: From *Lepra*, the host lichen.

Type: USA, Georgia, Union Co., Chattahoochee National Forest, along Duncan Ridge Trail from Wildcat Gap to Coosa Bald, off Forest Service Road 39, c. 1.4 mi NNW of GA 180 at Wolf Pen Gap, $34^{\circ}46'\text{N}$, $83^{\circ}57'\text{W}$, 1145–1285 m, moist hardwoods, on corticolous *Lepra oahuensis*, 6 Oct. 1998, W. R. Buck 34912 (NY – holotype).

Mycobank: MB844664

Basidiomata applanate, dark brown to blackish, gelatinous, very irregular in form, 0.3–2 mm diam. **Context** hy-



Tremella leprae, USA, Georgia, holotype. Basidiomata on the thallus of *Lepra oahuensis*. Scale bar: 500 μm .

phae not observed; subbasidial hyphae thick-walled, 3–4.5 μm diam., clamps not seen; haustoria present, basal clamp not seen. **Hymenium** containing numerous probasidia; probasidial initials subspherical to ellipsoid or pyriform, often with a short stalk-like base, with a basal clamp. **Basidia**, when mature, 2–4-celled, with longitudinal or rarely oblique septa, subspherical to ellipsoid, sometimes with a short stalk-like base, $17\text{--}36 \times 16\text{--}25\ \mu\text{m}$ (short stalk-like base included); epibasidia subcylindrical, 3.5–5 μm diam., up to at least 55 μm long. **Basidiospores** shortly ellipsoid, $10\text{--}11.5 \times 8.5\text{--}10\ \mu\text{m}$, producing subspherical to ellipsoid yeast-like cells, $4.5\text{--}7 \times 3\text{--}6\ \mu\text{m}$ diam. **Conidial stage** unknown.

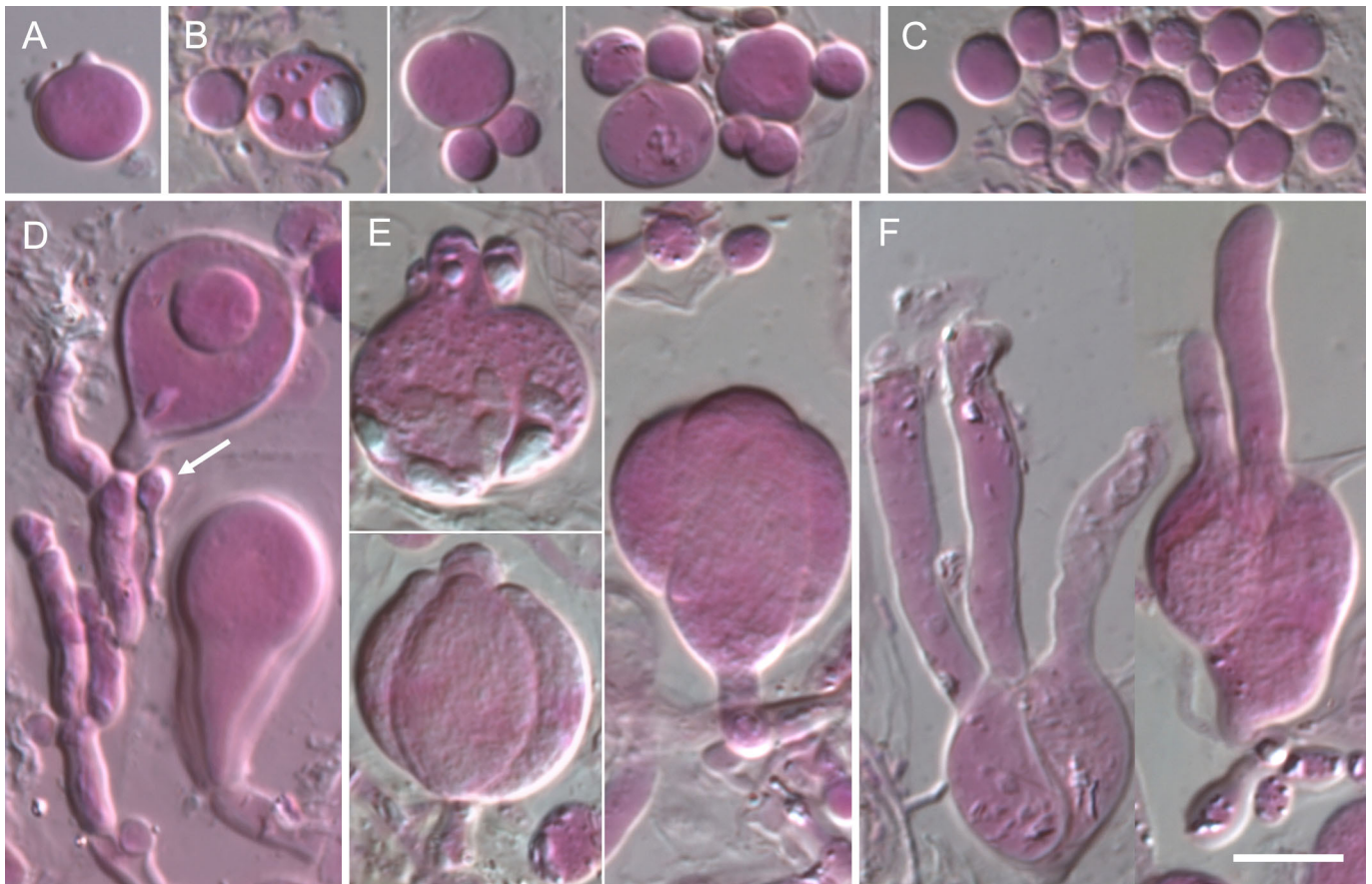
Notes. This species is distinguished from most other lichenicolous *Tremella* species by the flattened, blackish, irregularly formed basidiomata, and by the relatively large basidia and basidiospores.

Ecology and host. On the thallus of *Lepra oahuensis* (lichenanthone, trace of stictic acid).

Distribution. North America (USA: Georgia), known only from the type locality.



Tremella leprae



Tremella leprae, USA, Georgia, holotype. A, Basidiospore. B, Basidiospores producing yeast-like cells. C, Yeast cells. D, Subbasidial hyphae, probasidia and haustorium (arrow). E, Mature, 3–4-celled basidia. F, Mature basidia with epibasidia. In phloxine. Scale bar: 10 µm.

***Tremella leprariae* Diederich, sp. nov.**

Diagnosis: Characterized by the small, brown, gelatinous basidiomata, 0.1–0.3 mm diam., developing between the soredia of *Lepraria finkii*, and the longitudinally (rarely obliquely) 1-septate basidia, 15–21.5 × 7–10 µm.

Etymology: From *Lepraria*, the host lichen.

Type: USA, Michigan, Cheboygan Co., Pigeon River Country State Forest, W of McMasters Creek, E of Osmun Road, 7.5 mi S of MI-68, 45°16'47"N, 84°25'13"W, 250 m (816 ft), swamp forest dominated by *Thuja* and *Abies* with *Betula*, *Acer* and *Picea*, on 'soil' mound, on *Lepraria finkii*, 20 May 2015, R. C. Harris 60862 (NY – holotype; BR – isotype).

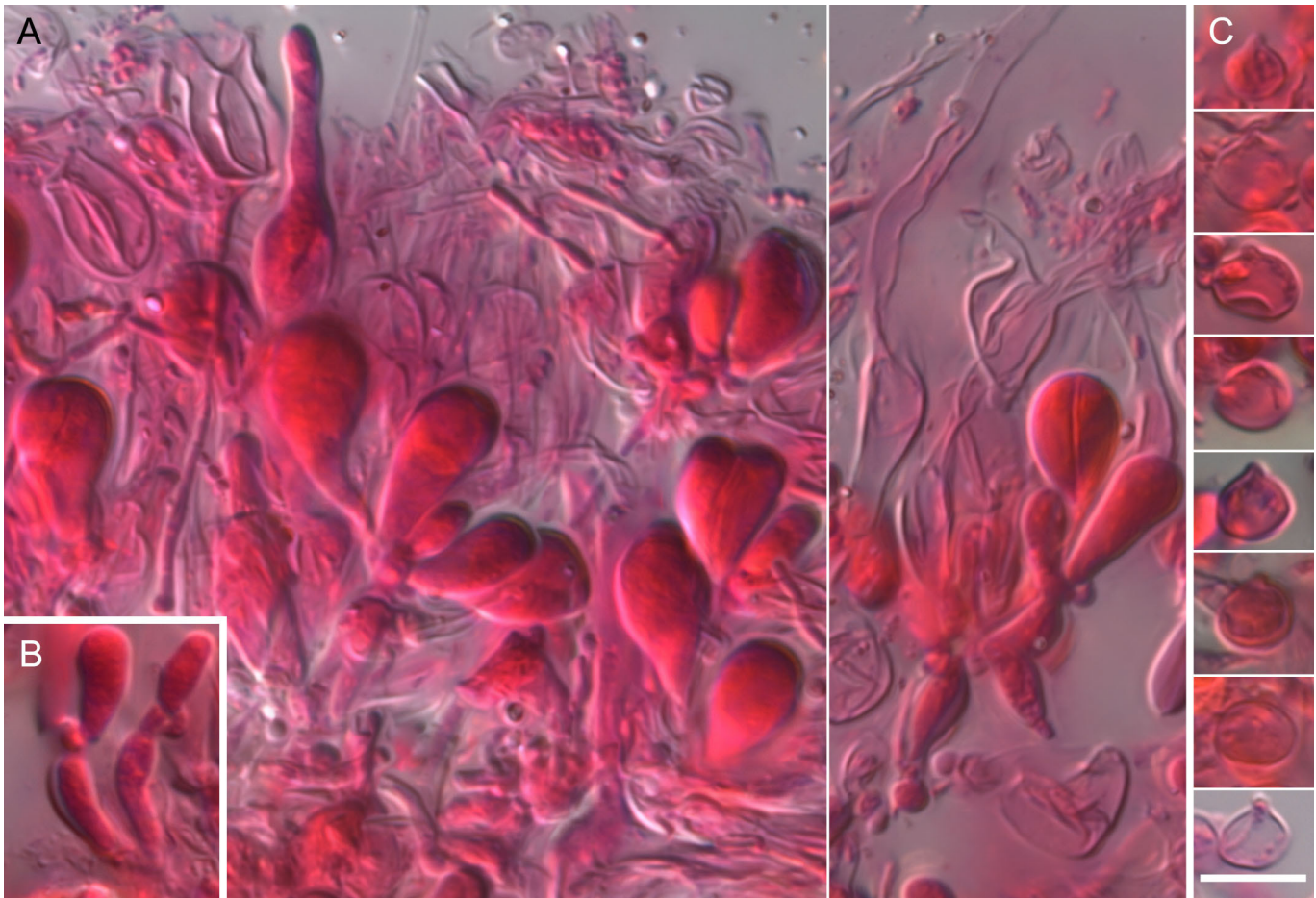
Mycobank: MB844665

Basidiomata not gall-inducing, intermixed with host soredia, partly immersed to superficial, pulvinate or irregular in form, gelatinous, orange-brown, 0.1–0.3 mm diam., becoming larger when agglomerated. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2.5–4.5 µm diam.; haustoria rare, basal clamp not observed. **Hymenium** containing numerous ellipsoid to pyriform probasidia, with a basal clamp. **Basidia**, when mature, ellipsoid to pyriform, not stalked, 2-celled, with one lon-

gitudinal, rarely oblique or almost transversal septum, 15–21.5 × 7–10 µm; epibasidia cylindrical, up to 60 µm long and 2.5–4 µm thick. **Basidiospores** abundant, broadly ellipsoid, c. 6–8.5 × 5.5–7 µm (mainly overmature spores not staining in phloxine have been observed). **Asexual stage** unknown.



Tremella leprariae, USA, Michigan, holotype. Basidiomata on the thallus of *Lepraria finkii*. Scale bar: 500 µm.



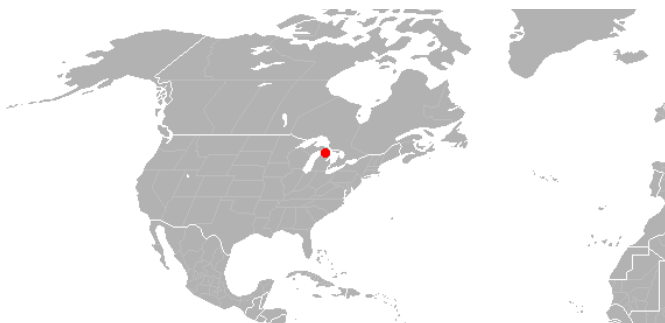
Tremella leprariae, USA, Michigan, holotype. A, Basidia in different stages of development. B, Probasidial initials with a basal clamp. C, Basidiospores. In phloxine. Scale bar: 10 μ m.

Notes. By its small, brown, gelatinous basidiomata not inducing galls on the host thallus, and the medium-sized, mainly longitudinally 1-septate basidia, this species resembles several other lichenicolous species: *Tremella phaeographidis* has much larger basidiomata, 0.4–0.7 mm diam., and transversely septate basidia dominate; basidiomata of *T. coccocarpiæ* and *T. microcarpa* rarely exceed 0.2 mm in diam.; and basidiomata of *T. montis-wilhelmii*, *T. normandinae* and *T. parmeliellae* are not gelatinous.

Although the type specimen is very rich with abundant young, mature and overmature basidia, no basidiospores in a good condition have been observed.

Ecology and host. On terricolous *Lepraria finkii*, not visibly damaging the host.

Distribution. North America (USA: Michigan), known only from the type locality.



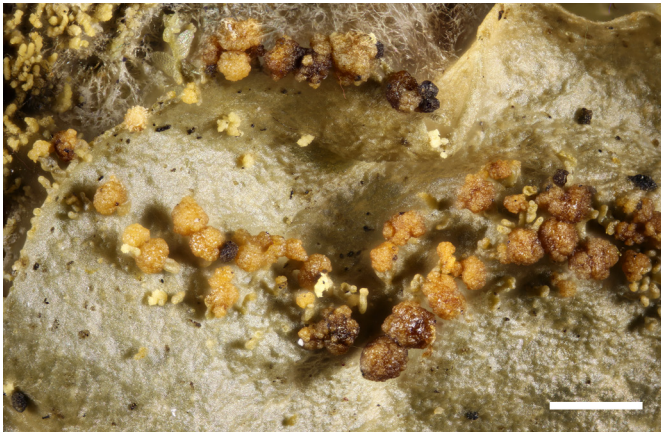
Tremella leprariae

Tremella leptogii Diederich

Bibl. *Lichenol.* 61: 95 (1996). **Type:** Peru, Dept. San Martín, Cerro Escalera (NE of Tarapoto), NW of the tunnel, on *Leptogium* sp., 15 March 1981, R. Santesson & G. Thor P74:54 (UPS – holotype; BR – isotype).

= *Tremella* sp. 6, in Diederich, *Bibl. Lichenol.* 61: 175 (1996)

Basidiomata growing on the isidia of the host, not inducing gall formation, convex, subglobose, waxy-gelatinous, orange-brown, mainly 0.12–0.22 mm diam., when old, strongly tuberculate and darker, up to 0.4 μ m diam. **Context hyphae** thin-walled, 2–2.5 μ m diam., clamps not ob-



Tremella leptogii, Peru, isotype. Basidiomata on *Leptogium* sp. Scale bar: 500 μ m.

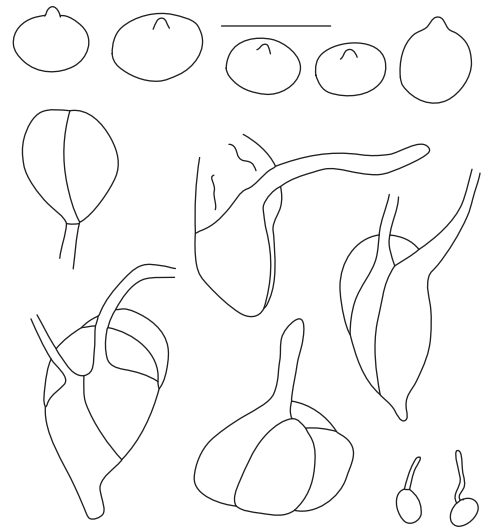
served; haustoria present. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, 2–4-celled, with longitudinal or slightly oblique septa, $10\text{--}14 \times 5.5\text{--}10 \mu\text{m}$; epibasidia subcylindrical, $1\text{--}1.5 \mu\text{m}$ diam., c. $10\text{--}14 \mu\text{m}$ long. *Basidiospores* broadly ellipsoid to subspherical, $6\text{--}8 \times 5\text{--}6.5 \mu\text{m}$ diam. *Asexual stage* unknown.

Notes. This species is similar to *Tremella stictae*, from which it mainly differs by the 2–4-celled basidia; the basidiomata are also a little smaller and more orange-brown. Diederich (1996) reported a hymenium containing conspicuous swollen hyphidia: these are now interpreted as belonging to the host.

Ecology and hosts. On the thallus, often on isidia of *Leptogium* sp., *L. burgesii*, *L. cf. cyanescens*, *L. phyllocarpum* and *L. vesiculosum*.

Distribution. North America (Mexico: Baja California; USA: Arkansas), Central America (Panama), South America (Bolivia; Brazil; Colombia; Ecuador; Peru) and Oceania (Papua New Guinea).

Additional specimens examined (all on *Leptogium*). **Bolivia:** Camino de las orquídeas, zona media, $17^{\circ}50'27''\text{S}$, $64^{\circ}49'58''\text{W}$,



Tremella leptogii, Peru, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 μ m.

2415 m, 2012, Etayo 28104 (LPB, herb. Etayo). **USA: Arkansas:** Faulkner Co., Cove Creek Natural Area, along W side of Cover Creek just above confluence with Cadron River, at E end of Conway Co. Rd. JD, c. 6.2 mi NNW of jct AR285 & AR25 in Wooster, 35.29°N , 92.48°W , 2010, Lendemer 26261 (NY).

References. Diederich 1996 [Diederich 2003, Etayo 2002, 2017, Millanes et al. 2011, van den Boom et al. 2017].

Tremella lethariae Diederich

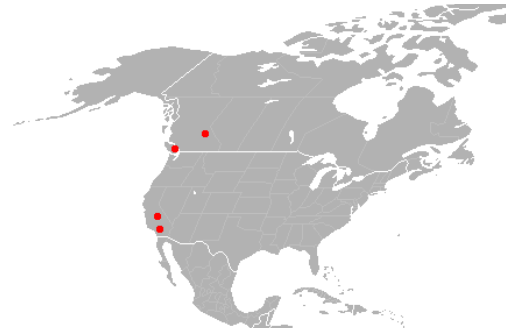
Herzogia 16: 83 (2003). *Type:* Canada, British Columbia, Gulf Islands, Saltspring Island, S of Fulford Harbour, between Mt. Bruce and Mt. Tuam, 6.5 km along Musgrave Rd. from junction Isabella Point Rd., somewhat uphill from road, 530 m, on *Pseudotsuga menziesii*, on *Letharia vulpina*, 14 Sept. 1989, T. Tønsberg 12725b (BG – holotype; BR – isotype).

= *Tremella* sp. 4, in Diederich, *Bibl. Lichenol.* 61: 173 (1996).

Basidiomata inducing gall-formation, convex, concolorous to the thallus, becoming orange-brown at maturity, 0.2–1.5 mm diam. *Context hyphae* not observed; subbasidial hyphae $3.5\text{--}4.5 \mu\text{m}$ diam., clamps not observed;



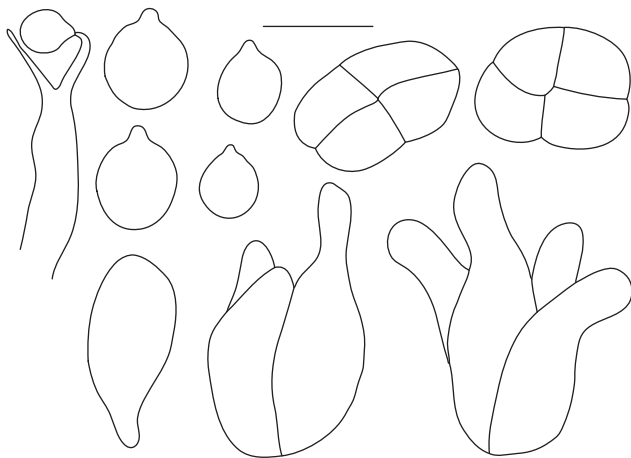
Tremella leptogii



Tremella lethariae



Tremella lethariae, Canada, British Columbia, isotype. Basidiomata on *Letharia vulpina*. Scale bar: 500 μ m.



Tremella lethariae, Canada, Poelt s. n. (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 μ m.

haustoria not observed. *Hymenium* containing numerous subspherical probasidia with a basal clamp. *Basidia*, when mature, 4-celled, with longitudinal septa, $15\text{--}20 \times 10\text{--}16$ μ m; epibasidia subcylindrical, at least 30 μ m in length, $2\text{--}4.5$ μ m diam. *Basidiospores* ellipsoid to subspherical, $6\text{--}8 \times 5.5\text{--}7.5$ μ m. *Asexual stage* unknown.

Notes. The species is characterized by the 4-celled non-stalked basidia and the formation of small galls first concolorous to the host thallus then becoming orange-brown.

Ecology and host. On the thallus of *Letharia vulpina*.

Distribution. North America (Canada: British Columbia; USA: California). Sequences from *Tremella lethariae* yeasts have also been obtained from asymptomatic *L. vulpina* thalli from Italy, Sweden and Switzerland (Tuovinen et al. 2018) (not shown on our distribution map).

References. Diederich 1996 as *Tremella* sp. 4, 2003, Tuovinen 2019 [Kocourková et al. 2012].

***Tremella leucodermae* Diederich, Etayo, Flakus & Millanes, sp. nov.**

Diagnosis: Characterized by the large, pale to medium or blackish brown, strongly convex, elongate basidiomatal galls on the thallus of *Leucodermia*, 0.3–1.5 mm long, the small, 2–4-celled basidia, $9\text{--}16 \times 4.5\text{--}7$ μ m, and the medium sized basidiospores, $5\text{--}7 \times 4.5\text{--}5.5$ μ m.

Etymology: From *Leucodermia*, the host lichen.

Type: Bolivia, Dept. Tarija, Prov. Aniceto Arce, Papachacra, $21^{\circ}41'41''$ S, $64^{\circ}29'35''$ W, 2330–2400 m, Bolivian-Tucuman montano forest, with *Alnus acuminata* and *Podocarpus* sp., on epiphytic *Leucodermia leucomelos*, 7 Aug. 2012, J. Etayo 28197, A. Flakus & M. Kukwa (LPB – holotype; BR, herb. Etayo – isotype).

Mycobank: MB844666

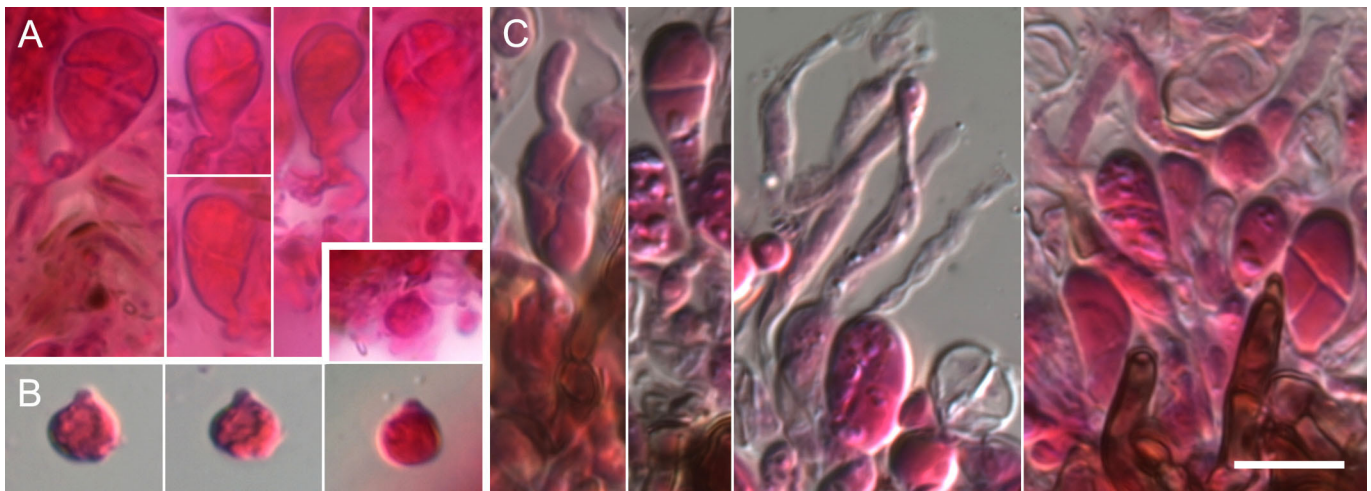
Basidiomata inducing large pale to medium brown or blackish galls, superficial, pulvinate, strongly convex, waxy-gelatinous, either roundish or elongate, 0.3–1.5 \times 0.3–0.7 mm, when on the host thallus, or narrowly elongate.



Tremella leucodermae, Bolivia, holotype. Basidiomata on the cilia of *Leucodermia leucomelos*. Scale bar: 500 μ m.



Tremella leucodermae, Bolivia, Etayo 27974. Basidiomata on the thallus of *Leucodermia vulgaris*. Scale bar: 1 mm.



Tremella leucodermae, Bolivia, A–B, holotype, C, Flakus 26268. A, C, Basidia and epibasidia. B, Basidiospores. In phloxine. Scale bar: 10 μ m.

gate and contorted, 0.3–1.5 \times 0.2–0.3 mm, when on the host cilia. *Context hyphae* thick-walled, 2–2.5 μ m diam.; subbasidial hyphae thick-walled, 1.5–2.5 μ m diam.; haustoria present, with a basal clamp. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid or pyriform, often with an elongate, narrower, stalk-like base, cruciately 2–4-celled, with longitudinal or oblique, rarely transverse septa, 9–16 \times 4.5–7 μ m; epibasidia cylindrical, tapering towards the apex, at least 15 μ m long. *Basidiospores* subspherical to ellipsoid, 5–7 \times 4.5–5.5 μ m. *Asexual stage* unknown.

Notes. This species is distinguished from most known lichenicolous *Tremella* species by the narrow, 2–4-celled basidia, less than 7 μ m wide, and the narrowly elongated and contorted galls induced when growing on the host cilia. *Tremella phaeophysciae* differs by longer basidia, 15–27 μ m long, larger basidiospores, 6–8 \times 5.5–7.5 μ m, and olivaceous basidiomata; *T. cladoniae* still has longer basidia, 15–27 μ m long, and larger basidiospores, 7–10 \times 6–8 μ m; and *T. parmeliellae* has longer basidia, 14–22 μ m long, and subspherical, not elongate basidiomata.



Tremella leucodermae

Ecology and hosts. On the thallus and cilia of epiphytic *Leucodermia leucomelos*, *L. boryi* and *L. vulgaris*.

Distribution. South America (Bolivia; Ecuador).

Additional specimens examined. **Bolivia:** Dept. La Paz: Prov. Nor Yungas, near Nogalani village, on the road Coroico-La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud, on *Leucodermia vulgaris*, Etayo 27974 (LPB, herb. Etayo); Prov. Franz Tamayo, Área Natural de Manejo Integrado Nacional Apolobamba, below Pelechuco, 14°49'07"S, 69°03'49"W, 3650 m, on cilia of *L. boryi*, 2014, Etayo 34451 (LPB, herb. Etayo); Prov. Murillo Sainani, Valle del Zongo, 16°07'03"S, 68°04'42"W, 2170 m, on *L. cf. boryi*, 2014, Flakus 26268 (KRAM, LPB). **Dept. Cochabamba:** Prov. Carrasco, Parque Nacional Carrasco, Wayra Mayu close to Monte Punku, lower montane Yungas cloud forest, 17°33'30"S, 65°16'08"W, 2750 m, on *L. leucomelos*, 2014, Etayo 34312 (LPB). **Ecuador:** Prov. Pichincha, sierra central, cráter Pululaua, Mitad del Mundo, on *L. leucomelos*, 2750 m, 1999, Etayo 17260 (herb. Etayo).

Tremella lichenicola Diederich

Lejeunea n. S. 119: 2 (1986). *Type:* Luxembourg, Larochette, Manzebaach, on *Violella fucata*, 16 May 1985, P. Diederich 6068 (LG – holotype; BR, IMI 300095 – isotypes).

Basidiomata dark brown to black, pulvinate, often with a central depression, strongly gelatinous, drying horny, surface generally rugose, rarely smooth, 0.2–1(–1.5) μ m diam. *Context hyphae* thick-walled, 1.5–2.5 μ m diam., with clamp connections; subbasidial hyphae thick-walled, 3–6 μ m diam.; haustoria frequent. *Hymenium* hyaline or greenish, containing numerous ellipsoid probasidia with a basal clamp, clamp often spur-like on the basidial base without being attached to the subtending hypha. *Basidia*, when mature, subglobose, 2–4-celled, with 1–3 longitudinal septa, 16–23 \times 10–19 μ m; epibasidia subcylindrical, reaching more than 100 μ m in length, 2–4.5 μ m diam. *Basidiospores* broadly ellipsoid to subspherical, 7–11 \times 7–9.5 μ m. *Asexual stage:*



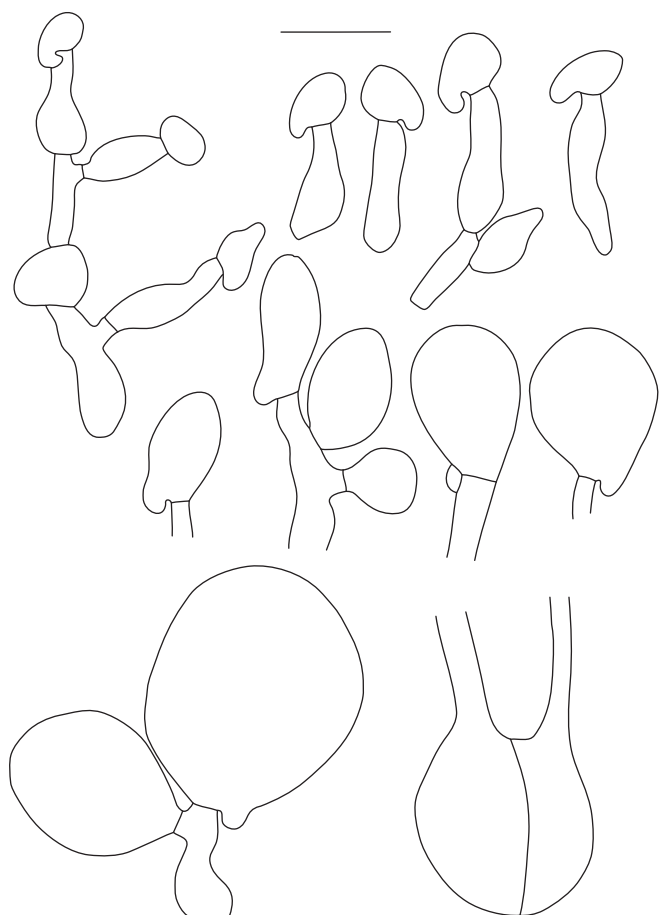
Tremella lichenicola, Luxembourg, isotype. Basidiomata on *Violella fucata*. Scale bar: 500 µm.

long irregular conidial chains are sometimes present in the hymenium; in addition, elongate ellipsoid conidia, $4\text{--}8 \times 2\text{--}4\text{ }\mu\text{m}$, are frequently observed in the hymenium.

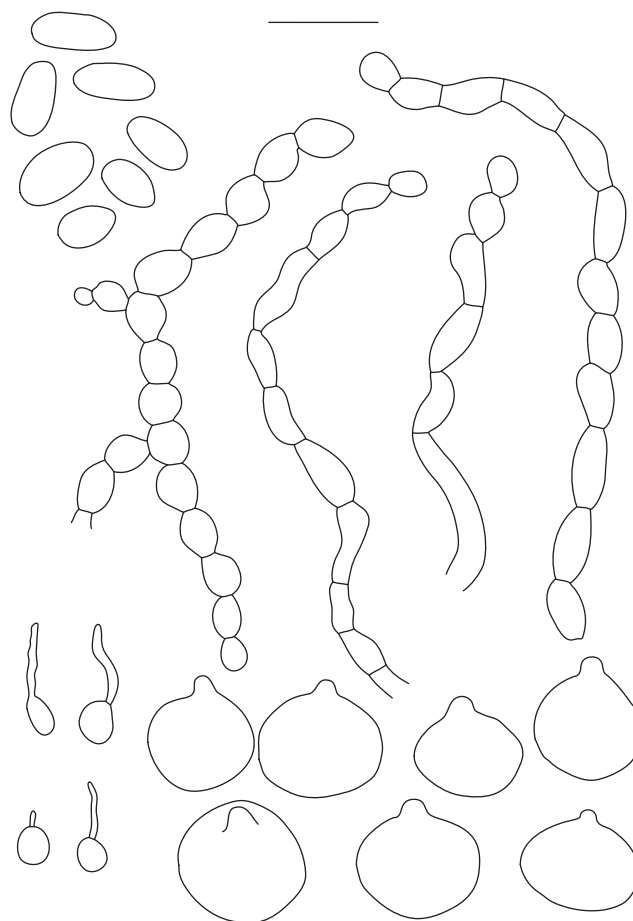
Notes. This was the first lichenicolous heterobasidiomycete to be described (with the exception of *Biatoropsis usnearum* and *Tremella caloplacae* that were earlier described without recognizing their nature as a basidiomycete) (Diederich 1986), and may also have been one of the most common species in Europe at that time. However, major changes in air pollution have dramatically reduced the populations of the host, *Violella fucata*, and at the same time of *Tremella lichenicola*.

It is distinguished from other lichenicolous taxa by a number of characters: it is one of the rare species with strongly gelatinised, black basidiomata; epibasidia are longer than in most lichenicolous heterobasidiomycetes; basidia have an unusual development, often being asymmetrical due to the spur-like clamp not attached to the subtending hypha.

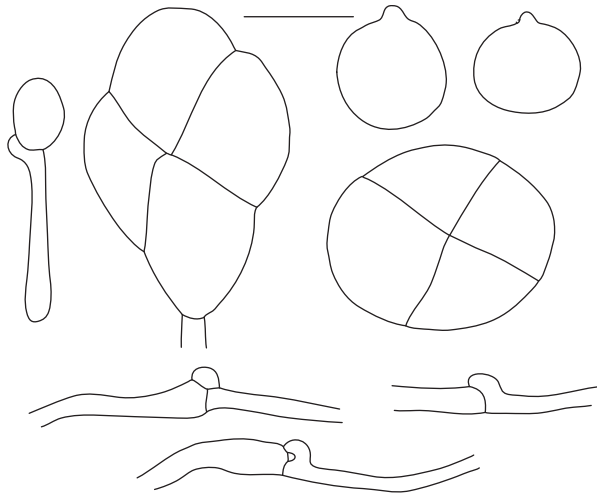
In most European collections, including the type, all basidia are 2-celled; in North American specimens, however, 4-celled basidia are dominant. These American specimens may represent a distinct taxon, but molecular data are needed to check this.



Tremella lichenicola, Luxembourg, Diederich 5448, except basidium bottom right: Germany, Diederich 5529 (modified from Diederich 1996). Probasidia and mature basidia, most with a spur-like basal clamp. Scale bar: 10 µm.



Tremella lichenicola, Luxembourg and Germany, holotype (left conidial chain), Diederich 5529 (basidiospores), Diederich 5448 (rest) (modified from Diederich 1996). Basidiospores, catenulate conidia, single conidia and haustorial branches. Scale bar: 10 µm.



Tremella lichenicola, Canada, Tønsberg 12665 (modified from Diederich 1996). 4-celled basidia, basidiospores and hyphae with clamp connections. Scale bar: 10 µm.



Tremella lichenicola

Ecology and host. On the thallus of *Violella fucata*.

Distribution. Europe (Austria; Belgium; Czech Republic; Denmark; Estonia; Finland; France; Germany; Lithuania; Luxembourg; Netherlands; Norway; Poland; Russia; Spain; Sweden; Switzerland; UK: England, Scotland) and North America (Canada: British Columbia; USA: Washington).

References. Coppins & James 1979, Diederich 1986, 1996 [Alstrup et al. 2004, Aptroot et al. 2005, Brackel 2007, 2014, Brackel et al. 2018, Christensen et al. 1995, Hafellner & Komposch 2007, Hafellner et al. 2004, Kocourková & van den Boom 2005, Kukwa 2004, 2005, Kukwa & Czarnota 2006, Kukwa & Flakus 2009, Kukwa et al. 2010, 2013, Malíček et al. 2018, Motiejūnaitė 2007, Motiejūnaitė et al. 2016, Roux 2020, Schiefelbein et al. 2012, Stepanchikova et al. 2010, 2017, 2019, 2020, Suija 2005].

***Tremella lobariacearum* Diederich & M. S. Christ. s. lat.**

in Diederich, *Bibl. Lichenol.* 61: 103 (1996). *Type:* Madeira, between Ponta do Sol and Porto Moniz, Rabaçal, on *Lobaria macaronesica*, 8 Apr. 1992, P. Diederich 4935 (LG – holotype; BR – isotype).

Basidiomata inducing the formation of gall-like swellings on the apex of isidia or on the soredia, more rarely on the corticated margin or even the lower surface of the host, pale to dark brown, often blackish, waxy to firm gelatinous, at the beginning subspherical, later generally applanate, sometimes tuberculate, often irregular in form, 0.2–1.6(–4) mm diam. *Context hyphae* thick-walled, 3–4 µm diam., connections not observed with certainty; haustoria present. *Hymenium* containing numerous ellipsoid to clavate probasidia with a basal clamp, sometimes intermixed with conidiogenous cells. *Basidia*, when mature, ellipsoid to clavate, some shortly stalked, 1-septate, septum oblique, rarely longitudinal or transverse, 16–23 × 7–10 µm; epibasidia subcylindrical, 2–3 µm diam., at least 30 µm long. *Basidiospores* shortly ellipsoid, 6.5–8.5 × 5.5–7 µm. *Asexual stage:* asteroconidia present, with 4 arms, 9–15 µm diam., individual arms 2–6 µm long; conidiogenous cells clavate to subcylindrical, not branched, 18–30 × 2.5–4 µm.

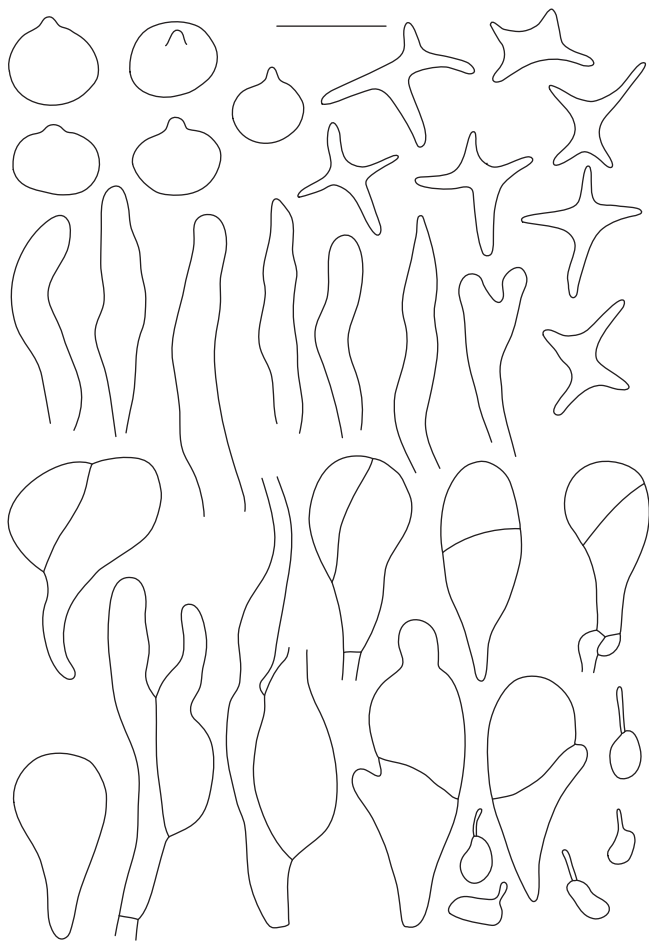
Notes. This species had been described in a wide sense, including populations on *Lobaria* s. lat. and *Pseudocyphellaria* s. lat., as no morphological differences, allowing the recognition of several species, were observed by Diederich (1996). Our molecular results have shown that *Tremella lobariacearum* is a species complex. Specimens on *Crocodia*, *Emmanuelia* and *Pseudocyphellaria* are described here as the new *Tremella flakusii*, *T. emmanueliae* and *T. pseudocyphellariae*, while those on *Lobaria* s. lat. need more study and are not revised here.

Ecology and hosts. *Tremella lobariacearum* s. str. grows on the tip of isidia of *Lobaria macaronesica*, while *T. lobariacearum* s. lat. inhabits isidia, soredia or the thallus of other *Lobaria* s. lat. species.

Distribution. *Tremella lobariacearum* s. str. on *Lobaria macaronesica* is known from Macaronesia (Azores; Ca-



Tremella lobariacearum, Madeira, isotype. Basidiomata on isidia of *Lobaria macaronesica*. Scale bar: 500 µm.



Tremella lobariacearum, Madeira, holotype (modified from Diederich 1996). Basidia, basidiospores, conidiogenous cells, asteroconidia and haustorial branches. Scale bar: 10 μ m.

nary Islands; Madeira), while *T. lobariacearum* s. lat. has been reported from Europe, Macaronesia, North and South America, Africa, Asia and Oceania. No distribution map is given.

Main references. Diederich 1996, Werth et al. 2013.

***Tremella macrobasidiata* J. C. Zamora, Pérez-Ortega & V. J. Rico**

Lichenologist 43: 408 (2011). *Type:* Spain, Castilla y León, Ávila, El Tiemblo, El Castañar, in the apothecia of *Lecanora chlarotera*, on bark of fallen *Castanea sativa*, 40°21'26"N, 4°30'34"W, 1120 m, 18 Sept. 2010, B. Zamora & J. C. Zamora (MA-Fungi 80867 – holotype; MA-Fungi 80868, MAF-Lich 16877 – isotypes).

Basidiomata developing in the hymenium of the host, inconspicuous at first but soon inducing the formation of waxy to gelatinous galls on the apothecia, 0.2–2 mm diam., brownish to dark green or blackish, sometimes with ochraceous, greyish, bluish or pale shades, convex to irregular,

often tuberculate or cerebriform. *Context hyphae* thin- to thick-walled, 2–3.5 μ m diam., clamps present; subbasidial hyphae thick-walled, 2–5 μ m diam.; haustoria present. *Hymenium* with many subspherical to narrowly ellipsoid probasidia with a basal clamp. *Basidia*, when mature, 2–4-celled, with transverse, oblique or longitudinal septa, often slightly constricted at the septa, subglobose, ovoid, broadly ellipsoid, ellipsoid, subfusiform, pyriform, clavate to narrowly clavate, sometimes with an attenuated stalk-like base, 20–51 \times 12–24 μ m, stalk-like base 1–15 μ m long; epibasidia subcylindrical, 3–6(–7) μ m thick, 40–65 μ m long. *Basidiospores* subspherical to broadly ellipsoid, (6.5–)7–12.5(–15) \times (6.5–)7.5–13(–15) μ m; basidiospore germination by formation of hyphae, ballistoconidia (resembling small basidiospores) and blastoconidia, 2–4 \times 1.5–2 μ m (yeast-like cells). *Asexual stage:* asteroconidia rare, mainly in old basidiomata; conidiogenous cells subcylindrical to narrowly fusiform, 14–35 \times 2–6.5 μ m, basal clamps not seen. [Modified from Zamora et al. 2011.]

Notes. *Tremella macrobasidiata* is characterized by its intrahymenial growth in *Lecanora chlarotera* apothecia, forming brownish to dark green galls, sometimes with ochraceous, greyish or even bluish tinges. It develops large and extremely variable basidia, and also rather large basidiospores.

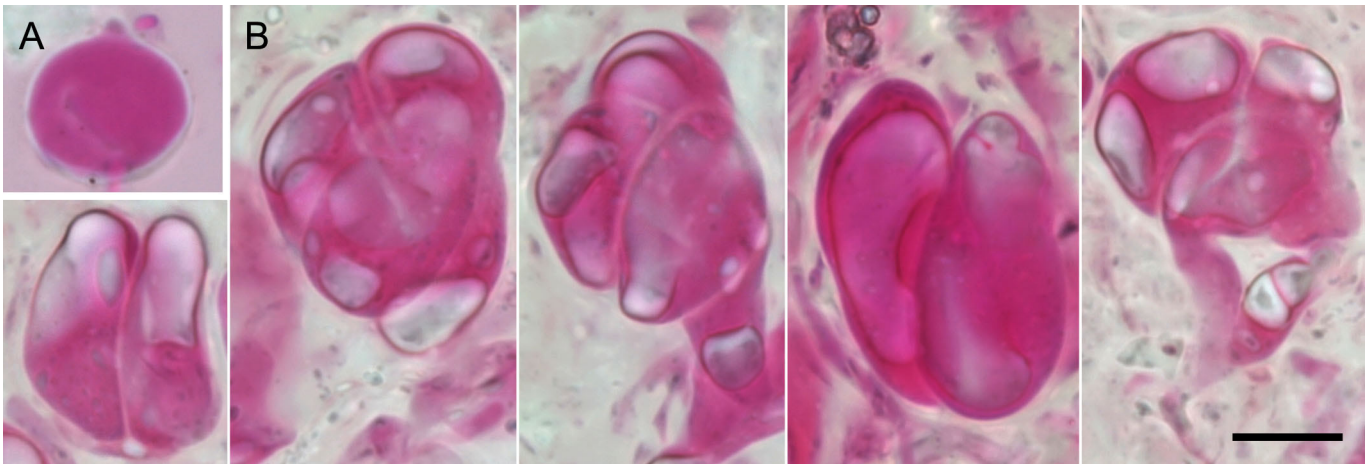
Ecology and host. On apothecia of *Lecanora chlarotera*, highly pathogenic, eventually killing the infected apothecia.

Distribution. Europe (Austria; Portugal; Spain; Sweden) and Asia (Türkiye).

Specimens examined (all on *Lecanora chlarotera*). **Austria:** *Oberösterreich:* Donautal, Engelhartzell, Kronschnig, 310 m, on *Juglans*, 2000, Berger 15049 (herb. Berger). *Steiermark:* Nordalpen, Nördliche Kalkalpen, Hochschwab-Gruppe, an der Strasse



Tremella macrobasidiata, Spain, holotype. Basidiomata on apothecia of *Lecanora chlarotera*. Photo: J. C. Zamora. Scale bar: 1 mm.



Tremella macrobasidiata, Austria, Hafellner 78394. A, Basidiospore. B, Mature 2–4-septate basidia. In phloxine. Scale bar: 10 µm.

von Thörl zum Gasthof Bodenbauer, c. 1.8 km NNW von St. Ilgen, kurz N des Weilers Innerzwain, 47°33'30"N, 15°09'05"E, 780 m, on *Fraxinus*, 2010, Hafellner 78394 (GZU). **Spain:** *Madrid:* Villaviciosa de Odón, urbanización Campodón, on *Prunus*,



Tremella macrobasidiata, Spain, Villaviciosa de Odón, Zamora. Brown basidiomata on apothecia of *Lecanora chlarotera*. Scale bar: 500 µm.



Tremella macrobasidiata, Spain, Horcajo de la Sierra, Zamora. Blackish basidiomata on apothecia of *Lecanora chlarotera*. Scale bar: 500 µm.



Tremella macrobasidiata

2011, Zamora (BR); Horcajo de la Sierra, 41.0594°N, 3.5881°W, 1620 m, on *Fraxinus*, 2011, Zamora (BR).

References. Zamora et al. 2011, 2016 [Ekman et al. 2019, Kocakaya et al. 2018, Tuovinen et al. 2021].

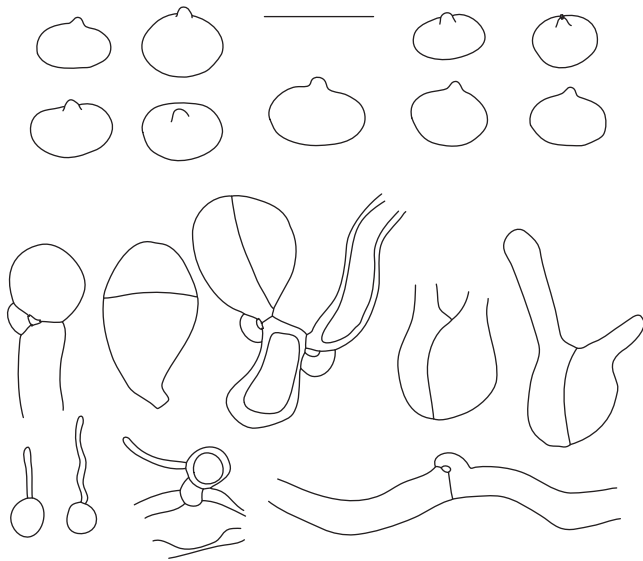
Tremella macroceratis Diederich & Hafellner

in Diederich, *Bibl. Lichenol.* 61: 108 (1996). *Type:* Norway, Sogn og Fjordane, Gem. Luster, Sognefjell, S der Straße von Skolden nach Lom, W von Hervassbu, alt. 1320 m, Blockschuttheide, on *Cladonia macroceras*, 23 Aug. 1984, J. Hafellner 14310 & A. Ochsenhofer (GZU – holotype; BR – isotype).

Basidiomata superficial, subglobose to pulvinate, pale to dark reddish brown, shiny, waxy-gelatinous, 0.2–0.8 mm diam. *Context hyphae* thick-walled, with clamp connections, 3–5 µm thick; haustoria frequent, with clamps. *Hymenium* containing numerous subspherical probasidia with a basal clamp. *Basidia*, when mature, subspherical, with one longitudinal septum, 8.5–12 × 7–8.5 µm, rarely ellipsoid, with one oblique or transverse septum, up to 14 µm long; epibasidia subcylindrical, 1.5–2.5 µm diam., at



Tremella macroceratis, Norway, isotype. Basidiomata on *Cladonia macroceras*. Scale bar: 500 µm.



Tremella macroceratis, Norway, holotype (modified from Diederich 1996). Basidia, basidiospores, hyphae and haustorial branches. Scale bar: 10 µm.

least 17 µm long. *Basidiospores* ellipsoid, $5.5\text{--}7.5(-8) \times (3.5\text{--})4\text{--}5.5$ µm. *Asexual stage* unknown.

Notes. This species is very similar to *Tremella papuana*. Basidiomata are variable in colour, at first pale, concolorous with the thallus, then brownish, later often dark reddish brown. It differs from *T. cladoniae* and also *Zygyomyces bachmannii*, both confined to *Cladonia* hosts, by the basidiomata that are not gall-inducing.

Ecology and host. On the lower part of the podetia of *Cladonia macroceras*.

Distribution. Europe (Norway), known only from the type locality.

Reference. Diederich 1996.



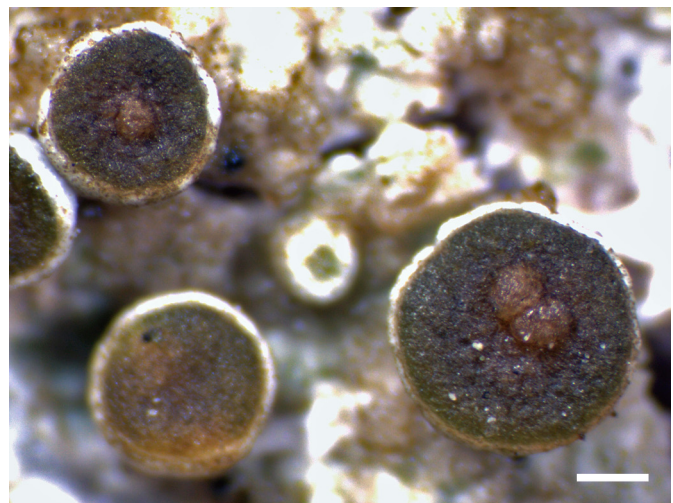
Tremella macroceratis

***Tremella mayrhoferi* J. C. Zamora, Millanes, Etayo & Wedin**

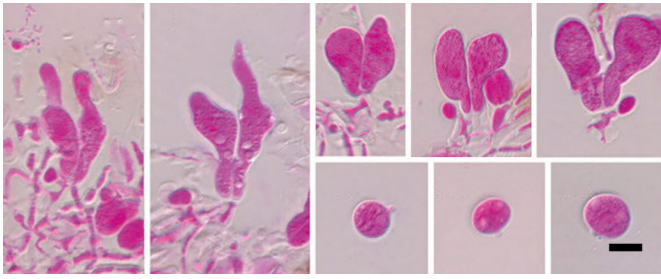
Herzogia 31: 670 (2018). *Type:* Sweden, Uppland, Uppsala parish, Bondkyrko, Hågadalen, 400 m W of Stora Djurgården farmhouse, $59^{\circ}48'50''\text{N}$, $17^{\circ}36'2''\text{E}$, on *Lecanora allophana* apothecia, on bark of young *Populus tremula* trees (mixed forest with *Populus*, *Quercus*, *Corylus*, and *Betula*), 29 Jan. 2018, J. C. Zamora & A. M. Millanes s. n. (UPS L-877384 – holotype).

Basidiomata growing in the hymenium of the host, inducing the formation of broadly convex galls, pale to dark brown, firm to waxy, 0.05–0.4(–0.5) mm diam. *Context hyphae* 2–4 µm thick, clamps not seen; subbasidial hyphae thick-walled, 3–9 µm thick; haustoria present. *Hymenium* containing numerous subspherical, broadly ellipsoid to clavate probasidia with a basal clamp. *Basidia*, when mature, 2–4-celled, with longitudinal, rarely oblique septa, individual cells elongating and growing separately, each $13\text{--}35 \times 7\text{--}20$ µm; epibasidia 6–8 µm thick, up to 20 µm long. *Basidiospores* subspherical to broadly ellipsoid, $8.5\text{--}12 \times 9\text{--}14$ µm. *Asexual stage:* catenulate conidia sometimes present, cells 3–6 µm thick. [Modified from Zamora et al. 2018.]

Notes. *Tremella mayrhoferi* is distinguished from most other lecanoriicolous *Tremella* species by the basidial cells



Tremella mayrhoferi, Sweden, holotype. Basidiomata in the hymenium of *Lecanora allophana*. Photo: J. C. Zamora. Scale bar: 500 µm.



Tremella mayrhoferi, Sweden, holotype (modified from Zamora et al. 2018). Basidia in different stages of development and basidiospores. Scale bar: 10 µm.



Tremella mayrhoferi

that elongate at maturity. This character is also known from the new *T. zamorae*, but basidiomata in that species inhabit the host thallus, not the hymenium.

Ecology and host. In apothecia (hymenium) of *Lecanora allophana*.

Distribution. Europe (Finland; Norway; Spain; Sweden) and North America (USA: Minnesota).

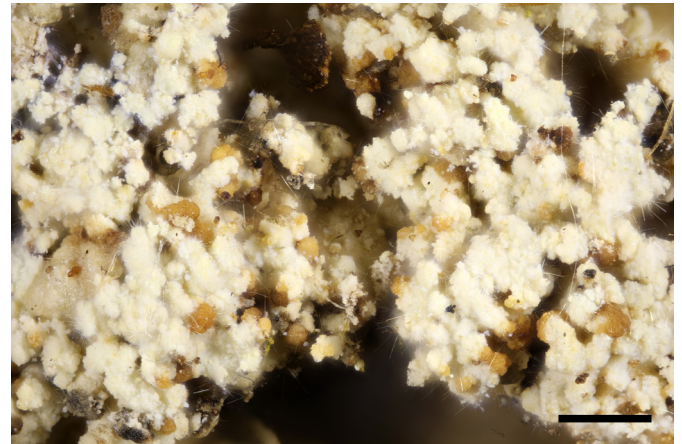
Reference. Zamora et al. 2018.

Tremella microcarpa Diederich

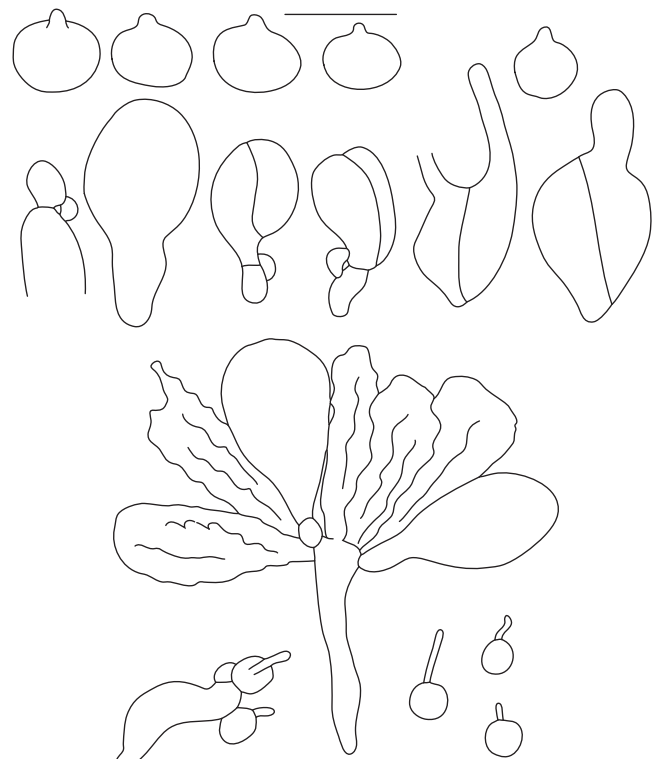
Bibl. Lichenol. 61: 110 (1996). **Type:** Papua New Guinea, Eastern Highlands Province, Mount Gahavisuka Provincial Park, N of Goroka, 6°01' S, 145°25' E, alt. 2400 m, on a sterile sorediate, crustose, corticolous lichen, 3 Aug. 1992, P. Diederich 10493 (LG – holotype; BR – isotype).

Basidiomata waxy-gelatinous, pale yellowish or reddish brown, becoming darker when old, pulvinate when young, later sometimes tuberculate, 0.04–0.2(–0.3) mm diam. **Context hyphae** thin-walled, 1.5–2 µm diam., clamp connections not observed; haustoria frequent, with clamps. **Hymenium** containing numerous ellipsoid to clavate probasidia, often with an attenuated base, with a basal clamp. **Basidia**, when mature, 2-celled, with one longitudinal or oblique septum, ellipsoid and 9.5–12.5 × 7–11 µm, or stalked, 17–20 × 8–10.5 µm; epibasidia subuliform to subcylindrical, 2.5–4 µm diam., 18–25 µm long. **Basidiospores** ellipsoid, 5.5–8.5 × 4.5–7 µm. **Asexual stage** unknown.

Notes. This species is distinguished by the extremely small basidiomata, similar to those of *Tremella coccocarpiæ*,



Tremella microcarpa, Papua New Guinea, isotype. Basidiomata on an unidentified sterile sorediate lichen (cf. *Megalospora*). Scale bar: 500 µm.



Tremella microcarpa, Papua New Guinea, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.

in which basidiospores are, however, smaller, 5.5 × 4–4.5 µm, and basidia slightly longer and narrower.

Ecology and host. On an unidentified sterile sorediate corticolous lichen, perhaps belonging to the genus *Megalospora*.

Distribution. Oceania (Papua New Guinea).

Reference. Diederich 1996.



Tremella microcarpa

Tremella monospora Diederich

Bibl. Lichenol. 61: 113 (1996). *Type:* Peru, Huanuco, Prov. Huanuco, Cerro Carpish, N of the tunnel, 9°38'S, 76°04'W, 2300 m, on *Leptogium*, 22 Febr. 1981, R. Santesson & R. Moberg P44:30 (UPS – holotype; BR – isotype).

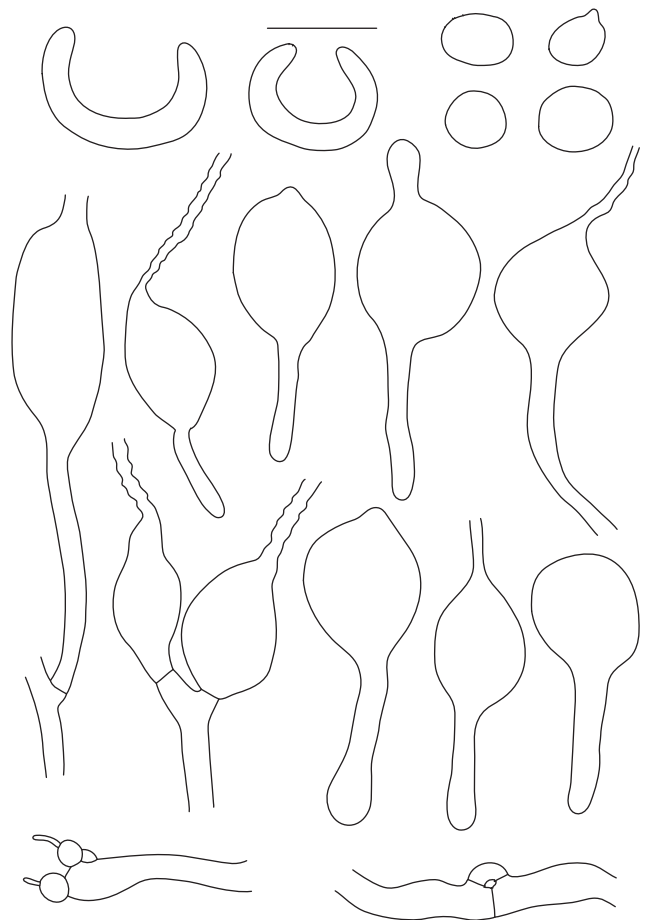
Basidiomata pale brown, waxy-gelatinous, more or less convex, roundish or irregular, 0.1–0.6 mm diam., sometimes confluent. *Context hyphae* thin-walled, 2–3 µm diam., with clamp connections; haustoria present. *Hymenium* containing numerous claviform to ellipsoid probasidia with a long stalk, clamp connections not observed. *Basidia*, when mature, aseptate, 1-celled, with one epibasidium, with a long stalk (5–)8–14(–17) × 1–3 µm, upper part (stalk not included) 9–17 × 7–10 µm, ellipsoid to subspherical, at maturity sometimes separated from the stalk by a septum; epibasidia subulate to subcylindrical, 2–3 µm diam., at least 23 µm long. *Basidiospores* subspherical, 5–7 × 4.5–6 µm. *Asexual stage:* lunate conidia have been observed.

Notes. This is one of the very few known *Tremellales* species with 1-celled basidia, the others being *T. endosporogena* and *Heteroacanthella ellipsospora*, both intrahymenial in the apothecia of *Lecanora carpinea*. It is rapidly distinguished from both by the basidia having a long stalk-like base.

Ecology and host. On the thallus of *Leptogium* sp.

Distribution. South America (Peru), known only from the type locality.

Reference. Diederich 1996.



Tremella monospora, Peru, holotype (modified from Diederich 1996). Basidia, basidiospores, lunate conidia and haustorial branches. Scale bar: 10 µm.



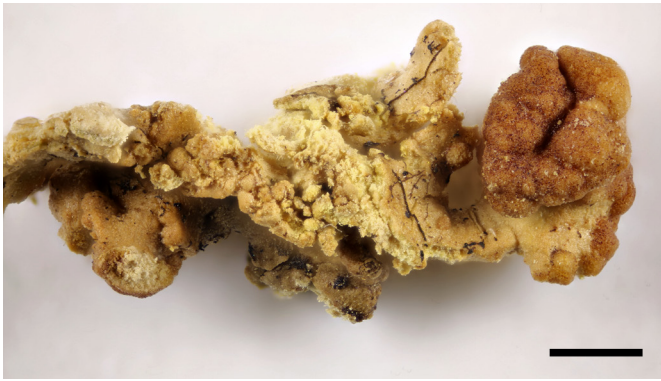
Tremella monospora, Peru, isotype. Brownish basidiomata on the thallus of *Leptogium* sp. Scale bar: 500 µm.



Tremella monospora

Tremella montis-wilhelmii Diederich

Bibl. Lichenol. 61: 116 (1996). *Type:* Papua New Guinea, Simbu Province, Mount Wilhelm, Pindaunde valley, near the hut on the S-shore of lake Piunde, 3600 m, on *Normandina simodense*, 14 March 1987, H. Sipman 22.094 (B – holotype; BR – isotype).



Tremella montis-wilhelmii, Papua New Guinea, isotype. Basidioma on *Normandina simodense*. Scale bar: 500 µm.

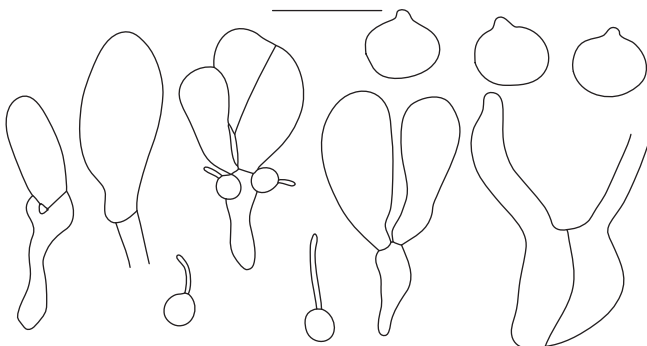
Basidiomata superficial, convex, with a constricted base, when young subglobose, later tuberculate to cerebriform, reddish brown, waxy-gelatinous, not shiny, 0.1–1.4 mm diam. **Context hyphae** 1–2.5 µm diam., clamps not observed; haustoria not rare. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid to clavate, with one transverse, oblique or rarely longitudinal septum, 12–17(–22) × (6–)7–9 µm; epibasidia subcylindrical, 1.5–3 µm diam., at least 20 µm long. **Basidiospores** subglobose, 6–7 × 5–6 µm. **Asexual stage** unknown.

Notes. *Tremella montis-wilhelmii* is morphologically similar to several other lichenicolous species, especially *T. normandinae*, a species with broader basidia, 8.5–11.5 µm broad, that also grows on *Normandina*. No molecular data are available yet from both hosts to test their distinctiveness.

Ecology and host. On the thallus of *Normandina simodense*.

Distribution. Oceania (Papua New Guinea), known only from the type locality.

Reference. Diederich 1996.



Tremella montis-wilhelmii, Papua New Guinea, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.



Tremella montis-wilhelmii

Tremella nashii Diederich

Opuscula Philolichenum 4: 15 (2007). **Type:** USA, Arizona, Apache Co., White Mountains, Apache National Forest, Mount Baldy Wilderness, near beginning of trail 94 along W fork of Little Colorado River at Sheep's Crossing, 33°58'N, 109°31'W, 2860 m, on *Usnea sorediifera*, 7 June 1998, T. Nash 41941 (ASU – holotype; BR – isotype).

Basidiomata waxy-gelatinous, very pale to sometimes dark brown, convex, subspherical or more often elongate, often irregular in form, 0.3–2.5 × 0.2–0.7 mm. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2.5–4 µm diam., at least some with clamp connections; haustoria present, with clamp connections. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, 2–4-celled (in some specimens all 2-celled, in others all 4-celled), with longitudinal or oblique septa, subspherical to ellipsoid, often distinctly stalked, 8–20(–24) × 8.5–12 µm (incl. stalk); epibasidia subcylindrical, 2–4 µm thick, at least 30 µm long. **Basidiospores** subspherical to shortly ellipsoid, 5–8 × 4–6 µm. **Asexual stage** unknown.

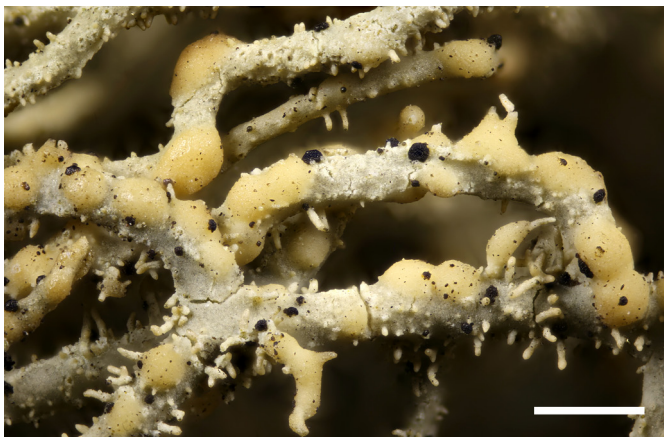
Notes. This species is common on *Usnea hirta* in the USA, Arizona, where it is frequently accompanied by *Biatoropsis hirtae*. Basidiomata often start as elongated, sometimes poorly delimited swellings of the host thallus and are typically pale brown, only exceptionally medium or dark brown. *Biatoropsis hirtae*, on the contrary, has roundish,



Tremella nashii, USA, Arizona, isotype. Basidiomata on the thallus of *Usnea sorediifera*. Scale bar: 500 µm.

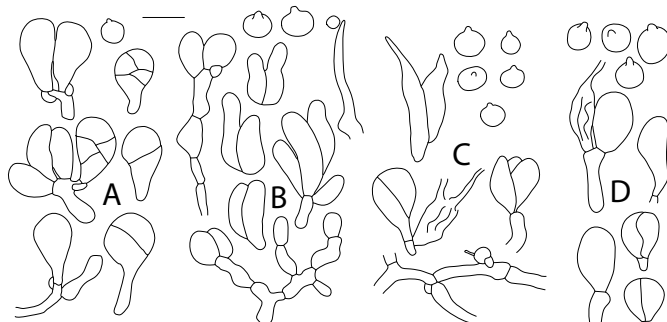


Tremella nashii, USA, Arizona, Thayer 39. Basidiomata on the thallus of *Usnea hirta*. Scale bar: 500 µm.

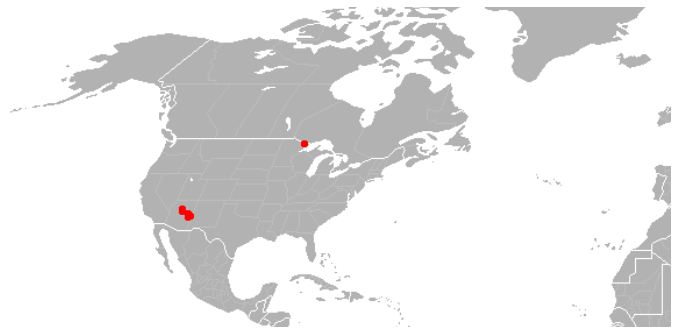


Tremella nashii, USA, Arizona, Walden 10. Basidiomata on the thallus of *Usnea hirta*. Scale bar: 500 µm.

often slightly stipitate basidiomata with a more or less flat surface, that are typically more orange-brown, and has elongate, transversely septate basidia. *Tremella santessonii* Diederich also has transversely septate basidia. *Tremella stevensiana* Diederich has longitudinally septate basidia



A–C, *Tremella nashii*, USA, Arizona. A, holotype, B, Nash 42005, C, Nash 27172. D, *Tremella* aff. *nashii*, Norway, Holien 7110 (modified from Diederich 2007). Basidia, basidiospores and hypha with haustorial branch. Scale bar: 10 µm.



Tremella nashii

that are constantly 2-celled, basidiomata are much smaller, applanate to pulvinate, 0.1–0.3(–0.5) mm diam., and is characterized by the abundant conidiophores, located between basidia, consisting of a 9–21 µm long conidiogenous cell, bearing in the upper part 5–30 ellipsoid conidia.

Ecology and hosts. On the thallus of *Usnea sorediifera*, *U. hirta* and *Usnea* sp.

Distribution. North America (USA: Arizona, Minnesota).

Additional specimens examined. USA: Arizona: Coconino Co., Coconino National Forest, c. 3.58 km SW Crystal Springs and 4.81 km N of Meyers, 34.5015°N, 111.3661°W, on *Pinus ponderosa*, on *Usnea hirta*, 2018, Thayer 39 (BR); Greenlee Co., Apache-Sitgreaves National Forest, c. 26.4 km S Alpine and 10.1 km W of New Mexico border, 33.6104°N, 109.1554°W, on *U. hirta*, 2019, Walden 10 (BR). Minnesota: Lake Co., Superior National Forest, c. 12.58 km NW of Taconite Harbor and 18.81 km N of Little Marais in the Nine Mile Lake Campground, 47.5782°N, 91.0742°W, on *U. sp.*, 2018, Gockman 5585 (BR).

Reference. Diederich 2007.

Tremella aff. *nashii*

Notes. Three Norwegian specimens resemble *Tremella nashii*, but are distinguished by the darker basidiomata.



Tremella cf. *nashii*, Norway, Holien 7227. Basidiomata on the thallus of *Usnea* sp. Scale bar: 500 µm.

Basidia are longitudinally 1-septate, $10\text{--}16 \times 8.5\text{--}9.5\ \mu\text{m}$, and basidiospores are $5\text{--}8.5 \times 5\text{--}8\ \mu\text{m}$. Fresh material in a better condition is needed to assess the identity of these populations.

Ecology and host. On the thallus of an unidentified *Usnea* species.

Distribution. Europe (Norway).

Specimens examined (all on *Usnea*). **Norway:** Trøndelag: Overhalla, W of Foss in a ravine, 1997, Holien 7110 (TRH, BR); Afjord, N-facing slope along river Skjerva, 1997, Holien 7223 (TRH); Trondheim, Byneset, E of Berg, 1997, Holien 7227 (TRH, BR).

Tremella nephromatis Diederich

Bibl. Lichenol. 61: 118 (1996) **Type:** Canada, British Columbia, Kispiox area, c. 9 km NNW of town, N of Date Creek, $55^{\circ}25' \text{N}$, $127^{\circ}48' \text{W}$, on *Nephroma parile*, 16 June 1992, T. Goward & H. Knight 92–350 (UBC – holotype; BR – isotype).

Basidiomata superficial, often developing on soredia of the host, waxy-gelatinous, dark reddish brown, surface matt, strongly convex, subspherical when young, later often irregular, lobate or tuberculate, often alveolate, $(0.1)0.6\text{--}4\ \text{mm}$ diam. **Context hyphae** thin-walled, $1\text{--}2\ \mu\text{m}$ diam., clamps not observed; haustoria present, but rare. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, longitudinally, obliquely or transversely 1-septate, not constricted at the septum, $11\text{--}20 \times 7.5\text{--}10\ \mu\text{m}$; epibasidia subcylindrical, $2\text{--}3.5\ \mu\text{m}$ thick, $20\text{--}26\ \mu\text{m}$ long. Basidiospores subspherical to ellipsoid, $5.5\text{--}8 \times 5\text{--}6(7.5)\ \mu\text{m}$. **Asexual stage** unknown.



Tremella nephromatis, Canada, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: $10\ \mu\text{m}$.



Tremella nephromatis, Canada, British Columbia, isotype. Basidiomata on the thallus of *Nephroma parile*. Scale bar: $500\ \mu\text{m}$.



Tremella nephromatis

Notes. This species is characterized by the large, strongly convex, often irregular, dark reddish brown basidiomata on the thallus of *Nephroma parile*.

Ecology and host. On the thallus, most commonly on soredia of *Nephroma parile*, including var. *endoxantha*.

Distribution. Europe (Russia) and North America (Canada: British Columbia; USA: Alaska, Minnesota).

Additional specimen examined. USA: Minnesota: St Louis Co., Iron Range OHV State Recreation Area, c. $3.77\ \text{km}$ E of Franklin and $4.84\ \text{km}$ N of Gilbert, 47.5322°N , 92.4697°W , on *Nephroma parile*, 2019, Gockman 5804 (BR).

References. Diederich 1996 [Diederich 2003, Spribille et al. 2010, 2020, Zhurbenko 2004].

Tremella nephromopsidis Diederich, sp. nov.

Diagnosis: Characterized by the large, pale to medium brown basidiomatal galls on the thallus of *Nephromopsis* that are initially convex, later resemble apothecia with a narrow base and a large flat or slightly convex disk and a sharp rim, $0.3\text{--}1.2\ \text{mm}$ diam., and the small, longitudinally 1-septate basidia, $10\text{--}17 \times 5\text{--}9\ \mu\text{m}$.

Etymology: From *Nephromopsis*, the host lichen.

Type: USA, California, Marin Co., Mt. Tamalpais State Park, rocky headlands along Hwy 1, c. $1\ \text{mi}$ S of Stinson Beach, hill over-



Tremella nephromopsidis, USA, California, holotype. Convex basidiomatal galls on the lower thallus surface of *Nephromopsis orbata*. Scale bar: 500 μ m.



Tremella nephromopsidis, USA, California, holotype. Basidiomatal galls on the upper thallus surface of *Nephromopsis orbata* simulating apothecia. Scale bar: 500 μ m.

looking Rocky Pt. parking area, 90 m (300 ft), on Douglas fir (*Pseudotsuga menziesii*), on *Nephromopsis orbata*, 10 Febr. 2001, R. Robertson 5710 (NY – holotype; BR – isotype).

Mycobank: MB844667

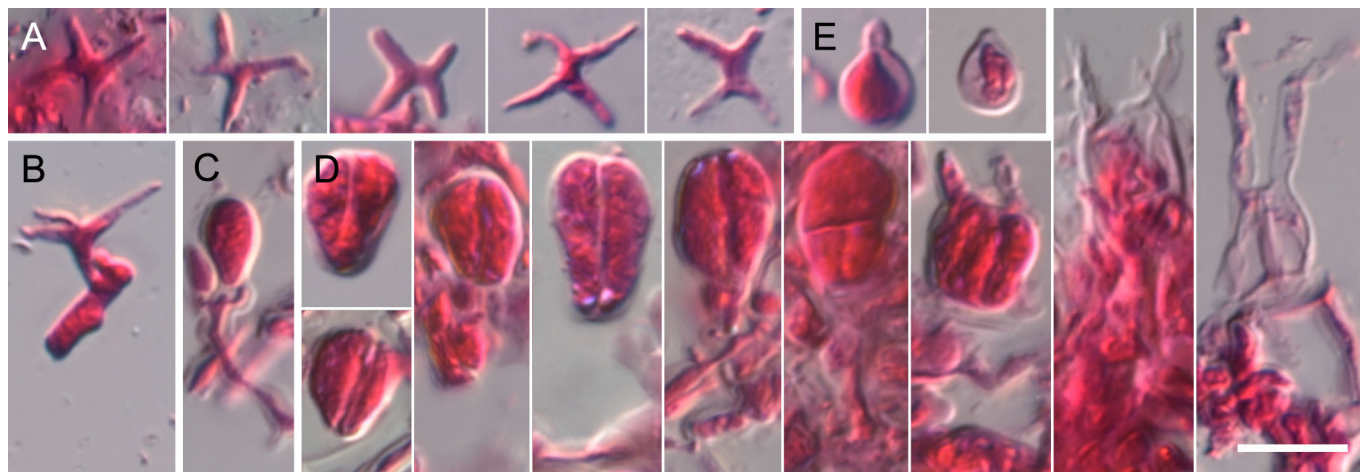
Basidiomata superficial, gall-inducing, at first small and convex, later becoming larger, with a narrow base and a flat or slightly convex upper surface, and a sharp rim, imitating host apothecia, not gelatinous, pale to medium brown, 0.3–1.2 mm diam. *Context hyphae* not observed; sub-basidial hyphae thick-walled, 2–3.5 μ m diam.; haustoria present, basal clamp not observed. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, shortly to elongate ellipsoid or pyriform, not stalked, 2-celled, with a longitudinal or rarely oblique septum, 10–17 \times 5–9 μ m; epibasidia cylindrical, at least 28 μ m long. *Basidiospores* in a poor condition, almost all collapsed in the holotype, subspherical to ellipsoid, c. 6 \times 6.5

μ m (one observed). *Asexual stage*: asteroconidia abundant, individual arms 3.5–8 μ m long, conidiogenous cells 9–18 \times 2–5.5 μ m, apically with several short, irregular branches having produced asteroconidia.

Notes. Amongst the lichenicolous *Tremella* species with small, longitudinally 1-septate basidia and pale to medium brown, gall-inducing basidiomata, this species is distinguished by the large galls that eventually simulate apothecia, with a narrow base and a large flat ‘disk’ surrounded by a sharp rim. The type specimen presents numerous basidia and conidiogenous cells producing asteroconidia. Basidiospores, however, are rare and too old, mostly collapsed, so that only one could be measured.

Ecology and host. On the thallus of *Nephromopsis orbata*.

Distribution. North America (USA: California), known only from the type locality.



Tremella nephromopsidis, USA, California, holotype. A, Asteroconidia. B, Conidiogenous cell producing an asteroconidium. C, Basally clamped probasidium. D, Basidia in different stages of development, E, Basidiospores. In phloxine. Scale bar: 10 μ m.

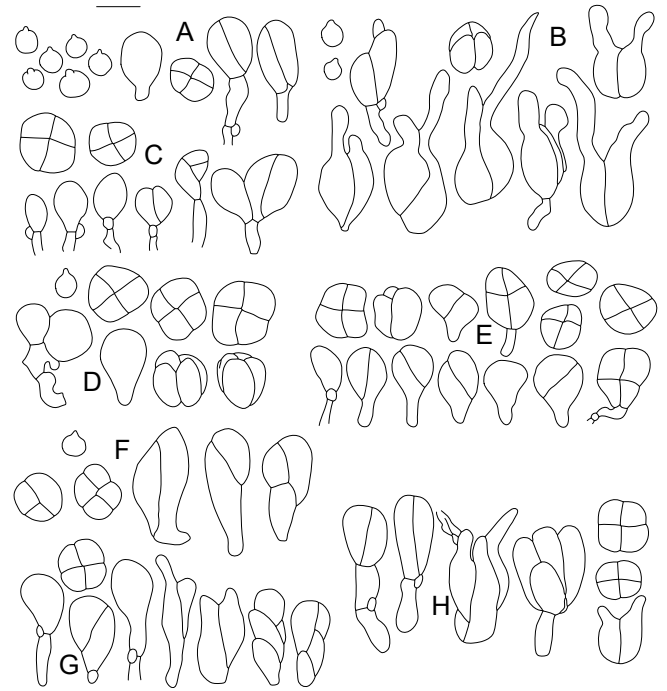
*Tremella nephromopsidis**Tremella nieblae****Tremella nieblae* Diederich & van den Boom**

in Diederich, *Opuscula Philolichenum* 4: 16 (2007). *Type*: USA, California, Monterey Co., SSW of Carmel, Point Lobos State Reserve, Bird Island Trail, 121°56'W, 36°28'N, 25 m, on *Niebla cephalota*, 23 July 2002, P. van den Boom 29018 (BR – holotype; BR, herb. van den Boom – isotypes).

Basidiomata indistinct, inducing the formation of large, convex, subspherical or elongate to bullate galls on the



Tremella nieblae, USA, California, isotype. Basidiomatal gall on the thallus of *Niebla cephalota*. Scale bar: 500 μ m.



Tremella nieblae, USA and Mexico. A, holotype, C, Cole 7909F, D, Tucker 34216B, B, Cole 7909, E, Wetmore 75724a, F, van den Boom 29229, H, van den Boom 29474, G, van den Boom 29214 (modified from Diederich 2007). Basidia and basidiospores. Scale bar: 10 μ m.



Tremella nieblae, USA, California, Robertson 6545. Bullate basidiomatal gall on the thallus of *Niebla homalea*. Scale bar: 2 mm.

host thallus, mostly 0.8–10 mm diam.; gall surface similar to that of the host, but frequently more intensively pigmented, either darker or more orange-brown. *Context hyphae* not observed; subbasidial hyphae 2–4 μ m diam., with clamp connections; haustoria not observed. *Hymenium* containing numerous subspherical, ellipsoid or pyriform probasidia with a basal clamp. *Basidia*, when mature, 4-celled, with longitudinal or rarely oblique septa, some not stalked, others slightly or distinctly stalked, 11–28 \times 8.5–15 μ m (incl. stalk); epibasidia subcylindrical, 2.5–4.5 μ m thick, up to at least 30 μ m long. *Basidiospores* subspherical to shortly ellipsoid, 4–5.5(–6.5) \times 4–5.5(–6) μ m. *Asexual stage* unknown.

Notes. This common taxon is inducing large, convex galls on the thallus of *Niebla* species. Basidiomata are often

indistinct: basidia are intermixed with host hyphae in the cortical layer of the galls, and basidiospores are rarely observed.

Ecology and hosts. On the thallus and apothecial margin of *Niebla cephalota* and *N. homalea*, inducing the formation of distinct, relatively large, subspherical or elongate, on *N. homalea* frequently bullate galls.

Distribution. North America (Mexico: Baja California; USA: California), obviously very common.

References. Diederich 2007 [Kocourková et al. 2012].

Tremella normandinae Diederich

Bibl. Lichenol. 61: 120 (1996). **Type:** Hawaii, Oahu, Pupukea, on sunny, dead *Acacia koa* in open forest of introduced *Eucalyptus* and *Mimisops*, alt. 300 m, on *Normandina pulchella*, 29 July 1965, O. & I. Degener (M 4837 – holotype [ex herb. Klement]).

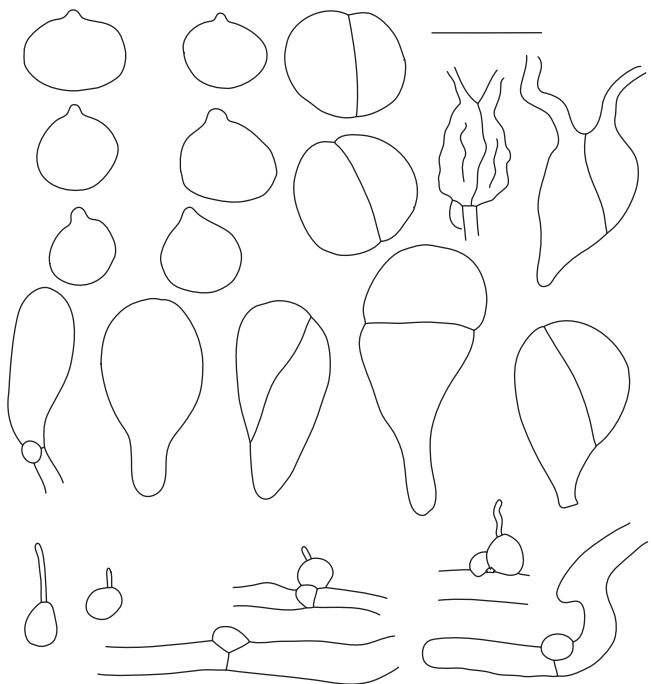
Basidiomata superficial, convex, often with a constricted base, pale or pinkish brown, waxy, not shiny, 0.2–0.6 mm diam. **Context hyphae** 1.5–2.5 µm diam., clamp connections not observed; haustoria frequent. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid to clavate, with one transverse, oblique or longitudinal septum, (12–)14.5–21(–24) × 8.5–11.5 µm; epibasidia subcylindrical, 1.5–3 µm diam., at least 30 µm long. **Basidiospores** subglobose, 6.5–8.5 × 6–7 µm. **Asexual stage** unknown.

Notes. This is a rare species inducing the formation of convex galls on the thallus of *Normandina pulchella*. *Tremella montis-wilhelmii*, described from *N. simodense*, is distinguished by the narrower basidia, 12–17 × 7–9 µm and larger basidiomatal galls, 0.1–1.4 mm diam.

Ecology and host. On the thallus of *Normandina pulchella*.

Distribution. Europe (UK: Scotland) and Oceania (Hawaii).

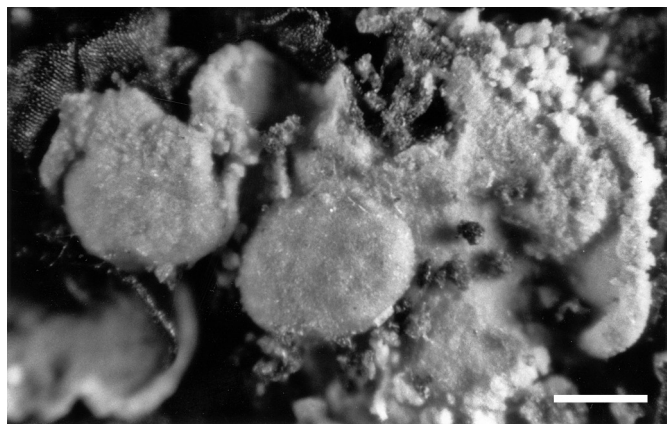
Reference. Diederich 1996.



Tremella normandinae, Hawaii, holotype (modified from Diederich 1996). Basidia, basidiospores, hyphae and haustorial branches. Scale bar: 10 µm.



Tremella normandinae



Tremella normandinae, Hawaii, holotype (modified from Diederich 1996). Basidiomata on *Normandina pulchella*. Scale bar: 250 µm.

Tremella occultixanthoriae Diederich, Geyselings & Millanes, sp. nov.

Diagnosis: Characterized by the pulvinate, pale orange-brown, waxy-gelatinous basidiomata growing on the lower thallus surface of *Xanthoria parietina*, the subspherical to ellipsoid, 4-celled, longitudinally septate basidia, 8.5–11.5 × 8–10.5 µm, and the reduced epibasidia acting as conidiogenous cells, producing hyaline, aseptate conidia, 4.5–5.5 × 4–4.5 µm, most with a hyaline basal appendage.

Etymology: From *occultus*, hidden, referring to the basidiomata hiding under the host thallus, and *Xanthoria*, the host lichen.

Type: Belgium, Leuven, city cemetery, Nieuwe Kerkhofdreef, 3001 Heverlee, 50.8701°N, 4.7149°E, 40 m, on horizontal and vertical surface of hard limestone of a grave, on *Xanthoria parietina*, 3 July 2021, P. Diederich 19596 & D. Ertz (BR – holotype; NY, S – isotypes).



Tremella occultixanthoriae, Belgium, type locality. All examined saxicolous and some corticolous thalli of *Xanthoria parietina* were infected.



Tremella occultixanthoriae, Belgium, Geyseling (BR). Basidiomata on the lower thallus surface of *Xanthoria parietina*. Scale bar: 500 μ m.

MycoBank: MB844668

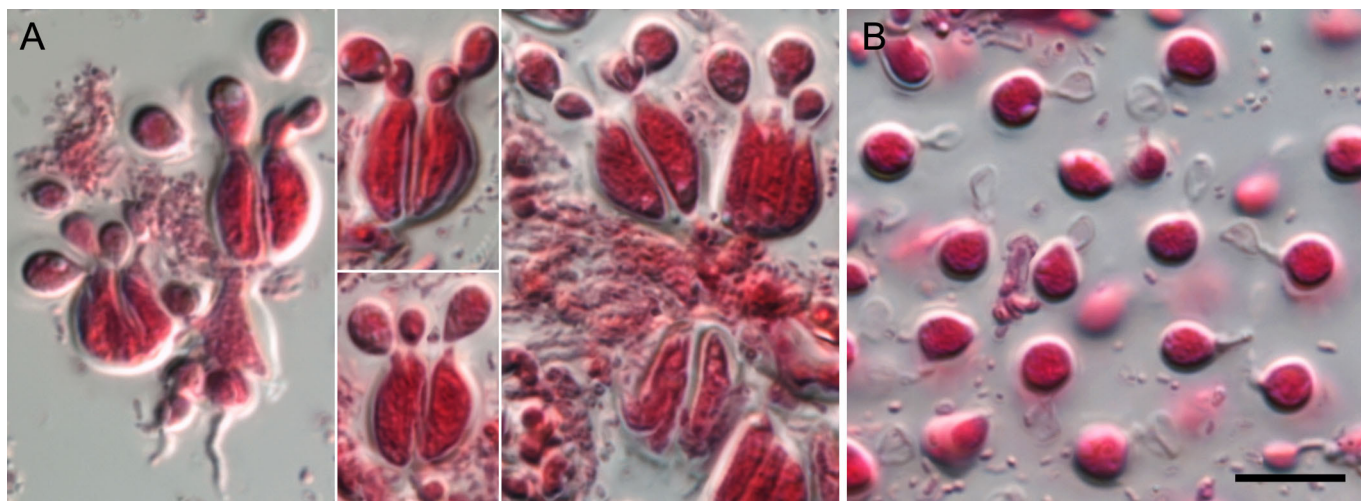
Basidiomata developing on the lower surface of the host thallus, pulvinate, waxy-gelatinous, pale orange-brown, roundish to slightly elongate, well delimited, dispersed but occasionally fusing, 0.25–0.6 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3.5–4.5 μ m thick; haustoria present, tremelloid, subspherical to ellipsoid, 3–4.5 μ m diam. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid, 4-celled, with longitudinal septa, 8.5–11.5 \times 8–10.5 μ m, wall 0.8–1 μ m; epibasidia reduced, functioning as conidiogenous cells, with conidia appearing as produced directly from the basidia. *Basidiospores* unknown. *Conidiogenesis* probably holoblastic. *Conidia* hyaline, aseptate, ellipsoid, 4.5–5.5 \times (3.5–)4–4.5 μ m, wall c. 0.5 μ m thick, basally truncate, frequently with a hyaline basal appendage, 3.5–6 \times 1.5–4 μ m.

Notes. This species is unusual in two ways. First, basidiomata develop exclusively on the lower surface of the host thallus, making them thus invisible in the field, unless thalli are removed from the substrate, and second, epibasidia are reduced or missing and basidiospores not produced, while basidia produce instead sessile conidia. A similar conidiogenesis is known from *Tremella cetraculeata* and *T. cetrariae*, which differ by the black, gelatinous, pustulate basidiomata and conidia lacking a basal appendage.

Ecology and host. On the lower thallus surface of *Xanthoria parietina*, mainly saxicolous on a grave, also on an old *Fagus*.

Distribution. Europe (Belgium), known only from the type locality.

Additional specimens examined. **Belgium:** Same locality as the type, Geyselings (BR); id., on *Fagus*, Diederich 19597 (BR).



Tremella occultixanthoriae, Belgium, holotype. A, Basidia, conidia and haustoria (left photo). B, Conidia, each with a hyaline basal appendage. In phloxine. Scale bar: 10 μ m.



Tremella occultixanthoriae

***Tremella octosporae* Diederich & Sérus., sp. nov.**

Diagnosis: Characterized by the small, subspherical or elongate, pale to medium brown, waxy-gelatinous basidiomata on the thallus of *Agonimia octospora*, 0.15–0.35 mm diam., basidiospores $6\text{--}7 \times 6.5\text{--}7.5 \mu\text{m}$, and the mainly longitudinally 1-septate basidia, $9\text{--}16.5 \times 8\text{--}13 \mu\text{m}$.

Etymology: From *Agonimia octospora*, the host lichen.

Type: France, Pyrénées-Atlantiques, vallée de la Bidouze, entre les sources et le captage d'eau, 500–600 m, futaie de hêtres, mélangée de *Fraxinus*, *Ulmus* et *Tilia* dans le fond de la vallée et sous-bois de *Corylus*, on *Agonimia octospora*, 9 July 1989, E. Sérusiaux 10490 (LG – holotype; BR – isotype).

Mycobank: MB844672

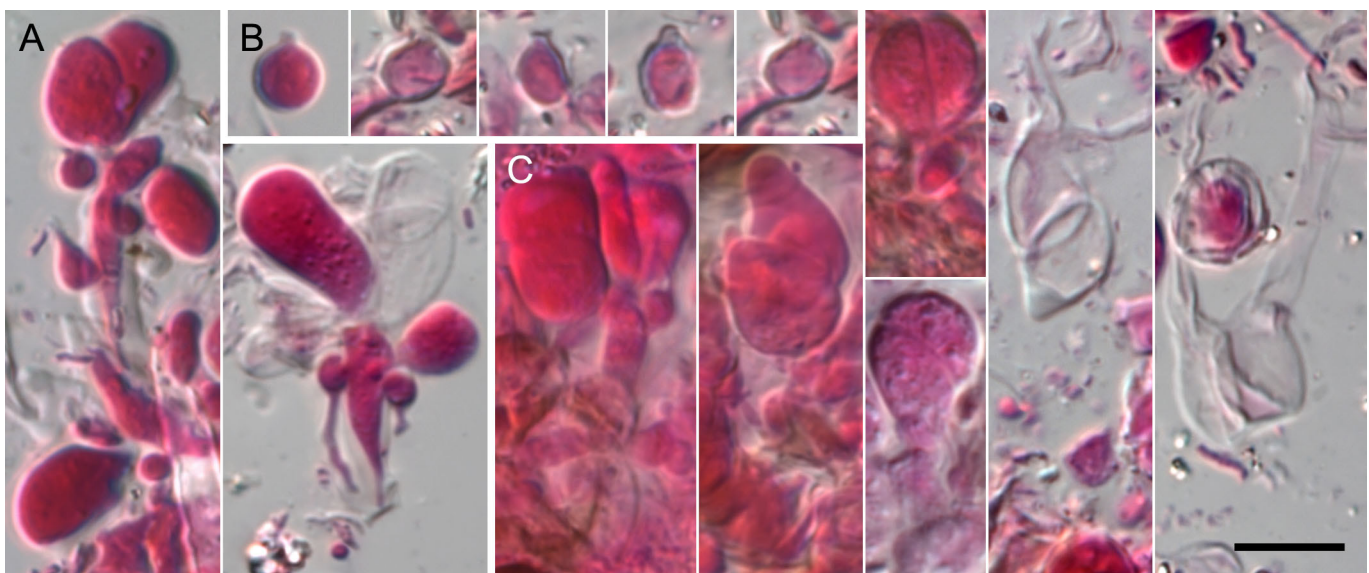
Basidiomata superficial, pulvinate, subspherical or elongate, waxy-gelatinous, pale to medium brown, 0.15–0.35 mm diam., gall inducing, with a rough, not shiny surface. **Context hyphae** $1.5\text{--}3 \mu\text{m}$ diam.; subbasidial hyphae thick-walled, $3\text{--}5.5 \mu\text{m}$ diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous subspherical probasidia with a basal clamp. **Basidia**, when mature, sub-



Tremella octosporae, France, holotype. Basidiomata on the thallus of *Agonimia octospora*. Scale bar: 500 μm .

spherical to ellipsoid, 2-celled, with a longitudinal, rarely oblique or transverse septum, $9\text{--}16.5 \times 8\text{--}13 \mu\text{m}$; epibasidia cylindrical, at least $30 \mu\text{m}$ long. **Basidiospores** subspherical, $6\text{--}7 \times 6.5\text{--}7.5 \mu\text{m}$. **Asexual stage** not observed.

Notes. This taxon needs to be compared with the lichenicolous *Tremella* species inducing small brownish galls on the host thallus and with mainly longitudinally 1-septate basidia. Basidiomata of *Tremella coccocarpiæ* and *T. microcarpa* are much smaller, usually $< 0.2 \text{ mm}$; *T. papuana* and *T. microceratis* have narrower basidiospores, $< 5.5 \mu\text{m}$; basidia in *T. parmeliellæ* are mainly transversely septate; and *T. montis-wilhelmii* and *T. normandinae* have larger basidiomata and more elongate basidia. The differences with *T. pacificæ*, also growing on *Agonimia*, are given under that species.



Tremella octosporae, France, holotype. A, Fertile hyphae, probasidia and haustoria. B, Basidiospores. C, Basidia in different stages of development. In phloxine. Scale bar: 10 μm .

*Tremella octosporae*

Ecology and host. On the thallus of *Agonimia octospora* in a *Fagus*-dominated forest.

Distribution. Europe (France), known only from the type locality in the Pyrénées-Atlantiques.

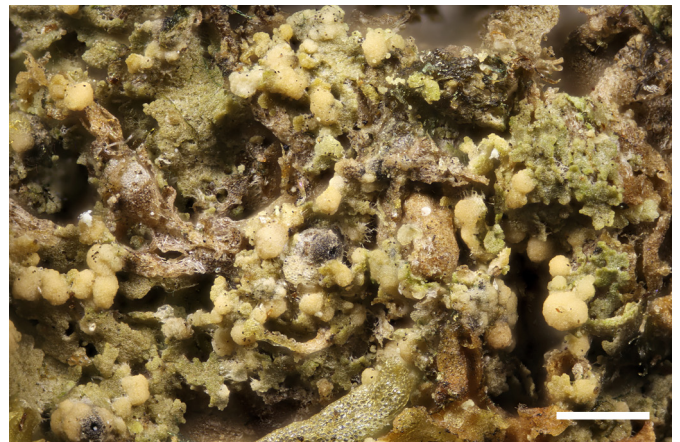
***Tremella pacifica* Diederich & van den Boom, sp. nov.**

Diagnosis: Characterized by the small, subspherical, pale brown, waxy-gelatinous basidiomata on the thallus of *Agonimia pacifica*, 0.1–0.3 mm diam., the particularly small basidiospores, $3.5\text{--}4.5 \times 3.5\text{--}4\text{ }\mu\text{m}$, and the mainly longitudinally 1-septate basidia, $7.5\text{--}15.5 \times 5\text{--}8\text{ }\mu\text{m}$.

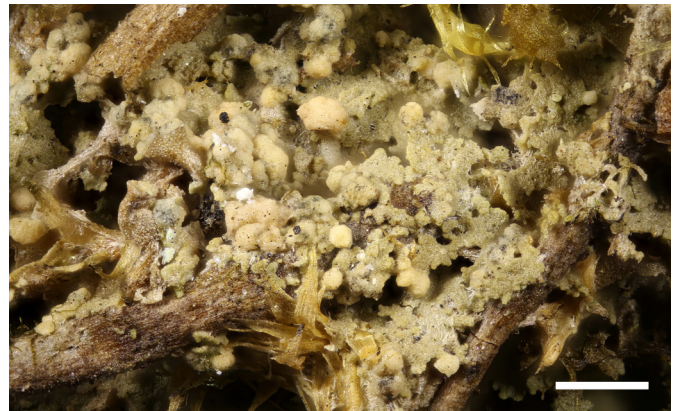
Etymology: From *Agonimia pacifica*, the host lichen.

Type: Dominican Republic, Prov. Puerto Plata, S of Puerto Plata, Parc National 'Isabel de Torres', Pico Isabel de Torre, $19^{\circ}45.73'\text{N}$, $70^{\circ}42.68'\text{W}$, 770 m, botanical garden with damp and open forest with mixed trees and shrubs, on palm, on *Agonimia pacifica*, 29 Jan. 2008, P. van den Boom 39090 (BR – holotype; herb. van den Boom – isotype).

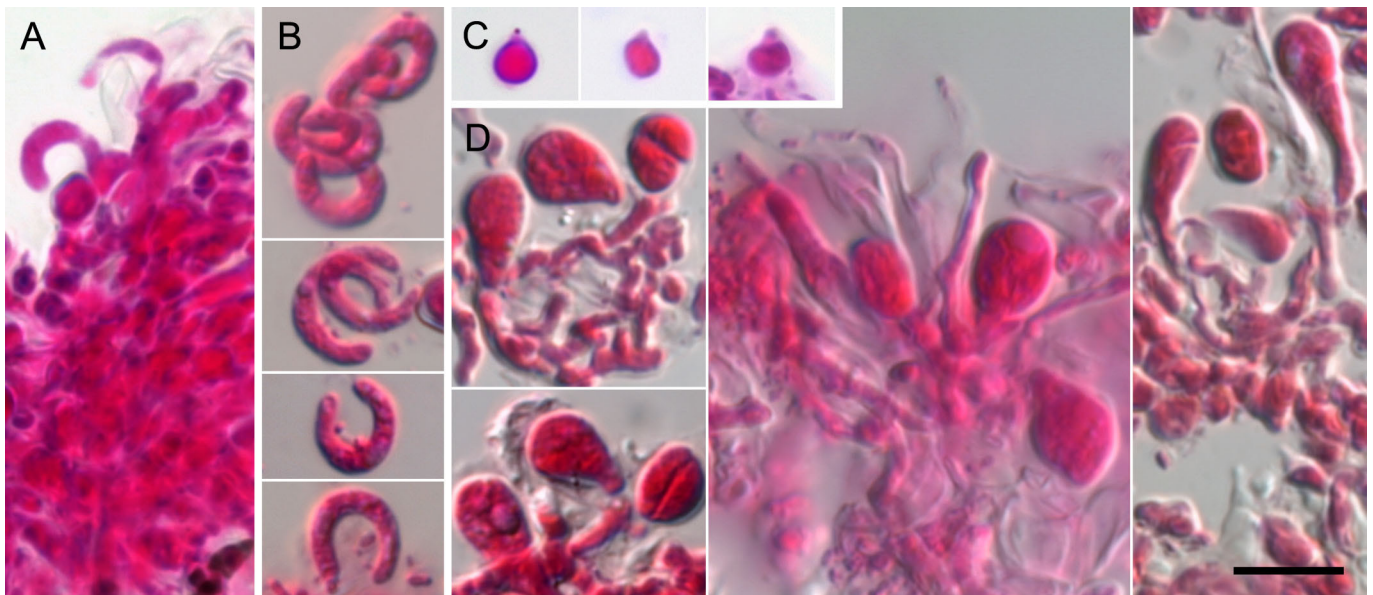
Mycobank: MB844673



Tremella pacifica, Dominican Republic, holotype. Basidiomata on the thallus of *Agonimia pacifica*. Scale bar: 500 μm .



Tremella pacifica, Dominican Republic, holotype. Basidiomata on the thallus of *Agonimia pacifica*. Scale bar: 500 μm .



Tremella pacifica, Dominican Republic, holotype. A, Developing lunate conidia, still attached to conidiogenous cells. B, Mature lunate conidia. C, Basidiospores. D, Basidia in different stages of development. In phloxine. Scale bar: 10 μm .

Basidiomata superficial, pulvinate, subspherical, sometimes slightly tuberculate, waxy-gelatinous, pale brown, 0.1–0.3 mm diam., gall inducing, with a smooth surface. *Young galls* entirely composed of subspherical to ellipsoid host cells, $5.5\text{--}8 \times 3\text{--}5 \mu\text{m}$; fertile hymenium developing in some regions, later occupying the entire the gall. *Context hyphae* not observed; subbasidial hyphae thick-walled, $2\text{--}3 \mu\text{m}$ diam.; haustoria present, with a basal clamp. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, ellipsoid, 2-celled, with a longitudinal or oblique septum, $7.5\text{--}15.5 \times 5\text{--}8 \mu\text{m}$, sometimes with an elongate lower cell and then up to $18 \mu\text{m}$ long; epibasidia cylindrical, at least $30 \mu\text{m}$ long. *Basidiospores* subspherical, $3.5\text{--}4.5 \times 3.5\text{--}4 \mu\text{m}$. *Asexual stage*: lunate conidia present (some still attached to the conidiogenous cell have been observed), c. $7.5\text{--}12.5 \mu\text{m}$ diam. (largest outer diam.) and $2\text{--}3 \mu\text{m}$ thick.

Notes. This species is distinguished from almost all other known lichenicolous *Tremella* species by the particularly small basidiospores. *T. psoroglaenae*, with similarly sized basidiospores ($4\text{--}5 \times 3.5\text{--}4.5 \mu\text{m}$), is readily distinguished by the medium to dark brown basidiomata, the often slightly broader basidia, $10\text{--}16 \times 7\text{--}10 \mu\text{m}$, and the different host choice, *Psoroglaena* sp. *Tremella octosporae*, also developing on *Agonimia*, has much larger basidiospores, $6\text{--}7 \times 6.5\text{--}7.5 \mu\text{m}$, slightly darker basidiomatal galls with a rough, not smooth surface, and constantly broader basidia, $9\text{--}16.5 \times 8\text{--}13 \mu\text{m}$.

Diederich (1996) reported the observation of lunate conidia in *Tremella lobariacearum*, *T. monospora* and *Zyzygomyces* species, but never observed where they were produced and thus was not sure whether they really belonged to the basidiomycete. In the type of *Tremella pacifica*, numerous lunate conidia have been observed, including two fixed at the end of conidiogenous cells within the fertile hymenium. The conidiogenous cells were obscured by the other cells from the hymenium and could not be studied.

Ecology and host. On the thallus of *Agonimia pacifica* on a palm in a tropical botanical garden.

Distribution. Caribbean ([Dominican Republic](#)), known only from the type locality.



Tremella pacifica

Tremella papuana Diederich

Bibl. Lichenol. 61: 123 (1996). *Type*: Papua New Guinea, Eastern Highlands Province, Mount Gahavisuka Provincial Park, N of Goroka, along trail to lookout, little disturbed mossy mountain forest, on *Hypogymnia pseudobitteriana*, 2400 m, $6^{\circ}1' \text{ S}$, $145^{\circ}25' \text{ E}$, 3 Aug. 1992, P. Diederich 10494 (LG – holotype; BR – isotype).

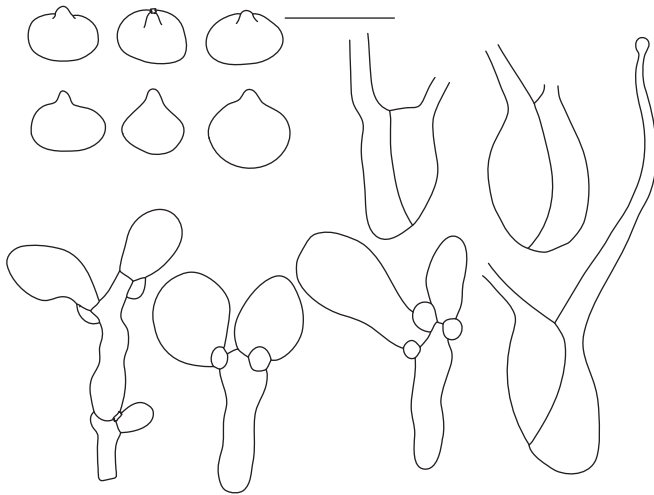
Basidiomata applanate to pulvinate, discoid, waxy-gelatinous, shiny, whitish or pale greyish brown when young, becoming almost black when old, always darker in the centre, $0.2\text{--}0.5 \text{ mm}$ diam. *Context hyphae* $1\text{--}2 \mu\text{m}$ diam., clamps not observed; subbasidial hyphae thick-walled, $2.5\text{--}3.5 \mu\text{m}$ diam., with clamps; haustoria with clamps. *Hymenium* containing numerous ellipsoid probasidia with a basal clamps. *Basidia*, when mature, ellipsoid, with one longitudinal or slightly oblique septum, the two cells sometimes not equal in size, $11\text{--}15 \times 6.5\text{--}8.5 \mu\text{m}$; epibasidia cylindrical, $1.5\text{--}2.5 \mu\text{m}$ thick, at least $30 \mu\text{m}$ long. *Basidiospores* ellipsoid, $6\text{--}7.5 \times 3.5\text{--}6 \mu\text{m}$. *Asexual stage* unknown.



Tremella papuana, Papua New Guinea, isotype. Basidiomata on *Hypogymnia pseudobitteriana*. Scale bar: $500 \mu\text{m}$.



Tremella papuana, Canada, British Columbia, Goward 99-335. Basidiomata on *Hypogymnia imshaugii*. Scale bar: $500 \mu\text{m}$.



Tremella papuana, Papua New Guinea, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 μ m.



Tremella papuana

Notes. This is a poorly known and rarely recorded *Tremella* taxon having distinct basidiomata on the thallus of *Hypogymnia* species. *Tremella hypogymniae* and *T. tubulosae*, on the contrary, are inducing convex galls. Macroscopically, it strongly resembles *Tremella macroceratis*, described from *Cladonia* thalli.

Ecology and hosts. On the thallus of *Hypogymnia pseudo-bitteriana* and *H. imshaugii*.

Distribution. North America (Canada: British Columbia) and Oceania (Papua New Guinea).

References. Diederich 1996 [Diederich 2003].

Tremella parmeliarum Diederich

Bibl. *Lichenol.* 61: 125 (1996). **Type:** Papua New Guinea, Madang prov., Huon Peninsula, Finisterre Range, Yupna valley, Teptep village, on *Parmotrema reticulatum*, 30 July 1992, P. Diederich 10816 (LG – holotype; BR – isotype).

Basidiomata inducing the formation of convex galls with a strongly constricted base, medium to dark chestnut brown, except sometimes delimited parts that are concolorous with

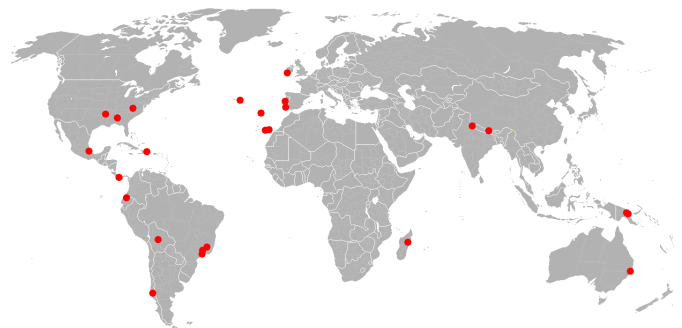


Tremella parmeliarum, Papua New Guinea, isotype. Basidioma on *Parmotrema reticulatum*. Scale bar: 500 μ m.

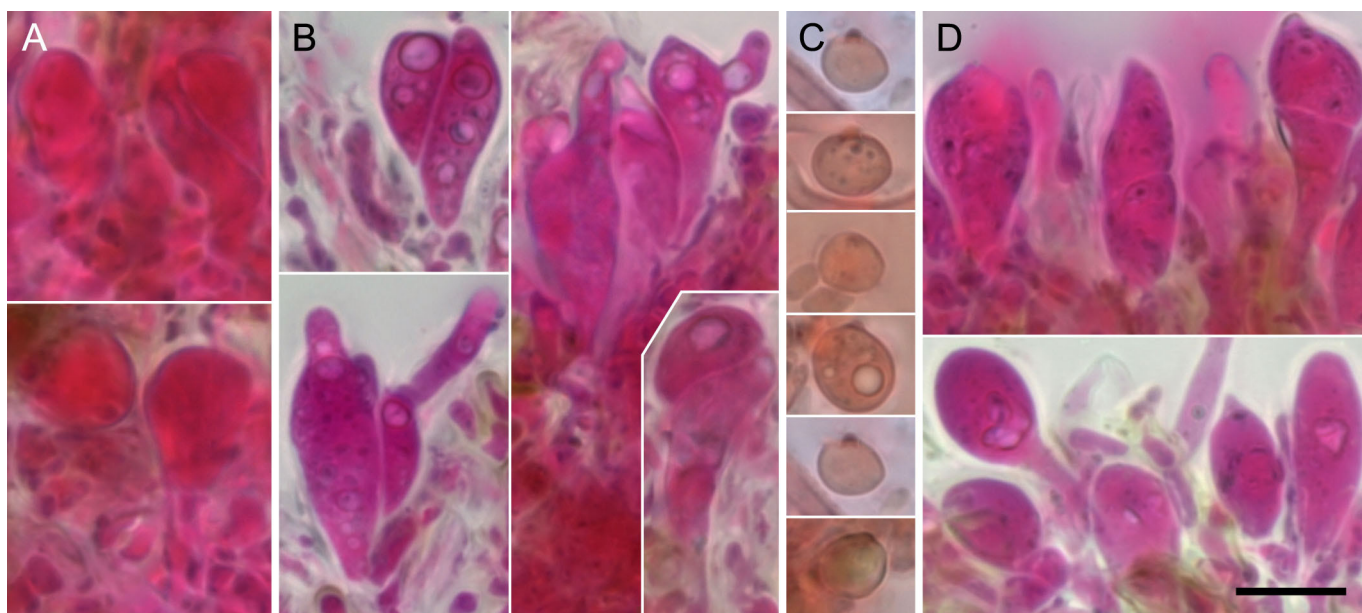
the host thallus, 0.25–5 mm diam.; surface smooth, shiny, sometimes with a central depression, rarely becoming almost cerebriform. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2–3 μ m diam.; haustoria not observed. *Hymenium* containing numerous ellipsoid or subspherical probasidial initials, basal clamps not observed. *Basidia*, when mature, subspherical to ellipsoid, longitudinally or obliquely 1-septate, 10–22 \times 6.5–13 μ m, rarely transversely septate and then clavate and sometimes with an attenuated stalk-like base, 22–30 \times 10–11.5 μ m; epibasidia 3–4 μ m diam., at least 30 μ m long. *Basidiospores* ellipsoid, 6–8 \times 5–6(–7.5) μ m.

Notes. This species forms very characteristic large, strongly convex, chestnut brown, shiny basidiomata on the thallus of *Parmotrema reticulatum*. Former reports from other *Parmotrema* species by Diederich (1996) are here regarded as belonging to other species. Basidia are constantly 1-septate.

Ecology and host. On the thallus of *Parmotrema reticulatum*. Del-Prado et al. (2016) showed that the *P. reticulatum*-*pseudoreticulatum* complex is heterogeneous and includes at least eight genetically distinct species, which are, however, not yet formally described. Therefore it is not possible at this moment to establish how many of these are inhabited by *Tremella parmeliarum*.



Tremella parmeliarum



Tremella parmeliarum. A, Papua New Guinea, holotype, B–C, Brazil, ISE 52077, D, Bolivia, Etayo 33998B. A–B, D, Basidia, in phloxine. C, Basidiospores, in ammoniacal Congo red. A–B, D, in phloxine. Scale bar: 10 μ m.



Tremella parmeliarum, Azores, Sao Miguel, Diederich 16977. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, Canary Islands, Tenerife, Diederich 16574. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, Brazil, Oliveira (ISE 52077). Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, Brazil, Buck 26480. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, USA, Arkansas, Wetmore 85928. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, USA, Arkansas, Wetmore 85928. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, Mexico, 2007, Egan. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.



Tremella parmeliarum, Mexico, 2007, Egan. Basidiomata on *Parmotrema reticulatum*. Scale bar: 1 mm.

Distribution. Europe (Ireland; Portugal), Macaronesia (Azores; Canary Islands; Madeira), North America (Mexico; USA: Alabama, Arkansas, Virginia), Central America (Panama), Caribbean (Dominican Republic), South America (Bolivia; Brazil; Chile; Ecuador), Indian Ocean (Madagascar), Asia (India; Nepal) and Oceania (Australia; [Papua New Guinea](#)).

Additional specimens examined (all on *Parmotrema reticulatum*).

Australia: *Queensland*: Lamington National Park, c. 100 km S of Brisbane, Binna Burra, 153°10'E, 28°20'S, 700 m, 1999, Aptroot 46128 (M). **Azores:** *Sao Miguel*: Furnas, Terra Nostra Park, 37°46'15"N, 25°18'42"W, 220 m, 2010, Diederich 16977 (BR). **Bolivia:** Dte. Cochabamba, Prov. Carrasco, P. N. Carrasco, between Meruvia and Monte Punku, 17°34'46"S, 65°15'27"W, 3080 m, *Podocarpus* forest, 2014, Etayo 33998B (LPB, herb. Etayo). **Brazil:** *Minas Gerais*: prope Caldas, on '*Rimelia* cf. *reticulata*', 1873, Mosén 2313 (UPS); Catas Altas, Serra do Caraça, Parque Natural do Caraça, near monastery Santuário do Caraça, 20°06'S, 43°29'W, 1300 m, on sandstone, 1997, Aptroot 40644 (M); *São Paulo*: Campos do Jordão, 22°45'S, 45°36'W, 1994, Buck 26480 (BR, NY). **Canary Islands:** Tenerife, S of Los Silos, c. 1 km W

of Erjos, Monte del Agua, 28°19'N, 16°48'W, 1140 m, on trees in laurisilva, 2007, Diederich 16574 (BR, S-F102497). **Chile:** Valdivia prov., Valdivia, Collico, 1940, Santesson 8311bis (UPS). **Dominican Republic:** Prov. La Vega, Jarabacoa, grounds of Hotel Mantaña, 1800 ft, 1982, Buck 8530A (BR, NY). **Madagascar:** Prov. de Tamatave, Préf. d'Ambatondrazaka, Moramanga, Ambavaniasy c. 8 km E de Beforona, sentier vers Fanovana, 18°55'50"S, 48°32'30"E, 900 m, 1994, Scheidegger (herb. Scheidegger). **Mexico:** Estado de Veracruz, Sierra Madre Oriental, just W of Xico along Coyopolan River, 19°25'33"N, 97°01'27"W, 1360 m, 2007, Egan (BR, OMA). **Nepal:** Khumbu Himal, Chourikharka, 1981, Remus & Menzel 38 (UPS). **Papua New Guinea:** Same locality as type, Aptroot 32325 (M); Eastern Highlands prov., Mount Kiss-Kiss, 1 km E of Goroka, 1987, Aptroot 18918 (M); Eastern Highlands prov., Mount Gahavisuka Provincial Park, 11 km N of Goroka, 2300 m, 1992, Aptroot 32517 (M); Morobe prov., Huon Peninsula, Saruwaged Range, Honzeukngon village S of Derim airstrip in Timbe valley, 1987, Sipman 24396 (B); Simbu prov., Daulo Pass, on road from Kundiawa to Goroka, 1992, Diederich 10001 (BR). **Portugal:** Algarve, Serra de Monchique, 1 km N of Caldas de Monchique, 1993, van den Boom 14847 (BR, herb. van den Boom). **USA:** Arkansas, Garland Co., Hot Springs National

Park, peak NW of DeSoto Park on Sunset Trail, 34°33'22"N, 93°02'16"W, 1020 ft, 2001, Wetmore 85928 (BR). Virginia, Wythe Co., Mount Rogers National Recreation Area, Jefferson National Forest, along Cole Branch Drive, c. 3.5 km S of intersection with Pope Rd., just SW of Collins Cove Horse Camp, near Raven Cliff Karst Area, 36°48'26"N, 81°02'54"W, 2400 ft, 2008, Hodkinson 9228, 9235, 9352 (DUKE).

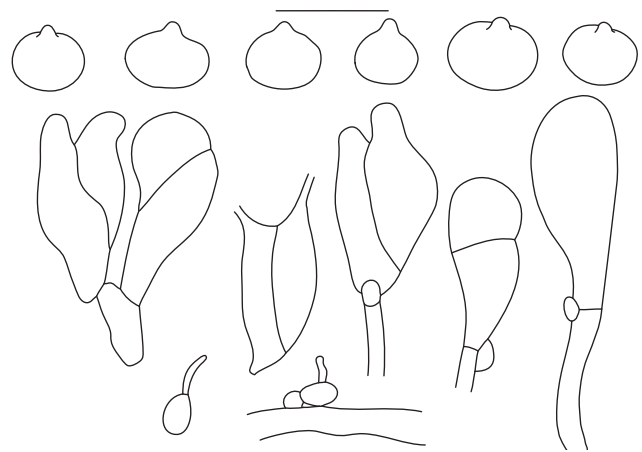
References. Diederich 1996 [Berger & Zimmermann 2016, Diederich 2003, Etayo 2017, Hafellner 2002, Hodkinson 2010, Joshi et al. 2018, van den Boom 2015, van den Boom & Clerc 2015, van den Boom & Etayo 2017, van den Boom & Giralto 2012, van den Boom et al. 2017].

Tremella parmeliellae Diederich & Sérus.

in Diederich, *Bibl. Lichenol.* 61: 130 (1996). *Type:* Papua New Guinea, Eastern Highlands Province, Mt. Gahavisuka Provincial Park, 11 km N of Goroka, 2400 m, 6°01' S, 145°25' E, little disturbed mossy mountain forest, on *Parmeliella foliicola*, Aug. 1992, E. Sérusiaux 13762–26 (LG – holotype; BR – isotype).

Basidiomata convex, pulvinate to subspherical, pale brownish to black, waxy-gelatinous, 0.1–0.6 mm diam. *Context hyphae* sometimes with clamp connections, 2–3 µm diam.; haustoria frequent, with clamp connections. *Hymenium* 30–50 µm high, containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, with one transverse, oblique or rarely almost longitudinal septum, rarely constricted at the septum, the lower cell with an attenuated base, often longer than the upper cell, 14–22 × 5–9 µm; epibasidia subcylindrical, 1.5–2.5 µm diam. *Basidiospores* ellipsoid to subspherical, 5–8 × 4–6 µm. *Asexual stage* unknown.

Notes. The two known specimens look rather different: basidiomata in the type are pale brown, 0.1–0.3 mm diam., while those in another specimen (Sérusiaux, LG) are mostly 0.2–0.6 mm diam. and black. Microscopically, both specimens look the same. It is difficult to know whether they rep-



Tremella parmeliellae, Papua New Guinea, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.



Tremella parmeliellae

resent two distinct species or extreme forms of one species. More material will be needed to answer that question.

Ecology and host. On the thallus and apothecia of *Parmeliella foliicola*.

Distribution. Oceania (Papua New Guinea).

Reference. Diederich 1996.

Tremella parmogardneri Diederich, Etayo & Millanes, sp. nov.

Diagnosis: Characterized by the resupinate, medium to dark brown basidiomata over the thallus of *Parmotrema gardneri*, 1–4 mm diam., the elongate ellipsoid, 1-septate basidia, 16–28(–36) × 7–10 µm, and the shortly ellipsoid basidiospores, 6–8 × 5–7 µm.

Etymology: A noun in apposition, from *Parmo[trema]* and *gardneri*, the host lichen.

Type: USA, Florida, Hernando Co., Withlacoochee State Forest, Richloam Wildlife Management Area, N Grade Rd. at Lion Rd., 0.7 mi E of Fla. Hwy 471, 16.5 mi N of US 98, 28°29'N, 82°04'W, small cypress dome, on *Taxodium*, on *Parmotrema gardneri*, 4 Dec. 1992, R. C. Harris 29787-A (NY 02690975 – holotype; BR – isotype).

Mycobank: MB844674

Basidiomata not gall-inducing, resupinate over the thallus of the host, flat or very slightly convex, roundish to elliptical,



Tremella parmeliellae, Papua New Guinea, isotype. Basidiomata on *Parmeliella foliicola*. Scale bar: 500 µm.



Tremella parmogardneri, USA, Florida, isotype. Basidiomata on *Parmotrema gardneri*. Scale bar: 1 mm.

rather well delimited, medium to dark brown, matt, waxy-gelatinous, 1–4 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2.5–4 µm diam.; haustoria present, basal clamp not observed. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, elongate ellipsoid, transversely 1-septate, 16–28(–36) × 6–10 µm, exceptionally longitudinally septate, 15–16 × 11–12 µm; epibasidia cylindrical, 2.5–4.5 µm thick, at least 12 µm long. *Basidiospores* shortly ellipsoid, 6–8 × 5–7 µm. *Asexual stage* unknown.

Notes. This species differs from the other sexual *Tremella* species confined to *Parmotrema* hosts by the entirely flat basidiomata. From *T. parmohypotropi* and *T. parmoperforati*, it further differs by the constantly 1-septate basidia, and from *T. parmeliarum* by the mainly transversely septate basidia.

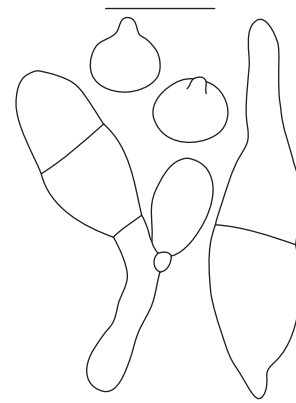
Ecology and host. On the thallus of *Parmotrema gardneri*.

Distribution. North America (USA: Florida) and South America (Bolivia).

Additional specimen examined. **Bolivia:** Dept. La Paz: Prov. Larecaja, near Achiquiri village and Charapampa, 18 km from Mapiri on the road to Apolo, Yungas inferior secondary forest,



Tremella parmogardneri



Tremella parmogardneri, USA, Florida, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 µm.

15°13'31"S, 68°13'49"W, 1071 m, on *Parmotrema gardneri*, 2011, Etayo 27223 (BR, LPB, herb. Etayo); Prov. Murillo, Sainani, Valle del Zongo, open area with shrubs and scattered trees, 16°07'01"S, 68°04'49"W, 2100 m, on *P. cf. gardneri*, 2014, Etayo 34342 (LPB, herb. Etayo).

Tremella parmohypotropi Diederich, Gockman & Milanes, sp. nov.

Diagnosis: Characterized by the large, strongly convex, basally constricted, pale to dark brown galls over the thallus of *Parmotrema hypotropum*, 0.3–5 mm diam., the large, mainly longitudinally or obliquely 2–4-celled basidia, 17–36 × 12–18 µm, and the large, subspherical to shortly ellipsoid basidiospores, 7.5–9.5 × 7–9 µm.

Etymology: From *Parmo[trema] hypotropum*, the host lichen.

Type: USA, Texas, Limestone Co., c. 4.2 km S of Groesbeck and 9.3 km NE of Thornton, 31.4837°N, 96.5282°W, on the bark of *Prosopis glandulosa* in a pasture, on *Parmotrema hypotropum*, 10 Dec. 2018, O. Gockman 5784 (BR – holotype).

Mycobank: MB844675

Basidiomata inducing the formation of strongly convex galls with a constricted base, pale to dark brown, often with a greyish µm tinge, 0.3–5 mm diam.; surface matt, at the beginning often with a irregular central depression, sometimes becoming slightly lobulate or tuberculate. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2–4 µm diam.; haustoria not observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, ellipsoid, occasionally with an attenuated stalk-like base, 2–4-celled, with longitudinal, oblique or rarely transverse septa, 17–36 × 12–18 µm; epibasidia cylindrical, up to 85 µm long, 3–5 µm thick. *Basidiospores* subspherical to shortly ellipsoid, 7.5–9.5 × 7–9 µm. *Asexual stage* unknown.

Notes. This species differs from *Tremella parmeliarum* by the basidiomata that are more greyish brown, not chestnut brown,



Tremella parmohypotropi, USA, Texas, holotype. Basidiomata on *Parmotrema hypotropum*. Scale bar: 1 mm.



Tremella parmohypotropi, USA, Texas, holotype. Basidiomata on *Parmotrema hypotropum*. Scale bar: 1 mm.



Tremella parmohypotropi, USA, Texas, Walden 0031. Basidiomata on *Parmotrema hypotropum*. Scale bar: 1 mm.



Tremella parmohypotropi, USA, Texas, Walden 0031. Basidiomata on *Parmotrema hypotropum*. Scale bar: 1 mm.

with a more irregular and matt surface, by the much larger, 2–4-celled basidia, and by the distinctly larger basidiospores.

Ecology and host. On the thallus of *Parmotrema hypotropum*.

Distribution. North America (USA: Texas).

Additional specimen examined. USA: Texas: Blanco Co., Pedernales Falls State Park, c. 16.9 km E of Johnson City and 7.6 km S of Cypress Mill, 30.3131°N, 98.2416°W, on branches of *Quercus*, on *Parmotrema hypotropum*, 2019, Walden 0031 (BR).



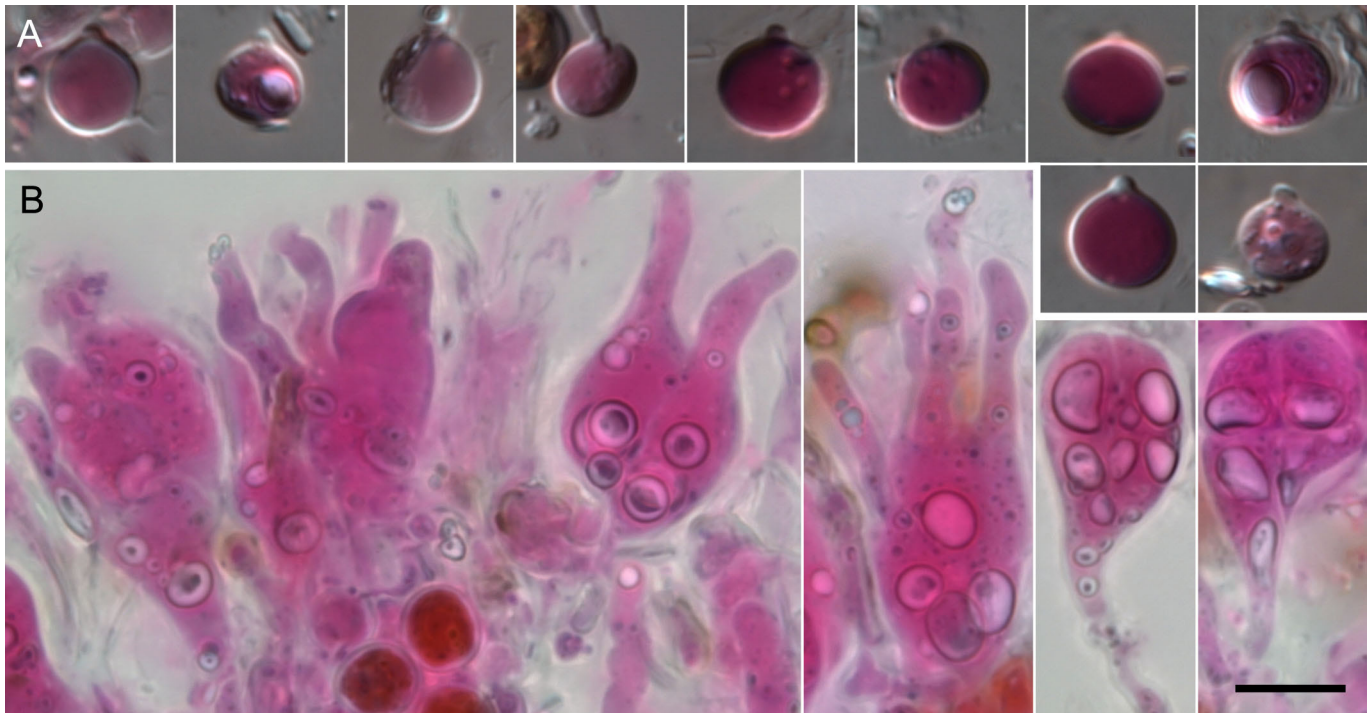
Tremella parmohypotropi

Tremella aff. *parmohypotropi*

Notes. A specimen on *Parmotrema hypoleucinum* morphologically resembles *Tremella parmohypotropi*, but is distin-



Tremella aff. *parmohypotropi*, USA, California, Tucker 34441. Basidiomata on *Parmotrema hypoleucinum*. Scale bar: 1 mm.



Tremella parmohypotropi, USA, Texas, holotype. A, Basidiospores. B, Basidia in different stages of development. In phloxine. Scale bar: 10 μ m.



Tremella aff. *parmohypotropi*, USA, California, Tucker 34441. Basidiomata on *Parmotrema hypoleucinum*. Scale bar: 1 mm.



Tremella aff. *parmohypotropi*, USA, California, Tucker 34441. Basidiomata on *Parmotrema hypoleucinum*. Scale bar: 1 mm.

guished by the often darker basidiomatal galls. No molecular data could be obtained. Sequences from fresh material on the same host should allow us deciding whether this belongs to *T. parmohypotropi* or represents a genetically distinct species.

Ecology and host. On the thallus of *Parmotrema hypoleucinum*, a taxon that is only doubtfully different from *P. hypotropum* (Widhalm et al. 2016).

Distribution. North America (USA: California).

Specimen examined. USA: California: Santa Barbara Co., Santa Barbara, Montecito, Ashley Road, grounds of “Lotusland” Botanic Garden, on *Pittosporum undulatum*, on *Parmotrema hypoleucinum*, 1996, Tucker 34441 (BR, SBBG).

Tremella parmoperforati Diederich & Millanes, sp. nov.

Diagnosis: Characterized by the slightly convex, basally not constricted, pale to medium brown galls with a smooth and matt surface over *Parmotrema perforatum*, 0.4–2 mm diam., medium-sized, longitudinally (2–)4-celled basidia, 11–17.5 \times 8.5–14 μ m, and medium-sized, shortly ellipsoid basidiospores, 5–7.5 \times 3.5–7 μ m.

Etymology: From *Parmo[trema] perforatum*, the host lichen.

Type: USA, Louisiana, Washington par., hardwood forest 4.5 mi E of Angie, on W bank of Pearl River, Pope property E of La. Rte 438 (E end), 30°59'N, 89°44'W, on *Parmotrema perforatum*, 21 March 1982, S. Tucker 24600 (SBBG – holotype; BR – isotype).

Mycobank: MB844676



Tremella parmoperforati, USA, Louisiana, isotype. Basidiomata on *Parmotrema perforatum*. Scale bar: 1 mm.



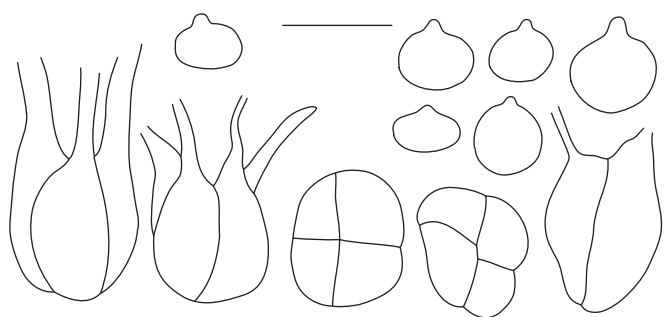
Tremella parmoperforati, USA, Louisiana, isotype. Basidiomata on *Parmotrema perforatum*. Scale bar: 1 mm.



Tremella parmoperforati, USA, Louisiana, isotype. Basidiomata on *Parmotrema perforatum*. Scale bar: 1 mm.



Tremella parmoperforati, USA, Louisiana, Tucker 31070. Basidiomata on *Parmotrema perforatum*. Scale bar: 1 mm.



Tremella parmoperforati, USA, Louisiana, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 μ m.

Basidiomata inducing superficial galls, 0.4–2 mm diam., when young slightly convex with an indistinct margin, basally not constricted, pale to medium brown, when older, with an elevated, often well delimited margin, medium brown, with a smooth and matt surface. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3–4.5 μ m

diam.; haustoria not observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid, base not attenuated, cruciately (2–)4-celled, with longitudinal septa, 11–17.5 \times 8.5–14 μ m; epibasidia cylindrical, up to 60 μ m long, 1–3 μ m. *Basidiospores* shortly ellipsoid, 5–7.5 \times 3.5–7 μ m. *Asexual stage* unknown.



Tremella parmoperforati

Notes. This species differs from *Tremella parmeliarum* and *T. parmogardneri* by the 4-celled (vs 2-celled) basidia, and from the former by the flattened basidiomatal galls that are usually not constricted at the base, and that are medium brown and matt (vs darker chestnut brown and shiny). It differs from *T. parmohypotropi* by the flattened basidiomatal galls with a non-constricted base and a more or less smooth surface, and the much smaller basidia and basidiospores.

Ecology and host. On the thallus of *Parmotrema perforatum*.

Distribution. North America (USA: Louisiana).

Additional specimen examined. USA: Louisiana: West Feliciana par., between Thompson Creek and Hamner Creek, along state Rte 966, 30°47'N, 91°15'W, on *Parmotrema perforatum*, 1991, Tucker 31070 (BR, SBBG).

***Tremella pertuceracea* Diederich, Flakus & Rodr. Flakus, sp. nov.**

Diagnosis: Characterized by the applanate to slightly convex, pale pinkish brown, waxy-gelatinous basidiomata with a smooth and slightly shiny surface, spreading over the thallus of *Pertusaria* sp. and becoming almost resupinate, up to 2.5 mm diam., the longitudinally or obliquely septate 2–4-celled basidia often having a long and narrow stalk-like base, 13.5–33 × 11–16 µm (incl. stalk), upper part 13.5–23 µm long, stalk 0–18 µm long, the basidiospores 7.5–8 × 6.5–8 µm, and the absence of clamp connections.

Etymology: From *Pertu[saria]*, the host lichen genus, and *ceracea*, waxy.

Type: Bolivia, Dept. La Paz, Prov. Franz Tamayo, Área Natural de Manejo Integrado Nacional Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'22"S, 69°00'11"W, 2480 m, lower montane Yungas forest, on corticolous *Pertusaria* sp., 16 Nov. 2014, A. Flakus 25096 (KRAM – holotype; BR, LPB – isotypes).

Mycobank: MB844677

Basidiomata superficial, applanate to slightly convex, basally not constricted, pale pinkish brown, waxy-gelatinous, surface uneven, smooth and slightly shiny, delimited and roundish when young, at least 0.4 mm diam., becoming larger, spreading over the host thallus, fusing with neighbouring basidiomata and then almost resupinate with a smooth or slightly tuberculose surface, up to 2.5 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2.5–5 µm diam., septa without clamps; haustoria present, without a basal clamp. *Hymenium* containing numerous ellipsoid probasidia, often with a long stalk-like base, without a basal clamp. *Basidia*, when mature, 2–4-celled, with longitudinal or oblique septa, ellipsoid, often with a distinct stalk, 13.5–33 × 11–16 µm (stalk included), upper part (without stalk) 13.5–23 µm long, stalk 0–18 µm long; epibasidia subulate to subcylindrical, 2.5–6 µm diam., 40–75 µm long. *Basidiospores* subspherical to ellipsoid, 7.5–8 × 6.5–8 µm. *Exospores* developing on the



Tremella pertuceracea, Bolivia, holotype. Basidiomata on the thallus of *Pertusaria* sp. Scale bar: 1 mm.



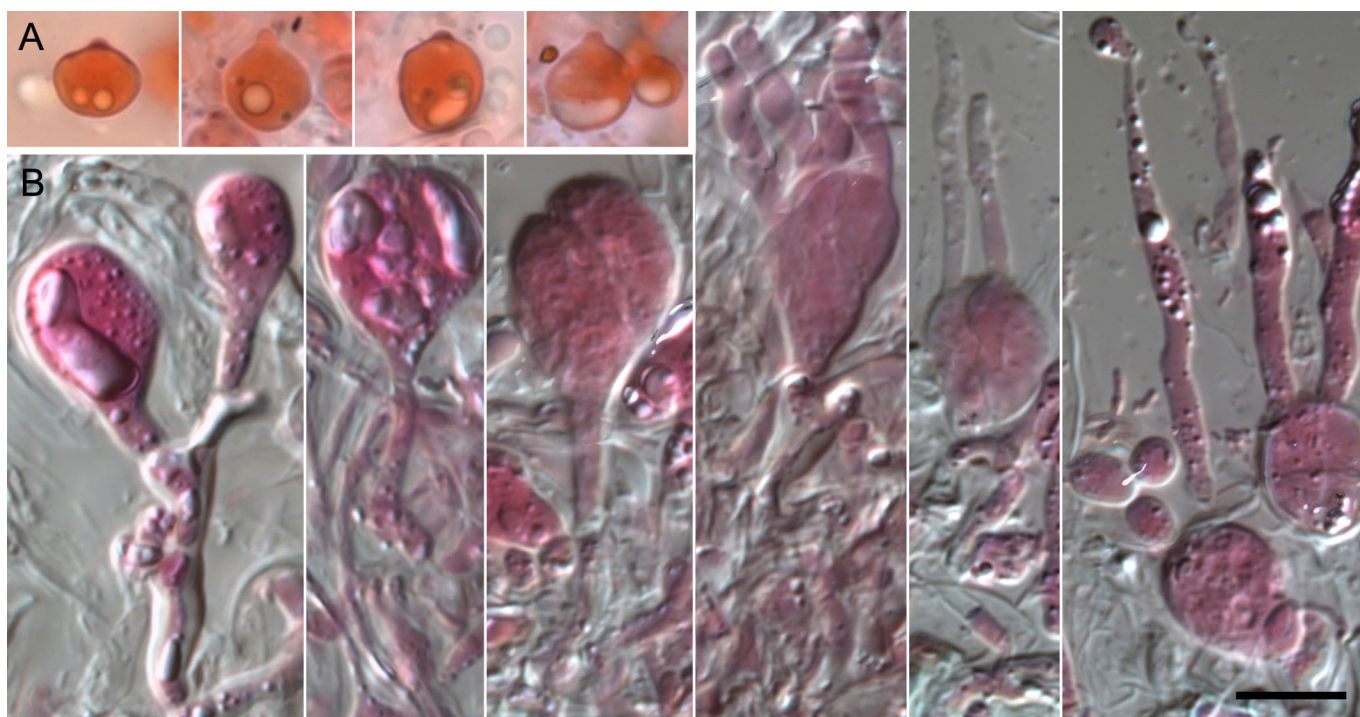
Tremella pertuceracea, Bolivia, holotype. Basidiomata on the thallus of *Pertusaria* sp. Scale bar: 1 mm.



Tremella pertuceracea, Bolivia, holotype. Basidiomata on the thallus of *Pertusaria* sp. Scale bar: 500 µm.

outer wall of old basidia, mostly observed free-swimming, ellipsoid, aseptate, 3.5–4.5 × 2.5–3.5 µm.

Notes. This species is characterized by the pale pinkish brown, waxy-gelatinous, only slightly convex basidiomata



Tremella pertuceracea, Bolivia, holotype. A, Basidiospores, in ammoniacal Congo red. B, Basidia in different stages of development; note the three 'exospores' in the right photo, in phloxine. Scale bar: 10 μ m.

spreading over the host thallus, and the 2–4-celled, clampless basidia that are much smaller than in most other species of the *Tremella pertusariae* complex. *Tremella pertuthalamiae* has similarly sized basidia, but is distinguished by strongly convex, more strongly coloured basidiomata, and by larger basidiospores.

Ecology and host. On the thallus of an unidentified *Pertusaria* species characterized by verruciform apothecia, 8-spored asci, uniseriate ascospores $82\text{--}110 \times 32\text{--}41 \mu\text{m}$, and the presence of perlatolic acid. Both *P. achroiza* and *P. tuberculifera* differ by the presence of 2-O-methylperlatolic acid, difficult to separate from perlatolic acid by TLC.

Distribution. South America (Bolivia), known only from the type locality.



Tremella pertuceracea

Tremella pertusae Diederich, Millanes, Brackel & Etayo, sp. nov.

Diagnosis: Characterized by basidiomata inducing convex, concolorous to beige galls on the thallus of *Pertusaria pertusa*, 0.2–2.5 mm diam., large 2–4-celled basidia, often with a long and narrow stalk-like base, $27\text{--}52 \times 15\text{--}26 \mu\text{m}$ (incl. stalk), upper part $19\text{--}29 \mu\text{m}$ long, stalk $4\text{--}32 \mu\text{m}$ long, large basidiospores, $9.5\text{--}11.5 \times 8.5\text{--}10 \mu\text{m}$, and the absence of clamp connections.

Etymology: From [*Pertusaria*] *pertusa*, the host lichen.

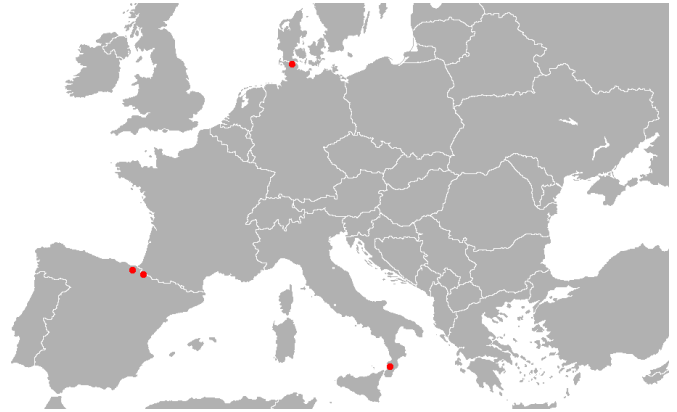
Type: Italy, Calabria, Prov. di Reggio di Calabria, Piana di Gioia Tauro, W Polistena, $38^{\circ}25'37.7''\text{N}$, $16^{\circ}02'11.3''\text{E}$, 145 m, on *Olea europaea*, on *Pertusaria pertusa*, 7 May 2015, W. von Brackel 7593 & D. Puntillo (BR – holotype).

Mycobank: MB844678

Basidiomata inducing the formation of galls on the host thallus; galls strongly convex, often as tall as broad, basally often constricted, concolorous to beige, surface smooth and matt, becoming cerebriform when old, 0.2–2.5 mm diam. **Context hyphae** not observed; subbasidial hyphae thick-walled, $2.5\text{--}4.5 \mu\text{m}$ diam., septa without clamps; haustoria not seen. **Hymenium** containing numerous ellipsoid probasidia, often with a long stalk-like base, basal clamp not seen. **Basidia**, when mature, 2–4-celled, with longitudinal, oblique or transverse septa, ellipsoid, often with a very long stalk, $27\text{--}52 \times 15\text{--}26 \mu\text{m}$ (stalk included), upper part (without stalk) $19\text{--}29 \mu\text{m}$ long, stalk $4\text{--}32 \mu\text{m}$ long; epibasidia subulate to subcylindric.



Tremella pertusae, Italy, holotype. Basidiomatal galls on the thallus of *Pertusaria pertusa*. Scale bar: 1 mm.



Tremella pertusae

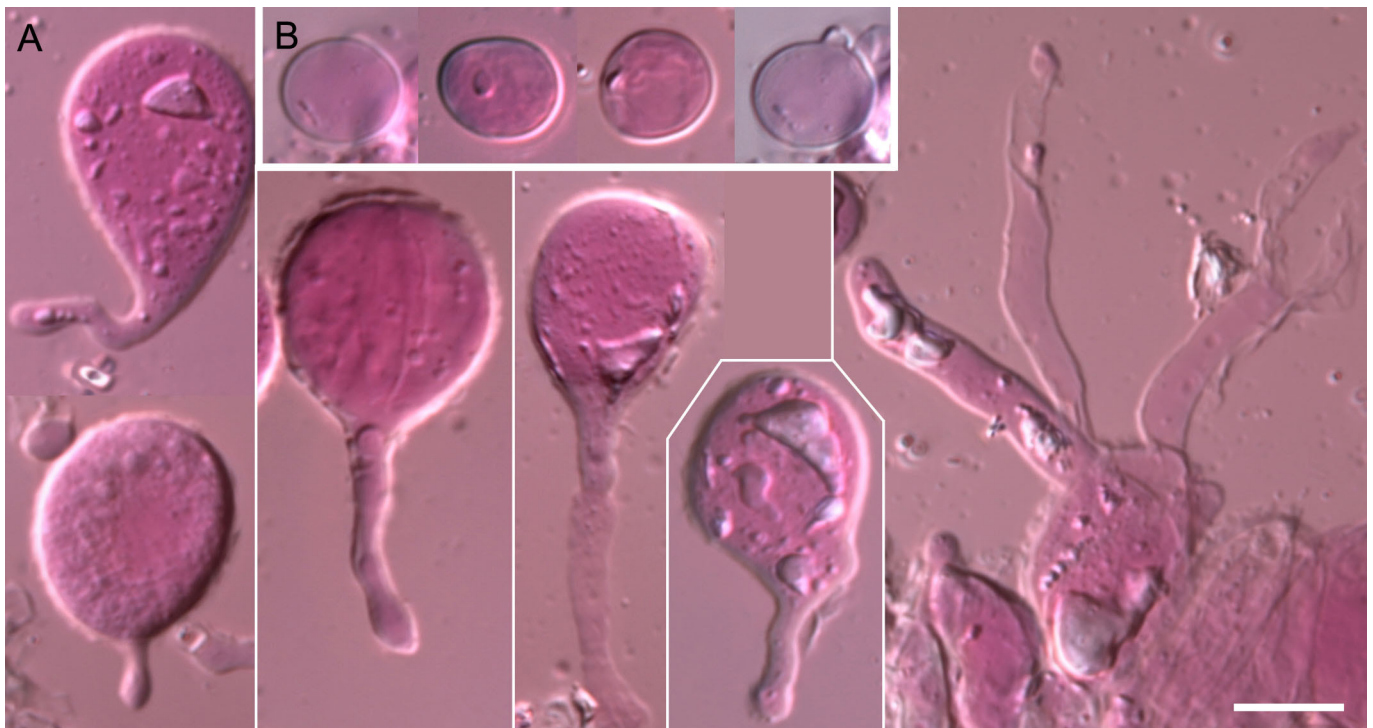
cal, 4.5–6 μm diam., 35–55 μm long. *Basidiospores* ellipsoid, 9.5–11.5 \times 8.5–10 μm . *Asexual stage* unknown.

Notes. A German specimen of this species was included in *Tremella pertusariae* by Diederich (1996), a species confined to apothecia of *Pertusaria hymenea*. That species differs by the waxy-gelatinous basidiomata that are not gall-inducing. A further Italian specimen of '*T. pertusariae*' on *P. pertusa* (herb. Brackel 6394, Brackel 2015) has been examined by us: it may be a young *T. pertusae*, but no basidia could be observed.

Ecology and host. On the thallus of *Pertusaria pertusa*, gall-inducing.

Distribution. Europe (Germany; Italy; Spain).

Additional specimens (all on *Pertusaria pertusa*). **Germany:** Schleswig-Holstein: Kreis Flensburg, 1939, Erichsen 167 (UPS) (studied by Diederich 1996, not re-examined in 2022). **Spain:** Basque Country: Gipuzkoa, S^a de Aralar, track from Lizarrusti to Otxondo, on *Fagus*, 42°57'10"N, 2°06'11"W, 650–900 m, 2011, Etayo 27176 (herb. Etayo). Navarra: S^a of S. Miguel de Aralar, path from parking place to forestry house, 42°57'31"N, 2°02'57"W, 1000 m, on *Fagus*, 2018, Etayo 31720 (herb. Etayo); S^a de Urbasa, *Fagus* forest near Balcón de Pilatos viewpoint, 42°48'08"N, 2°08'23"W, 947 m, on *Fagus*, 2018, Etayo 31241 (herb. Etayo); S^a de Urbasa, Crezmendi mountain, on *Fagus*, 42°50'24"N, 2°10'06"W, 910 m, 1993, Etayo 12496 (herb. Etayo); Selva de Irati, Orbaiceta, 200 m from Azpegui refuge, path going to the east, *Fagus* forest below Mendilatz, 43°01'30"N, 1°13'27"W, 1050 m, on *Fagus*, 2018, Etayo 31421 (herb. Etayo).



Tremella pertusae, Italy, holotype. A, Probasidia, mature basidia and epibasidia. B, Basidiospores. In phloxine. Scale bar: 10 μm .

Tremella pertusariae Diederich

Bibl. Lichenol. 61: 133 (1996). *Type*: UK, Northern Ireland, VC H33, Fermanagh, Crom, Knockenbrass, on *Pertusaria hymeneae*, 14 July 1993, B. J. Coppins 15805 & A. M. O'Dare (E – holotype; BR – isotype).

Basidiomata intrahymenial, soon slightly to strongly convex, pale pinkish brown, rarely becoming dark brown, waxy-gelatinous, 0.3–0.8 mm diam. *Context hyphae* thick-walled, 2.5–4 µm diam., clamp connections not observed; subbasidial hyphae thick-walled, 2.5–3.5 µm diam.; haustoria present, without clamps. *Hymenium* hyaline, containing numerous claviform probasidia, some with a long stalk, clamp connections not observed. *Basidia*, when mature, 2–4-celled, with longitudinal, oblique or rarely transverse septa, ellipsoid, basally often attenuated, 22–45 × 15–28 µm (without stalk), rarely with a basal stalk and then up to 55 µm long, stalk up to 20 µm long; epibasidia subulate to subcylindrical, 4–7.5 µm diam., at least 30–60 µm long. *Basidiospores* subspherical, 8.5–9 × 8–8.5 µm (one observed). *Exospores* developing on the outer wall of an old cell (basidiospore or basidium?) ellipsoid, aseptate, 4.5–6 × 4–5 µm. *Endospores* developing inside old basidia after basidiospore production shortly ellipsoid, aseptate, 3–7.5 × 2.5–6 µm.

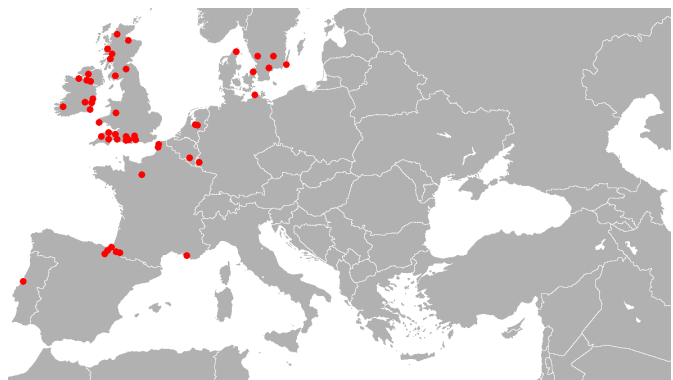
Notes. This species was described for *Tremella* specimens growing over *Pertusaria*, most with distinct basidiomata, while one was inducing galls on the host thallus (Diederich 1996). It was characterized by the particularly large, 2–4-celled basidia, the very large basidiospores and the absence of clamp connections. However, the host-specificity of European populations developing in the hymenium of *Pertusaria hymeneae*, the host-specificity of European populations inducing galls on *P. pertusa*, and American specimens developing basidiomata on the host thallus, suggested a complex of several species. Our molecular results confirm this hypothesis, as sequences from *P. hy-*

menina grouped together, those on *P. pertusa* represented a sister clade, while those from American specimens were distinct and sister to the European clade. Consequently, we regard *Tremella pertusariae* s. str. as being host-specific on *P. hymenina*, while all specimens from other hosts belong to distinct species. Several American specimens reported by Diederich (1996, 2003) have not been restudied.

Ecology and host. In the hymenium of *Pertusaria hymeneae*.

Distribution. W Europe (Belgium; Denmark; France; Germany; Ireland; Luxembourg; Netherlands; Portugal; Spain; Sweden; UK: England, Northern Ireland, Scotland).

Additional specimens examined (all in the hymenium of *Pertusaria hymeneae*). **Belgium:** St Hubert, valley of Masblette, near Pont Mauricy, 1997, Diederich 12607, 12649 (BR). **France:** *Pas-de-Calais:* S of Boulogne-sur-Mer, forêt domaniale d'Hardelot, 2000, Diederich 14335 (BR); forêt domaniale de Boulogne, 2000, Diederich 14246 (BR). *Pyrénées-Atlantiques:* Forêt de Sare entre Sare et le col de Lizarieta, 2006, Diederich 16331 (BR); *ibid.*, 2015, Diederich 18152 (BR); 20 km SE of Saint-Jean-Pied-de-Port, forêt d'Iraty, 43.0313°N, 1.0796°W, 2015, Diederich 18135 (BR). **Ireland:** Stoneyford, Mount Juliet, field NW of Ballyfin



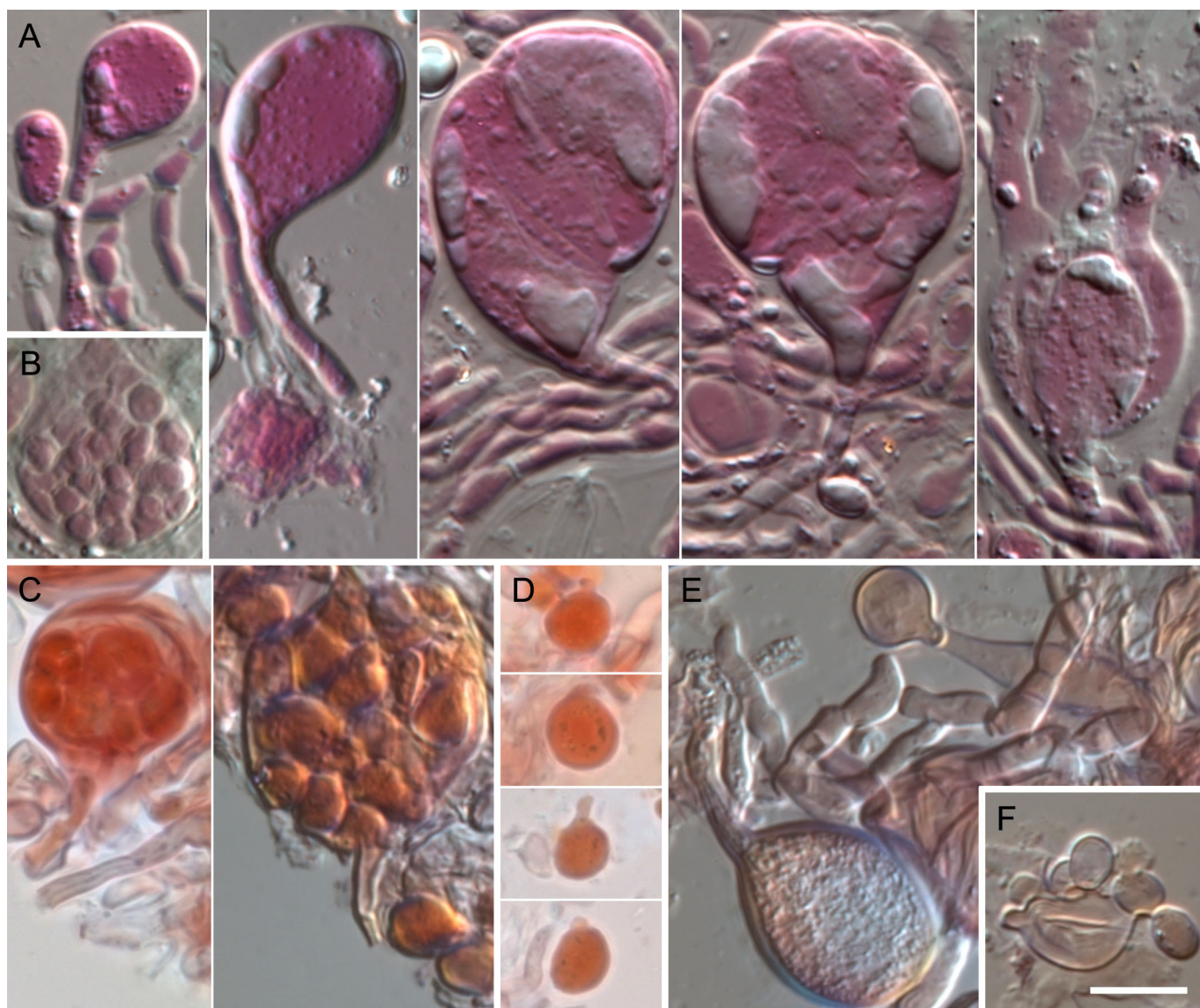
Tremella pertusariae



Tremella pertusariae, Ireland, isotype. Basidiomata arising from the hymenium of *Pertusaria hymeneae*. Scale bar: 500 µm.



Tremella pertusariae, France, Pyrenees, Diederich 18152. Basidiomata arising from the hymenium of *Pertusaria hymeneae*. Scale bar: 1 mm.



Tremella pertusariae. A–B, UK, Northern Ireland, holotype, C–D, France, Diederich 18152, E–F, France, Diederich 12649. A, Basidia in different stages of development. B, ‘Endospores’ in old basidium. C, ‘Endospores’ in old basidia. D, Basidiospores. E, Stalked basidium, epibasidium and basidiospore. F, ‘Exospores’ on old basidium. A–B, in phloxine, C–F, in ammoniacal Congo red. Scale bar: 10 µm.

bridge, 1996, Fox 65 (DBN). **Luxembourg:** Entre Berdorf et Mullerthal, versant droit de l’Ernz Noire, Schnellert, 1998, Diederich 13592 (BR). **Portugal:** Beira Litoral, Condeixa-a-Velha, archeological site Conímbriga, 40.0995°N, 8.4912°W, 115 m, on *Olea*, 2021, Diederich 19600 (BR).

References. Diederich 1996 [Brand et al. 2013, Cross & Sanderson 2012, Diederich 2003, Millanes et al. 2014a, Moore 2011, Roux & Gueidan 2002, Schiefelbein et al. 2014].

Tremella pertusariicola Diederich, Flakus, Etayo & Rodr. Flakus, sp. nov.

Diagnosis: Characterized by the immersed and erumpent to superficialy, pulvinate, dark brown to black, gelatinous basidiomata with a central depression on the thallus of *Per-*

tusaria cf. *rigida*, 0.3–0.8 mm diam., the relatively large, 2–4-celled basidia with mainly longitudinal or oblique septa, 21–40 × 10–19 µm, the large basidiospores, 10–11 × 8–9.5 µm, the exospores produced on the outer wall of old basidia and epibasidia, and the absence of clamp connections.

Etymology: From *Pertusaria*, the host lichen, and *incola*, dweller.

Type: Bolivia, Dept. Tarija, Prov. Burnet O’Connor, old road between Tarija and Entre Ríos, 21°27’50”S, 64°12’51”W, 1924 m, Bolivian-Tucuman forest with epiphytes exposed NW, on corticolous *Pertusaria* cf. *rigida*, 30 July 2015, A. Flakus 27677 (KRAM – holotype; BR, LPB – isotypes).

Mycobank: MB844679



Tremella pertusariicola, Bolivia. A–B, holotype, C–E, Etayo 30665. Probasidia and mature basidia. B, Basidia filled with parasitic hyphae. C, Basidiospores. D, ‘Exospores’ developing on the outer wall of old basidia and epibasidia. E, Mature basidia with epibasidia. In phloxine. Scale bar: 10 μ m.



Tremella pertusariicola, Bolivia, holotype. Basidiomata on the thallus of *Pertusaria* cf. *rigida*. Scale bar: 500 μ m.



Tremella pertusariicola, Bolivia, holotype. Basidiomata on the thallus of *Pertusaria* cf. *rigida*. Scale bar: 500 μ m.

Basidiomata first immersed then erumpent, finally superficial, pulvinate, basally not or slightly constricted, typically with a central depression, dark brown to black from the beginning, gelatinous, with a rough surface, 0.3–0.8 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2.5–3.5 μ m diam., septa without clamps; haustoria present, without a basal clamp. *Hymenium* containing numerous ellipsoid to claviform probasidia, often with a short stalk-like base, without a basal clamp. *Basidia*, when mature, 2–4-celled, with longitudinal or oblique, rarely transversal septa, ellipsoid, basally often attenuated, 21–40 \times 10–19 μ m (short stalk-like base included); epibasidia subulate to subcylindrical, 3.5–5.5 μ m diam., 35–60 μ m long. *Basidiospores* shortly ellipsoid, 10–11 \times 8–9.5 μ m. *Exospores* developing on old basidia or epibasidia after basidiospore production ellipsoid, aseptate, 5.5–8 \times 3.5–6.5 μ m.

Notes. This species is distinguished from the other known pertusariicolous *Tremella* species by the often immersed, then erumpent basidiomata that are dark brown to black from the beginning, typically with a central depression, at least when young. ‘Exospores’ developing on the outer wall of old basidia and epibasidia have been observed in specimen Etayo 30665. These are known in several per-

tusariicolous species and seem to be homologous to ‘endospores’, developing inside old basidia.

In all basidiomata examined from the type, and in older ones from specimen Etayo 30665, c. 5–10 % of the basidia were parasitised by hyphae that entered through the basidial wall, then multiplied inside until filling the entire basidial volume.

Ecology and host. On the thallus of *Pertusaria* cf. *rigida*. The type host has verruciform apothecia, 6–8-spored asci, biseriate ascospores 80–100 \times 30–40 μ m, and the presence of 4,5-dichlorolichexanthone. It differs from typical *P. rigida* by the finely verruculose ascospores. Specimen Etayo 30665 resembles morphologically and has ascospores 75–86 \times 30–31 μ m.

Distribution. South America (**Bolivia**), known from two nearby localities.

Additional specimen examined. **Bolivia:** Dept. Tarija, Prov. Burnet O’Connor, 60 km from Tarija, new road between Tarija and Entre Ríos, 21°28’52”S, 64°17’41”W, 1837 m, Bolivian-Tucuman forest with *Podocarpus*, on *Pertusaria*, 2015, Etayo 30665 (LPB, herb. Etayo).



Tremella pertusariicola

Tremella pertutexanae Diederich, Millanes & Common, sp. nov.

Diagnosis: Characterized by the applanate to pulvinate, pale pinkish brown, greyish brown to blackish, gelatinous basidiomata on the thallus of *Pertusaria texana*, 0.15–0.5 mm diam., the very large, (2–)4-celled basidia with longitudinal or oblique septa, 26–50 \times 11–25 μ m, the very large basidiospores, 9–12 \times 8–11.5 μ m, the exospores produced by 2–5 on the outer wall of old epibasidia, 5–7.5 \times 4–6 μ m, and the absence of clamp connections.

Etymology: From *Pertu[saria] texana*, the host lichen.

Type: USA, Florida, Sumter Co., Richloan Wildlife Management Area, 28.44°N, 82.084°W, 35 m, on branches of unidenti-



Tremella pertutexanae, USA, Florida, holotype. Basidiomata on the thallus of *Pertusaria texana*. Scale bar: 500 μ m.



Tremella pertutexanae, USA, Florida, Common 10165C. Basidiomata on the thallus of *Pertusaria texana*. Scale bar: 500 μ m.



Tremella pertutexanae, USA, Florida, Common 10194C. Basidiomata on the thallus of *Pertusaria texana*. Scale bar: 500 μ m.



Tremella pertutexanae, USA, Louisiana, Tucker 31284. Basidiomata on the thallus of *Pertusaria texana*. Scale bar: 500 μ m.

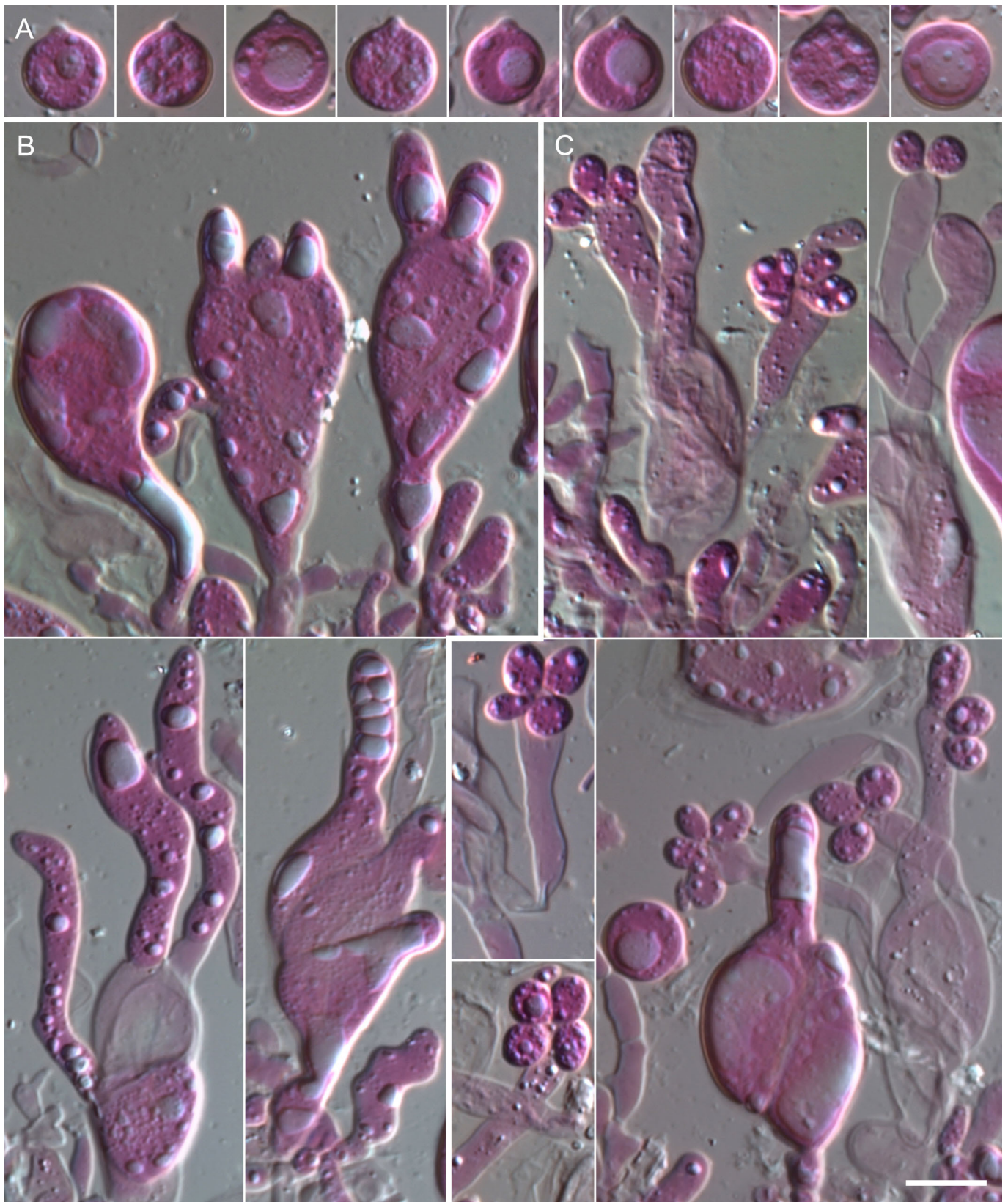


Tremella pertutexanae, USA, Oklahoma, Harris 48928. Basidiomata on the thallus of *Pertusaria texana*. Scale bar: 500 μ m.

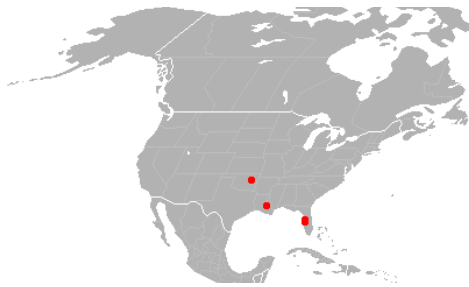
fied shrub, on *Pertusaria texana*, 9 June 2019, R. Common 10254D (BR – holotype).

Mycobank: MB844680

Basidiomata partly immersed to superficial, appanate to pulvinate and then basally slightly constricted, from pale pinkish brown, to greyish brown or blackish, gelatinous, with an often slightly uneven and matt surface, 0.15–0.5 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2.5–4.5 μ m diam., septa without clamps; haustoria present, without a basal clamp. *Hymenium* containing numerous ellipsoid to claviform probasidia, rarely with a short stalk-like base, without a basal clamp. *Basidia*, when mature, (2–)4-celled, with longitudinal or oblique septa, ellipsoid, basally often attenuated, (20–)26–50 \times 11–25 μ m (stalk present in a few specimens included); epibasidia subulate to subcylindrical, 3–7.5 μ m diam., 25–57 μ m long. *Basidiospores* subspherical to rarely ellipsoid, 9–12 \times 8–11.5 μ m. *Exospores* developing apically or laterally on old epibasidia after basidiospore production, usually by 2–5, shortly ellipsoid, aseptate, 5–7.5 \times 4–6 μ m. *Endospores* developing inside old basidia after basidiospore production possibly observed once, similar to exospores.



Tremella pertutexanae, USA, Florida, holotype. A, Basidiospores. B, Basidia in different stages of development. C, Old epibasidia producing 'exospores'. In phloxine. Scale bar: 10 μ m.



Tremella pertutexanae

Notes. This species belongs to the *Tremella pertusariae* complex, characterized by the very large, 2–4-celled basidia, the very large basidiospores, and lacking clamp connections. It is remarkable by the development of ‘exospores’ [this term used as the counterpart of ‘endospores’, designating mitospores born inside old basidia, first described from *Tremella endosporogena*] that have been observed on most specimens examined. Endospores in an old basidium have possibly been observed in specimen Common 10165C.

Ecology and host. On the thallus of corticolous *Pertusaria texana*.

Distribution. North America (**USA:** Florida, Louisiana, Oklahoma).

Additional specimens examined (all on *Pertusaria texana*). **USA:** **Florida:** Pasco Co., Zephyrhills, Woodfern Ave., 28.246°N, 82.192°W, 35 m, on an ornamental tree, 2019, Common 10321C (BR); *ibid.*, Samuel W. Pasco Recreation Area, 28.213°N, 82.157°W, 25 m, on windfall oak twigs, 2019, Common 10194C (BR); Sumter Co., 28.5783°N, 82.0916°W, 20–40 m, dead branches of *Quercus*, 2016, Common 10165C (BR). **Louisiana:** Baton Rouge, Burden Research Plantation, Essen Lane, 30°24′30″N, 91°06′45″W, bottomland hardwood forest, 1991, Tucker 31284 (BR, LSU). **Oklahoma:** Cherokee Co., Cookson Wildlife Management Area, W of Blue Top Road, 2 mi S of headquarters, 35°39′23″N, 94°49′46″W, along small stream over chert bedrock, 2004, Harris 48928 (NY).



Tremella pertuthalamiae, USA, Florida, holotype. Basidiomata on the thallus of *Pertusaria tetralthalamia*. Scale bar: 1 mm.

Tremella pertuthalamiae Diederich & Millanes, sp. nov.

Diagnosis: Characterized by the applanate to strongly convex, pale orange-brown, waxy-gelatinous basidiomata with a smooth and slightly shiny surface on the thallus of *Pertusaria tetralthalamia*, 0.3–1.5 mm diam., the longitudinally or obliquely septate (2–)4-celled basidia often having a long and narrow stalk-like base, 17–48 × 12–17 µm (incl. stalk), upper part 17–22 µm long, stalk 7–28 µm long, the very large basidiospores, 9.5–12 × 8–10.5 µm, and the absence of clamp connections.

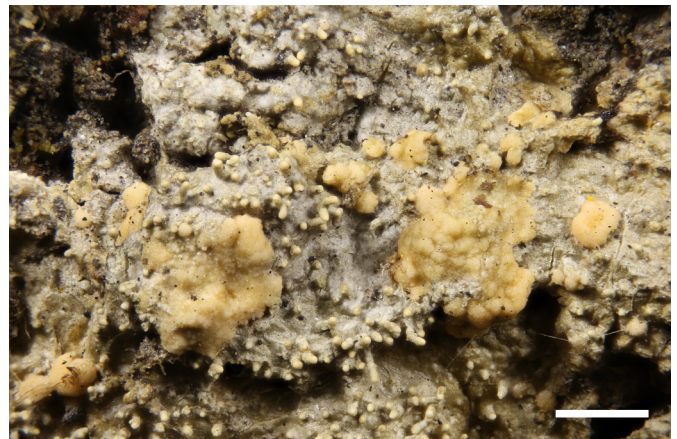
Etymology: From *Pertusaria tetralthalamia*, the host lichen of the holotype.

Type: USA, Florida, Osceola Co., Bull Creek Wildlife Management Area, along Interpretive Drive, 1.5 mi ESE of Check-in Station, 28°05′N, 80°56′W, small *Taxodium* swamp, on *Vitis*, on *Pertusaria tetralthalamia*, 9 Jan. 1996, R. C. Harris 37569 (NY 2690974 – holotype; BR – isotype).

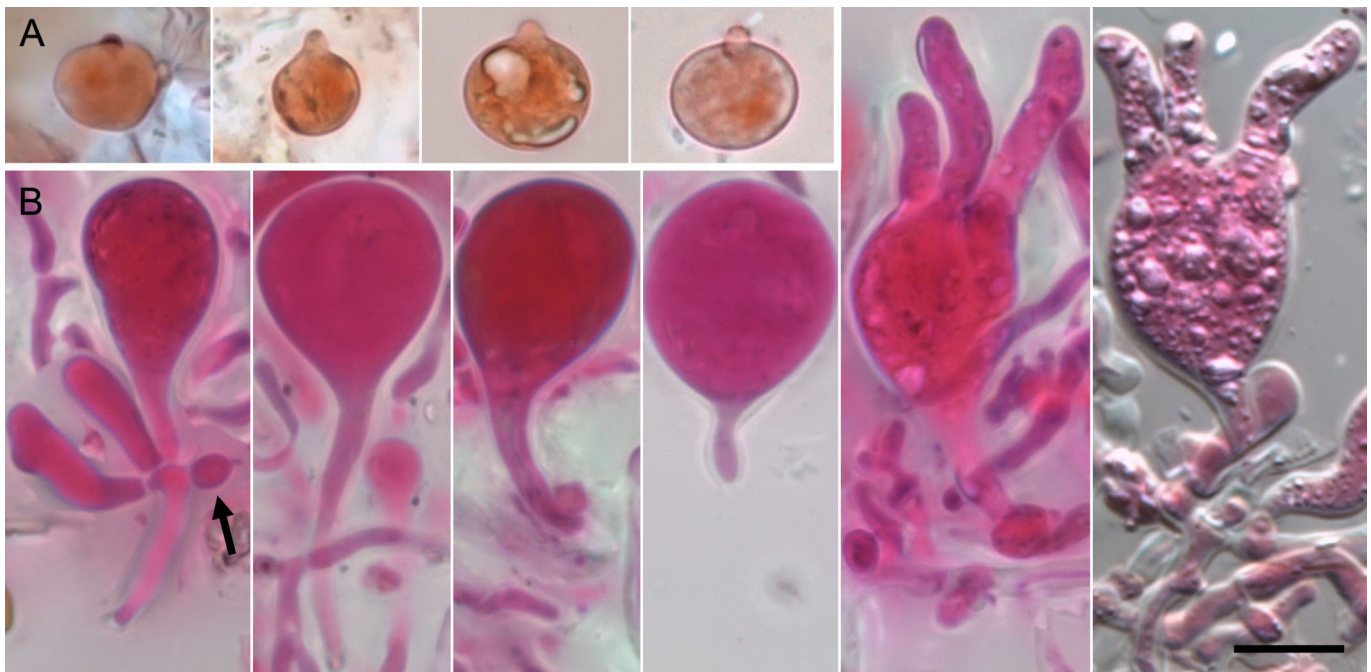
Mycobank: MB844681

Basidiomata partly immersed to superficial, applanate to strongly convex and then basally constricted, constantly pale orange-brown, waxy-gelatinous, surface smooth and slightly shiny, 0.3–1.5 mm diam. **Context hyphae** thick-walled, 2.5–4 µm diam.; subbasidial hyphae thick-walled, 2.5–4 µm diam., septa without clamps; haustoria present, without a basal clamp. **Hymenium** containing numerous ellipsoid probasidia, often with a long stalk-like base, without a basal clamp. **Basidia**, when mature, 2–4-celled, with longitudinal or oblique septa, ellipsoid, often with a distinct stalk, 17–48 × 12–17 µm (stalk included), upper part (without stalk) 17–22 µm long, stalk 7–28 µm long; epibasidia subulate to subcylindrical, 3.5–5.5 µm diam., 40–65 µm long. **Basidiospores** shortly ellipsoid, 9.5–12 × 8–10.5 µm. **Asexual stage** unknown. [Description of holotype.]

Notes. This species belongs to the *Tremella pertusariae* complex, resembles *T. pertutexanae* morphologically,



Tremella pertuthalamiae, Taiwan, Sparrius 6105. Basidiomata on the thallus of *Pertusaria* sp. Scale bar: 1 mm.



Tremella pertuthalamiae, USA, Florida, holotype. A, Basidiospores, in ammoniacal Congo red. B, Basidia in different stages of development, and haustorium (arrow), in phloxine. Scale bar: 10 μ m.

and occurs on a macroscopically similar host. It is distinguished by a number of partly subtle differences: basidiomata are waxy-gelatinous, with a smooth and shiny surface (vs gelatinous, with an often matt and rough surface), pale orange-brown also when old (vs often greyish to dark brown or blackish), 0.3–1.5 μ m diam. (vs 0.15–0.5 μ m); basidia often have a long and narrow stalk-like base (vs stalk mostly short or absent), the main basidial body without stalk is 17–22 μ m long (vs 26–50 μ m), and exospores have not been observed.

We tentatively include in this species a second specimen from Taiwan on an unidentified, sterile, isidiate *Pertusaria* species. Basidiomata are similar in colour and consistency, although older ones become more flattened. Basidia similarly often have a long and thin stalk, while the main basidial body is almost spherical. Basidia measure 22–36 \times 15–23 μ m (stalk included), upper part (without stalk) 19–24 μ m long, stalk 5–15 μ m long. The main difference from *T. pertuthalamiae* consists in the upper part of the basidia

being much broader, subspherical, sometimes broader than tall, and abruptly passing over to the stalk. More similar specimens, together with molecular data, will be necessary to identify whether populations on hosts other than *Pertusaria tetrathalamia* belong to *T. pertuthalamiae*, or if they represent distinct, possibly semi-cryptic species.

Ecology and hosts. On the thallus of *Pertusaria tetrathalamia* and of an unidentified, isidiate *Pertusaria* species.

Distribution. North America (USA: Florida) and Asia (Taiwan). Further specimens on *Pertusaria tetrathalamia* from Alabama and Florida (Diederich 2003 as *Tremella pertusariae*) need to be revised.

Additional specimen examined. **Taiwan:** Hualien Co., 43 km WNW of Hualien, Meifeng, 24°06'N, 121°11'E, 2250 m, roadside with relict mature trees, on mature *Castanopsis*, on *Pertusaria*, 2001, Sparrius 6105 (BR).



Tremella pertuthalamiae

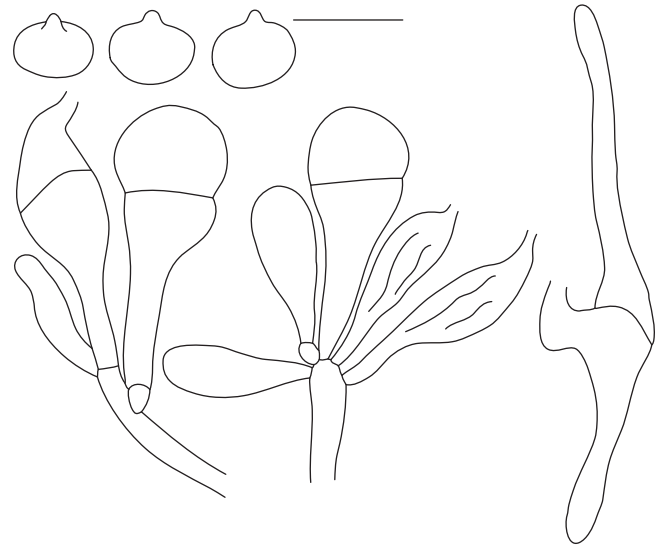
Tremella phaeographidis Diederich, Coppins & Bandoni

in Diederich, *Bibl. Lichenol.* 61: 136 (1996). Type: UK, VC 4, North Devon, Bideford, Clovelly, Gallantry Bower, by coastal path (21/30.26), on *Phaeographis smithii*, 14 Oct. 1994, B. J. Coppins 16483 & A. M. O'Dare (E – holotype; BR – isotype).

Basidiomata flattened or little convex, pulvinate, pale to dark brown, often reddish brown, waxy-gelatinous, 0.4–0.7 mm diam. **Context hyphae** 1.5–2.5 μ m diam.; clamp connections not observed; haustoria present, but rare. **Hymenium** containing numerous probasidia and conidiogenous



Tremella phaeographidis, UK, isotype. Basidiomata on *Phaeographis smithii*. Scale bar: 500 μm .



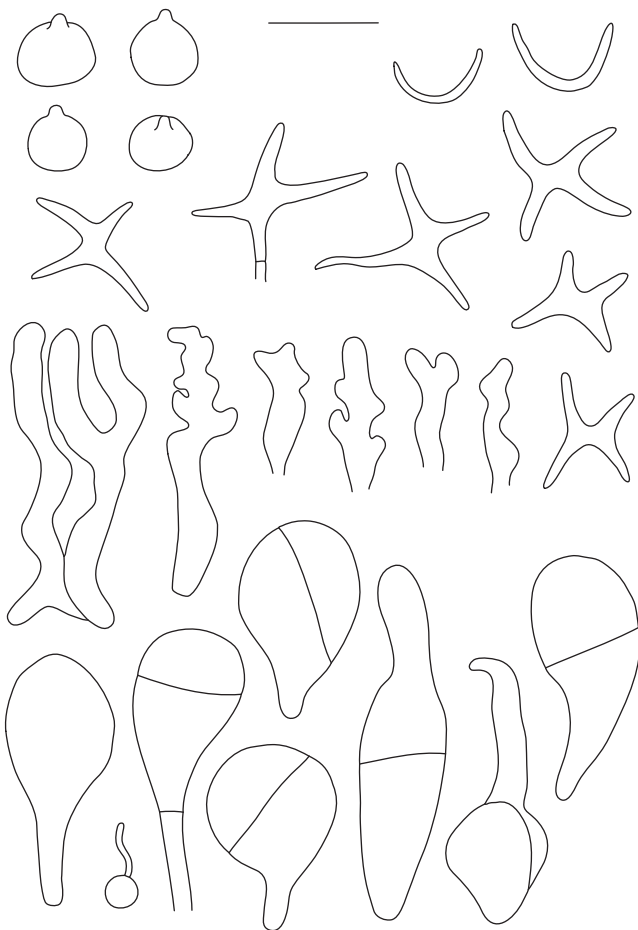
Tremella phaeographidis, Thailand, Bandoni 10272 (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 μm .

cells; probasidial initials ellipsoid, with a basal clamp. *Basidia*, when mature, with one transverse or oblique, rarely transverse septum, the lower cell with an attenuated, often

stalk-like base, longer than the upper cell, $16\text{--}24 \times 8\text{--}12 \mu\text{m}$; epibasidia subcylindrical, at least $25 \mu\text{m}$ long, $3\text{--}4 \mu\text{m}$ diam. *Basidiospores* ellipsoid to subspherical, $5.5\text{--}7.5 \times 5\text{--}6 \mu\text{m}$. *Asexual stage*: asteroconidia of $12\text{--}17 \mu\text{m}$ diam., with 4 arms of $4\text{--}9 \mu\text{m}$ in length, are frequently produced; conidiogenous cells $15\text{--}27 \mu\text{m}$ long, $2\text{--}3.5 \mu\text{m}$ diam., very irregular in form, with few apical branches; thin lunate conidia have been observed in a squash preparation.

Notes. This is a poorly known species originally described for a *Tremella* collected on *Phaeographis* in the UK and in Thailand. In the mean time, it has repeatedly been reported from atlantic regions in W France on *Phaeographis smithii* (Roux 2020) and SW England on *Leiorreuma lyellii* and several *Phaeographis* species (<https://species.nbnatlas.org/species/BMSSYS0000018799>), while it has never been recollected in the tropics. Molecular data are needed to identify whether one or two distinct species are involved.

Tremella phaeographinae, originally described from *Phaeographina* sp. in Florida, but now known to inhabit several *Phaeographis* s. lat. species in the SE USA, is distinguished by the characteristic basidia with one transverse



Tremella phaeographidis, UK, holotype (modified from Diederich 1996). Basidia, basidiospores, conidiogenous cells, asteroconidia, lunate conidia and a haustorial branch. Scale bar: 10 μm .



Tremella phaeographidis

and one longitudinal septum, and by growing in the hymenium of the hosts.

Ecology and hosts. On the thallus, rarely apothecia of *Leiorreuma lyellii*, *Phaeographis smithii*, *P. dendritica* and *Phaeographis* sp.

Distribution. Europe (France; UK: England) and Asia (Thailand).

References. Diederich 1996 [Roux 2020].

Tremella phaeographinae Diederich & Aptroot

in Diederich, *Bibl. Lichenol.* 61: 140 (1996). *Type:* USA, Florida, Collier County, Big Cypress National Preserve, road 94, on cypress trees in cypress forest, 25°40' N, 80°40' W, 5 m, on *Phaeographis* s. lat., June 1989, A. Aptroot 26229 (B – holotype; BR, herb. Aptroot – isotypes).

Basidiomata at first reduced, growing in the hymenium of the host, soon superficial on the hymenium, reddish to orange-brown, roundish or elongate, applanate to convex, often with a whitish pruina, waxy-gelatinous, $0.3\text{--}1.2 \times 0.2\text{--}0.5$ mm. **Context hyphae** thick-walled, with clamp connections, $2.5\text{--}4$ μm diam.; haustoria frequent, with clamp connections. **Hymenium** containing numerous elongate claviform probasidia with an attenuated base and a basal clamp. **Basidia**, when mature, with one transverse septum, often constricted at the septum, the lower part longer than the upper part, with an attenuated base, the lower part sometimes with one additional oblique septum, the upper part often with one additional longitudinal septum, $22\text{--}32 \times 9.5\text{--}11$ μm , basidia rarely with only one longitudinal septum; epibasidia subcylindrical, $3\text{--}4$ μm diam., at least 30 μm long. **Basidiospores** subspherical, $5.5\text{--}7.5 \times 5\text{--}6.5$ μm . **Asexual stage:** blastoconidia abundant, ellipsoid, with a truncate base, hyaline, smooth-walled, thin-walled, $5\text{--}7 \times 2.5\text{--}4$ μm .

Notes. This species is well characterized by the intrahymenial growth on *Phaeographis* s. lat., and by the unusual, 3-celled basidia, typically with one transverse and one longitudinal septum.

Ecology and hosts. In the hymenium of *Phaeographis* s. lat. The host of the holotype may belong in *Platygramme*, whilst the host of a paratype (Buck 22971, NY) is *Platy-*

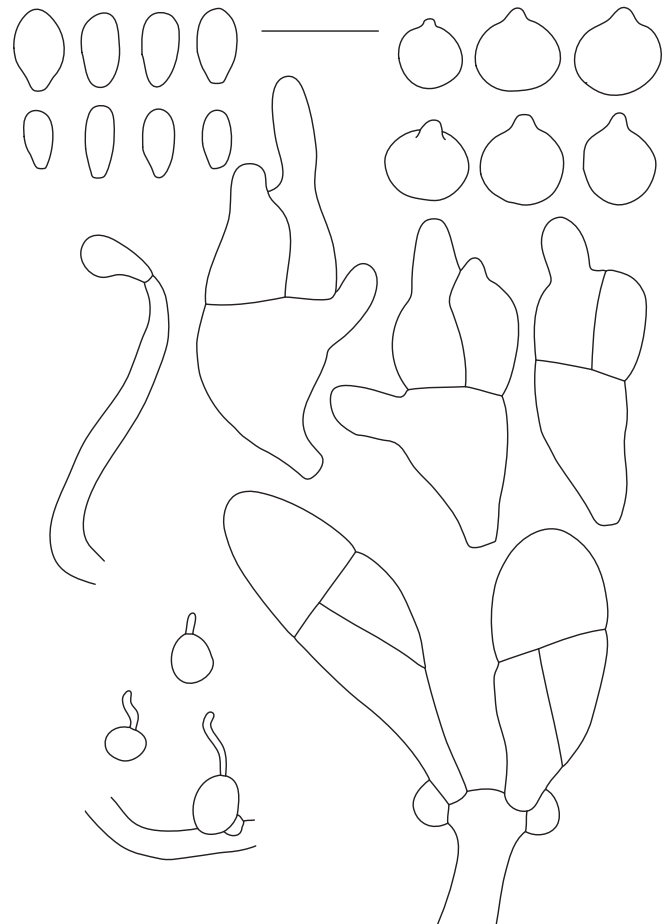


Tremella phaeographinae



Tremella phaeographinae, USA, Florida, isotype. Basidiomata on *Phaeographina* sp. Scale bar: 500 μm .

gramme pachnodes. The hosts of further specimens are *Leiorreuma explicans* and *Phaeographis leiogrammoides*. Both *Leiorreuma* and *Platygramme* belong to the *Phaeographis* clade, which might represent a single large genus



Tremella phaeographinae, USA, holotype (modified from Diederich 1996). Basidia, basidiospores, conidia and haustorial branches. Scale bar: 10 μm .

Phaeographis, but none of the known host species has yet been included in a phylogenetic analysis.

Distribution. North America (USA: Florida, Georgia).

References. Diederich 1996 [Ariyawansa et al. 2015, Diederich 2003, Diederich et al. 2019].

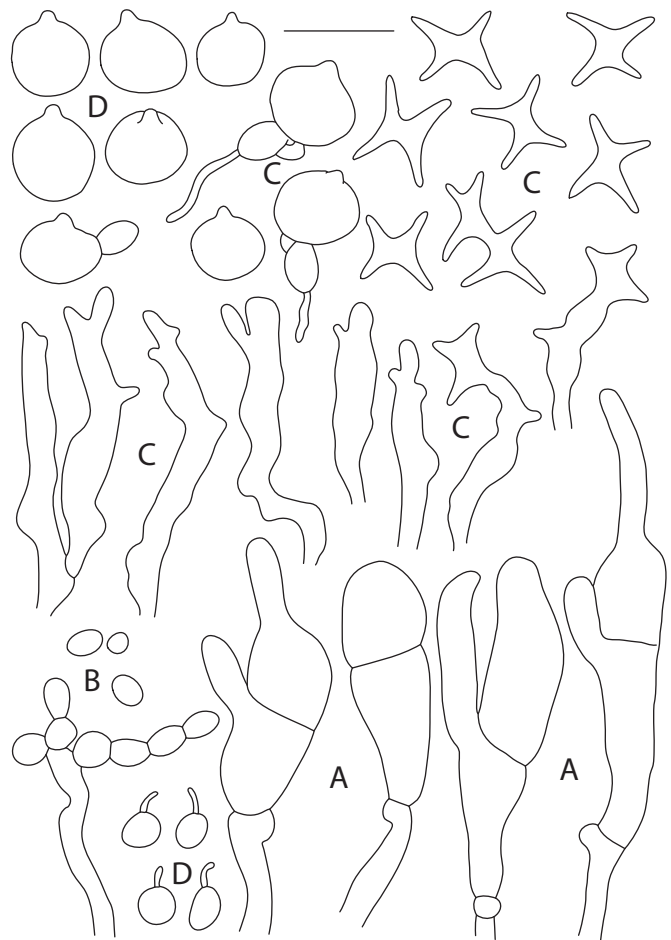
***Tremella phaeophysciae* Diederich & M. S. Christ.**

in Diederich, *Bibl. Lichenol.* 61: 142 (1996). *Type:* Denmark, Zealand, Jungshoved, on *Phaeophyscia orbicularis*, 12 Aug. 1966, M. S. Christiansen 2351 (C – holotype; BR – isotype).

Basidiomata inducing the formation of olivaceous to brownish, sometimes reddish brown, flat to slightly convex galls with a matt surface, 0.4–2 mm diam., when old, developing into dark brown and strongly convex, sometimes tuberculate, gelatinous basidiomata. *Context hyphae* 3–4 µm diam., clamps not observed; haustoria frequent. *Hymenium* 35–55 µm tall, containing numerous conidiogenous cells intermixed with clavate probasidia with a basal clamp. *Basidia*, when mature, 2–4-celled, septa transverse or oblique, rarely longitudinal, 15–27 × 4.5–8 µm; epibasidia subcylindrical, 2–3 µm diam., 25–50 µm long. *Basidiospores* subspherical to ellipsoid, 6–8 × 5.5–7.5 µm. *Asexual stage:* asteroconidia are frequent in older basidiomata, with 4 arms, 8–11 µm diam., individual arms 2.5–5 µm long; conidiogenous cells irregularly cylindrical, with a few short, 1–4 µm long ramifications near the apex, 18–28 × 2.5–3.5 µm; catenulate conidia have been observed in some specimens, individual cells 3–4 × 2.5–3 µm.

Notes. This is a distinct and common species inducing the formation of brownish olivaceous galls on the thallus of *Phaeophyscia* species. No other *Tremella* or *Zyzygomysces* species are known from this host genus.

Ecology and hosts. On the thallus of *Phaeophyscia orbicularis*, more rarely *P. cernohorskyi*, *P. cf. nashii*, *P. poeltii* and *Physciella melanchra*.



Tremella phaeophysciae. A, Denmark, holotype; B, Luxembourg, Diederich 8523; C, UK, Coppins 15946; D, Poland, Sipman 22644 (modified from Diederich 1996). Basidia, basidiospores, conidiogenous cells, asteroconidia, catenulate conidia and haustorial branches. Scale bar: 10 µm.

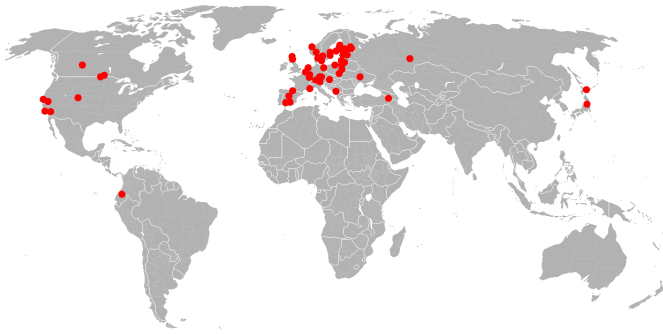
Distribution. Europe (Austria; Belgium; Denmark; Estonia; Finland; France; Germany; Lithuania; Luxembourg; Monte-



Tremella phaeophysciae, Denmark, isotype. Basidiomata on the thallus of *Phaeophyscia orbicularis*. Scale bar: 500 µm.



Tremella phaeophysciae, Scotland, Coppins 15946. Basidiomata on the thallus of *Phaeophyscia orbicularis*. Scale bar: 1 mm.

*Tremella phaeophysciae*

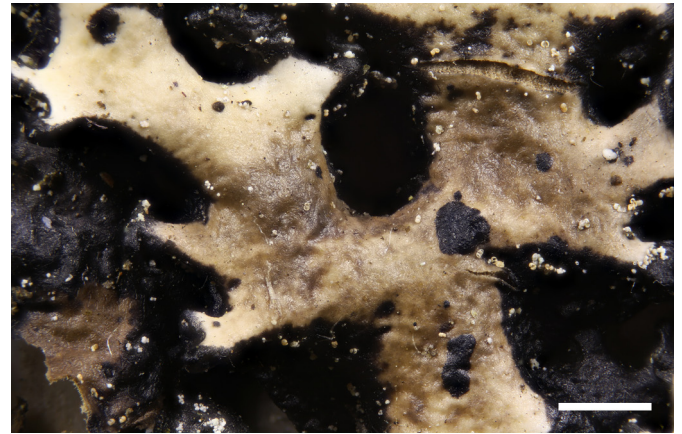
negro; Netherlands; Norway; Poland; Russia; Spain; Sweden; UK: Scotland; Ukraine), North America (Canada: Alberta, Manitoba; USA: California, Colorado, North Dakota), South America (Ecuador) and Asia (Armenia; Japan; Russia).

Additional specimens examined. **Canada:** Manitoba: South West Co., Turtle Mountain P. P., 7 km W of Co. Road 10 Brandon and 6 km S of McKinney Rd., Max Lake Shoreline, 49.0691°N, 100.1434°W, on *Phaeophyscia orbicularis*, 2013, Lewis 1493 (NY). **Japan:** Honshu, Shimotsuke Province, Tochigi Prefecture, Nikko City administrative region, Nikko National Park, Yumoto village, 36°48'26"N, 139°25'13"E, 1507 m, on *P. cf. orbicularis*, 2019, Ertz 24692 (BR). **USA:** California: Riverside Co., E of Los Angeles, Joshua Tree National Monument, road from Hidden Valley to Keys View, 0.5 km N of Keys View, 33°55.7'N, 116°10.3'W, 1240 m, on *P. cf. nashii*, 2002, van den Boom 29523 (herb. van den Boom); Santa Barbara Co., Santa Barbara, close to Mission Creek, Rocky Nook County Park (N end on Mission Oaks Lane, S of Foothill Blvd), on *P. cernohorskyi*, 2004, Tucker 38116B (SBBG); Tulumne Co., Riverside Park, on N Fork of Tuolumne River, Buchanan Mine Rd, E of Sonora, Canyon along rocky stream, on *P. orbicularis*, 2005, Tucker 38625 (SBBG). **North Dakota:** Bottineau Co., 10 mi N, 4 mi E of Bottineau, Lak Metigoshe State Park, 48°59.08'N, 100°19.82'W, 670 m, on *P. orbicularis*, 2009, Advaita 8065, 8101-B (NY); McHenry Co., 2 mi N, 1/2 mi E of Upham, J. Clark Salyer National Wildlife Refuge, 48°37.02'N, 100°43.75'W, 442 m, on *Physciella melanchra*, 2009, Advaita 8152 (NY).

References. Diederich 1996, Pippola & Kotiranta 2008 [Aptroot et al. 2005, Bilovitz 2014, Brackel 2014, Diederich 2003, Etayo 2009, 2017, Gasparyan et al. 2015, Hafellner 2018, Khodosovtsev & Darmostuk 2017, Kocourková & Brackel 2005, Kocourková et al. 2012, Kukwa 2004, 2005, Motiejūnaitė 2000, 2007, Motiejūnaitė et al. 2016, Puolasmaa et al. 2008, Roux 2020, Shiryayev et al. 2010, Suija 2005, Thell et al. 2014, Thor & Söchting 2018, van den Boom 2000, Zhurbenko et al. 2015].

Tremella pinaultii Diederich & Millanes, sp. nov.

Diagnosis: Characterized by the missing basidiomata, the mycelium immersed in necrosed thalli of *Hypogymnia physodes*, the 1-septate basidia, 11–17 × 7–13 µm, and the subspherical to shortly ellipsoid basidiospores, 6.5–7.5 × 5–7 µm.



Tremella pinaultii, France, holotype. Necrosed, brownish thallus of *Hypogymnia physodes*, in which basidia are located. Scale bar: 1 mm.



Tremella pinaultii, France, holotype. Necrosed, brownish thallus of *Hypogymnia physodes*, in which basidia are located. Scale bar: 1 mm.

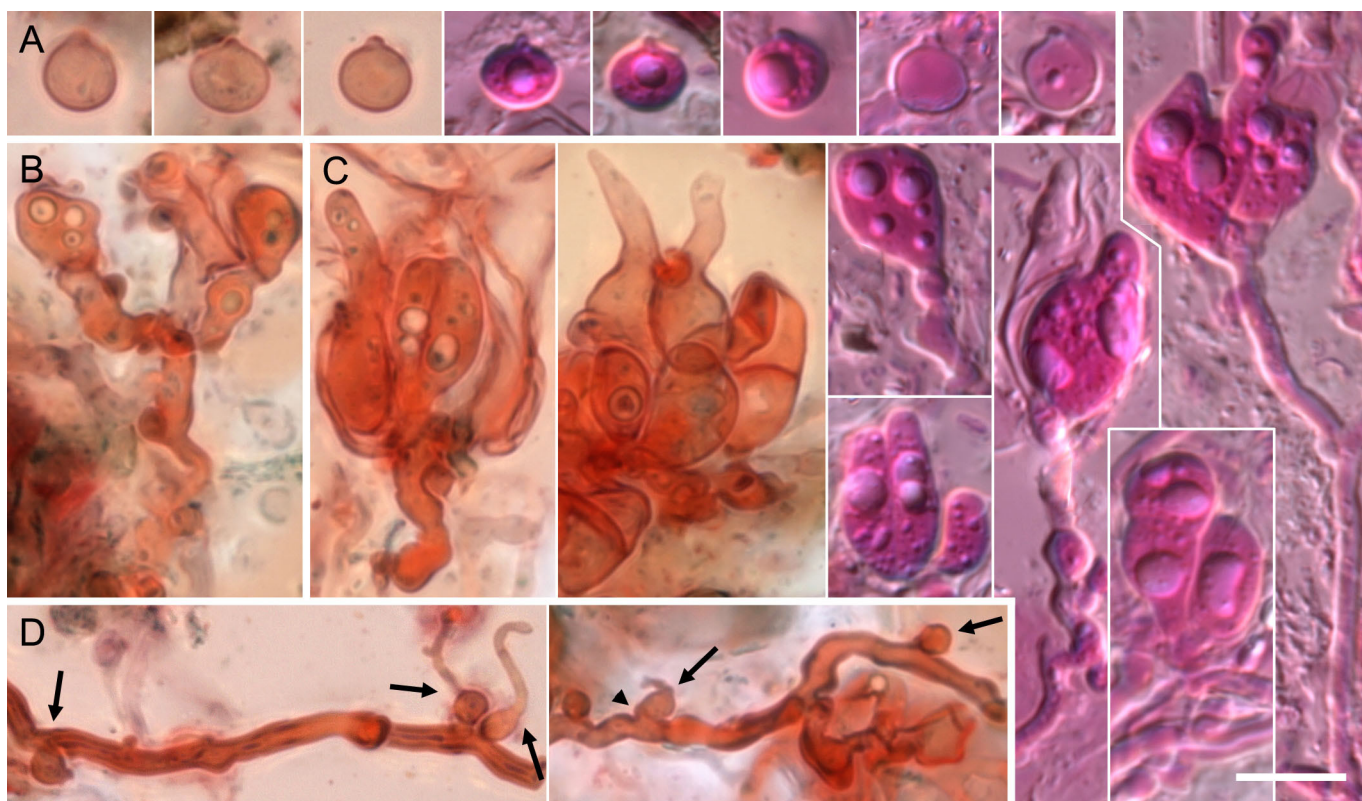
Etymology: Named after Patrick Pinault, France, collector of the new species.

Type: France, Puy-de-Dôme, Saint-Ours, SSW of Vulcania park, 45.8074°N, 2.9309°E, 930 m, on *Betula*, on *Hypogymnia physodes*, 1 Aug. 2020, P. Pinault (BR – holotype).

Mycobank: MB844682

Basidiomata and hymenium absent; mycelium located within necrosed, brownish to blackish portions of the host thallus. **Context hyphae** thick-walled, 2–3.5 µm diam.,

*Tremella pinaultii*



Tremella pinaultii, France, holotype. A, Basidiospores. B, Fertile hyphae with probasidial initials. C, Probasidia and mature basidia in different stages of development. D, Context hyphae with haustoria (arrows), one showing a basal clamp (arrow head). In ammoniacal Congo red (left) or phloxine (right). Scale bar: 10 µm.

most septa without clamps; subbasidial hyphae thick-walled, 2.5–4 µm diam.; haustoria present, with a basal clamp. *Probasidial initials* subspherical to ellipsoid, with a basal clamp. *Basidia*, when mature, in groups of 2 to 6, ellipsoid, 2-celled, with a longitudinal, oblique or transverse septum, 11–17(–20.5) × 7–13 µm; epibasidia cylindrical, 2.5–4 µm thick, 25–35 µm long. *Basidiospores* subspherical to shortly ellipsoid, with a distinct apiculus, 6.5–7.5 × 5–7 µm. *Asexual stage* unknown.

Notes. As this is the first known *Tremella* species developing inside lichen thalli and devoid of basidiomata, we initially thought that it might be unrelated to other lichenicolous taxa. However, *Tremella pinaultii* has typical tremelloid basidia, epibasidia, basidiospores and haustoria, and is therefore described within *Tremella* s. lat.

Some thallus lobes in the type collection are also infected by *Trichonectria anisopora*, and so it is not known with certainty whether the new *Tremella* is associated with *Hypogymnia physodes* or with *T. anisopora*.

It is a pleasure for us to dedicate the new species to Patrick Pinault, Châteaugay, Puy-de-Dôme, France, excellent collector of lichenicolous fungi, who discovered this new species and kindly allowed us to describe it.

Ecology and host. In the thallus of *Hypogymnia physodes*, infected portions being necrosed, brownish to black.

Distribution. Europe (France), known only from the type locality.

Tremella pisutiellae Diederich & W. R. Buck, sp. nov.

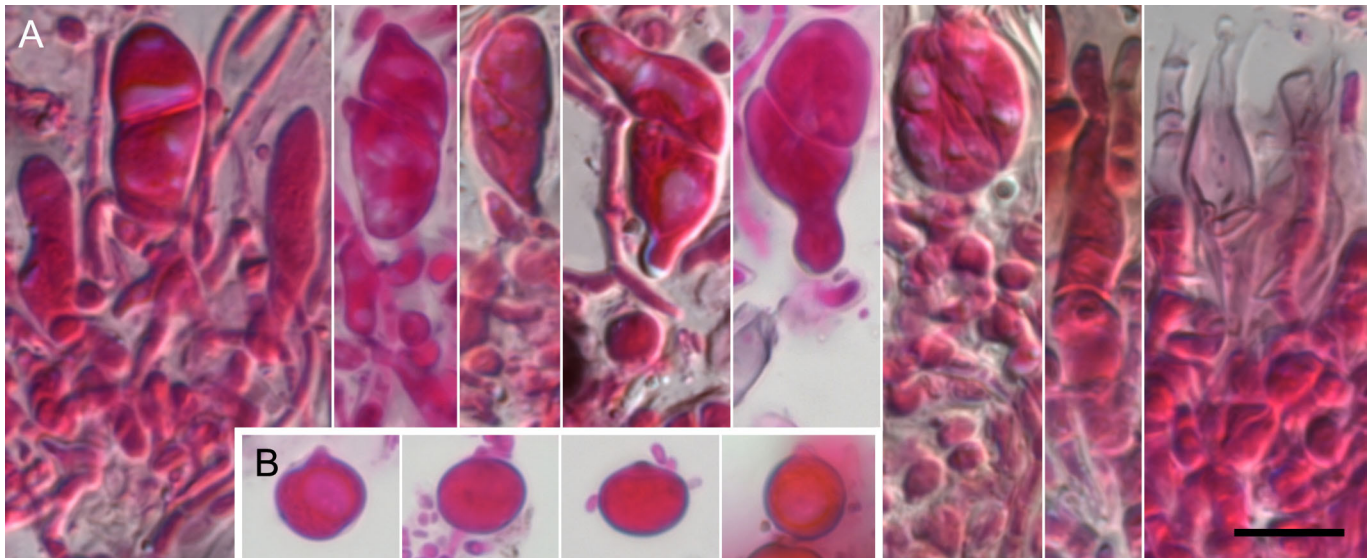
Diagnosis: Characterized by the intrahymenial growth in the apothecia of *Pisutiella conversa* that become swollen, the transversely 1-septate basidia, 17–24 × 7–10 µm, and the ellipsoid basidiospores, 6.5–8.5 × 6–7.5 µm.

Etymology: From *Pisutiella*, the host lichen.

Type: USA, Missouri, Christian Co., Mark Twain National Forest, S of Chadwick Road at jet of Monarch Road, 2.6 mi W of MO UU, 36°54'29"N, 92°58'14"W, overgrown dolomite glade on S-facing slope above Harmon Spring, in apothecia of *Pisutiella conversa*, 21 May 2003, W. R. Buck 44536 (NY – holotype).

Mycobank: MB844683

Basidiomata reduced, developing in the hymenium of the host, macroscopically visible as swellings of the apothecial disk that becomes taller than the apothecial margin. *Context hyphae* not observed; subbasidial hyphae 2.5–4 µm diam.; haustoria frequent. *Hymenium* reduced, probasidia intermixed with the asci and paraphyses of the host, ellipsoid,



Tremella pisutiellae, USA, Missouri, holotype. A, Basidia in different stages of development. B, Basidiospores. In phloxine. Scale bar: 10 μ m.

basal clamp not observed. *Basidia*, when mature, elongate ellipsoid, transversely 1-septate, not or slightly constricted at the septum, (13–)17–24 \times 7–10 μ m; epibasidia cylindrical, up to 4.5 μ m diam., at least 40 μ m long. *Basidiospores* ellipsoid, 6.5–8.5 \times 6–7.5 μ m. *Asexual stage* unknown.

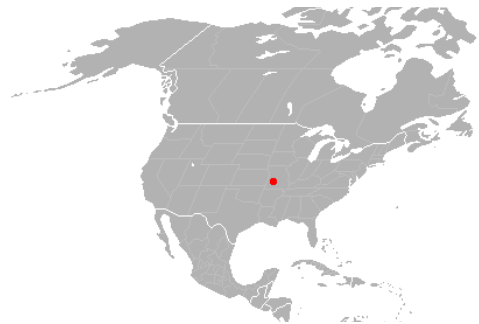
Notes. This is an intrahymenial species that can be detected by the slightly swollen apothecia of the host. As with most other intrahymenial species, it is poor in distinctive morphological characters. It is most similar to *Tremella rinodinae*, a species apparently confined to *Rinodina oleae*, that frequently develops conspicuous basidiomata over the host apothecia when mature.

Ecology and host. In the hymenium of saxicolous *Pisutiella conversa*.

Distribution. North America (USA: Missouri), known only from the type locality.



Tremella pisutiellae, USA, Missouri, holotype. Basidiomata in the hymenium of *Pisutiella conversa*. Scale bar: 500 μ m.



Tremella pisutiellae

Tremella placynthiellae Diederich & W. R. Buck, sp. nov.

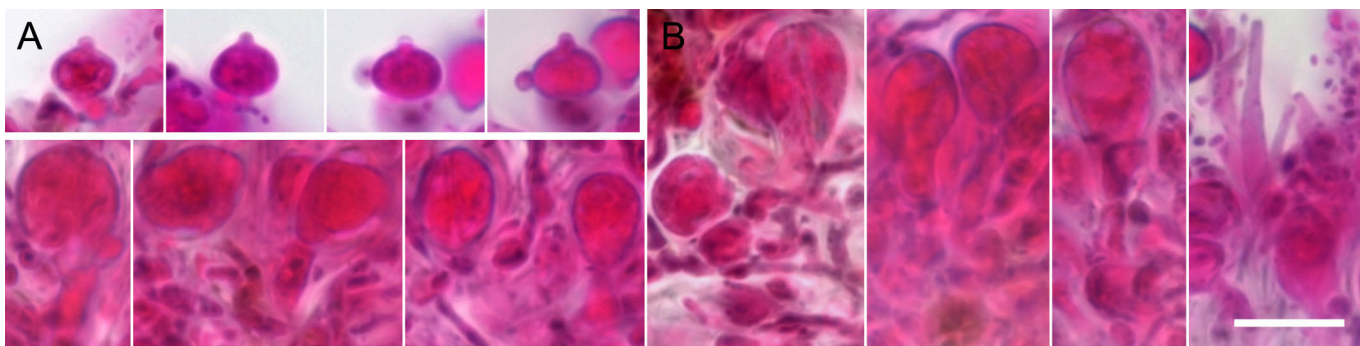
Diagnosis: Characterized by the small, subspherical, pale brown, waxy-gelatinous basidiomata on the thallus of *Placynthiella icmalea*, 0.04–0.16 mm diam., the medium-sized basidiospores, 5–6.5 \times 4.5–6.5 μ m, and the particularly small, longitudinally, obliquely or transversely 1-septate basidia, 6.5–12(–14) \times 5.5–9 μ m.

Etymology: From *Placynthiella*, the host lichen.

Type: USA, Missouri, Wayne Co., Sam A. Baker State Park, Mudlick Mountains, along road to fire tower, 37°15'27"N, 90°31'23"W, 300 m, T.30N., R.5E., sec. 29, oak-hickory forest with rhyolite boulders, on *Placynthiella icmalea*, 15 Oct. 2003, W. R. Buck 45306 (NY – holotype).

Mycobank: MB844684

Basidiomata developing at the apices of host goniocysts, superficial, subspherical, waxy-gelatinous, with a smooth surface, pale brown, minuscule, 0.04–0.16 mm diam., often confluent, sometimes tuberculate and then up to 0.4 mm diam. *Context hyphae* thick-walled, 1.5–2.5 μ m; subbasidial hyphae thick-walled, 2–3.5 μ m diam.; haustoria not



Tremella placynthiellae, USA, Missouri, holotype. A, Basidiospores. B, Basidia in different stages of development. Scale bar: 10 µm.



Tremella placynthiellae, USA, Missouri, holotype. Basidiomata on the thallus of *Placynthiella icmalea*. Scale bar: 500 µm.

observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid or pyriform, 2-celled, with a longitudinal, oblique or transverse septum, $6.5\text{--}12\text{--}(14) \times 5.5\text{--}9\text{ }\mu\text{m}$; epibasidia cylindrical or tapering, $10\text{--}30\text{ }\mu\text{m}$ long. *Basidiospores* ellipsoid, $5\text{--}6.5 \times 4.5\text{--}6.5\text{ }\mu\text{m}$. *Asexual stage* unknown.

Notes. This species is distinguished from most other lichenicolous *Tremella* species by the extremely small, pale brown basidiomata, most not exceeding 0.16 mm in diam., and the very small basidia. *Tremella coccocarpiae* differs by the smaller basidiospores, $5.5 \times 4\text{--}4.5\text{ }\mu\text{m}$, and the longer basidia, $11\text{--}15 \times 6.5\text{--}9\text{ }\mu\text{m}$; *T. microcarpa* differs by the abundant haustoria, the slightly larger basidia, $9.5\text{--}12.5 \times 7\text{--}11\text{ }\mu\text{m}$, the occasional presence of stalked basidia, $17\text{--}20 \times 8\text{--}10.5\text{ }\mu\text{m}$, and the slightly larger basidiospores, $5.5\text{--}8.5 \times 4.5\text{--}7\text{ }\mu\text{m}$.

Ecology and host. On the thallus (goniocysts) of *Placynthiella icmalea* over rotten wood.

Distribution. North America (USA: Missouri), known only from the type locality.



Tremella placynthiellae

Tremella protoparmeliae Diederich & Coppins

in Diederich, *Bibl. Lichenol.* 61: 147 (1996). *Type*: UK, VC 62, Farndale, Cleveland, on *Protoparmelia badia*, Sept. 1856, A. C. Maingay s. n. (E – holotype).

Basidiomata reduced, in the hymenium of the host, macroscopically not visible. *Context hyphae* not observed; haustoria present on subbasidial hyphae, with clamp connections. *Hymenium* reduced, clavate probasidia with a basal clamp situated in the hymenium of the host. *Basidia*, when mature, narrowly ellipsoid to subcylindrical, with one transverse septum (never oblique or longitudinal), distinctly constricted at the septum, the lower cell only a little longer than the upper cell, with an attenuated stalk-like base, $29\text{--}39 \times 8\text{--}10\text{ }\mu\text{m}$ (incl. stalk); epibasidia $3.5\text{--}4.5\text{ }\mu\text{m}$ thick, at least $30\text{ }\mu\text{m}$ long. *Basidiospores* subglobose, $8.5\text{--}9.5 \times 6.5\text{--}8\text{ }\mu\text{m}$. *Asexual stage* unknown.

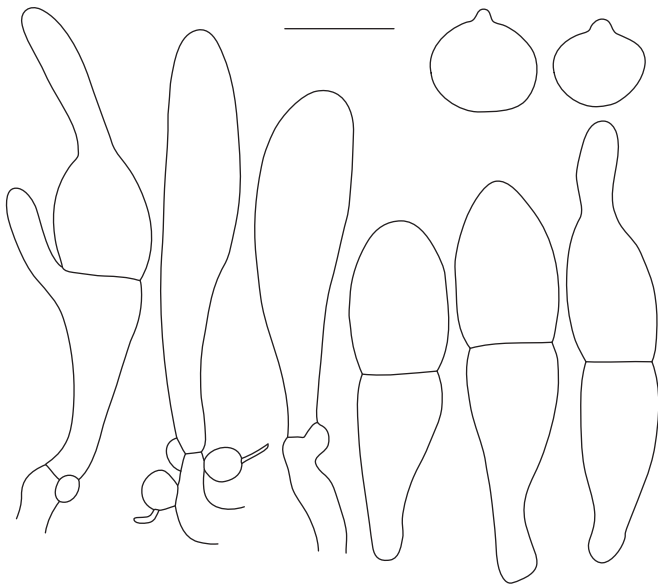
Notes. This taxon is distinguished from most other intrahymenial species by the very long 1-septate basidia. The similar *T. rhizocarpicola* differs by the dark brown swellings on infected apothecia.

Ecology and host. In the hymenium of *Protoparmelia badia*.

Distribution. Europe (Norway; Sweden; UK: England, Scotland).

Additional specimen (identified and communicated by B. Coppins). **Norway**: Oppland, Ringebu komm., highest point on road between Enden and Ringebu, near Muvatn, on saxicolous *Protoparmelia badia*, 1977, Dalby (E).

References. Diederich 1996 [Millanes et al. 2014a].



Tremella protoparmeliae, UK, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 μ m.



Tremella protoparmeliae

***Tremella pseudocyphellariae* Diederich, Millanes & Ertz, sp. nov.**

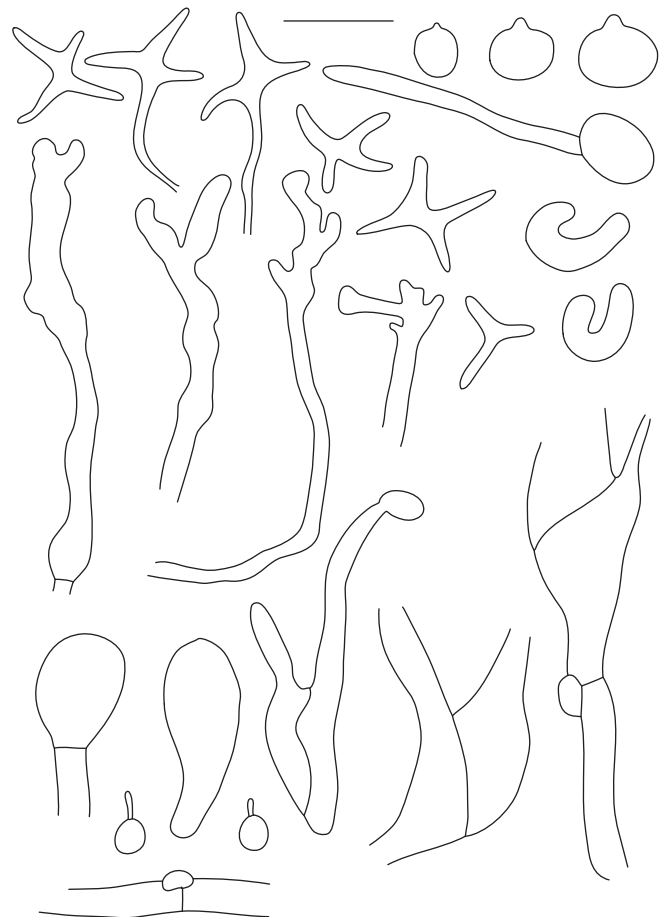
Diagnosis: Characterized by the large, medium to dark brown or blackish, waxy-gelatinous, subspherical to irregular basidiomata with a constricted base, 0.2–1.6 mm diam., on the thallus of *Pseudocyphellaria*, the mainly obliquely 1-septate basidia, $13\text{--}22 \times 8.5\text{--}13 \mu\text{m}$, and the shortly ellipsoid basidiospores, $6\text{--}10 \times 5\text{--}7.5 \mu\text{m}$.

Etymology: From *Pseudocyphellaria*, the host lichen.

Type: Mauritius, Savanne District, Black River Gorges National Park, along the trail to Mt Cocotte, 20.4417°S , 57.4711°E , 720–750 m, on corticolous *Pseudocyphellaria desfontainii*, 1 Sept. 2019, P. Diederich 18851 & D. Ertz (MAU – holotype; BR – isotype).

MycoBank: MB844685

Basidiomata growing on soralia, isidia or pseudocyphellae of the host, medium to dark brown or blackish, waxy to firm gelatinous, at the beginning subspherical, later irregular in form, 0.2–1.6 mm diam. *Context hyphae* thick-walled, 2–3 μm diam., with clamp connections; haustoria present. *Hymenium* containing numerous ellipsoid to clavate probasidia with a basal clamp, occasionally intermixed with conidiogenous cells. *Basidia*, when mature, ellipsoid, rarely subspherical or elongate ellipsoid, 1-septate, septum oblique, rarely longitudinal or transverse, $13\text{--}22 \times 8.5\text{--}13 \mu\text{m}$; epibasidia subcylindrical, 2–3 μm diam., up to 50 μm long. *Basidiospores* shortly ellipsoid, $6\text{--}10 \times 5\text{--}7.5 \mu\text{m}$, smaller ones $4\text{--}4.5 \times 3.5 \mu\text{m}$ probably representing secondary spores. *Asexual stage*: lunate conidia $13.5\text{--}14.5 \times 2.5\text{--}3 \mu\text{m}$ have been seen, but conidiogenesis not observed; asteroconidia 9–13 μm diam., individual arms 3–6 μm long, conidiogenous cells 1–3 μm diam., up to 75 μm long, with a few or several branches close to the apex up to 6 μm long.



Tremella pseudocyphellariae, Papua New Guinea, Diederich 10819 (modified from Diederich 1996). Basidia, basidiospores (one with a germ tube, conidiogenous cells, asteroconidia, lunate conidia, a hypha with a clamp connection and haustoria. Scale bar: 10 μ m.



Tremella pseudocyphellariae, Mauritius, holotype. Basidiomata on isidia of *Pseudocyphellaria desfontainii*. Scale bar: 500 μ m.



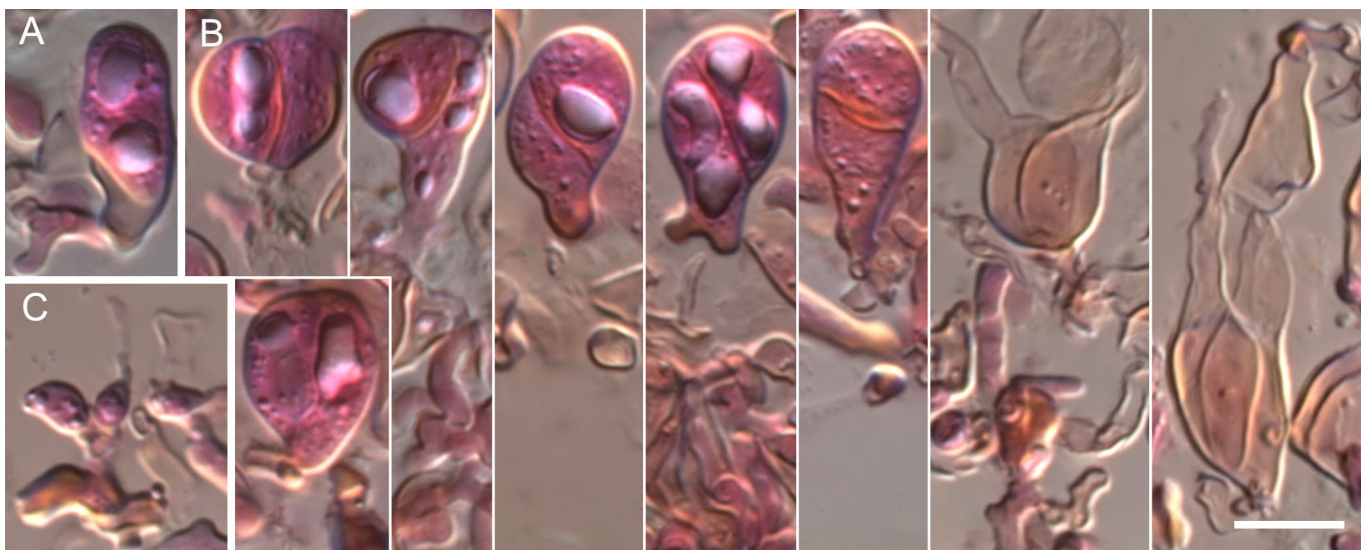
Tremella pseudocyphellariae, Papua New Guinea, Diederich 10035. Basidioma on pseudocyphellae of *Pseudocyphellaria argyracea*. Scale bar: 500 μ m.



Tremella pseudocyphellariae, Papua New Guinea, Diederich 10059. Basidiomata on isidia of *Pseudocyphellaria argyracea*. Scale bar: 500 μ m.



Tremella pseudocyphellariae, Papua New Guinea, Diederich 11321. Basidiomata on soralia of *Pseudocyphellaria* sp. Scale bar: 500 μ m.



Tremella pseudocyphellariae, Mauritius, holotype. A, Probasidium. B, Basidia in different stages of development. C, Haustoria. In phloxine mixed with ammoniacal Congo red. Scale bar: 10 μ m.

Notes. This species was included in *Tremella lobariacearum* by Diederich (1996). A recently collected specimen from Mauritius has been sequenced and our phylogeny suggests a new species. The material from Papua New Guinea is morphologically so similar that we consider it as conspecific. Further specimens from Madagascar and Réunion (Diederich 1996) have not been re-examined, but almost surely belong to the same species. *Tremella flakusii*, inhabiting species of *Crocodia*, is distinguished by the larger basidiospores and basidia, and by the pale to dark reddish brown, never blackish basidiomata.

Ecology and hosts. On the tip of isidia, soredia or pseudocyphellae of *Pseudocyphellaria desfontainii*, *P. argyracea*, *P. crocata*, *P. insculpta*, *P. intricata*, *P. multifida* and *P. cf. neglecta*.

Distribution. Indian Ocean (Madagascar; Mauritius; Réunion) and Oceania (Papua New Guinea).

Additional specimens examined. **Madagascar:** Antsiranana (Diego Suarez) Province: Diana Region, Diego II District, Joffreville Commune, Forontany (Morafeu), Parc National de la Montagne d'Ambre, summit Olioly, 12°32'35"S, 49°08'46"E, 1350 m, crest forest of mostly short trees on ridge, on corticolous *Pseudocyphellaria desfontainii*, 2014, Ertz 19447 (BR). **Toliara (Tuléar) Province:** c. 25 km au nord-ouest de Fort Dauphin (Tolagnaro), Parc National de Andohahela, partie sud de la parcelle 1 à 5 km à l'ouest du village de Malio, 24°55'44.8"S, 46°44'26.2"E, 380 m, forêt dense humide de fond de vallon, on *P. desfontainii*, 2019, Ertz 25182 (BR). **Papua New Guinea:** Eastern Highlands Province: Mount Gahavisuka Provincial Park, N of Goroka, on *Pseudocyphellaria crocata*, *P. multifida* and *P. sp.*, 1992, Diederich 10484, 10489, 10491, 10597 (BR). **Madang Province:** Huon Peninsula, Finisterre range, Yupna valley, Teptep village, on *P. crocata*, 1992, Diederich 10819 (BR). **Simbu Province:** Mount Wilhelm, Pindaunde valley, surroundings of upper lake (lake Aunde), 3600 m, on *P. crocata*, 1992, Diederich 10022 (BR); *ibid.*, near lake Piunde, on *P. argyracea*, 1992, Diederich 10035, 10059, 10085 (BR); Mount Wilhelm area, c. 11 km on new road under construction from Gembogl to Goroka, on *P. crocata*, *P. intricata* and *P. sp.*, 1992, Diederich 11321, 11322, 11323 (BR); Mount Wilhelm area, Bundi Gap, on road Keglsugl-Bundi, on *P. insculpta*, 1992, Diederich 11065 (BR).

References. Diederich 1996 as *Tremella lobariacearum*.



Tremella pseudocyphellariae

Tremella psoroglaenae Diederich

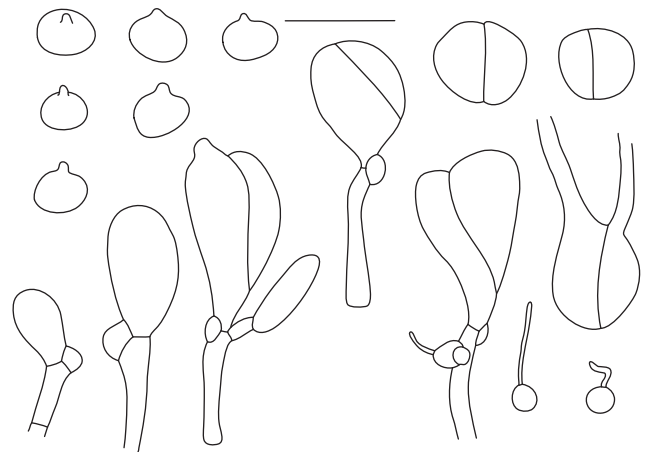
Bibl. Lichenol. 61: 149 (1996). **Type:** Papua New Guinea, Simbu Province, Mount Wilhelm area, c. 11 km on new road under construction from Gembogl to Goroka, mossy mountain forest, on *Psoroglaena* sp., 2800 m, 5°55'S, 145°9'E, 9 Aug. 1992, P. Diederich 12231 (LG – holotype; BR – isotype).

Basidiomata appanate to pulvinate, discoid, waxy-gelatinous, brown, 0.1–0.45 mm diam. **Context hyphae** 1–2.5 µm diam., clamps not observed; haustoria frequent. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid, with one longitudinal or slightly oblique septum, the two cells sometimes not equal in size, 10–16 × 7–10 µm; epibasidia cylindrical, 1.5–2.5 µm thick. **Basidiospores** ellipsoid, 4–5 × 3.5–4.5 µm. **Asexual stage** unknown.

Notes. This is a poorly known species that should be searched for in tropical countries where the hosts, *Psoroglaena* species, are common.



Tremella psoroglaenae, Papua New Guinea, isotype. Brown convex basidioma (centre of photo) on the thallus of *Psoroglaena* sp. Scale bar: 500 µm.



Tremella psoroglaenae, Papua New Guinea, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.



Tremella psoroglaenae

Ecology and host. On the thallus of *Psoroglaena* sp. (similar to *P. cubensis* Müll. Arg. var. *cubensis*).

Distribution. Oceania (Papua New Guinea), known only from the type locality.

Reference. Diederich 1996.

Tremella psoromicola Diederich

Bibl. Lichenol. 61: 150 (1996). **Type:** Chile, Prov. Valdivia, Lago Riñihue, Enco, on tree trunks in the dense forest above Enco, on *Psoroma* sp., 28 Sept. 1940, R. Santesson 7579 (UPS – holotype; BR – isotype).

Basidiomatal galls convex, pulvinate, medium brown, not waxy, 0.2–0.8 mm diam. **Context hyphae** thick-walled, with clamp connections, 2–3 µm diam.; haustoria frequent, with clamp connections. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, with one transverse or slightly oblique septum, constricted at the septum, the lower cell with an attenuated base, much longer than the upper cell, 17–24 × 8.5–11.5 µm; epibasidia subcylindrical, 2.5–3.5 µm diam., at least 20–25 µm long. **Basidiospores** ellipsoid to subspherical, 7–9 × 6.5–8 µm. **Asexual stage** unknown.

Notes. This poorly known species is characterized by the pulvinate, brown basidiomatal galls on the thallus of *Psoroma*.

Ecology and host. On the thallus of *Psoroma* sp.

Distribution. South America (Chile), known only from the type locality.

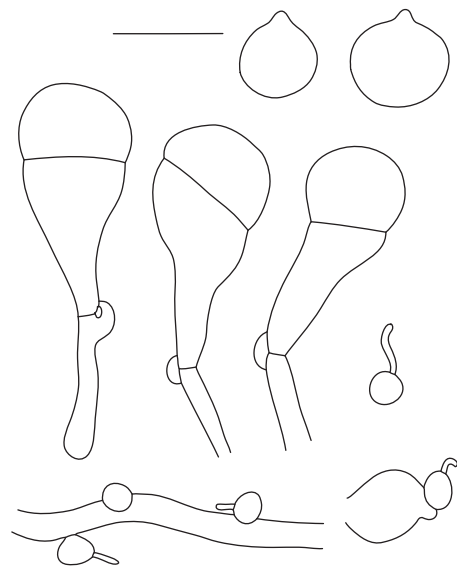
Reference. Diederich 1996.



Tremella psoromicola



Tremella psoromicola, Chile, isotype. Basidiomata on *Psoroma* sp. Scale bar: 500 µm.



Tremella psoromicola, Chile, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 µm.

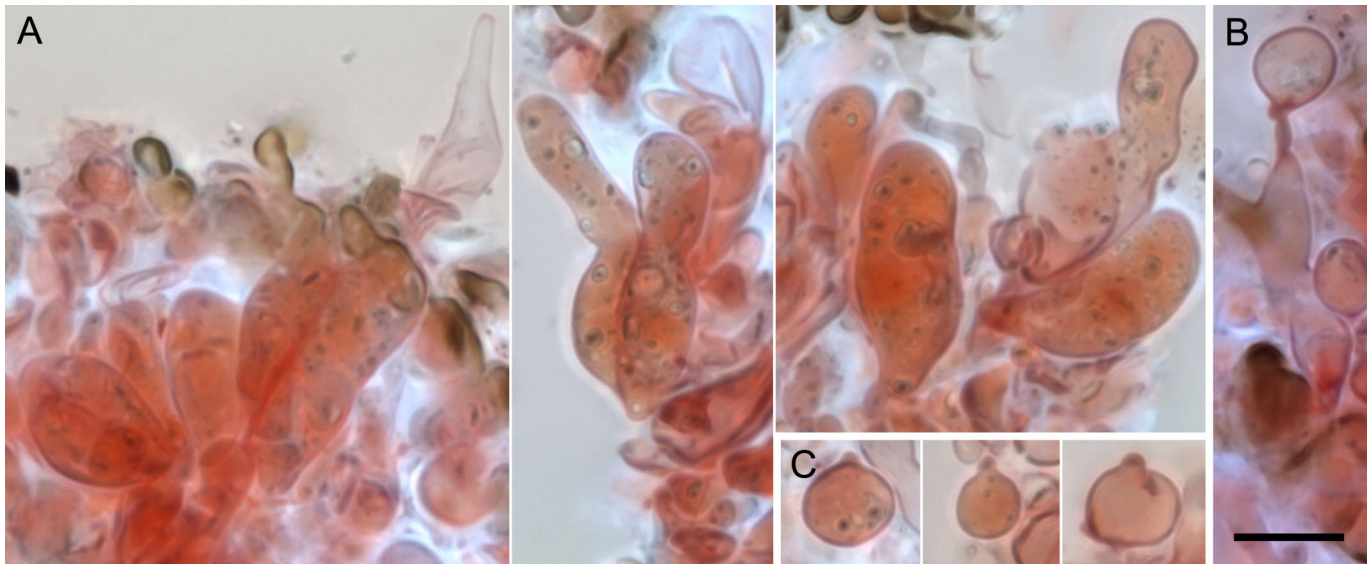
Tremella puncteliae Diederich, Etayo & Millanes, sp. nov.

Diagnosis: Characterized by the large, medium to dark brown, waxy-gelatinous, strongly convex basidiomata with a constricted base, 0.3–5 mm diam., on the thallus of *Punctelia borrieri*, the mainly longitudinally 1-septate basidia, 11.5–23.5 × 8–11.5 µm, the large, 4.5–7.5 µm thick epibasidia, and the large, subspherical to shortly ellipsoid basidiospores, 6–10 × 6–10 µm.

Etymology: From *Punctelia*, the host lichen.

Type: Mexico, surroundings of Popocatepetl, Barranca de Huiloac, 19°04'45"N, 98°35'05"W, 3190 m, ash way (lajar) with *Pinus*, *Alnus* and *Salix*, on *Pinus*, on *Punctelia borrieri*, 1 Nov. 2008, J. Etayo 25013 (MEXU – holotype; herb. Etayo – isotype).

MycoBank: MB844686



Tremella puncteliae, Mexico, holotype. A, Basidia in different stages of development. B, Epibasidium with basidiospore. C, Basidiospores. In ammoniacal Congo red. Scale bar: 10 μ m.

Basidiomata superficial, pulvinate, medium to strongly convex and then with a constricted base, often over gall-like swellings of the host, waxy-gelatinous, medium to dark brown, 0.3–5 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3–4.5 μ m diam.; haustoria not observed. *Hymenium* containing numerous subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, ellipsoid, 2-celled, with a longitudinal or oblique, more rarely transverse septum, 11.5–23.5 \times 8–11.5 μ m; epibasidia cylindrical, at least 40 μ m long, 4.5–7.5 μ m thick. *Basidiospores* subspherical to shortly ellipsoid, 6–10 \times 6–10 μ m. *Asexual stage* unknown.

Notes. This species is distinguished by the large, strongly convex, medium to dark brown basidiomata, the mainly longitudinally 1-septate basidia with particularly thick epi-



Tremella puncteliae

basidia, and the relatively large basidiospores. *Tremella parmeliarum*, a species confined to *Parmotrema reticulatum*, is distinguished by the large, dark, chestnut brown basidiomatal galls with an often smooth and slightly shiny surface.

Ecology and hosts. On the thallus of corticolous members of the *Punctelia borreri* complex.

Distribution. North America ([Mexico](#)).

Additional specimens examined (all on *Punctelia* cf. *borreri*). **Mexico:** Same locality as type, Etayo 25020 (herb. Etayo); from Refugio de Popocatepetl to repetidor, 19°03'39"N, 98°37'57"W, 3950 m, on old *Pinus hartwegii* wood, 2008, Etayo 24889 (herb. Etayo); way from Paso de Cortés to Amecameca, 19°05'11"N, 98°40'44"W, 3200–3330 m, on *Abies religiosa* wood near the way in the slope, 2008, Etayo 24956 (herb. Etayo).

Tremella aff. *puncteliae*

Notes. A Canadian specimen on *Punctelia caseana* macroscopically and microscopically resembles *Tremella puncteliae*, although basidiomatal galls are more strongly convex. As no sequences could be obtained from this specimen, we provisionally treat it as *T. aff. puncteliae*.



Tremella puncteliae, Mexico, holotype. Basidiomata on the thallus of *Punctelia borreri*. Scale bar: 1 mm.



Tremella aff. *puncteliae*, Canada, Brinker 5347. Basidiomata on the thallus of *Punctelia caseana*. Scale bar: 1 mm.



Tremella aff. *puncteliae*, Canada, Brinker 5347. Basidiomata on the thallus of *Punctelia caseana*. Scale bar: 1 mm.

Ecology and host. On the thallus of *Punctelia caseana*.

Distribution. North America (Canada: Ontario).

Specimen examined. **Canada:** Ontario: Rainy River Co., Quetico Provincial Park, 74 km SE of Atikokan, 250 N of NE corner of Emerald Lake, 48.1391°N, 91.2197°W, dry, rocky cliff rim, on *Pinus banksiana*, on *Punctelia caseana*, 2016, Brinker 5347 (herb. Brinker).

***Tremella puncteliotegens* Diederich, Etayo & Millanes, sp. nov.**

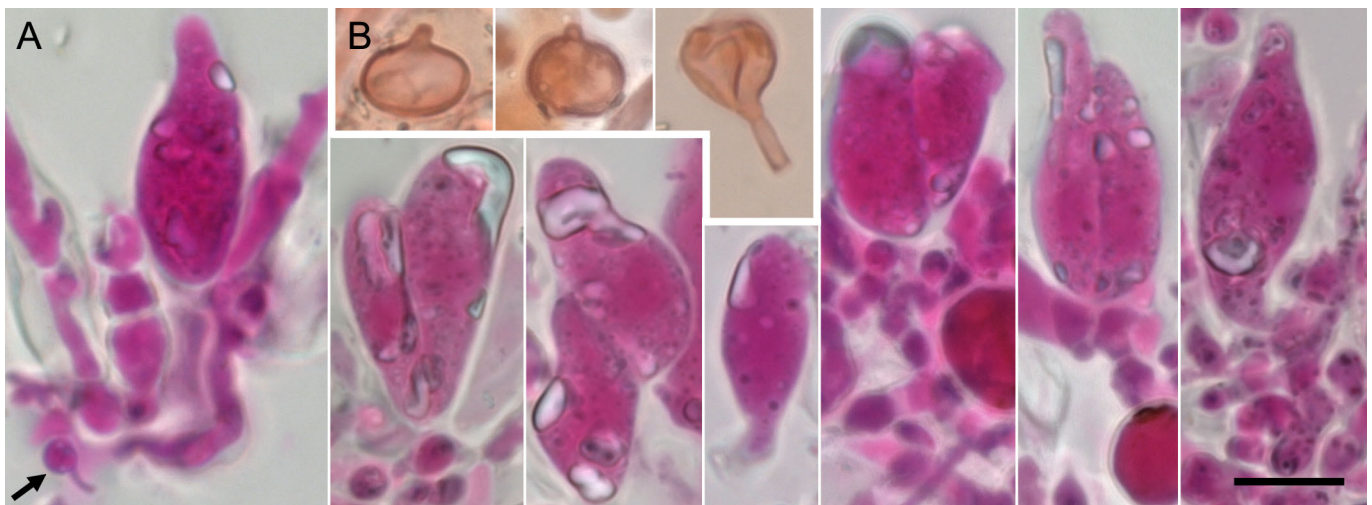
Diagnosis: Characterized by the large, medium brown, waxy-gelatinous basidiomata that are mainly resupinate over the thallus of *Punctelia borreri*, up to 5 mm diam., the mainly longitudinally or obliquely 1-septate basidia, 20–32 × 9–14.5 µm, the relatively thin, 3.5–4 µm thick epibasidia, and the large, subspherical to shortly ellipsoid basidiospores, 9–10.5 × 7–10.5 µm.

Etymology: From *Punctelia*, the host lichen, and *tegens*, covering.

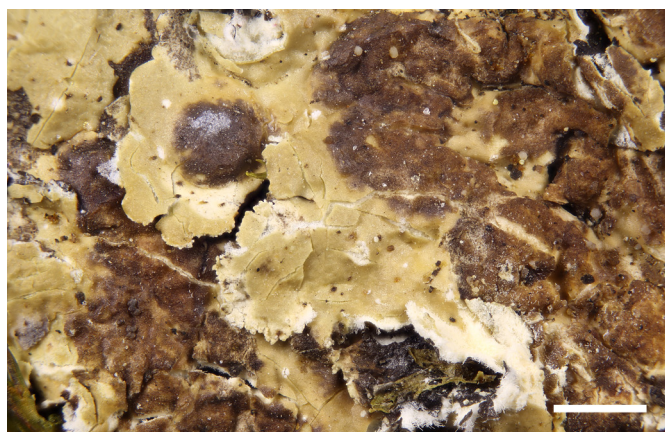
Type: New Zealand, South Island, Southland, Hedgehope, SH 96, Glencoe Memorial, on branches of a solitary tree of '*Fraxinus aurea*', on *Punctelia borreri* s. lat., 14 Sept. 2008, D. J. Galloway (MAF-Lich – holotype).

Mycobank: MB844687

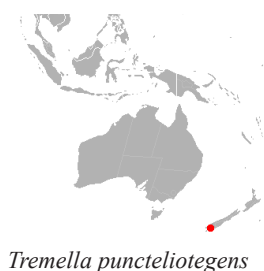
Basidiomata superficial, waxy-gelatinous, medium brown, resupinate, covering large areas of the host thallus, up to 5 mm diam., with an irregular surface composed of a continuous agglomeration of basidiomata, rarely with isolated, delimited basidiomata. **Context hyphae** not observed; subbasidial hyphae thick-walled, 3–5 µm diam.; haustoria present, basal clamp not observed. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid, 2-celled, with a longitudinal or oblique, more rarely transverse septum, 20–32 × 9–14.5 µm; epibasidia cylindrical, at least 35 µm



Tremella puncteliotegens, New Zealand, holotype. A, Basidia in different stages of development, and haustorium (arrow), in phloxine. B, Basidiospores, one still attached to epibasidium, in ammoniacal Congo red. Scale bar: 10 µm.



Tremella puncteliotegens, New Zealand, holotype. Delimited basidioma (left) and resupinate basidiomata (right and bottom left) on the thallus of *Punctelia borrieri*. Scale bar: 1 mm.



Tremella puncteliotegens

long, 3.5–4 μm thick. *Basidiospores* subspherical to short-ly ellipsoid, 9–10.5 \times 7–10.5 μm . *Asexual stage* unknown.

Notes. This species is distinguished from *Tremella puncteliae* by the medium brown resupinate basidiomata, the much larger basidia, 20–32 μm vs 11.5–23.5 μm long, and the much thinner epibasidia, 3.5–4 μm vs 4.5–7.5 μm thick. Both species are phylogenetically closely related, but distinct in our phylogeny.

Ecology and host. On the thallus of corticolous *Punctelia borrieri*.

Distribution. Oceania (New Zealand), known only from the type locality.

***Tremella purpurascensis* Diederich, Common & Mil-
lanes, sp. nov.**

Diagnosis: Characterized by the large, medium brown, waxy-gelatinous basidiomata that are resupinate over the thallus of *Dirinaria purpurascens*, 0.3–6 mm diam., the longitudinally or obliquely, rarely transversely 1-septate basidia, 16–30 \times 10–17.5 μm , the large, shortly ellipsoid basidiospores, 8.5–10 \times 7–9 μm , and the development of endospores in old basidia and basidiospores.

Etymology: From *Dirinaria purpurascens*, the host lichen.



Tremella purpurascensis, USA, Florida, holotype. Three young basidiomata on the thallus of *Dirinaria purpurascens*. Scale bar: 1 mm.



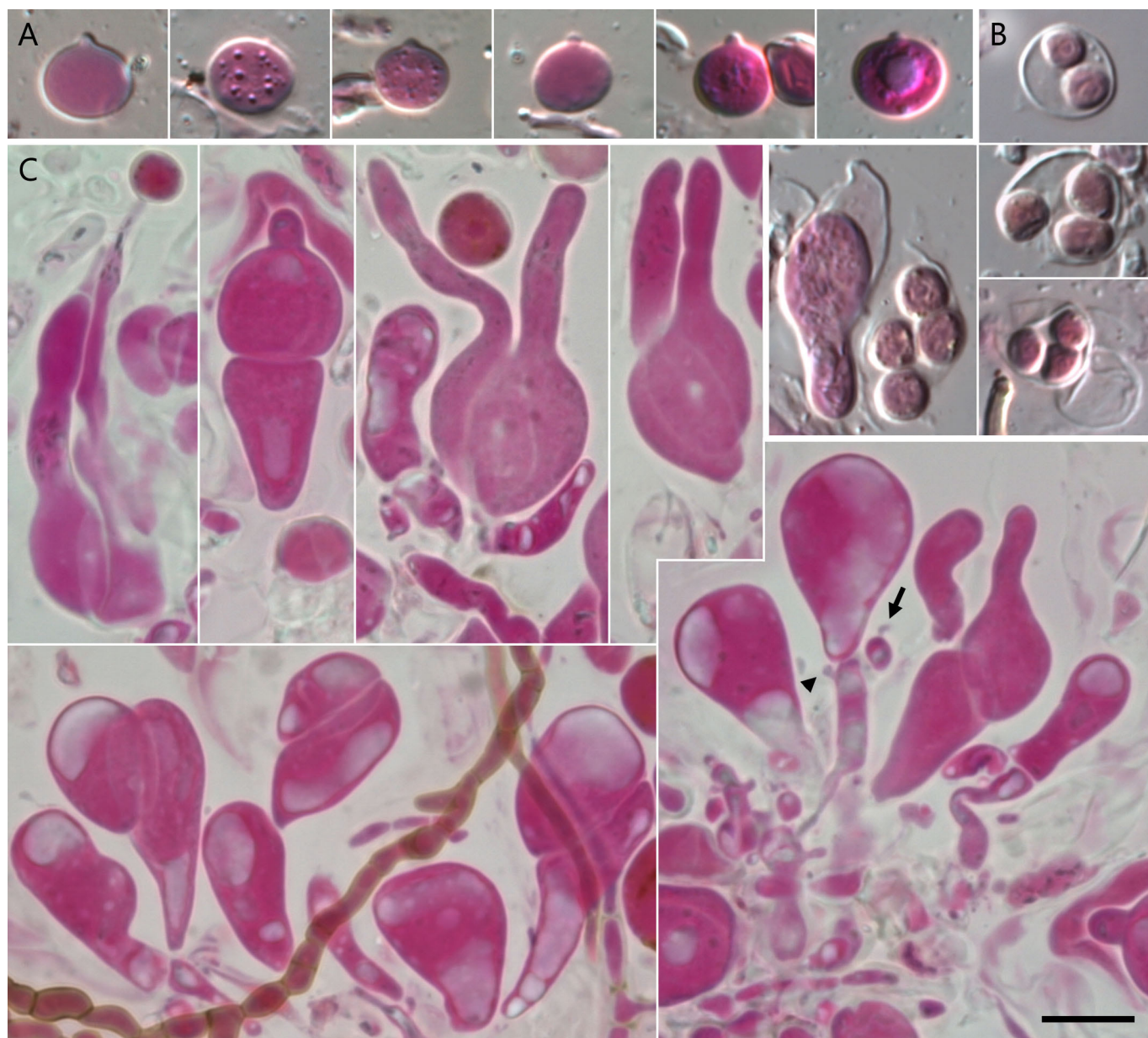
Tremella purpurascensis, USA, Florida, holotype. Old basidioma on the thallus of *Dirinaria purpurascens*. Scale bar: 1 mm.

Type: USA, Florida, Pasco Co., Zephyrhills, near post office, 28.2482°N, 82.1863°W, 45 m, windfall twigs, on *Dirinaria purpurascens*, 14 April 2015, R. Common 9891C (BR – holotype).

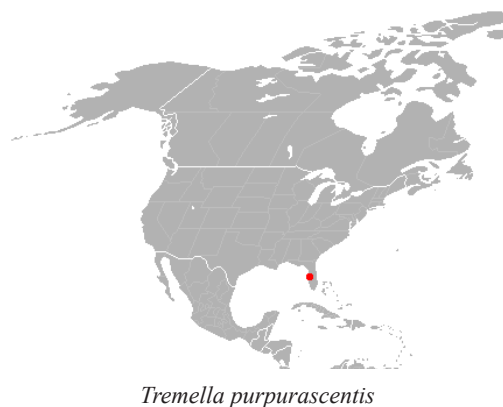
Mycobank: MB844688

Basidiomata superficial, waxy-gelatinous, medium brown, resupinate, covering large areas of the host thallus, up to 0.3–6 mm diam., c. 0.1 mm thick. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2.5–4 μm diam.; haustoria present, basal clamp not observed. **Hymenium** containing numerous pyriform to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, pyriform to ellipsoid, rarely subspherical, 2-celled, with a longitudinal or oblique, more rarely transverse septum, 16–30 \times 10–17.5 μm ; epibasidia cylindrical, 3.5–6 μm thick, 25–45 μm long. **Basidiospores** shortly ellipsoid, 8.5–10 \times 7–9 μm . **Endospores** developing inside old basidia and basidiospores, shortly ellipsoid, aseptate, 4–8 \times 3.5–7 μm .

Notes. *Tremella dirinariae*, known from *Dirinaria aegialita* in Florida, is distinguished by the smaller, black, pulvinate basidiomata, 0.25–0.35(–1) mm diam., that are



Tremella purpurascens, USA, Florida, holotype. A, Basidiospores. B, Endospores developing in old basidia and basidiospores. C, Basidia in various stages of development, with haustorium (arrow) and basal clamp (arrow head). In phloxine. Scale bar: 10 μ m.



often taller than broad, up to 0.3 mm tall, the mostly transversely septate, distinctly smaller basidia, (15–)17–24 \times 6.5–10(–12) μ m, the much smaller basidiospores, 6–8 \times 5.5–6.5 μ m, and the unknown endospores.

Ecology and host. On the thallus of corticolous *Dirinaria purpurascens*.

Distribution. North America (USA: Florida), very abundant, probably overlooked elsewhere.

Additional specimens examined. USA: Florida: Zephyrhills, 2013–19, on *Dirinaria purpurascens*, Common 9572B, 9621B, 9917C, 9944B, 9983B, 10008B, 10034B, 10066B, 10338 (BR).

Tremella pyrenaica Diederich, Poumarat, Daval & Milanes, sp. nov.

Diagnosis: Characterized by the intrahymenial growth in apothecia of *Lecanora* gr. *polytropa* that become swollen and brown, the transversely 1-septate basidia, $16.5\text{--}29\text{--}(35) \times 6\text{--}10\ \mu\text{m}$, and the ellipsoid basidiospores, $8.5\text{--}11 \times 6.5\text{--}9\ \mu\text{m}$.

Etymology: From the adjective *pyrenaicus*, meaning Pyrenean, or pertaining to the Pyrenees Mountains.

Type: France, Pyrénées-Atlantiques, Laruns, pic du Midi d'Ossau, 2080 m, sur une falaise verticale de roches non calcaires, on *Lecanora* gr. *polytropa*, 24 Oct. 2020, G. Daval (BR – holotype).

Mycobank: MB844689

Basidiomata developing in the hymenium of the host, macroscopically visible as convex brownish swellings of the host apothecia. **Context hyphae** not observed; subbasidial hyphae thick-walled, $2.5\text{--}4\ \mu\text{m}$ diam.; haustoria present, with a basal clamp. **Hymenium** intermixed with the host



Tremella pyrenaica, France, holotype population. Swollen apothecia of *Lecanora* gr. *polytropa* with intrahymenial basidia. Photo: G. Daval.

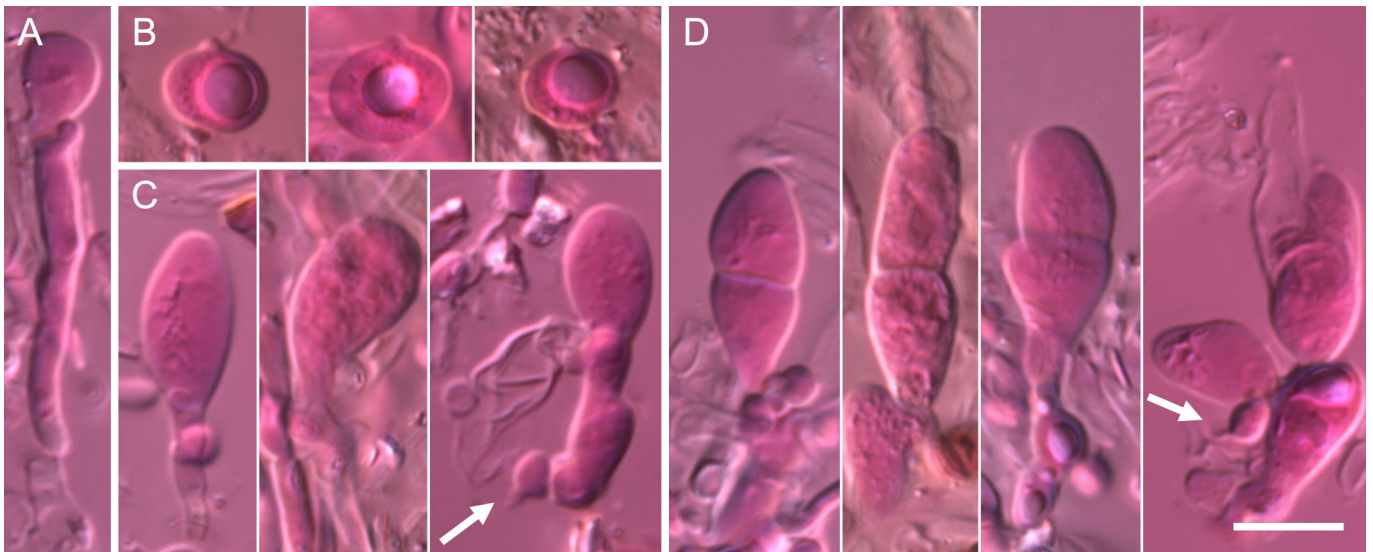


Tremella pyrenaica, France, holotype. Swollen apothecia of *Lecanora* gr. *polytropa* with intrahymenial basidia. Scale bar: 500 μm .



Tremella pyrenaica

hymenium, probasidia ellipsoid with a basal clamp. **Basidia**, when mature, ellipsoid to elongate ellipsoid, sometimes with an attenuated stalk-like base, with one transverse septum, $16.5\text{--}29\text{--}(35) \times 6\text{--}10\ \mu\text{m}$; epibasidia cylindrical, $3.5\text{--}4.5\ \mu\text{m}$ thick, at least $20\ \mu\text{m}$ long. **Basidiospores** ellipsoid, $8.5\text{--}11 \times 6.5\text{--}9\ \mu\text{m}$. **Asexual stage** unknown.



Tremella pyrenaica, France, holotype. A, Fertile hypha with clamped probasidial initial. B, Basidiospores. C, Probasidia with basal clamp. D, Mature, transversely 1-septate basidia. Arrows point to haustoria. In phloxine. Scale bar: 10 μm .

Notes. This species is distinguished from most other lecanoricolous *Tremella* species by the very narrow and constantly transversely 1-septate basidia.

Ecology and host. Intrahymenial in the apothecia of *Lecanora* gr. *polytropa*.

Distribution. Europe ([France](#)), known only from the type locality in the Pyrénées-Atlantiques.

Tremella pyrenulae Diederich, Millanes, Wedin & Common

in Ariyawansa et al., *Fungal Diversity* 75: 243 (2015). *Type:* USA, Florida, Hernando Co., Baypoint Park at end of CR 50/550, 28°32.166' N, 82°39.04' W, on *Pyrenula ochraceoflavens*, 25 Aug. 2011, R. Common 9170B (BR – holotype; S – isotype).

Basidiomata pale pinkish brown, pulvinate, waxy-gelatinous, surface rather smooth, roundish to slightly elongate, up to 0.5 × 0.4 mm, up to 0.3 mm tall, when mature with a constricted base. *Context hyphae* thin-walled, 2–3 µm diam., clamp connections not observed; haustoria not observed. *Hymenium* containing numerous ellipsoid to rarely clavate probasidia with a basal clamp. *Basidia*, when mature, 2-celled, with one longitudinal septum, slightly constricted at the septum, 13–17(–19) × 9.5–13 µm, generally without an attenuated stalk-like base; epibasidia subcylindrical, at least 45 µm long, 3–6 µm diam. *Basidiospores* ellipsoid to subspherical, 7–8 × 6.5–7.5 µm. *Asexual morph* not observed.

Notes. This seems to be a rather common Florida species, possibly confined to *Pyrenula ochraceoflavens*. It is characterized by the pink to pale brown basidiomata that do not induce gall-formation.

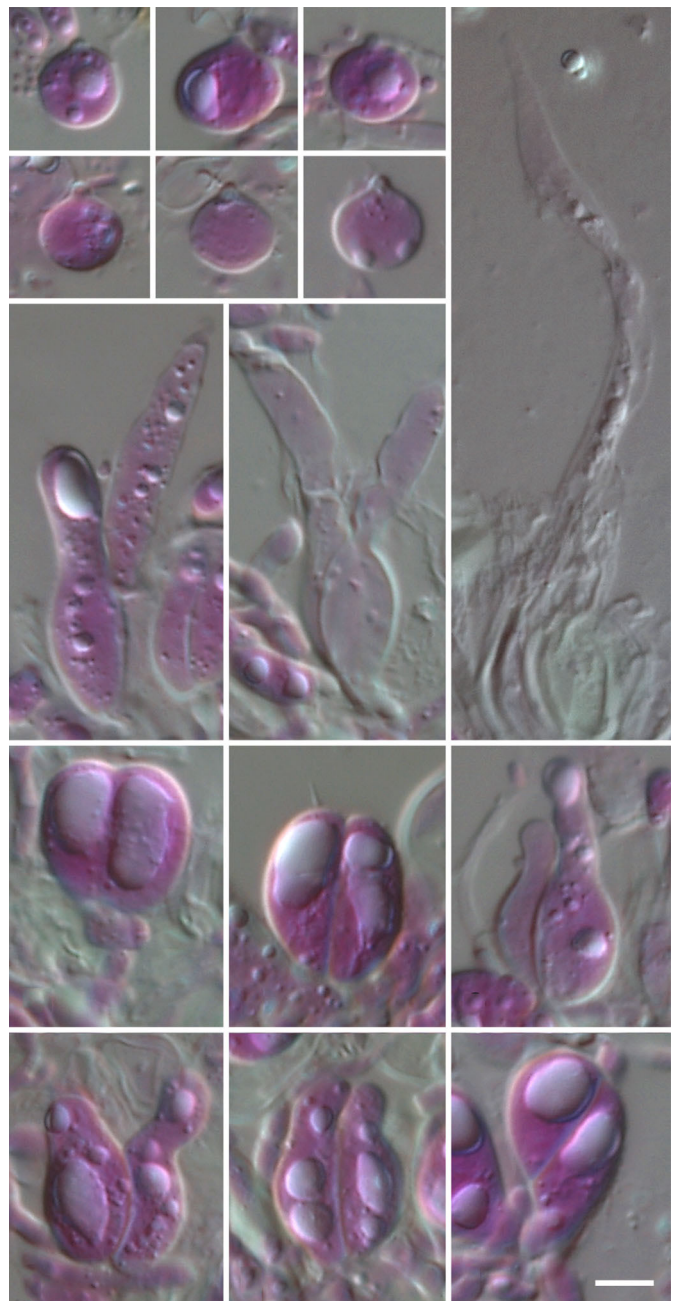
Ecology and host. On the thallus of *Pyrenula ochraceoflavens*.

Distribution. North America ([USA: Florida](#)).

Reference. Ariyawansa et al. 2015.



Tremella pyrenulae, USA, Florida, holotype. Basidiomata on the thallus of *Pyrenula ochraceoflavens*. Scale bar: 200 µm.



Tremella pyrenulae, USA, Florida, holotype (modified from Ariyawansa et al. 2015). Basidia and basidiospores. In phloxine. Scale bar: 5 µm.

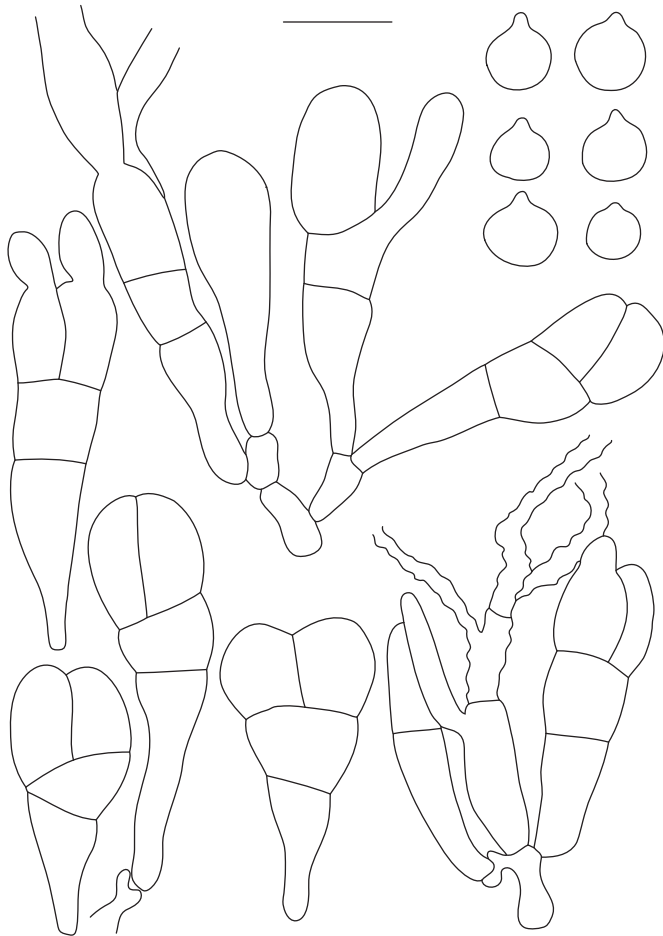


Tremella pyrenulae

***Tremella ramalinae* Diederich s. lat.**

Bibl. Lichenol. 61: 152 (1996). *Type:* Mexico, Baja California, near km 45 on road from San Quintin to Parador Punta Prieta, c. 10 km N of El Rosario, in Cañon del Rosario, 30°8' N, 115°46' W, on *Ramalina lacera*, 5 Jan. 1989, H. Sipman 24905 (B – holotype; BR – isotype).

Basidiomatal galls convex, subspherical-applanate, becoming tuberculate when old, often with a constricted base, firm gelatinous, yellowish to reddish brown, 0.4–3 mm diam. *Context hyphae* 1–1.7 µm diam., thin-walled, clamp connections not observed; haustoria present. *Hymenium* containing numerous clavate to pyriform probasidia with a basal clamp. *Basidia*, when mature, typically pyriform, with 2 transverse or oblique septa, the upper third with one longitudinal septum, constricted at the septa, 23–34 × 8–14 µm, the lower cell elongate, with an attenuated stalk-like base, 10–15(–18) µm long and 5–7 µm broad; epibasidia 2–4 µm thick, 25–35 µm long. *Basidiospores* subspherical, 5–6.5 × 4–6 µm. *Asexual stage* unknown. [Description modified from Diederich 1996, based on material on *Ramalina fraxinea* and *R. lacera*.]



Tremella ramalinae s. str., Mexico, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 µm.



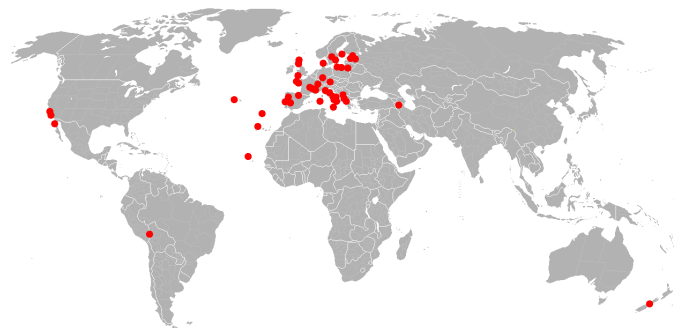
Tremella ramalinae s. str., Mexico, isotype. Basidioma on *Ramalina lacera*. Scale bar: 500 µm.

Notes. This species is characterized by the unusually septate basidia, in combination with the often convex basidiomatal galls with a constricted base. In some specimens, atypical basidia occur, but these are always 3–4-celled. *Tremella celata* (known from *Ramalina fraxinea*) and *T. tuckerae* (on several *Ramalina* species, including *R. fraxinea*) are distinguished by the resupinate, never basally constricted basidiomatal galls, and the 1(–3)-septate basidia.

Tremella ramalinae represents a species complex in need of further studies: On some hosts, such as *Ramalina australiensis*, *R. celastri* or *R. inflexa*, we have observed relatively flat basidiomatal galls, sometimes just representing slight swellings of the host thallus, thus resembling *T. celata* and *T. tuckerae*, but basidial septation is typical for *T. ramalinae*.

Ecology and hosts. *Tremella ramalinae* s. str. grows on the thallus of *Ramalina lacera*, while *T. ramalinae* s. lat. has been reported from *R. australiensis*, *R. celastri*, *R. fraxinea*, *R. inflexa*, *R. pollinaria* and *R. sinensis*.

Distribution. Europe (Albania; Austria; Denmark; Estonia; Finland; France; Germany; Greece; Italy; Montenegro; Poland; Portugal; Spain; Sweden; Switzerland; UK: England,



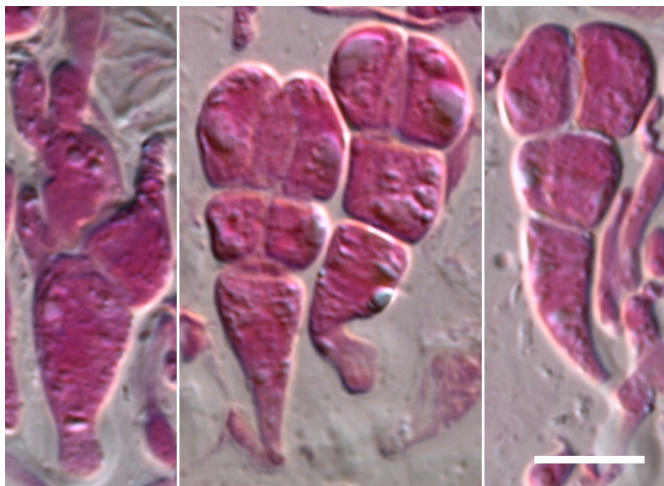
Tremella ramalinae s. lat. (New Zealand locality approximate)



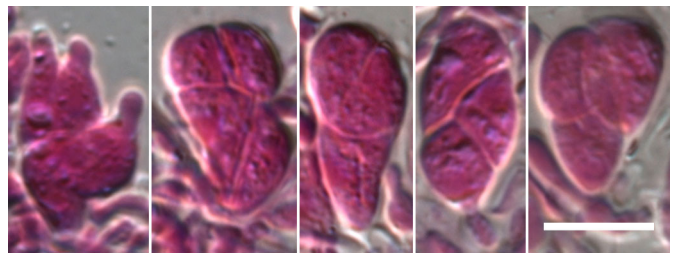
Tremella ramalinae s. lat., Spain, Etayo. Basidiomata on *Ramalina fraxinea*. Scale bar: 1 mm.



Tremella ramalinae s. lat., New Zealand, Bannister 1503. Basidiomata on *Ramalina australiensis*. Scale bar: 1 mm.



Tremella ramalinae s. lat., Spain, Etayo, on *Ramalina fraxinea*. Basidia. Scale bar: 10 µm.



Tremella ramalinae s. lat., New Zealand, Bannister 1503, on *Ramalina australiensis*. Basidia. Scale bar: 10 µm.

Scotland), Macaronesia (Azores; Canary Islands; Cape Verde; Madeira), North America (Mexico: Baja California; USA: California), South America (Bolivia), Asia (Iran) and Oceania (New Zealand).

Additional specimens examined. **Bolivia:** Depto La Paz, Prov. Bautista Saavedra, am Weg von Niño Corin zur unteren Brücke über den Rio Curva, 3200 m, on *Ramalina celastri*, 1982, Feuerer 15243 (BR). **New Zealand:** S. loc., on *R. australiensis*, Bannister 1503 (BR). **South Island:** S. loc., on *R. celastri*, Bannister 617, 978 (BR); s. loc., on *R. inflexa*, Bannister 1749 (BR). **Spain:** *Extremadura:* S. loc., on *R. fraxinea*, 1996, Izquierdo (BR, herb. Etayo). *La Rioja:* Tierra de Cameros, Gallinero de Cameros, 1000 m, on *R. fraxinea*, 1996, Etayo 14101 (BR, herb. Etayo). **USA:** *California:* Monterey Co., Pacific Grove, S of Ocean View Blvd, near lighthouse and at El Carmelo Cemetery, 36°38'N, 121°55.9'W, 10 m, on *Ramalina*, 2002, van den Boom 2002 (BR).

References. Diederich 1996, Pippola & Kotiranta 2008 [Aptroot et al. 2005, Berger & Zimmermann 2016, Brackel 2008, 2011, 2014, 2015, 2020, Brackel & Berger 2019, Brackel & Ko-

courková 2006, Brackel & Puntillo 2016, Diederich 2003, Etayo & López de Silanes 2020, Gagnon et al. 2004, Hafellner 2012, 2018, Halonen et al. 2000, Kocourková et al. 2012, Kowalewska & Kukwa 2003, Kukwa 2005, Kukwa & Czarnota 2006, Kukwa et al. 2013, Obermayer 2013, Roux 2020, Roux & Gueidan 2002, Sohrabi & Alstrup 2007, Suija 2005, Svoboda et al. 2012, Thell et al. 2014, van den Boom 2012, 2015, van den Boom & Alvarado 2019, van den Boom & Clerc 2017, Zimmermann & Feusi 2021].

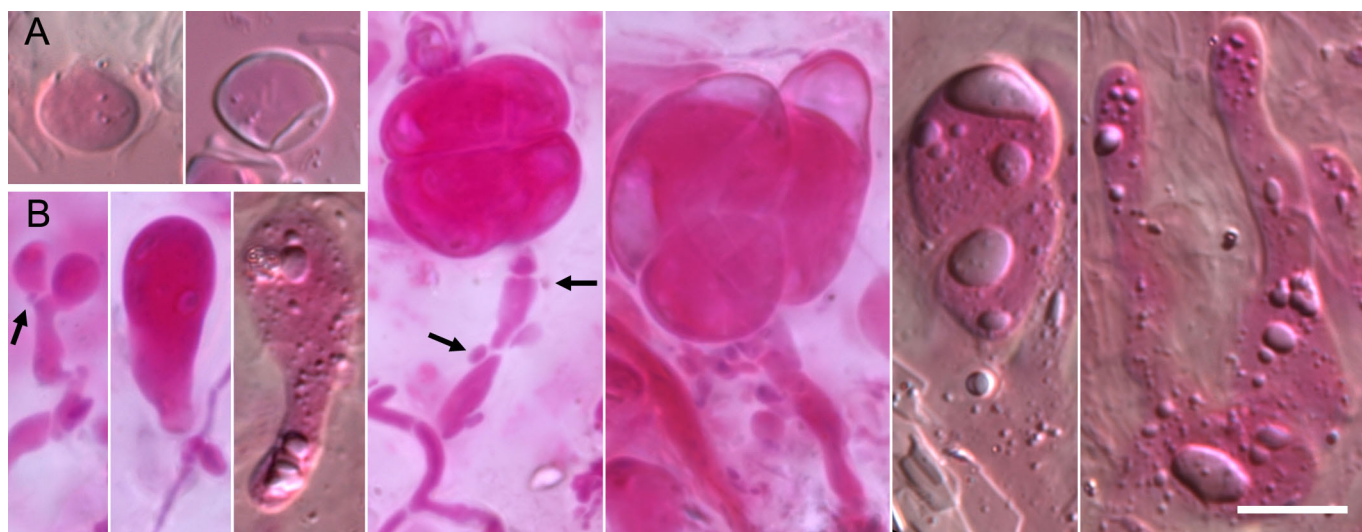
Tremella ramboldiae Diederich & W. R. Buck, sp. nov.

Diagnosis: Characterized by the small, waxy-gelatinous, amber-coloured basidiomata, 0.15–0.3 mm diam., developing on the thallus of *Ramboldia haematites*, the 2–4-celled basidia with longitudinal, oblique or transverse septa, 18–41 × 14–19 µm, and the large basidiospores, 9–11 × 7.5–9.5 µm.

Etymology: From *Ramboldia*, the host lichen.

Type: USA, South Carolina, Berkeley Co., Francis Marion National Forest, along Forest Service Road 121 (Ostrich Run Rd), at bridge over Whiskinboo Creek, 0.3 mi SE of jct with Forest Service Road 123 (Whiskinboo Rd), 33°16'01"N, 79°50'35"W, 27 m, floodplain of *Taxodium* and mixed hardwoods (*Acer*, *Quercus*, *Liquidambar*, *Nyssa*, *Ilex opaca*), on fallen oak branch, on *Ramboldia haematites*, 5 Dec. 2013, W. R. Buck 62056 (NY – holotype).

Mycobank: MB844690



Tremella ramboldiae, USA, South Carolina, holotype. A, Mature and overmature basidiospores. B, Probasidial initials, probasidia, mature basidia and epibasidia (arrows point at clamp connections). In phloxine. Scale bar: 10 μ m.



Tremella ramboldiae, USA, South Carolina, holotype. Basidiomata on the thallus of *Ramboldia haematites*. Scale bar: 500 μ m.



Tremella ramboldiae

Ecology and host. On the thallus of a corticolous norstictic acid deficient *Ramboldia haematites* (TLC: lichexanthone, pigment; no norstictic ac. crystals visible in 5% KOH; thallus cortex PD–, medulla PD+ slightly yellow).

Distribution. North America (USA: South Carolina).

Basidiomata half-immersed to superficial, pulvinate, waxy-gelatinous, amber-coloured, 0.15–0.3 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2.5–4.5 μ m diam.; haustoria absent. *Hymenium* containing numerous subspherical to ellipsoid probasidia, basal clamps not seen. *Basidia*, when mature, subspherical, ellipsoid, claviform to pyriform, 2–4-celled, with longitudinal, oblique or transverse septa, 18–41 \times 14–19 μ m; epibasidia cylindrical, 3.5–5 μ m thick, 30–48 μ m long. *Basidiospores* ellipsoid, 9–11 \times 7.5–9.5 μ m. *Asexual stage* unknown.

Notes. This species can easily be recognized by the small gelatinous, amber-coloured basidiomata probably confined to *Ramboldia* species, and by the large 2–4-celled basidia and basidiospores. Most basidiospores observed were overmature.

***Tremella rhabdodisci* Diederich, Thor, Ertz & Millanes, sp. nov.**

Diagnosis: Characterized by the relatively large, subspherical to irregular or tuberculate, medium brown, waxy-gelatinous basidiomata on the thallus of *Rhabdodiscus inallescens*, 0.2–1 mm diam., basidiospores c. 8 \times 5.5 μ m, and basidia with one longitudinal or oblique septum, 10.5–15.5 \times 10.5–14.5 μ m, or transverse septum, 19.5–26 \times 10–11.5 μ m.

Etymology: From *Rhabdodiscus*, the host lichen.

Type: Japan, Honshu, Tochigi Pref. (Shimotsuke Prov.), Nikko City, 20 km WNW of Nikko, Nikko National Park, 4.9 km ESE the village Yumoto, the Utsunomiya University Experiment forest, 36°47.88'N, 139°28.66'E, 1560 m, mixed partly oldgrowth forest, on *Tsuga diversifolia*, on *Rhabdodiscus inallescens*, 29 Sept. 2017, G. Thor 35584 (UPS – holotype).



Tremella rhabdodisci, Japan, holotype. Basidiomata on the thallus of *Rhabdodiscus inalbescens*. Scale bar: 500 μ m.



Tremella rhabdodisci

brown, 0.2–1(–1.3) mm diam., gall inducing, surface matt. *Context hyphae* thick-walled, 2–3 μ m diam., septa without clamps; subbasidial hyphae thick-walled, 3–5 μ m diam.; haustoria very abundant, with a basal clamp. *Hymenium* containing subspherical to ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid, 2-celled, with one longitudinal or rarely oblique septum, 10.5–15.5 \times 10.5–14.5 μ m, or transversely septate, 19.5–26 \times 10–11.5 μ m, sometimes with a short stalk-like base up to 4 μ m long; epibasidia cylindrical, 3–4.5 μ m diam., at least 20 μ m long. *Basidiospores* ellipsoid, only one overmature seen, 8 \times 5.5 μ m. *Asexual stage* unknown.

Notes. This is a beautiful species with large characteristic basidiomata on the thallus of *Rhabdodiscus*, and with medium-sized, 1-septate basidia. Unfortunately, most basidiomata examined are in a very poor condition, with no basidia, basidiospores, haustoria or septa with clamp connections, suggesting old basidiomata that did not change macroscopically after months or years. In the type, some mature basidiomata have been studied, but only one overmature basidiospore has been seen.

Ecology and host. On the thallus and apothecial margin of corticolous *Rhabdodiscus inalbescens*.

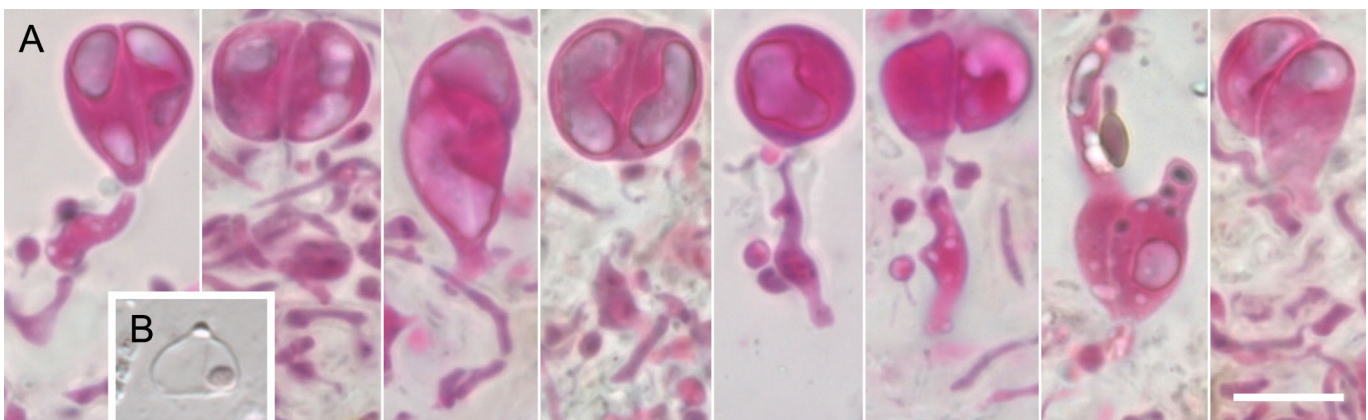
Distribution. Asia ([Japan](#)).

Additional specimens examined (all on *Rhabdodiscus inalbescens*).

Japan: Honshu, Tochigi Pref. (Shimotsuke Prov.), Nikko City, 20 km WNW of Nikko, Nikko National Park: 1.8 km N of Yumoto vil-

Mycobank: MB844691

Basidiomata superficial, pulvinate, subspherical to irregular or tuberculate, waxy-gelatinous, medium to rarely dark



Tremella rhabdodisci, Japan, holotype. A, Basidia, fertile hyphae and haustoria. B, Overmature basidiospore. In phloxine. Scale bar: 10 μ m.

lage (Yumoto Onsen), along the trail from Yumoto to Lake Karikomi and Lake Kirikomi, 36.8208°N, 139.4262°E, 1682 m, 2019, Thor 39727 (UPS); 5.3 km ESE of Yumoto village, the Utsunomiya University forest on the S slope of Mt. Taro, NE of where the dirt road ends, 36°47'59"N, 139°28'59"E, 1656 m, 2019, Ertz 24561 (BR); *ibid.*, 36°47'56"N, 139°28'56"E, 1600 m, 2019, Ertz 24603 (BR).

***Tremella rhizocarpicola* Diederich, Millanes & Wedin**

in Millanes et al., *MycKeys* 8: 32 (2014). *Type*: Norway, Rogaland, Suldal, on the N side of lake Stranddalsvatnet, 59°26.26'N, 6°43.48'E, 1000 m, on *Rhizocarpon lavatum*, 18 Aug. 1999, P. G. Ihlen 957 (BG L-68612 – holotype).

= *Tremella* sp. 3, in Diederich, *Bibl. Lichenol.* 61: 170 (1996).

Basidiomata inside the hymenium of the host, resulting in blackish swellings of the host apothecia. *Context hyphae* difficult to observe, 2.5–3.5 µm thick, thin-walled, with clamp connections; haustoria not observed. *Hymenium* containing numerous clavate probasidia with a basal clamp, intermixed with the hymenium of the host. *Basidia*, when mature, narrowly ellipsoid to subcylindrical, with one transverse septum (never oblique or longitudinal), slightly constricted at the septum, the lower cell elongate, with an attenuated stalk-like base, (14–)17–44 × 7–12(–13) µm (incl. stalk); epibasidia 3–3.5 µm thick, up to 65 µm long. *Basidiospores* subglobose, 7.5–9.5 × 6–8.5 µm. *Asexual stage*: conidial chains sometimes present in the hymenium; individual conidia subspherical, 3–5 µm diam.

Notes. This species is very similar to *T. protoparmeliae*, but may be distinguished by the formation of dark brown swellings on the host apothecia, whilst in *T. protoparmeliae* no symptoms are visible macroscopically.

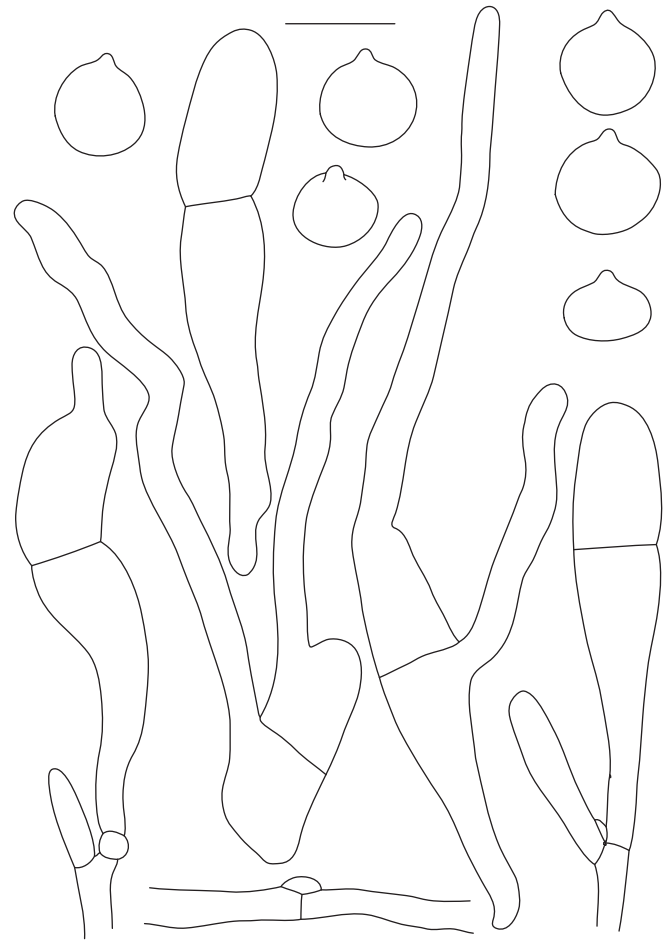
Ecology and host. In the hymenium of *Rhizocarpon lavatum* on siliceous rocks, often along shorelines or near water.

Distribution. Europe (Faroe Islands; Norway; Sweden).

References. Diederich 1996 as *Tremella* sp. 3, Millanes et al. 2014a.



Tremella rhizocarpicola, Scotland, Acton s. n. Basidiomata on the apothecia of *Rhizocarpon lavatum*. Scale bar: 1 mm.



Tremella rhizocarpicola, Sweden, Christiansen 6498 (modified from Diederich 1996). Basidia, basidiospores and a hypha with a clamp connection. Scale bar: 10 µm.



Tremella rhizocarpicola

***Tremella rinodinae* Diederich & M. S. Christ.**

in Diederich, *Bibl. Lichenol.* 61: 154 (1996). *Type*: Denmark, Zealand, Greve, Mosede Strand, on a perpendicular wall of concrete along a fresh-water ditch, near the sea-shore, 0.3–1 m above sea-level, on *Rinodina oleae*, 6 June 1981, M. S. Christiansen 1504 (C – holotype; BR – isotype).

Basidiomata developing in the hymenium of the host, later becoming distinct as brown swellings of the host apothecia,



Tremella rinodinae, Denmark, isotype. Basidiomata in swollen apothecia of *Rinodina oleae*. Scale bar: 500 μ m.

reddish to dark brown, firm gelatinous, up to 0.5 mm diam. *Context hyphae* thick-walled, with clamp connections, 2.5–3 μ m diam.; haustoria frequent, with clamp connections. *Hymenium* at first reduced, probasidia intermixed with the asci and paraphyses of the host, later becoming distinct and well developed over decaying apothecia of the host, containing numerous claviform probasidia with an attenuated base and a basal clamp. *Basidia*, when mature, with one transverse, rarely slightly oblique, exceptionally longitudinal septum, often constricted at the septum, the lower part longer than the upper part, with an attenuated base, (17–)20–26(–30) \times 8–10 μ m; epibasidia subcylindrical, 2.5–4.5 μ m diam., 30–50 μ m long, with a distinct sterigma, exceptionally with two sterigmata. *Basidiospores* subspherical to ellipsoid, 7–9 \times 5–8 μ m. *Asexual stage* unknown.

Notes. Amongst the *Tremella* species with reduced basidiomata growing in the hymenium of their host, this species is distinguished by the relatively short basidia and the basidiomata that are eventually visible as brown swellings of the host apothecia.

Ecology and host. In or on the hymenium of *Rinodina oleae* (incl. *R. gennarii*) and *R. oxydata*.

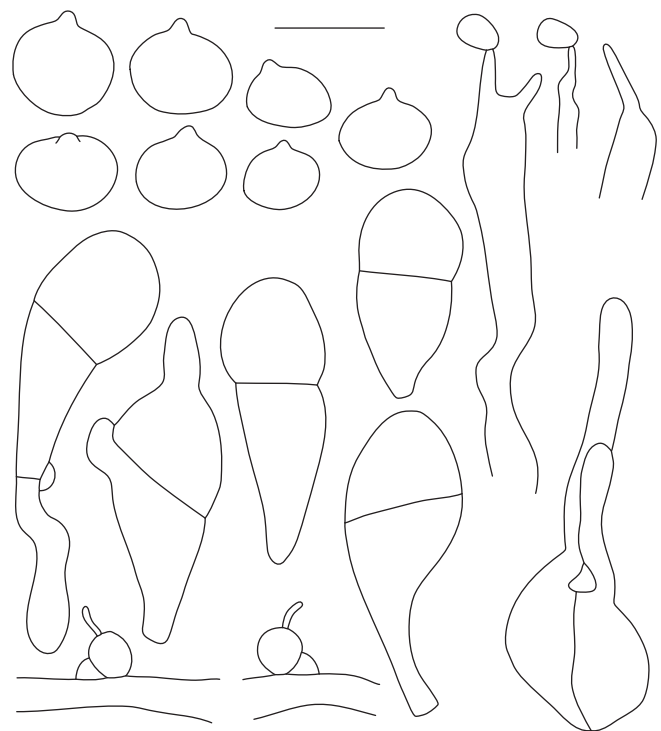
Distribution. Europe (Denmark; Netherlands; Sweden) and North America (USA: New Jersey).

Additional specimen examined. **Netherlands:** Dwingeloo, Mole-neinde, on saxicolous *Rinodina oleae*, 2022, Boers (BR).

References. Diederich 1996 [Millanes et al. 2014a].



Tremella rinodinae



Tremella rinodinae, Denmark, holotype (modified from Diederich 1996). Basidia, basidiospores and haustorial branches. Scale bar: 10 μ m.

***Tremella robusta* Diederich, Ertz, van den Boom & Millanes, sp. nov.**

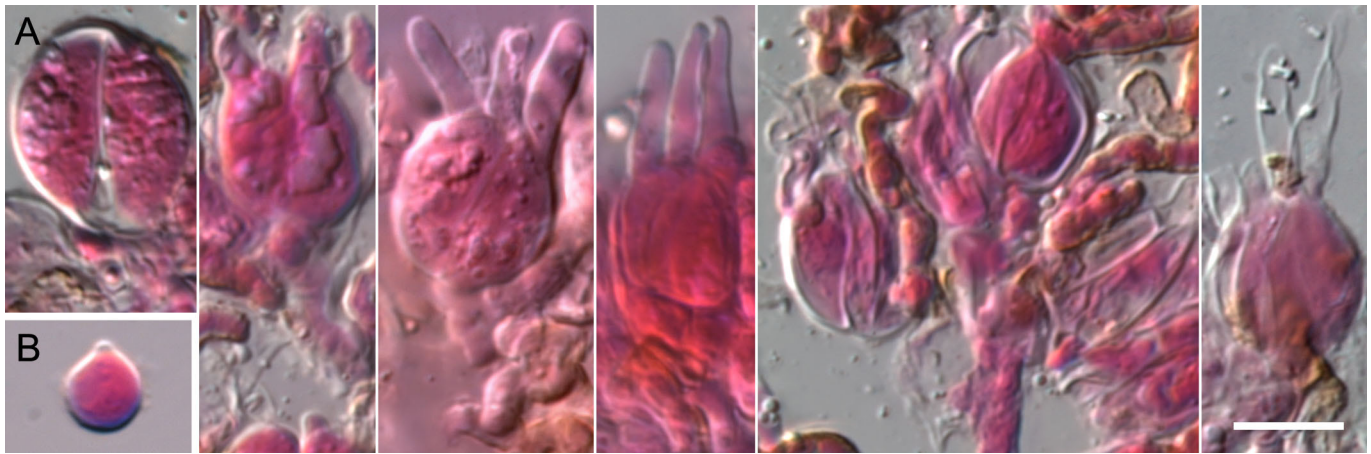
Diagnosis: Distinguished from *Tremella dendrographae* by the brown (not whitish) basidiomatal galls that do not become cerebriform when old, and by the slightly smaller basidia, 12–20 \times 12.5–18 μ m.

Etymology: From *robustus*, referring to the firm basidiomatal galls.

Type: USA, California, Monterey Co., Monterey, Carmel, Point Lobos State Reserve, North Shore Trail, 20 m, on corticolous *Dendrographa franciscana*, 18 July 2008, D. Ertz 12420 (BR LICH 6535-36 – holotype).



Tremella robusta, USA, California, holotype. Basidiomata on the apothecial margin of *Dendrographa franciscana*. Scale bar: 500 μ m.



Tremella robusta, USA, California, holotype. A, Basidia in different stages of development. B, Basidiospore. In phloxine. Scale bar: 10 μ m.

MycoBank: MB844692

Basidiomata gall-inducing, superficial, subspherical or irregularly convex, often with a narrower base, with a matt, non-corticated surface, medium brown, 0.2–1 mm diam., when confluent up to 4 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3–4.5 μ m diam.; haustoria not observed. *Hymenium* containing numerous subspherical to shortly ellipsoid probasidia with a basal clamp. *Basidia*, when mature, subspherical to shortly ellipsoid, not stalked, 2–4-celled, with longitudinal septa, 12–20 \times 12.5–18 μ m, exceptionally elongate ellipsoid, with oblique septa, up to 26 μ m long; epibasidia cylindrical, at least 23 μ m long, 3–3.5 μ m thick. *Basidiospores* subspherical, 7 \times 7.5 μ m (one mature observed; old spore not staining in phloxine: 5.7 \times 6 μ m). *Asexual stage* unknown.

Notes. This species strongly resembles *Tremella dendrographae* by the large, longitudinally septate, non-stalked basidia and the large convex basidiomatal galls. That species differs by the whitish galls becoming cerebriform when old, and slightly larger basidia, 17–24 \times 14–23 μ m. The species has been collected twice in nearby localities. Both specimens are rich, with numerous immature, mature and overmature basidia; nevertheless, basidiospores are extremely sparse in both specimens, as only two have been observed.

Ecology and host. On *Cupressus macrocarpa* over coastal granite rocks, developing on the apothecial margin of *Dendrographa franciscana*, large galls eventually covering parts of the apothecial disk.

Distribution. North America (USA: California), known only from the type locality.

Additional specimen examined. USA: California: Monterey Co., SSW of Carmel, Point Lobos State Reserve, Allen Memorial Grove, Cypress Grove Trail, 36°31.2'N, 121°57'W, 25 m, on *Cupressus macrocarpa*, on *Dendrographa franciscana*, 23 July 2002, van den Boom 29395 (herb. van den Boom).



Tremella robusta

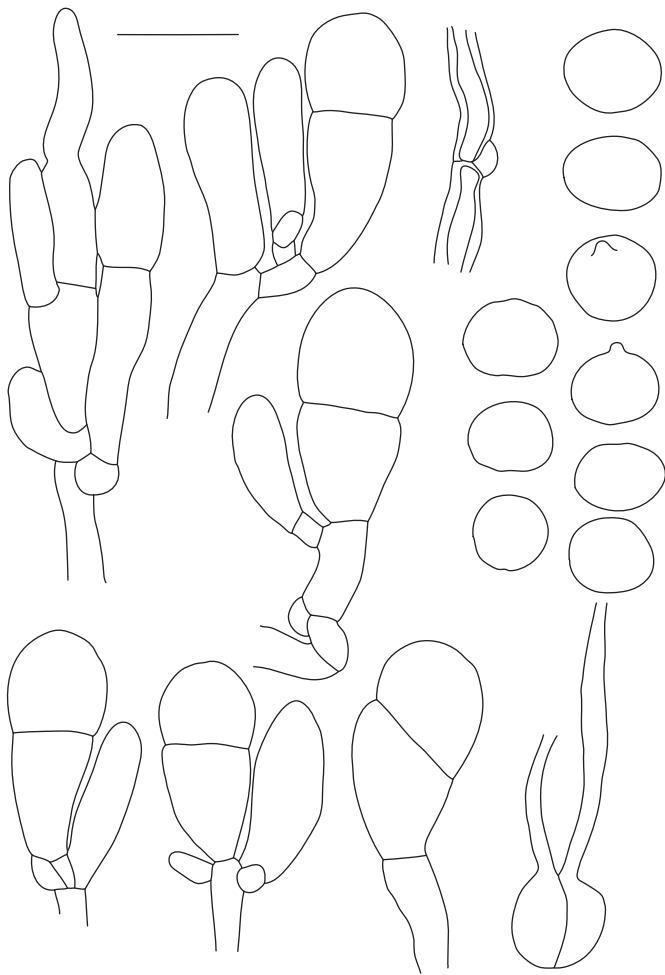
Tremella santessonii Diederich

in Diederich & Christiansen, *Lichenologist* 26: 55 (1994). *Type:* Zimbabwe ['Rhodésie'], entre Melsetter et Cashel, dans un fourré à *Philippia* et *Brachystegia*, on *Usnea*, 1900 m, 10 Jan. 1974, C. Vanden Berghen 748b (LG – holotype; BR, H – isotypes).

Basidiomata pulvinate, discoid, waxy-gelatinous, red-dish brown to almost black, 0.2–0.4 mm diam. *Context hyphae* of two kinds, either 2.5–6 μ m wide, thick-walled, with clamp connections, or 1–1.5 μ m diam., thin-walled, without clamp connections; haustoria not observed. *Hymenium* containing numerous clavate probasidia with a basal clamp. *Basidia*, when mature, elongate ellipsoid, with one transverse septum, constricted at the septum, 16–21 \times 8–9 μ m, the upper cell 7–10 μ m long and 8–9 μ m broad, the lower cell more elongate, with an attenuated stalk-like base, 9–13 μ m long and 6–10 μ m broad; septum rarely diagonal or longitudinal; epibasidia 2.5–3.5 μ m thick, up to 60 μ m long. *Basidiospores* subglobose, 6.5–8 \times 5.5–7 μ m. *Asexual stage* unknown.

Notes. *Tremella santessonii* is similar to several species of *Biatoropsis* with small, dark brown basidiomata, especially to *B. minuta*. It is readily distinguished by the particularly small basidiomata, hyphae having clamp connections, and the constantly 1-septate basidia with an apical cell being as long as broad, and a narrower elongate basal cell.

Ecology and hosts. On the thallus of *Usnea* species, not visibly damaging the host. The type collection consisted of an



Tremella santessonii, Zimbabwe, holotype (modified from Diederich 1994). Basidia, basidiospores and a hypha with a clamp connection. Scale bar: 10 μ m.



Tremella santessonii

assemblage of several *Usnea* species, in which a single species was attacked by the *Tremella*, and another species by *Biatoropsis*. In the Rwanda specimen the same thallus of *Usnea* was infected by both *T. santessonii* and *Biatoropsis*.

Distribution. Africa (Rwanda; [Zimbabwe](#)) and Oceania (Papua New Guinea).

References. Diederich 1996, Diederich & Christiansen 1994.



Tremella santessonii, Zimbabwe, isotype. Basidiomata on *Usnea* sp. Scale bar: 500 μ m.



Tremella santessonii, Rwanda, Lambinon 72-1083. Basidioma on the thallus of *Usnea* sp. Scale bar: 500 μ m.

Tremella sarcographae Diederich & Aptroot, sp. nov.

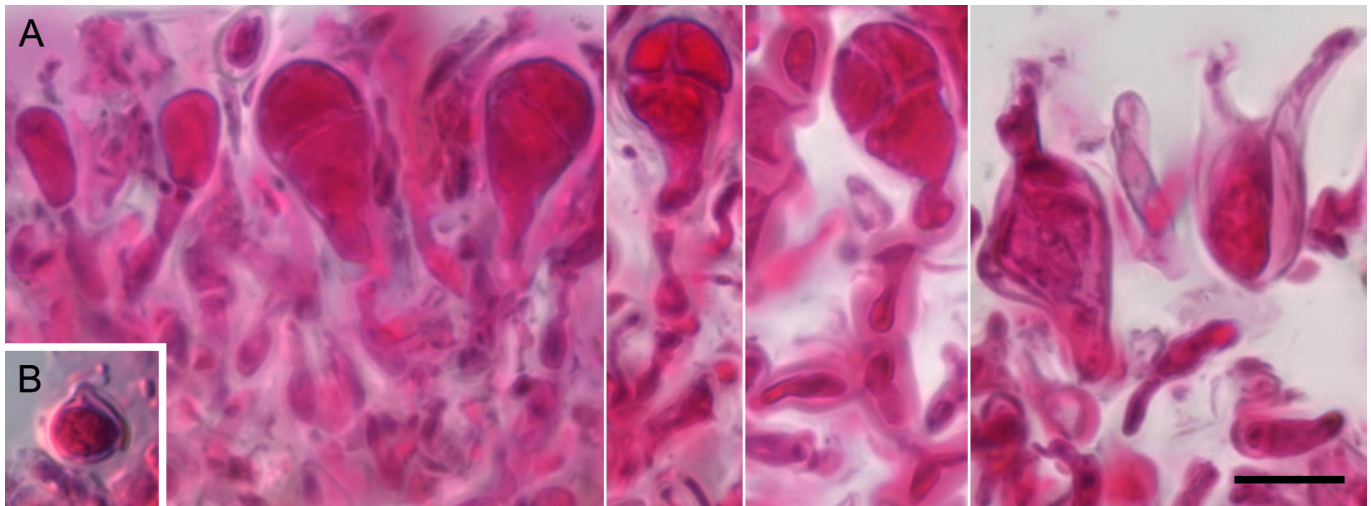
Diagnosis: Characterized by the large, strongly convex, medium brown, waxy-gelatinous basidiomata with a constricted base on the thallus of *Sarcographa medusulina*, 0.4–1.3 mm diam., basidiospores $4.5\text{--}7 \times 4.5\text{--}6 \mu\text{m}$, and the 2–4-celled basidia with transverse or oblique, rarely longitudinal septa, $13\text{--}24.5 \times 8\text{--}12 \mu\text{m}$.

Etymology: From *Sarcographa*, the host lichen.

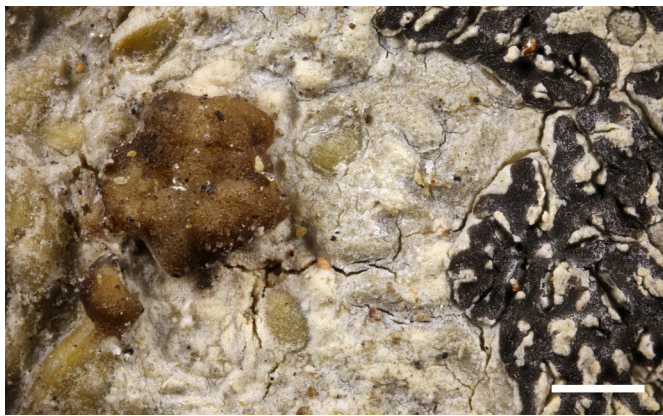
Type: Brazil, Sergipe, Aracaju, São Cristóvão, UFS campus, $10^{\circ}55'S$, $37^{\circ}06'W$, 10 m, on the bark of a tree in the university campus, on *Sarcographa medusulina*, 7 April 2014, M. Cáceres 21571 & A. Aptroot (ISE – holotype; BR – isotype).

Mycobank: MB844693

Basidiomata superficial, pulvinate, when young subspherical, later with an irregular and partly concave upper surface, waxy-gelatinous, medium brown, 0.4–1.3 mm diam. **Context hyphae** not observed; subbasidial hyphae thick-walled, $2.5\text{--}4.5 \mu\text{m}$ diam.; haustoria present, basal clamp not observed. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid to pyriform, with a frequently attenuated base, 2–4-celled, with transverse or oblique, rarely longitudinal septa, $13\text{--}24.5 \times 8\text{--}12 \mu\text{m}$; epibasidia



Tremella sarcographae, Brazil, holotype. A, Basidia in different stages of development. B, Basidiospore. In phloxine. Scale bar: 10 µm.



Tremella sarcographae, Brazil, isotype. Basidiomata on the thallus of *sarcographa medusulina*. Scale bar: 500 µm.



Tremella sarcographae

cylindrical, at least 30 µm long. *Basidiospores* subspherical, $4.5\text{--}7 \times 4.5\text{--}6$ µm. *Asexual stage* unknown.

Notes. Amongst the known lichenicolous *Tremella* species that do not induce gall-formation and with up to 4-celled, mostly non-stalked basidia, the new species is distinguished by the large, strongly convex, brown basidiomata with a constricted base, and the basidial size. The only known specimen shows numerous young, and some mature basidia, but only a few basidiospores could be observed. Their size range must therefore be re-evaluated when more specimens become available. Young basidia often develop one transverse septum. When mature, the upper part frequently becomes cruciately septate when observed laterally, owing to unequally long cells that partly overlap.

Ecology and host. On the thallus of corticolous *Sarcographa medusulina*.

Distribution. South America (Brazil), known only from the type locality.

Tremella stevensiana Diederich

in Diederich & Christiansen, *Lichenologist* 26: 57 (1994). *Type:* Australia, border of Queensland and New South Wales, Moss Garden Walk Lookout, $28^{\circ}18'S$, $152^{\circ}27'E$, 900 m, on *Usnea confusa*, 2 Febr. 1980, G. N. Stevens 4940 (MEL – holotype, BR [herb. Diederich 9824] – isotype).

Basidiomata applanate to pulvinate, discoid, waxy-gelatinous, pale yellowish brown to dark reddish brown, 0.1–0.3(–0.5) mm diam. **Context hyphae** 1–3.5 µm wide, thick-walled, often with clamp connections; haustoria rarely observed. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp and conidiogenous cells. **Basidia**, when mature, ellipsoid, with 1–3 longitudinal septa, $9\text{--}12 \times 7.5\text{--}9$ µm; epibasidia 1.5–3 µm thick. **Basidiospores** ellipsoid to subspherical, $5.5\text{--}6.5 \times 4.5\text{--}5.5$ µm. **Asexual stage** present, conidiophores very frequent, situated between the basidia, consisting of a conidiogenous cell, $9\text{--}21 \times 1.5\text{--}4$ µm, bearing in the upper part 5–30 young ellipsoid conidia $2\text{--}3 \times 1\text{--}2$ µm, developing successively to mature ellipsoid or irregular conidia $4\text{--}7 \times 2.5\text{--}5$ µm.

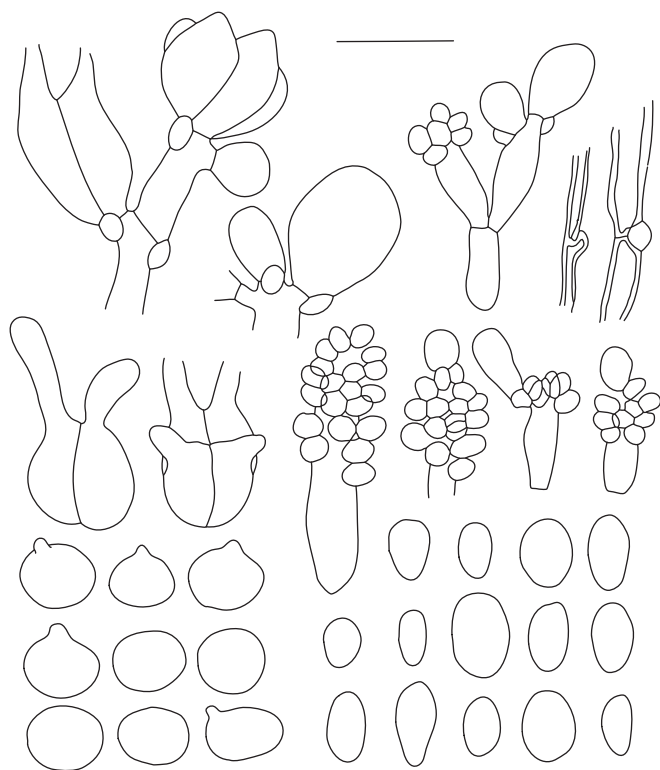
Notes. Macroscopically, this species is distinguished from the other heterobasidiomycetes growing on *Usnea* (*Biato-*



Tremella stevensiana, Australia, isotype. Basidiomata on *Usnea confusa*. Scale bar: 500 μ m.



Tremella stevensiana, Australia, Stevens 5060. Basidiomata on the thallus of *Usnea* sp. Scale bar: 500 μ m.



Tremella stevensiana, Australia, holotype (modified from Diederich 1994). Basidia, basidiospores, conidiophores with mainly young conidia, mature conidia and hyphae with clamp connection. Scale bar: 10 μ m.



Tremella stevensiana

ropsis spp., *Cyphobasidium usneicola*, *Tremella nashii* and *T. santessonii*) by the very small basidiomata concolorous to the thallus or reddish brown, resembling small papillae of the lichen. It is easily distinguished from the other *Tremellales* growing on *Usnea* by the tremelloid basidia with longitudinal septa, and by the characteristic asexual stage. Most conidiogenous cells only bear young conidia. Occasionally, a young apical conidium develops into a much larger mature conidium, soon becoming detached.

Ecology and hosts. On the thallus of *Usnea confusa*, *U. cf. bismolliuscula* and *U. undulata*.

Distribution. Oceania (Australia; Papua New Guinea).

References. Diederich 1996, Diederich & Christiansen 1994.

Tremella stictae Diederich

Bibl. Lichenol. 61: 159 (1996). **Type:** Rwanda, Butare, au-dessus du guest-house de l'I. N. R. S., 1700 m, on *Sticta weigeli*, 17 Dec. 1972, J. Lambinon 71/1020 (LG – holotype; BR – isotype).

Basidiomata growing on the margin of the host thallus, rarely on the lower surface, mainly on the top of the isidia, convex, subglobose, tuberculate when old, waxy-gelatinous, pale brownish when young, dark brown when old, 0.1–0.5(–0.8) mm diam., tuberculate basidiomata up to 2 mm diam. **Context hyphae** thick-walled, with clamp connections, 2–2.5 μ m diam., or thin-walled, without clamp connections, 1.5–2 μ m diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous ellipsoid probasidia with a basal clamp. **Basidia**, when mature, 2-celled, with a longitudinal, oblique or transverse septum, 10–16 \times 6–8.5 μ m; epibasidia subcylindrical, at least 10 μ m long and 1.5–2 μ m diam. **Basidiospores** ellipsoid, 5–7.5 \times 4–5.5 μ m diam. **Asexual stage:** asteroconidia of 10–13 μ m diam. have been observed in one specimen, with four arms 4–7 μ m long, attached with one arm to a conidiogenous cell.



Tremella stictae, Rwanda, isotype. Basidiomata on the thallus of *Sticta weigelii*. Scale bar: 500 µm.



Tremella stictae, Papua New Guinea, Diederich 10112. Basidiomata on the dendriscocauloid thallus of *Sticta* sp. Scale bar: 1 mm.

Notes. Diederich (1996) reported a hymenium containing conspicuous swollen hyphidia: these are now interpreted as belonging to the host. The similar *Tremella emmanuelleae* is distinguished by the longer basidia, mainly $14.5\text{--}26 \times 4.5\text{--}9\text{ }\mu\text{m}$, and *T. leptogii* by the 4-celled basidia.

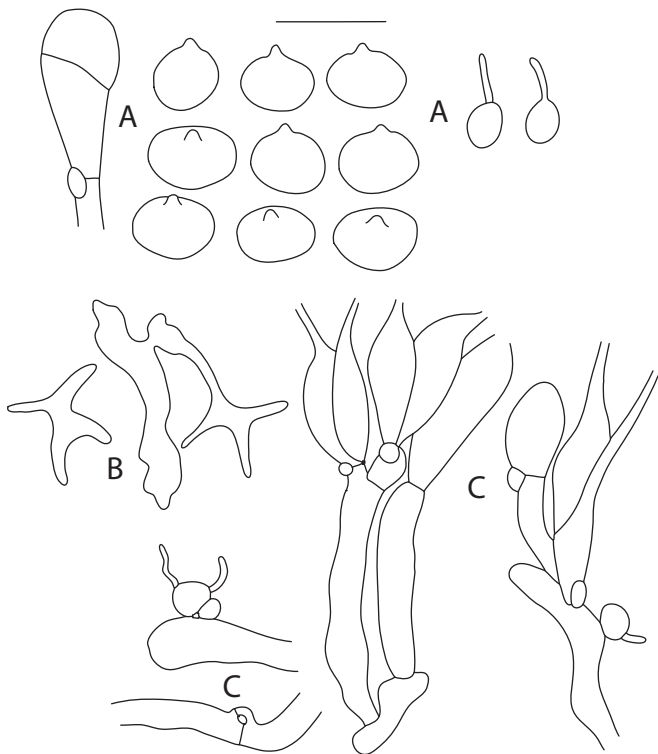
Ecology and hosts. On the upper surface, margin or rarely lower surface of the thallus of *Sticta weigelii*, *S. fuliginosa*, *S. madagascarensis*, *S. orbicularis*, *S. weigelii* and

unidentified *Sticta* species, including a dendriscocauloid species from Papua New Guinea. All specimens recently examined by us have a cyanobacterial photobiont. As the genus *Sticta* is currently undergoing regional revisions, with the recognition of many genetically distinct species, the identifications above must be regarded as provisional.

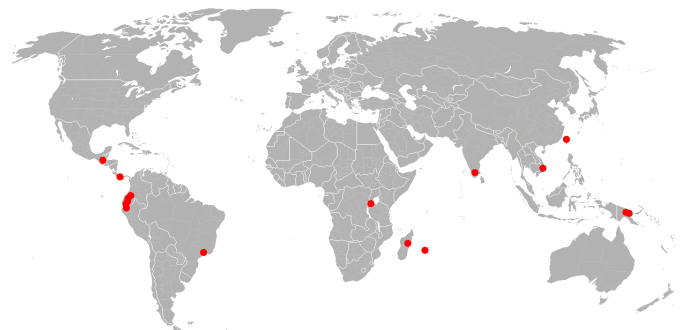
Distribution. Central America (Guatemala; Panama), South America (Brazil; Colombia; Ecuador), Africa (Rwanda), Indian Ocean (Madagascar; Réunion), Asia (India; Taiwan; Vietnam) and Oceania (Papua New Guinea).

Additional specimens examined. **Réunion:** Cirque de Salazie, W of Hell Bourg, just outside the village, along the road to îlet à Vidot, $21^{\circ}03.4'S$, $55^{\circ}31.2'E$, 975 m, on *Sticta*, 2008, van den Boom 40972 (herb. van den Boom). **Taiwan:** Nantou Co., 15 ENE of Puli, near Wushe, river gorge, $24^{\circ}00'23''N$, $121^{\circ}06'03''E$, 950 m, on *Machilus thunbergii*, on *S. orbicularis*, 2001, Aptroot 52032 (BR). Prov. Ilan, Mt Nanfuta-san, 2400–2600 m, on *Sticta*, 1964, Kurokawa 1000, *Kurokawa Lich. Rar. Crit. Exs.* 44 *Peltigera nigripunctata* (LG, on thallus of intermixed *Sticta*).

References. Diederich 1996 [Diederich 2003, Etayo 2002, 2017, Etayo & van den Boom 2006, Joshi et al. 2018, van den Boom et al. 2017, Zhurbenko et al. 2020].



Tremella stictae, Rwanda, holotype (A) and Papua New Guinea, Diederich 10111 (B), Aptroot 32328 (C) (modified from Diederich 1996). Basidia, basidiospores, conidiogenous cell, asteroconidia, hyphae and haustorial branches. Scale bar: 10 µm.



Tremella stictae

***Tremella strigulae* Diederich, sp. nov.**

Diagnosis: Characterized by the yellowish brown, flat and thin, often poorly delimited, eventually sometimes pulvinate, not gall-inducing, waxy-gelatinous basidiomata, 0.2–0.5(–0.9) mm diam., developing over the thallus of *Strigula stigmatella*, the transversely or obliquely 1-septate basidia, $14\text{--}22 \times 7.5\text{--}12\ \mu\text{m}$, and the subspherical to shortly ellipsoid basidiospores, $6.5\text{--}7.5 \times 6\text{--}6.5\ \mu\text{m}$.

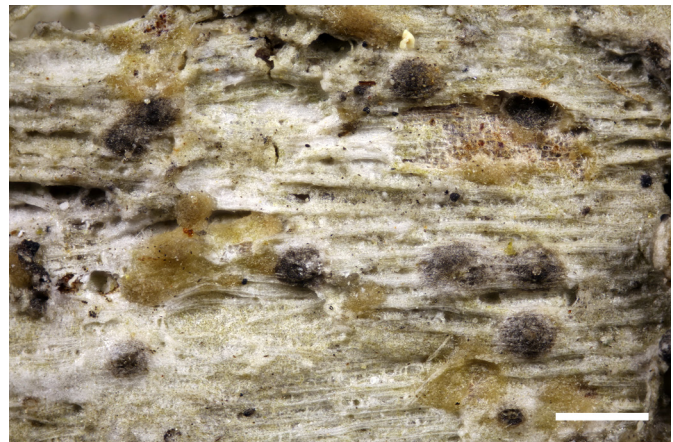
Etymology: From *Strigula*, the host lichen.

Type: USA, Vermont, Orleans Co., town of Craftsbury, Craftsbury Outdoor Center, at S end of Great Hosmer Pond, W of Black River, $44^{\circ}41'04''\text{N}$, $72^{\circ}21'47''\text{W}$, 325 m, *Thuja* swamp, on trunk of *Thuja*, on *Strigula stigmatella*, 16 May 2005, R. C. Harris 51490-A (NY – holotype; BR – isotype)

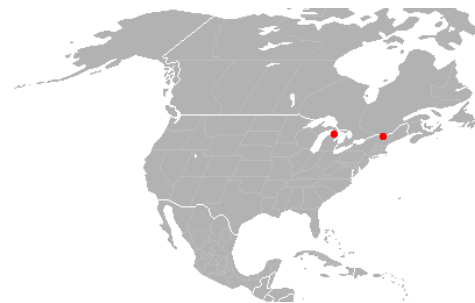
MycoBank: MB844694

Basidiomata superficial, initially flat and very thin, later becoming slightly convex to sometimes pulvinate, often poorly delimited, waxy-gelatinous, yellowish brown, 0.2–0.5(–0.9) mm diam. **Context hyphae** thick-walled, $2.5\text{--}4\ \mu\text{m}$ diam., septa with clamps; subbasidial hyphae thick-walled, $2.5\text{--}4\ \mu\text{m}$ diam.; haustoria abundant, basal clamp not observed. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid to pyriform, 2-celled, with a transverse or oblique septum, $14\text{--}22 \times 7.5\text{--}12\ \mu\text{m}$; epibasidia cylindrical, at least $30\ \mu\text{m}$ long. **Basidiospores** subspherical to shortly ellipsoid, $6.5\text{--}7.5 \times 6\text{--}6.5\ \mu\text{m}$. **Asexual stage** unknown.

Notes. Amongst the lichenicolous *Tremella* species with transversely to obliquely 1-septate basidia and developing basidiomata over the host thallus without inducing galls, this species is distinguished by the yellow-brown, never dark brown basidiomata; those from *Tremella phaeo-*



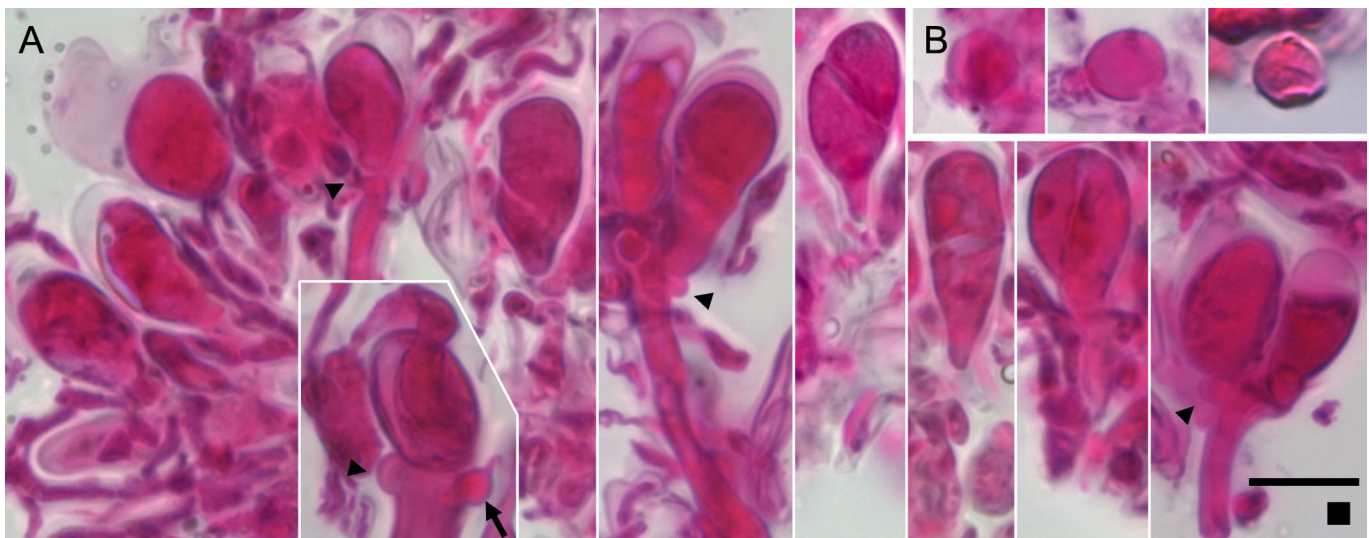
Tremella strigulae, USA, Vermont, holotype. Basidiomata on the thallus of *Strigula stigmatella*. Scale bar: 500 μm .



Tremella strigulae

graphidis are pale to dark, often reddish brown, and from *T. santessonii* reddish brown to almost black.

Ecology and host. On the thallus of corticolous *Strigula stigmatella*.



Tremella strigulae, USA, Vermont, holotype. A, Basidia in different stages of development, with basal clamps (arrow heads) and haustorium (arrow). B, Basidiospores. In phloxine. Scale bar: 10 μm .

Distribution. North America (USA: Michigan, Vermont).

Additional specimen examined. USA: Michigan: Cheboygan Co., Pigeon River Country State Forest, W of McMasters Creek, E of Osmun Road, 7.5 mi S of MI-68, 45°16'47"N, 84°25'13"W, c. 250 m (816 ft), swamp forest dominated by *Thuja* and *Abies* with *Betula*, *Acer* and *Picea*, on *Thuja*, on *Strigula stigmatella*, 2015, Harris 60859 (NY),

***Tremella sulcaria* Diederich & M. S. Christ.**

in Diederich, *Bibl. Lichenol.* 61: 163 (1996). Type: China, Yunnan, Lijiang, Mt. Yulong Shan, Ganhaizi, alt. 3050 m, on *Sulcaria sulcata*, 18 Dec. 1964, J. C. Wei, *Wei Lichenes sinenses exsiccati* 27 (C – holotype; BR – isotype).

Basidiomata strongly convex, subspherical, black, surface rugulose, a little gelatinous, not waxy, 0.2–0.4 (–0.6) mm diam. **Context hyphae** difficult to observe; haustoria not observed. **Hymenium** containing numerous subspherical probasidia with a basal clamp. **Basidia**, when mature, ellipsoid, 2-celled, with one longitudinal septum, 9–14 × 6–8.5 µm; epibasidia subcylindrical, 2–3 µm diam., 20–25 µm long. **Basidiospores** ellipsoid, 7–8 × 4–6 µm. **Asexual stage** unknown.

Notes. This species is easily recognized by the strongly convex basidiomata that are black, even when young.

Ecology and host. On the thallus of *Sulcaria sulcata*.

Distribution. Asia (China; Nepal).

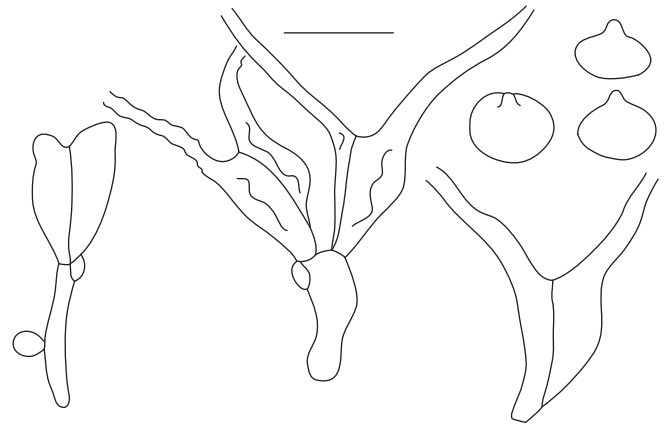
Reference. Diederich 1996.



Tremella sulcaria, China, isotype. Basidioma on *Sulcaria sulcata*. Scale bar: 500 µm.



Tremella sulcaria



Tremella sulcaria, China, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 µm.

***Tremella synarthoniae* Diederich & Common, sp. nov.**

Diagnosis: Characterized by the flat or slightly convex, orange-brown, gelatinous basidiomata on the thallus of *Synarthonia inconspicua*, 0.3–0.6 mm diam., the 2-celled basidia with a longitudinal or oblique septum, 11–20 × 7.5–11 µm, and the relatively large basidiospores 6–9.5 × 5.5–7.5 µm.

Etymology: From *Synarthonia*, the host lichen.

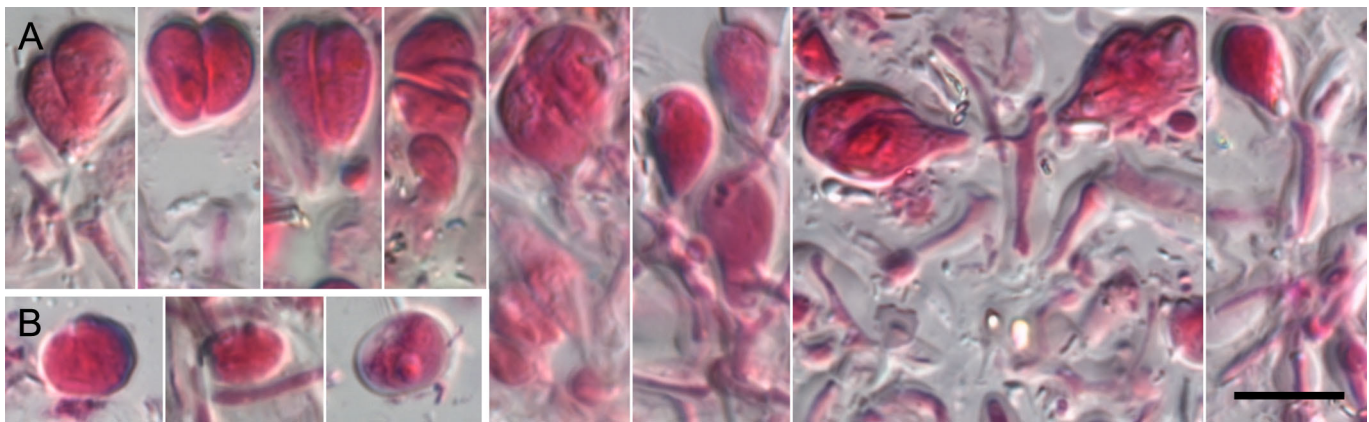
Type: USA, Florida, Collier Co., Collier-Seminole State Park, just W of boat basin, 25°59'N, 81°35'W, mangrove, on *Synarthonia inconspicua*, 7 Dec. 1992, R. C. Harris 30019-A (NY – holotype).

Mycobank: MB844695

Basidiomata superficial, flat or slightly convex, roundish, elongate or irregular in form, gelatinous, orange-brown, not gall-inducing, 0.3–0.6 mm diam. **Context hyphae** 1.5–2 µm diam.; subbasidial hyphae thick-walled, 3–4.5 µm diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when ma-



Tremella synarthoniae, USA, Florida, holotype. Basidiomata on the thallus and apothecia of *Synarthonia inconspicua*. Scale bar: 500 µm.



Tremella synarthoniae, USA, Florida, holotype. A, Basidia in different stages of development. B, Basidiospores. In phloxine. Scale bar: 10 μ m.



Tremella synarthoniae

ture, ellipsoid, rarely with a stalk-like base, 2-celled, with a longitudinal or oblique, rarely transverse septum, $11\text{--}20 \times 7.5\text{--}11 \mu\text{m}$; epibasidia cylindrical, at least 42 μm long. *Basidiospores* ellipsoid, $6\text{--}9.5 \times 5.5\text{--}7.5 \mu\text{m}$. *Asexual stage* unknown.

Notes. Amongst the known lichenicolous *Tremella* species with brownish gelatinous basidiomata developing on the host thallus, mainly longitudinally 1-septate basidia and relatively large basidiospores, *Tremella phaeographidis* differs by the slightly larger, often darker basidiomata, and the frequently transversely septate basidia; *T. montis-wilhelmii*, *T. normandinae* and *T. parmeliellae* differ by the strongly convex, less gelatinous basidiomata. *Tremella coniocarpi*, a species growing on a related host, differs by pale (not orange) brown basidiomata and 4-celled basidia.

Ecology and host. On the thallus of corticolous *Synarthonia inconspicua*.

Distribution. North America (USA: Florida), known from two nearby localities.

Additional specimen examined. USA: Florida: Collier Co., Fakahatchee Strand State Park, trail east of Big Cypress Boardwalk area, on US 41, 25.9475°N , 81.4714°W , 5 m, on hardwood scrub and Sabal Palm, on *Synarthonia inconspicua*, 2014, Common 98531 (BR).

Tremella teloschistis Diederich, Gockman, Walden & Millanes, sp. nov.

Diagnosis: Characterized by the orange, slightly convex, elongate, waxy-gelatinous basidiomata on the thallus of *Teloschistes exilis*, up to $1 \times 0.3 \text{ mm}$, the elongate ellipsoid to subclaviform, transversely 1-septate basidia, $12\text{--}23 \times 5.5\text{--}10 \mu\text{m}$, and the medium sized, subspherical basidiospores, $5\text{--}7.5 \times 4.5\text{--}6.5 \mu\text{m}$.

Etymology: From *Teloschistes*, the host lichen.

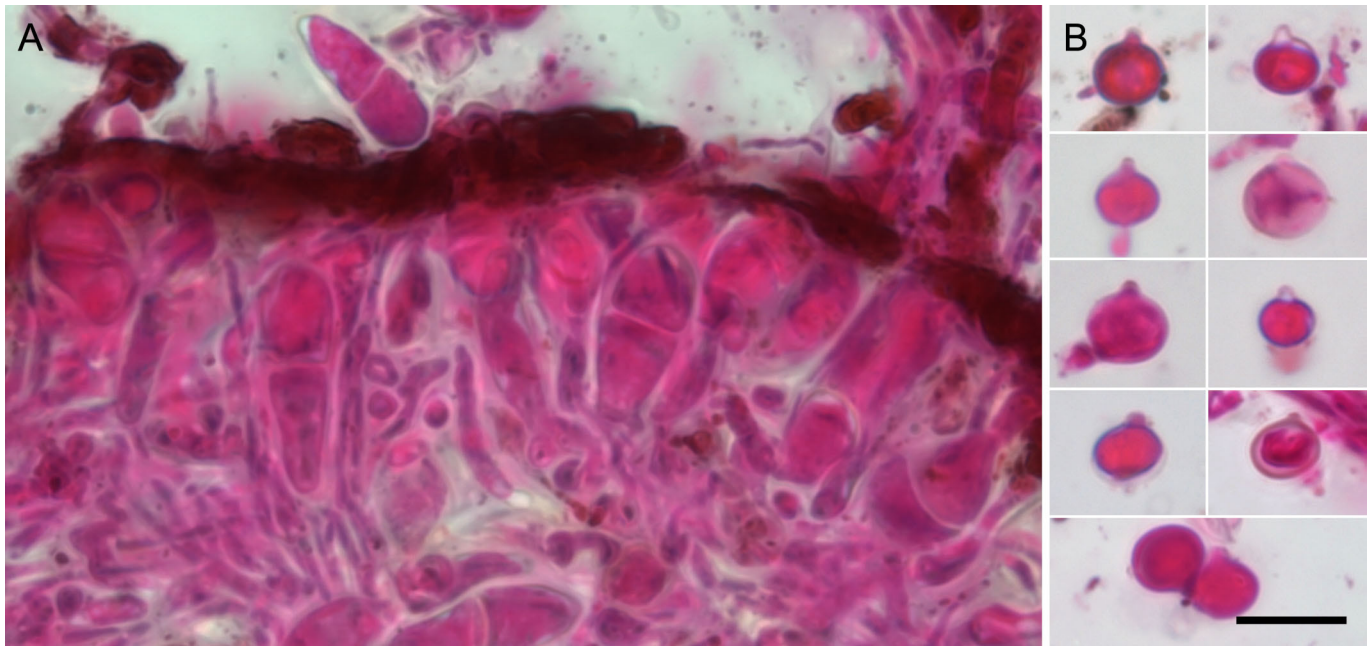
Type: USA, Texas, Parker Co., c. 6.4 km S of Authon and 14 km E of Mineral Wells, 32.8233°N , 97.9179°W , on *Quercus stellata* in a post oak savannah community, on *Teloschistes exilis*, 29 Jan. 2019, O. Gockman & J. Walden 5783 (BR – holotype).

MycoBank: MB844696

Basidiomata gall-inducing, resulting in orange, often curved swellings of the host thallus contrasting with the more yellow intact thallus, up to $1 \times 0.3 \text{ mm}$. **Context hyphae** not observed; subbasidial hyphae thick-walled, $2\text{--}3.5 \mu\text{m}$ diam.; haustoria present, basal clamp not observed. **Hymenium** containing numerous subspherical to ellipsoid



Tremella teloschistis, USA, Texas, holotype. Basidiomata on the thallus of *Teloschistes exilis*. Scale bar: 500 μ m.



Tremella teloschistis, USA, Texas, holotype. A, Hymenium with mature basidia. B, Basidiospores. In phloxine. Scale bar: 10 μ m.

probasidia with a basal clamp. *Basidia*, when mature, elongate ellipsoid to subclaviform, rarely subspherical, with one transverse septum, $12\text{--}23 \times 5.5\text{--}10 \mu\text{m}$; epibasidia cylindrical, at least $23 \mu\text{m}$ long. *Basidiospores* subspherical, $5\text{--}7.5 \times 4.5\text{--}6.5 \mu\text{m}$. *Asexual stage* unknown.

Notes. This species is easily recognized by the orange swellings contrasting with the more yellow host thallus, and a hymenium made of rather narrow, transversely 1-septate basidia.

Ecology and host. On the thallus of corticolous *Teloschistes exilis*, gall-inducing.

Distribution. North America (USA: Texas), obviously very common and possibly overlooked elsewhere.

Additional specimens examined (all on *Teloschistes exilis*). **USA:** Texas: Bandera Co., Lost Maples State Natural Area, c. 8.5 km NNW of Vanderpool and 32 km W of Medina, 29.8187°N , 99.5790°W , on branches of *Quercus virginiana*, 20 Jan. 2019, Walden 0018 & Gockman (BR); Blanco Co., Pedernales Falls State Park, c. 16.9 km E of Johnson City and 7.6 km S of Cypress Mill, 30.3131°N , 98.2416°W , on branches of *Quercus fusiformis* and *Diospyros texana*, 2 Febr. 2019, Walden 0030 & Milburn (BR); Medina Co., Hill Country State Natural Area, c. 16.8 km SW of Bandera and 22.1 km SSE of Medina, along the Medina Trail, 29.6077°N , 99.1817°W , on branches of *D. texana*, 16 Jan. 2019, Walden 0014, 0019 & Gockman (BR); Parker Co., Lake Mineral Wells State Park, c. 3.3 km NW of Cool and 4.1 km WSW of Garner, 32.8211°N , 98.0267°W , on branches of *Quercus stellata*, 31 Jan. 2019, Walden 0027 & Milburn (BR); Travis Co., Balcones Canyonland National Wildlife Refuge, c. 5.7 km W of Jonestown and 5.1 km N of Lago Vista, 30.5057°N , 97.9816°W , on branches of *Quercus buckleyi* and *Q. fusiformis*, 2 Febr. 2019, Walden 0033 & Milburn (BR).



Tremella teloschistis

***Tremella tornabeae* Diederich, Etayo, Pérez-Ortega & Millanes, sp. nov.**

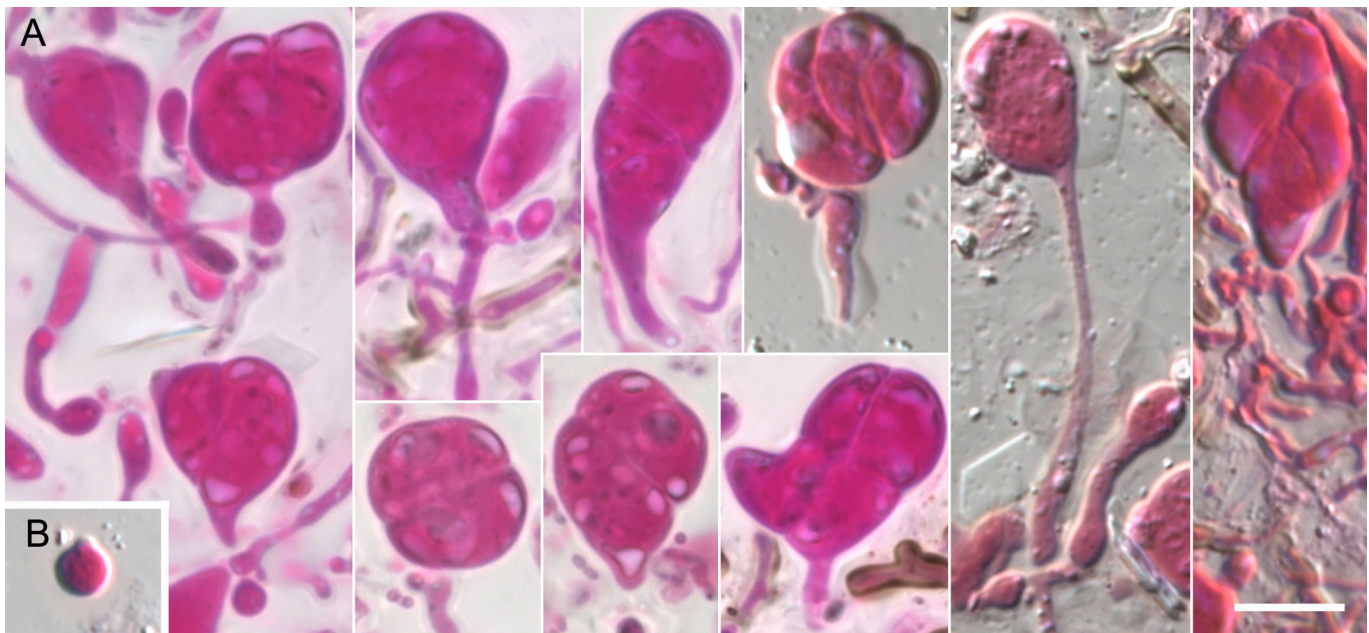
Diagnosis: Characterized by the dark brown to black, slightly convex, elongate, gelatinous basidiomata on the thallus of *Tornabea scutellifera*, $0.3\text{--}1 \times 0.2\text{--}0.5 \text{ mm}$, the (2–)4-celled basidia with longitudinal, oblique or transverse septa, $13.5\text{--}22.5 \times 8\text{--}14.5 \mu\text{m}$ (without stalk), often with a stalk up to $36 \mu\text{m}$ long, and the relatively small subspherical basidiospores, c. $5 \times 5 \mu\text{m}$.

Etymology: From *Tornabea*, the host lichen.

Type: Canary Islands, Lanzarote, NNE of Teguise, Ermita de las Nieves, 29.1067°N , 13.5297°W , 600 m, on branches of small bushes over rocks, on *Tornabea scutellifera*, 3 Sept. 2017, P. Diederich 18634 (BR – holotype).

Mycobank: MB844697

Basidiomata dark brown to black, exceptionally medium brown, slightly (rarely strongly) convex, base not or poorly constricted, gelatinous, surface rugose, elongate, up to $0.3\text{--}1 \times 0.2\text{--}0.5 \text{ mm}$. *Context hyphae* thick-walled, $2.5\text{--}3 \mu\text{m}$ diam.,



Tremella tornabeae, Canary Islands, Lanzarote, holotype. A, Basidia in different stages of development. B, Basidiospore. In phloxine. Scale bar: 10 µm.



Tremella tornabeae, Canary Islands, Lanzarote, holotype. Basidiomata on the thallus of *Tornabea scutellifera*. Scale bar: 500 µm.

without clamps; subbasidial hyphae thick-walled, 2.5–4 µm diam.; haustoria abundant, with a basal clamp. *Hymenium* containing numerous ellipsoid to pyriform probasidia with a basal clamp. *Basidia*, when mature, (2–)4-celled, septa longitudinal, oblique or transverse, sometimes cruciately septate at lateral view, subspherical, ellipsoid, or pyriform, often with a stalk-like base, upper part (without stalk) 13.5–22.5 × 8–14.5 µm, stalk up to 36 µm long; epibasidia subcylindrical, 3–4 µm diam., at least 17 µm long. *Basidiospores* subspherical, c. 5 × 5 µm (only one seen). *Asexual stage* unknown.

Notes. This species seems to be rather common on *Tornabea scutellifera* in Macaronesia, but often only a few basidiomata are present. These are typically blackish and elongate, with a rough surface.



Tremella tornabeae

Ecology and host. On the thallus of *Tornabea scutellifera* on branches of small bushes.

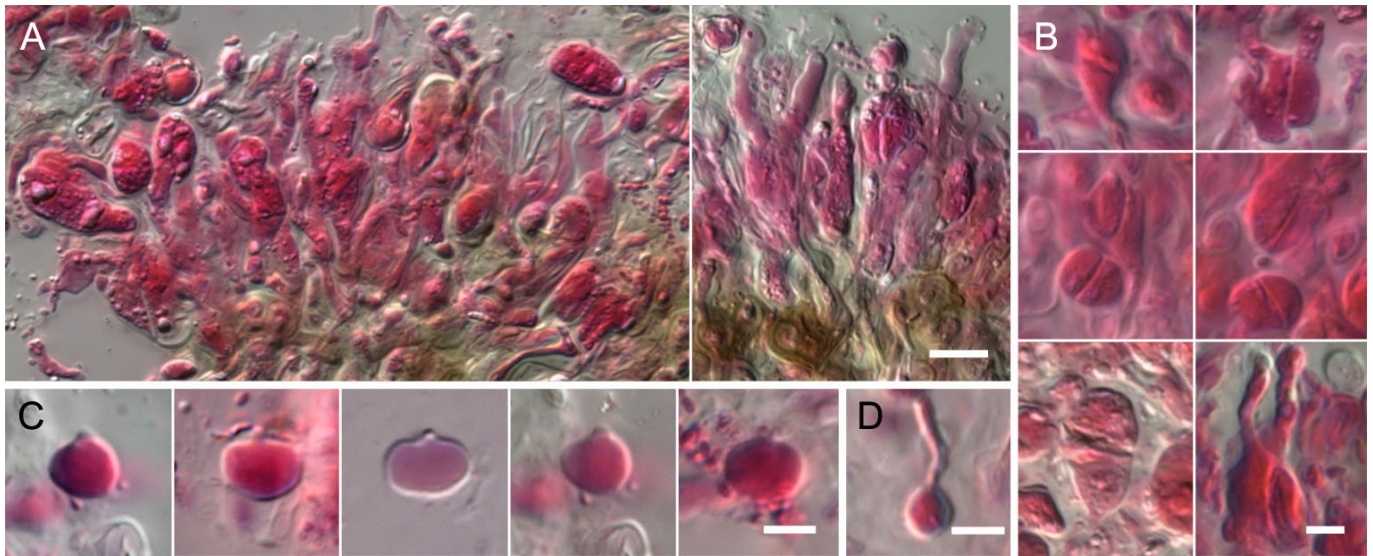
Distribution. Macaronesia (Canary Islands: Fuerteventura, Lanzarote, Tenerife).

Additional specimens examined (all on *Tornabea scutellifera*).

Canary Islands: *Fuerteventura*: Carretera de Antigua a Betancuria, Mirador de Morro Velosa, 585 m, 2004, Etayo 22045 (herb. Etayo); *ibid.*, 28.4384°N, 14.0532°W, 2015, Diederich 18204 (BR). *Tenerife*: Las Canteras, Montaña de Taco, volcanic outcrops, 28°22'20"N, 16°50'07"W, 385 m, 2018, Pérez-Ortega 7611 (MA-Lichen); Las Portelas, volcanic outcrops near Altos de Baracán, 28°19'42"N, 16°51'22"W, 810–870 m, 2018, Pérez-Ortega 8024 (MAF).

Tremella tubulosae Diederich, Coppins, J. C. Zamora, Millanes & Wedin

in Diederich et al., *Bull. Soc. Nat. luxemb.* 122: 243 (2020). *Type*: UK, Scotland, VC 92, South Aberdeen, Glen Fenzie, 38(NJ) 318 030, on *Juniperus*, on *Hypogymnia tubulosa*, 1 April 2008, B. J. Coppins 22916 & C. J. Ellis (E 00722365 – holotype).



Tremella tubulosae, UK, Scotland, holotype (modified from Diederich et al. 2020). A, Hymenium with basidia. B, Basidia. C, Basidiospores. D, Haustorium. In phloxine. Scale bars: A = 10 μ m, B–D = 5 μ m.



Tremella tubulosae, Scotland, holotype. Basidiomata on the thallus of *Hypogymnia tubulosa*. Scale bar: 2 mm.



Tremella tubulosae, Scotland, Coppins 18906. Basidiomata on the thallus of *Hypogymnia tubulosa*. Scale bar: 2 mm.

Basidiomata inducing the formation of convex galls on the host thallus, base not constricted, pale to dark brown or blackish, matt, 0.2–1.8 mm diam. Context hyphae thin-walled, 2–3 μ m diam., clamp connections not observed; subbasidial hyphae 2–5 μ m thick; haustorial branches present. Hymenium hyaline, containing numerous clavate probasidia with a basal clamp. Basidia, when mature, 2-celled, with one longitudinal, rarely oblique or transverse septum, slightly constricted at the septum, not or slightly stalked, (7–)10–17(–23) \times (7–)8–11(–15) μ m, rarely with an attenuated stalk-like base; epibasidia subcylindrical, 2.5–4.5 μ m diam., up to at least to 40 μ m long. Basidiospores subspherical to ellipsoid, 6–8 \times 5–7(–8) μ m. *Asexual stage* unknown.

Notes. This species is phylogenetically distinct and sister to *Tremella hypogymniae*, known from *Hypogymnia*

physodes (thallus). Both species induce distinct galls on their host thallus: those of *T. hypogymniae* are distinguished by being pale brown or orange to pinkish, only exceptionally dark brown. *Tremella papuana* differs by the



Tremella tubulosae

usually smaller basidiomata, 0.2–0.5 mm diam., that are constantly darker in the centre and do not induce galls, and frequently narrower basidiospores, 3.5–6 µm wide.

Ecology and host. On the thallus of *Hypogymnia tubulosa*.

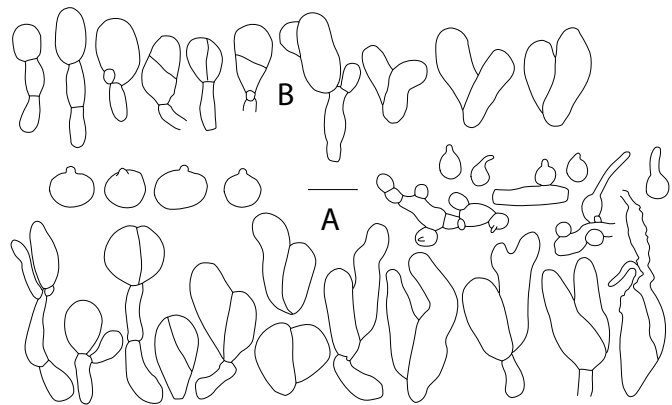
Distribution. Europe (Spain; UK: Scotland).

Reference. Diederich et al. 2020.

Tremella tuckerae Diederich

Opuscula Philolichenum 4: 18 (2007). *Type:* USA, New Mexico, Bernalillo Co., Sandia Mountains E of Albuquerque along NM route 536, Cibola National Forest, at Sandia Crest, along the North Crest trail No. 130N, 35°12'39"N, 106°26'57"W, 3250 m, on conifers in spruce-fir forest, on *Ramalina sinensis*, 12 Aug. 2001, S. Tucker 37335 (SBBG – holotype; BR – isotype).

Basidiomata resupinate over thin or thick, often irregular, frequently poor delimited gall-like swellings of the host thallus, waxy-gelatinous, pale brown (more orange-brown than the host thallus and therefore easily distinguishable) to blackish (in *Ramalina cuspidata*), 0.3–2 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled,



Tremella tuckerae. A, USA, New Mexico, holotype, B, Ireland, O'Dare (modified from Diederich 2007). Basidia, basidiospores and hyphae with haustoria. Scale bar: 10 µm.

2.5–5 µm diam., at least some with clamp connections; haustoria present, with clamp connections. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, 2-celled, with one longitudinal or rarely oblique septum, 10.5–15.5 µm diam., near the septum 12–17 µm long, both cells elongating at maturity, up to 30 µm long (epibasidium not included), in the upper part 4.5–7 µm diam.; epibasidia at least 30 µm long. *Basidiospores* subspherical to shortly ellipsoid, (5.5)7.5–9(–11) × (4–)6.5–8 µm. *Asexual stage* unknown.

Notes. This species is remarkable by the longitudinally 1-septate basidia in which each cell elongates when mature and becomes much longer than the septum. Several other lichenicolous species with similar basidia are known, e.g., *Tremella christiansenii* and *T. hypocenomycis*.

Tremella celata has similar basidiomatal galls, but is distinguished by the smaller basidia with cells that never elongate at maturity and is known only from *Ramalina fraxinea*. *Tremella ramalinae* is distinguished from both by the (3–)4-celled basidia with often two transverse or oblique and one apical longitudinal septa.



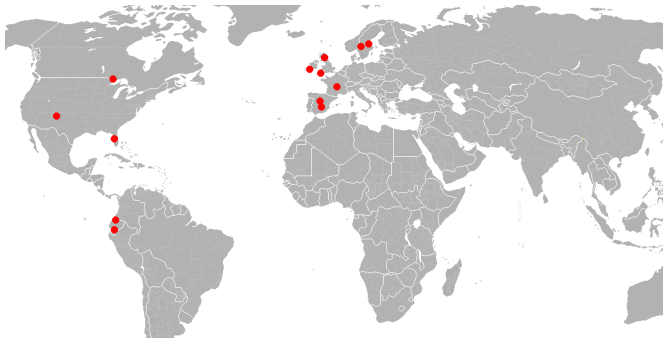
Tremella tuckerae, USA, New Mexico, isotype. Basidioma on the thallus of *Ramalina sinensis*. Scale bar: 500 µm.



Tremella tuckerae, Spain, Avila, Zamora (BR). Basidioma on the thallus of *Ramalina farinacea*. Scale bar: 1 mm.



Tremella tuckerae, France, Pinault. Basidioma on the thallus of *Ramalina fraxinea*. Scale bar: 1 mm.

*Tremella tuckerae*

Ecology and hosts. On the thallus of *Ramalina sinensis*, *R. celastri*, *R. cuspidata*, *R. farinacea*, *R. fraxinea*, *R. intermedia* and *R. stenospora*.

Distribution. Europe (France; Ireland; Spain; Sweden; UK: England, Scotland), North America (Canada: Ontario; **USA**: Florida, **New Mexico**) and South America (Ecuador).

Additional specimens examined. **Canada:** Ontario: 'Hi' Lake at portage to That Man Lake, 48.1289°N, 91.2640°W, on *Ramalina intermedia*, 2015, Scott 4528 (herb. Scott). **France:** Puy-de-Dôme: Saint-Genès-Champanelle, parking de la fontaine et chapelle de Saint-Aubin, 45.75°N, 2.99°E, 960 m, on *R. fraxinea*, 2022, Pinault (BR). **Spain:** Avila, El Tiemblo, El Castañar, 40.3544°N, 4.5184°W, 1100–1200 m, on *R. farinacea*, 2010, Zamora (BR). Jaén, Montizón, Venta de los Santos, 38.3928°N, 2.9039°W, 580–680 m, on *R. farinacea*, 2011, Zamora (BR). Huesca, Nueno, La Valle, on *R. farinacea*, 2014, Zamora (BR). **USA:** Florida: Pasco Co., Zephyrhills, Samuel W. Pasco Recreation Area, 28.213°N, 82.157°W, 25 m, on *R. stenospora*, 2019, Common 10238B (BR).

References. Diederich 2007 [Ekman et al. 2019, Etayo 2017, Zamora et al. 2016].

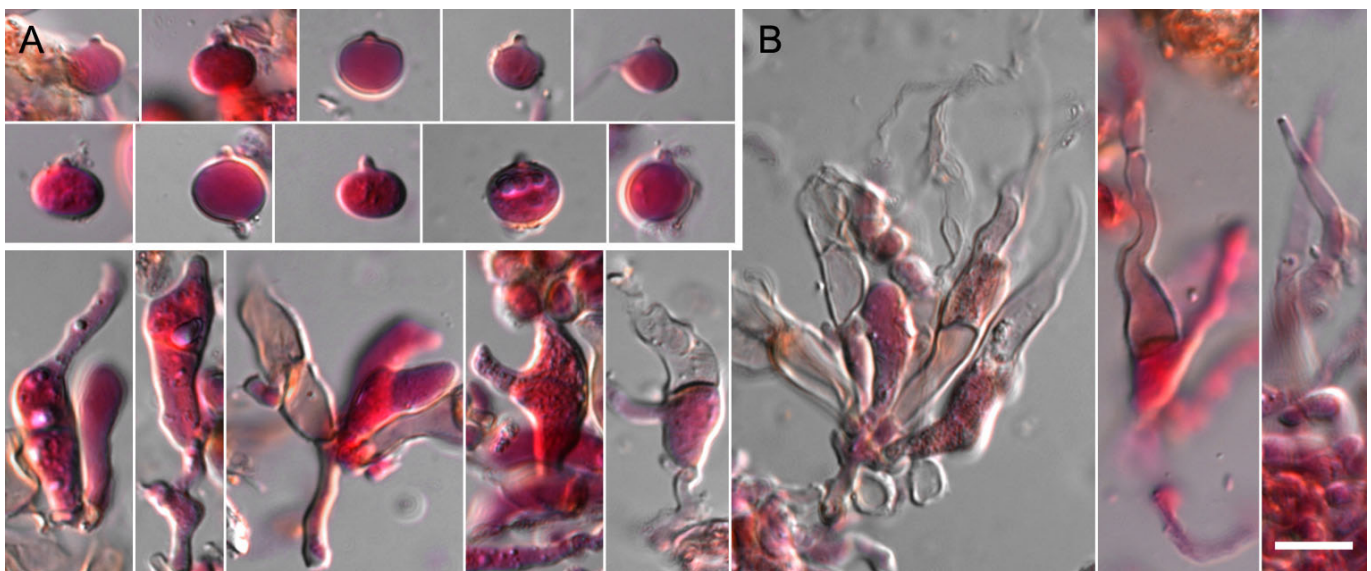
Tremella umbilicariae Diederich & Millanes

in Diederich et al., *Bull. Soc. Nat. luxemb.* 115: 170 (2014). *Type:* Peru, dept. Ancash, prov. Huaraz, pass W of Conococha (road Huaraz-Pativilca), 10°07'S, 77°23'W, 3900 m, on *Umbilicaria*, 1 March 1981, R. Santesson & R. Moberg P62:55 (UPS – holotype; BR – isotype).

Basidiomata inducing the formation of distinct convex galls on the host thallus, base not or slightly constricted, dark brown to blackish, relatively smooth, matt, frequently pruinose near the base, 0.6–2.5 mm diam., when very old sometimes almost tuberculate and with a cracked surface. *Context hyphae* thin-walled, 2.5–3 µm diam., often with clamp connections; haustoria present. *Hymenium* containing numerous clavate probasidia with a basal clamp. *Basidia*, when mature, 2-celled, with one transverse septum, slightly constricted at the septum, 19–25(–28) × (6.5)7–8 µm, rarely with an attenuated stalk-like base; epibasidia subcylindrical, 2.5–4 µm diam., up to 45 µm long. *Basidiospores* ellipsoid to subspherical, (6.5–)7.5–9.5(–10) × (5.5–)6–7.5(–8.5) µm. *Asexual stage* unknown.

Notes. This species induces conspicuous basidiomata on the thallus of *Umbilicaria*.

We have examined a further specimen of *Tremella* on *Umbilicaria* (France, Pyrénées-Orientales, Nyer, réserve naturelle de Nyer, immédiatement à l'ESE de coll del Pal, 42.4669°N, 2.2586°E, 2315 m, sur rocher de granite porphyroïde, sur *U. nylanderiana*, 2007, Roux 24368, MARSSJ) with similar basidiomatal galls; the specimen is immature, with only aseptate probasidia that are much larger (up to 41 × 15 µm) than basidia of *Tremella umbilicariae*. This specimen had already been published by Roux



Tremella umbilicariae, Peru, holotype (modified from Diederich et al. 2014). A, Basidiospores. B, Basidia with epibasidia. In phloxine + Congo red. Scale bar: 10 µm.



Tremella umbilicariae, Peru, holotype. Basidiomata on the thallus of *Umbilicaria*. Scale bar: 1 mm.



Tremella umbilicariae, Peru, holotype. Basidiomata on the thallus of *Umbilicaria*. Scale bar: 1 mm.



Tremella umbilicariae

et al. (2011) as ‘*Tremella umbilicariae* ad int.’. It probably represents a distinct, yet undescribed species.

Ecology and host. On the thallus of an unidentified *Umbilicaria* species, gall-inducing.

Distribution. South America (Peru), known only from the type locality.

Reference. Diederich et al. 2014.

Tremella varia Pérez-Ortega, Millanes, V. J. Rico & J. C. Zamora

in Zamora et al., *Mycologia* 108: 388 (2016). *Type*: Spain, Castilla-La Mancha, Toledo, Los Navalucillos, Parque Nacional de Cabañeros, near parking at the park entrance, 39°34'32"N, 4°39'36"W, 750 m, on *Lecanora varia* on *Cistus ladanifer*, 23 Oct. 2010, S. Pérez-Ortega 1748 & M. Arróniz-Crespo (MAF-Lich 19748 – holotype).

Fungus growing in the host thallus and apothecia exciple, inducing the formation of convex to bullate, rounded, waxy, greenish yellow at first (concolorous with host thallus) but soon cream to pale brown galls, 0.1–0.7 mm diam. *Context hyphae* 2–4(–5) μm diam., thick-walled, with clamps; sub-

basidial hyphae thick-walled; haustoria frequent. *Hymenium* often poorly developed, with numerous globose to broadly clavate probasidia. *Basidia* 2–4-celled, with longitudinal, rarely slightly oblique septa, sessile, subglobose to broadly ellipsoid or clavate, $15\text{--}26 \times 12\text{--}22 \mu\text{m}$; epibasidia subcylindrical, $12\text{--}28 \times (2.5\text{--})3\text{--}5 \mu\text{m}$. *Basidiospores* globose to subglobose, $(6.5\text{--})7\text{--}10.5 \times (6.5\text{--})7\text{--}11(12) \mu\text{m}$ diam. *Asexual stage* unknown. [Modified from Zamora et al. 2016.]

Notes. Contrary to several other lecanoriicolous *Tremella* species, basidiomata of *Tremella varia* are not intrahymenial, but induce the formation of convex galls on the host thallus and apothecial margin. The only other such species, the new *T. zamorae* described below, readily differs by basidia with individual cells much elongating at maturity, and by much larger basidiospores, $11.5\text{--}17.5 \times 10.5\text{--}18 \mu\text{m}$.

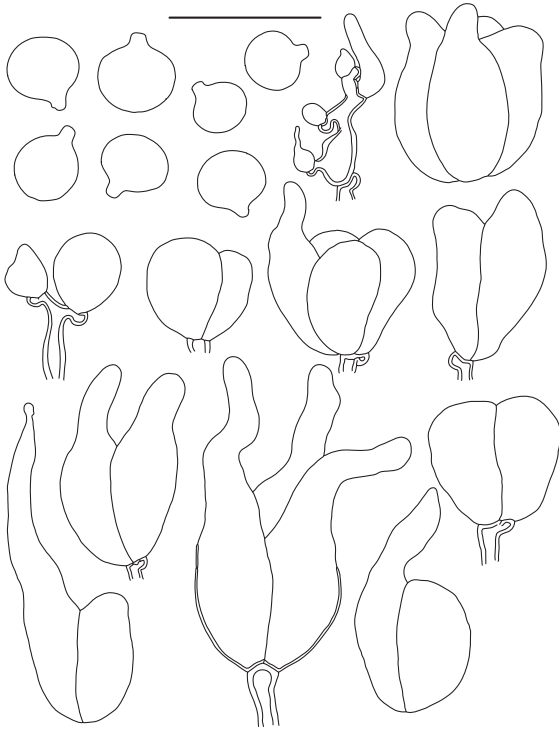
Ecology and host. On the thallus and apothecial margin of *Lecanora varia*.

Distribution. Europe (Spain).

References. Zamora et al. 2016 [Tuovinen et al. 2021].



Tremella varia, Spain, San Martín de Valdeiglesias, MAF-Lich 19751. Basidiomata on the thallus of *Lecanora varia*. Photo: J. C. Zamora.



Tremella variae, Spain, holotype (modified from Zamora et al. 2016). Basidia, basidiospores and hypha with haustoria. Scale bar: 10 µm.



Tremella variae

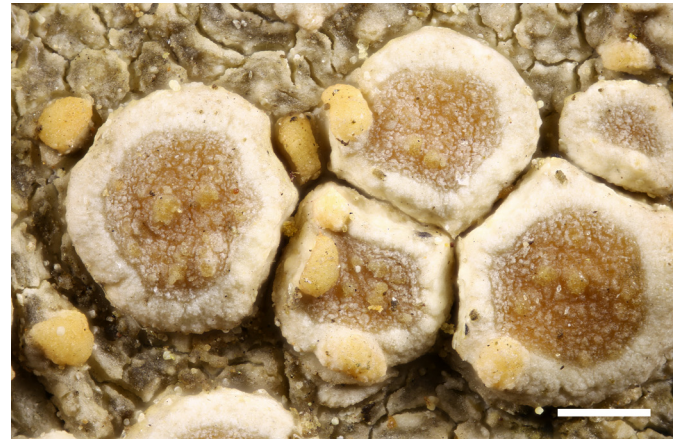
Tremella aff. *variae*

Basidiomata superficial, pulvinate, subspherical, waxy-gelatinous, pale yellowish brown, 0.15–0.7 mm diam. **Probasidial initials** with a basal clamp. **Basidia**, when mature, subspherical to ellipsoid, 2–4-celled, with longitudinal or rarely oblique septa, $20\text{--}30 \times (10\text{--})17\text{--}24$ µm. **Basidiospores** subspherical to shortly ellipsoid, $9\text{--}10 \times 7.5\text{--}10$ µm.

Notes. Two specimens on *Lecanora intumescens* strongly resemble *Tremella variae*. As both specimens are in a poor condition, more material on this host is needed to take a decision about its taxonomic status.

Ecology and host. On the thallus, apothecial margin and rarely apothecial disk of corticolous *Lecanora intumescens*.

Distribution. Europe (Portugal; Spain).



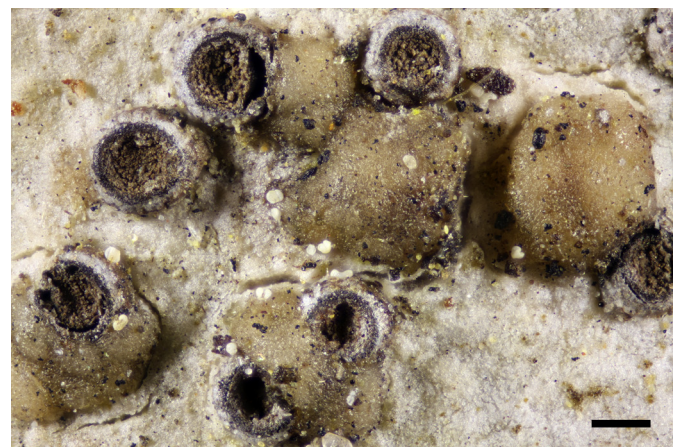
Tremella aff. *variae*, Spain, Etayo 19619. Basidiomata on the thallus and apothecia of *Lecanora intumescens*. Scale bar: 500 µm.

Specimens examined (both on *Lecanora intumescens*). **Portugal:** Trás-os-Montes, N of Bragança, Montesinho, NE of village, $41^{\circ}56.5'N$, $6^{\circ}45.2'W$, 1200 m, on *Betula*, on *Lecanora intumescens*, van den Boom 19495 (herb. van den Boom). **Spain:** Huesca, refugio de Gabardito, barranca de Agüerri, 1425 m, on *Fagus*, 2002, Etayo 19619 (herb. Etayo).

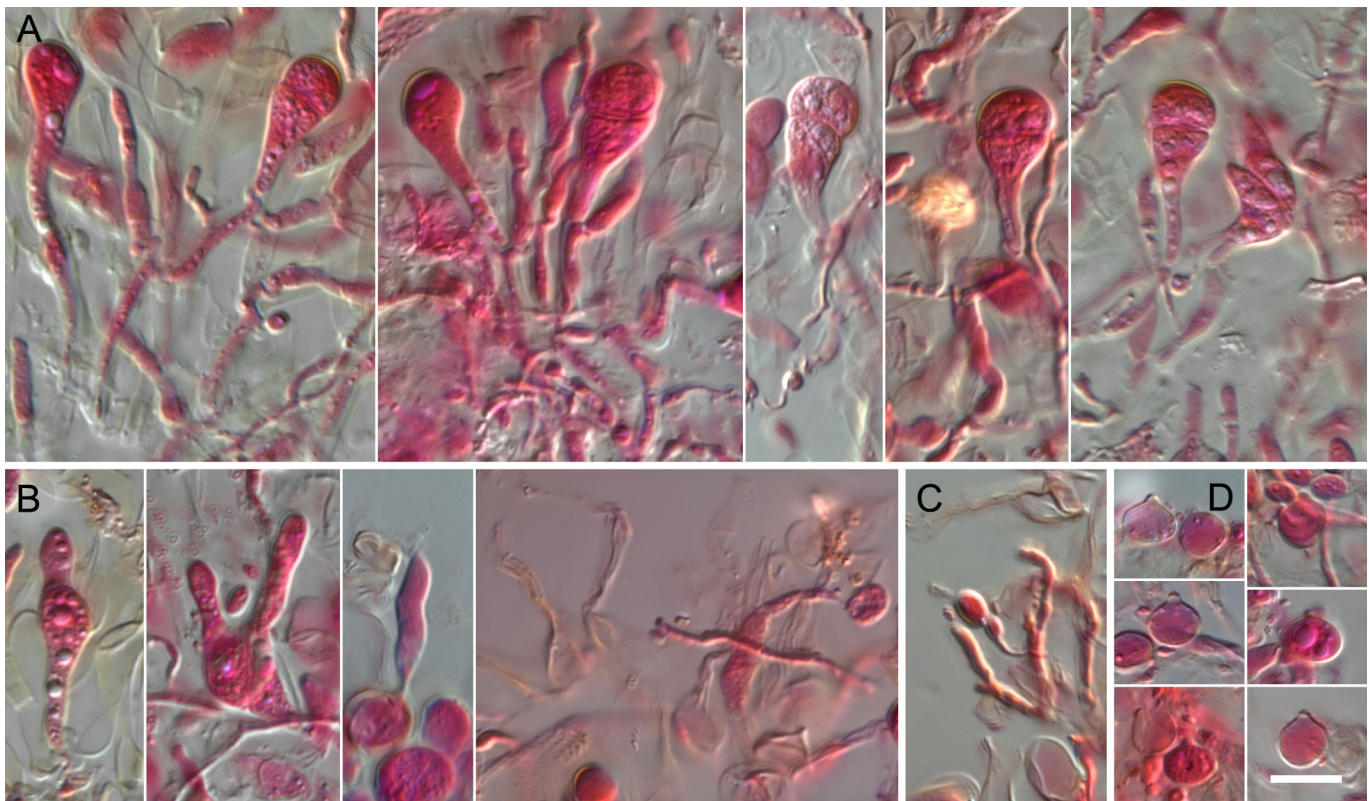
Tremella wedinii Diederich, Common & Millanes

in Diederich, Common, Braun, Heuchert, Millanes, Suija & Ertz, Plant and Fungal Systematics 64: 274 (2019). **Type:** USA, Florida, Pasco Co., Zephyrhills, near US 301, $28.239^{\circ}N$, $82.184^{\circ}W$, alt. 30 m, windfall oak twigs, on *Glyphis scyphulifera*, 8 May 2016, R. Common 10067B (BR 5030086825797 – holotype; MSC, S – isotypes).

Basidiomata pale brown, rarely becoming medium to dark brown when mature, pulvinate, waxy-gelatinous, surface rather smooth, roundish, elongate or irregularly formed, up to 0.5(–0.8) mm diam., flat or slightly convex, rarely strongly convex, with a constricted base. **Context hyphae**



Tremella wedinii, USA, Florida, isotype. Basidiomata on *Glyphis scyphulifera*. Scale bar: 200 µm.



Tremella wedinii, USA, Florida, holotype (modified from Diederich et al. 2019). A, Basidia. B, Basidia with epibasidia. C, Haustorium. D, Basidiospores. In phloxine + Congo red. Scale bar: 10 μ m.

thin-walled, 2–4 μ m diam., clamp connections not observed; haustoria present. Hymenium containing numerous ellipsoid to rarely clavate probasidia with a basal clamp. *Basidia*, when mature, 2-celled, with one transverse, rarely oblique or longitudinal septum, slightly constricted at the septum, often with a long attenuated stalk-like base, (16.5–)20–28.5(–31.5) \times (8–)9–10.5(–11) μ m (incl. stalk); epibasidia subcylindrical, 3–5 μ m diam., at least 45 μ m long. *Basidiospores* ellipsoid to subspherical, 7.5–9.5(–10) \times 6.5–8.5(–9) μ m. *Asexual stage* unknown.

Notes. This species is distinguished from most lichenicolous *Tremella* species by the mainly 1-transseptate basidia with a long attenuated stalk-like base. *Tremella anaptychia*

also has such stalked basidia but they are much broader, 10–15 μ m.

Ecology and host. On the thallus, more rarely the apothecia, of *Glyphis scyphulifera*.

Distribution. North America (USA: Florida, Louisiana), Caribbean (Puerto Rico).

Reference. Diederich et al. 2019.

Tremella wirthii Diederich

Bibl. Lichenol. 61: 164 (1996). *Type:* Germany, Bayern, Neu-Ulm, Holzheim, Obstgarten WSW Steinheim, MTB 7626/2, 470 m, on *Protoparmelia hypotremella*, 6 Febr. 1991, V. Wirth 21713 (STU – holotype).

Basidiomata convex, pulvinate, pale to dark greyish brown, gelatinous, not waxy, 0.15–0.5 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3–5 μ m diam.; haustoria frequent, with clamp connections. *Hymenium* containing numerous subspherical probasidia with a basal clamp. *Basidia*, when mature, subspherical to ellipsoid, rarely indistinctly stalked, 2–4-celled, with longitudinal septa, 18–24 \times 12–18 μ m; epibasidia subcylindrical, 3.5–5.5 μ m diam., up to at least 50 μ m long. *Basidiospores* subspherical, 9–10.5 \times 8–10 μ m. *Asexual stage* unknown.



Tremella wedinii



Tremella wirthii, Netherlands, van Herk. Basidiomata on *Prototarmelia hypotremella*. Scale bar: 500 μ m.

Notes. This is a distinctive species of *Tremella* with large 2–4-celled basidia and large basidiospores. It is similar to *T. haematommatis* in which basidiomata are either reduced and grow in the host hymenium, or superficial and amber-coloured. *Tremella prototarmeliae* grows on another species of *Prototarmelia*, *P. badia*, but differs in the intrahymenial growth and narrowly ellipsoid to subcylindrical, transversely 1-septate basidia, $29\text{--}39 \times 8\text{--}10 \mu\text{m}$.

Ecology and hosts. On the thallus of *Prototarmelia hypotremella* and *P. oleaginea*.

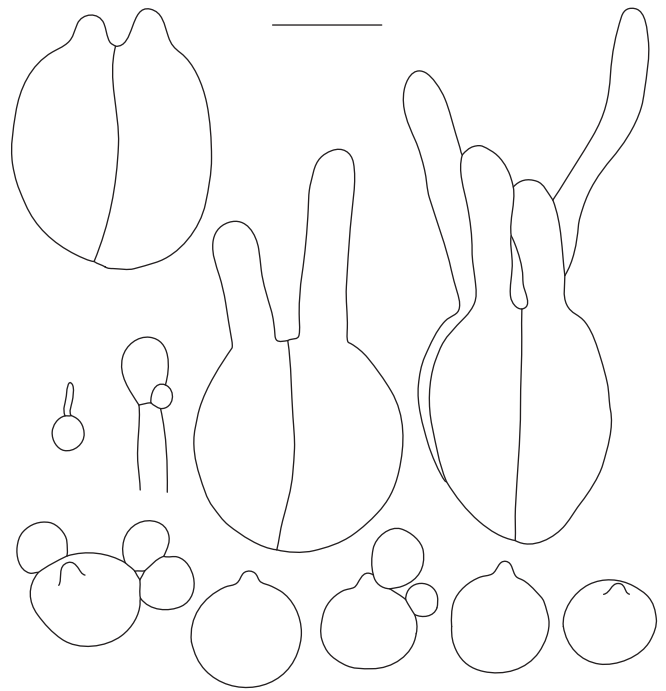
Distribution. Europe (Austria; Czech Republic; France; Germany; Netherlands; Norway; Sweden).

Specimen examined. **Norway:** Trøndelag: Steinkjer, Litl-Gaulstad, along the path towards Nummerein Gruvfjellet, 63.9743°N , 12.1198°E , 325 m, on *Prototarmelia oleaginea*, 2015, Haugan 151235 (BR).

References. Diederich 1996 [Aptroot et al. 1997, Brackel 2014, Holien et al. 2016, Roux 2020, Vondrak et al. 2022, Westberg et al. 2015].



Tremella wirthii



Tremella wirthii, Germany, Wirth 17412 (modified from Diederich 1996). Basidia, basidiospores and a haustorial branch. Scale bar: 10 μ m.

***Tremella xanthomendozae* Diederich, C. A. Morse & Brinker, sp. nov.**

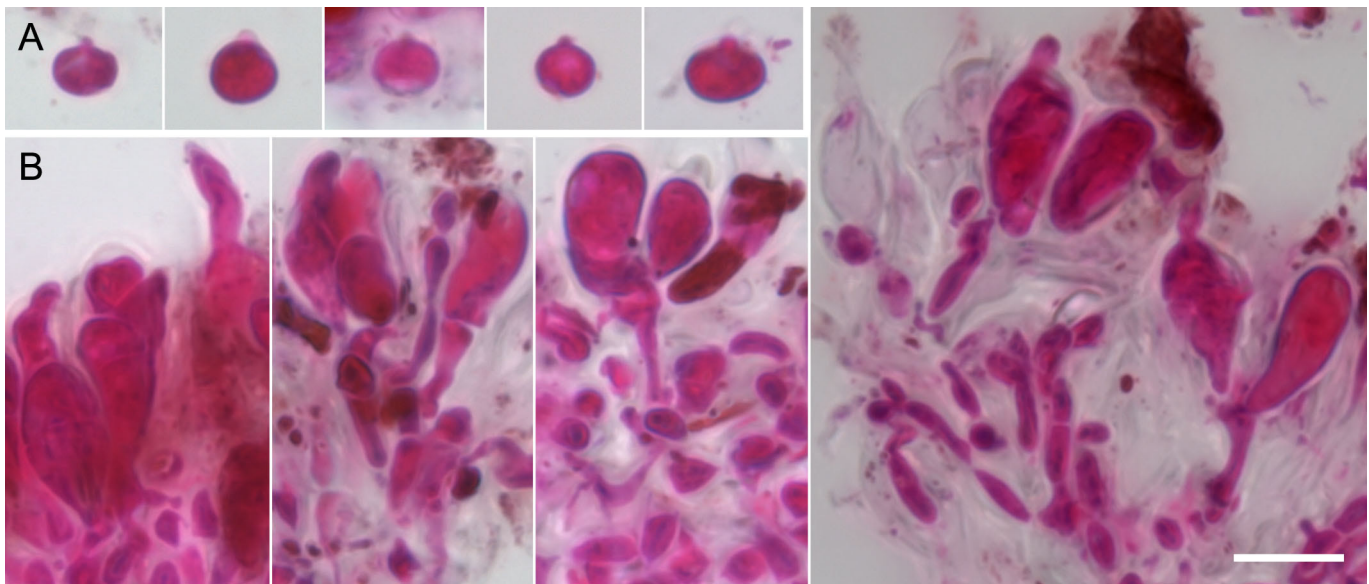
Diagnosis: Characterized by the orange, pulvinate, basally often constricted, waxy-gelatinous basidiomatal galls on the thallus of *Xanthomendoza weberi*, 0.15–0.6 mm diam., the elongate ellipsoid to subclaviform, transversely or obliquely 1-septate basidia, $13\text{--}22 \times 5.5\text{--}9 \mu\text{m}$, and the medium sized, shortly ellipsoid basidiospores, $5\text{--}7.5 \times 4.5\text{--}6 \mu\text{m}$.

Etymology: From *Xanthomendoza*, the host lichen.

Type: USA, Kansas, Douglas Co., c. $0.25\text{--}0.45 \text{ mi N}$, 1.75 mi E of jct of DG Co Rd 1055 & US Hwy 56 in Baldwin City, prop-



Tremella xanthomendozae, Canada, Brinker 8605. Basidiomata on the thallus of *Xanthomendoza weberi*. Scale bar: 500 μ m.



Tremella xanthomendozae, USA, Kansas, holotype. A, Basidiospores. B, Hymenium with mature basidia. In phloxine. Scale bar: 10 μ m.

erty of Ralph and Roma Earles, 38.7859°N, 95.1515°W, c. 300 m, on *Carya ovata*, on *Xanthomendoza weberi*, 15 April 2021, C. A. Morse 27743 (KANU – holotype; BR – isotype).

Mycobank: MB844698

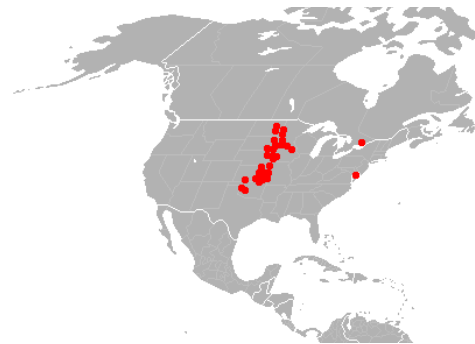
Basidiomatal galls on the host thallus superficial, pulvinate, subspherical, often with a constricted base, waxy-gelatinous, orange, 0.15–0.6 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2–6 μ m diam.; haustoria present. *Hymenium* containing numerous ellipsoid probasidia with a basal clamp. *Basidia*, when mature, elongate ellipsoid to subclaviform, sometimes with an attenuated, almost stalk-like base, 2-celled, septum transverse or oblique, 13–22 \times 5.5–9 μ m; epibasidia cylindrical, at least 22 μ m long. *Basidiospores* shorty ellipsoid, (4.5–)5–7.5 \times (3.5–)4.5–6 μ m. *Asexual stage* unknown.

Notes. This species can easily be recognized by the convex orange basidiomatal galls contrasting with the yellow thallus of the host.

Ecology and host. Gall-inducing on the thallus of *Xanthomendoza weberi*.

Distribution. North America (Canada: Ontario; **USA**: Delaware, Iowa, **Kansas**, Minnesota, Nebraska, North Dakota, Oklahoma, South Dakota).

Selected additional specimens examined (all on *Xanthomendoza weberi*). **Canada**: Ontario: Prince Edward Co., Massassauga Point, 6 km E of Rossmore off Massassauga Rd, Bay of Quinte, Massassauga Point Conservation Area, 44.1477°N, 77.3121°W, on *Juniperus virginiana*, 2020, Brinker 8605 (CANL, NY, herb. Brinker). **USA**: Delaware: Sussex Co., Georgetown, on *Ulmus*, 1985, Reed 125018 (NY). Kansas, Douglas Co., c. 1 mi S, 2 mi E of Vinland, 'Violet Hill', 38.8261°N, 95.1457°W, c. 300 m, on *Quercus*, 2021, Morse 27730 (BR, KANU).



Tremella xanthomendozae

Tremella zamorae Diederich & Millanes, sp. nov.

Diagnosis: Characterized by pale to orange-brown, waxy-gelatinous basidiomata, 0.2–0.7 mm diam., subspherical probasidia that become longitudinally cruciately septate, (2–)4-celled, 7.5–20 μ m diam., with individual cells eventually elongating and growing separately, without clearly differentiated epibasidia, 40–72 \times 6.5–19 μ m, very large subspherical basidiospores, 11.5–17.5 \times 10.5–18 μ m, and endospores developing inside old basidia, 3.5–9 \times 2.5–4.5 μ m.

Etymology: Named after J. C. Zamora (Geneva, Switzerland), expert of lecanoricolous *Tremella* species.

Type: USA, North Carolina, Hyde Co., Pocosin Lakes National Wildlife Refuge, Pungo Lake Unit, Pungo Lake Observation Platform, N of South Lake Road, 1 mi W of Allen Road, 35°41'22"N, 76°32'30"W, *Myrica-Ilex* scrub, on *Lecanora louisianae*, 11 Dec. 2012, R. C. Harris 58550 (NY – holotype; BR – isotype).

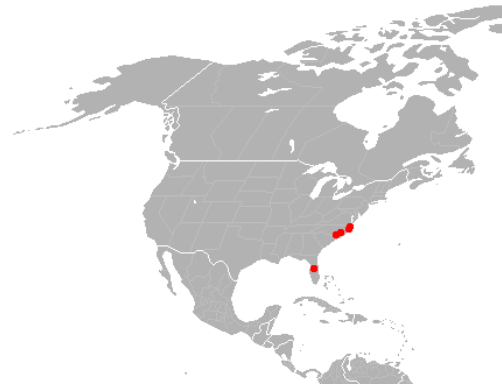
Mycobank: MB844699

Basidiomata pale to orange-brown, rarely dark brown, waxy-gelatinous, 0.2–0.7 mm diam. *Context hyphae*

and subbasidial hyphae thick-walled, 3.5–5 µm diam., clamps not observed; haustoria not observed. *Hymenium* with numerous subglobose probasidia; basal clamps indistinct. *Basidia* becoming longitudinally cruciately septate, (2–)4-celled, remaining for some time subspherical, 7.5–20 µm diam. (viewed from above); when mature, individual cells elongate and grow separately in length, without clearly differentiated epibasidia, 40–72 × 6.5–19 µm. *Basidiospores* subspherical, rarely broadly ellipsoid, 11.5–17.5 × 10.5–18 µm, able to germinate by producing a sterigma and a secondary ballistospore similar to a basidiospore but only 6–7 µm diam. *Endospores* developing inside old basidia, after basidiospore production, shortly ellipsoid, aseptate, 3.5–9 × 2.5–4.5 µm. *Asexual stage*: one lunate conidium observed (Buck 61628), c. 9.5–10.5 µm diam. (largest outer diam.) and 3.5–5 µm thick.

Notes. This species is remarkable by the initially subspherical basidia with individual cells eventually elongating separately, up to 72 µm long, without clearly differentiated epibasidia, the particularly large, subspherical basidiospores, and the presence of endospores within old basidia. Although it has not been successfully sequenced, it resembles *Tremella diderichiana* and related species so much that it certainly belongs to the same clade. *Tremella diderichiana* differs by the slightly smaller basidiospores, 10–12.5 × 10–14 µm, shorter basidial cells less than 50 µm long, the frequent haustoria, by inducing the formation of galls on the host thallus and apothecia, and by being confined to another host species, *Lecidea* aff. *erythrophaea*. The otherwise similar *Tremella endosporogena* is distinguished by the aseptate basidia and the predilection for *Lecanora carpinea* apothecia.

We dedicate this species to our friend and colleague Juan Carlos Zamora, prominent mycologist, for his important contributions to the study of ‘heterobasidiomycetes’.



Tremella zamorae

Ecology and host. On the thallus, rarely the apothecial margin of corticolous *Lecanora louisianae*.

Distribution. North America (USA: Florida, North Carolina).

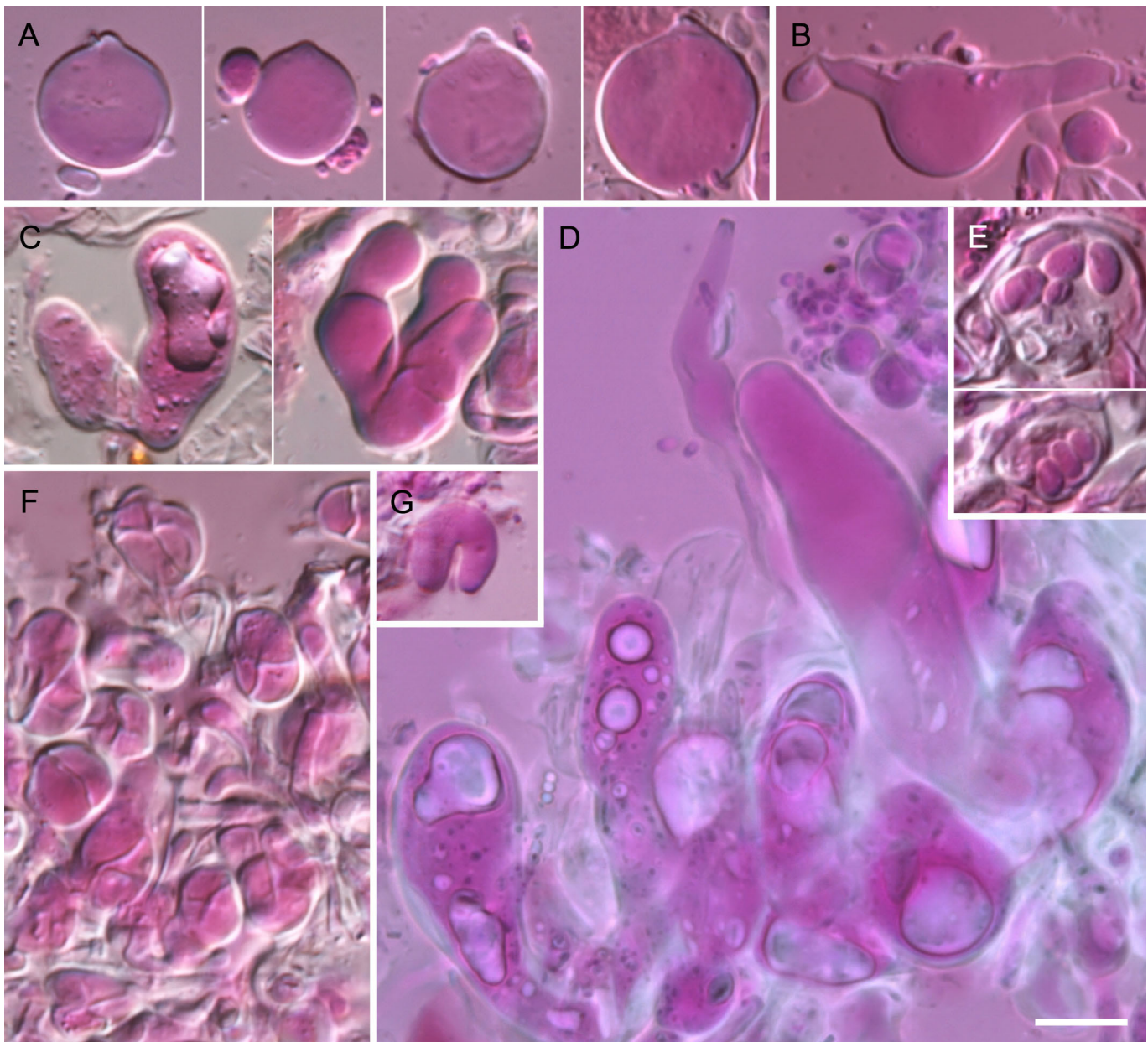
Additional specimens examined (all on *Lecanora louisianae*). USA: Florida: Polk Co., Nalcrest (retirement community 100 km E of Tampa), N side, edge of scrub, 27°51'30"N, 81°25'30"W, 25 m, Southern Florida Flatwoods, on *Myrica cerifera*, 1989, Wheeler, Obermayer *Lichenotheca Graecensis* 201 (G [examined by J. C. Zamora]). North Carolina: Same locality as type, on *Myrica*, 2012, Harris 58545 (NY). Bladen Co., Bay Tree Lake State Park, sand ridge 0.6 mi SE of NC41, 0.3 mi W of Shore of Bay Tree Lake, 34°40'07"N, 78°25'35"W, 80 ft, oak dominated sand ridge, on *Quercus*, 2016, Lendemer 48297 (NY). Dare Co., Alligator River National Wildlife Refuge, W of Brier Hall Road, 1.6 mi N of jct with US 64, 35°53'58"N, 75°56'24"W, *Liquidambar-Acer-Pinus* swamp forest, on fallen branch, 2012, Harris 58113 (NY). Pender Co., Angola Bay Game Land, along Bay Road, 0.2 mi W of jct with Pocosin Road, 34°40'46"N, 77°47'05"W, 30 ft, *Pinus-Gordonia-Cyrilla* pocosin, 2013, Buck 61628 (NY). Tyrell Co., Pocosin Lakes National Wildlife Refuge, Frying Pan Boating Access, S of Frying Pan Road, 6 mi E of jct with NY 94, 35°48'12"N, 76°06'30"W, *Acer*-dominated hardwood swamp, on fallen branch, 2012, Harris 58393-B (NY).



Tremella zamorae, USA, North Carolina, holotype. Basidiomata on the thallus of *Lecanora louisianae*. Scale bar: 500 µm.



Tremella zamorae, USA, North Carolina, Harris 58545. Basidiomata on the thallus of *Lecanora louisianae*. Scale bar: 500 µm.



Tremella zamorae, USA, North Carolina. A–B, E, Harris 58545, C, Lendemer 48297, D, holotype, F–G, Buck 61628. A, Basidiospores. B, Germinating basidiospore and secondary ballistospore (bottom right). C, Basidia with elongating cells. D, Mature basidia with very large cells. E, Old basidia filled with endospores. F, Young subspherical basidia with a cruciate septation. G, Lunate conidium. In phloxine. Scale bar: 10 μ m.

Tremella aff. *zamorae*

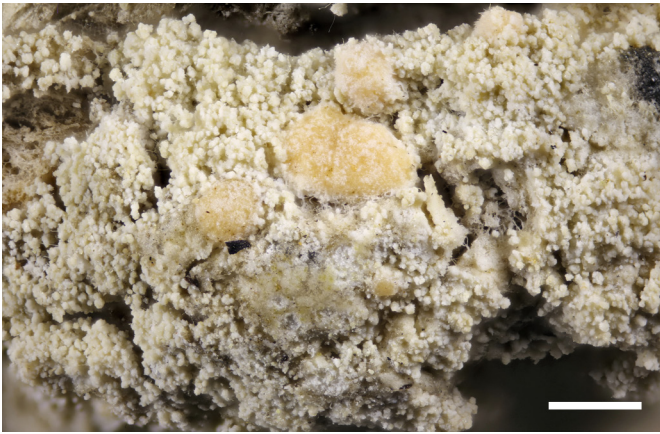
Basidiomata pale pinkish brown, waxy-gelatinous, 0.2–0.7 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 4.5–5.5 μ m diam., clamps not observed; haustoria not observed. *Hymenium* with numerous subspherical probasidia; basal clamps not seen. *Basidia* initially cruciate-septate, (2–)3(–4)-celled; when mature, individual cells elongate and grow separately in length, without clearly differentiated epibasidia, 4.5–8.5 μ m diam., up to 85 μ m long. *Basidiospores* not seen. *Asexual stage* not observed.

Notes. A specimen on *Lecanora nothocaesiella* resembles *Tremella zamorae* macroscopically and microscopically.

Ecology and host. On the thallus of *Lecanora nothocaesiella*.

Distribution. North America (USA: Wisconsin).

Specimen examined. **USA:** Wisconsin: Oneida Co., Town of Minocqua, Patterson Hemlocks State Natural Area, 1.2 mi S of St. Hwy 70 on West Clear Lake Road, 45°53'51"N, 89°57'45"W, 500 m, on *Acer saccharum*, on *Lecanora nothocaesiella*, 2002, Harris 46022 (NY).



Tremella aff. *zamorae*, USA, Wisconsin, Harris 46022. Basidiomata on the thallus of *Lecanora nothocaesiella*. Scale bar: 500 μ m.

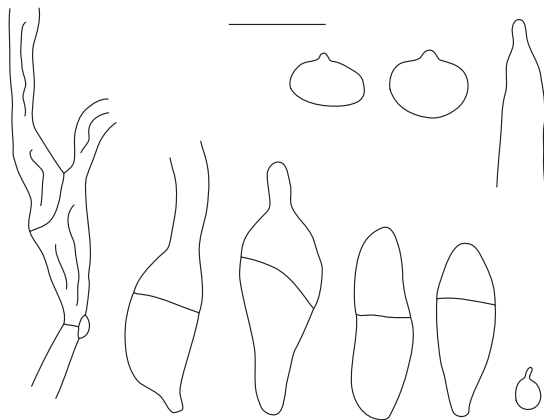
Tremella sp. 2 on *Lecanora rimicola*

Basidiomata intrahymenial, macroscopically not visible. *Context hyphae* not observed; haustorial branches present. *Hymenium* reduced, probasidia developed in the hymenium of the host; probasidial initials clavate, with a basal clamp. *Basidia*, when mature, narrowly ellipsoid to subcylindrical, with 1 transverse septum, not constricted at the septum, the lower cell a little longer than the upper cell, 15–21 \times 5–7 μ m; epibasidia 3–4.5 μ m thick, at least 40 μ m long. *Basidiospores* ellipsoid, with a large apiculus, 7.5–8 \times 5–5.5 μ m. *Asexual stage* unknown.

Notes. This species was briefly described by Diederich (1996), based on two microscopic slides prepared by M. S. Christiansen in 1984. We examined several apothecia, but none of them was infected by the fungus.

Ecology and host. On the hymenium of *Lecanora rimicola*.

Distribution. Europe (Denmark).



Tremella sp. 2 on *Lecanora rimicola*, Denmark, Christiansen 4411 (modified from Diederich 1996). Basidia, epibasidium, basidiospores and a haustorium. Scale bar: 10 μ m.



Tremella sp. 2 on *Lecanora rimicola*

Specimen examined. **Denmark:** NW Zealand, Faarevejle, on boulders in a salt meadow at the northern shore of the headland Ordrup Næs, Sejerø Bugt., on *Lecanora rimicola*, 1984, Christiansen 4411 (C).

Reference. Diederich 1996.

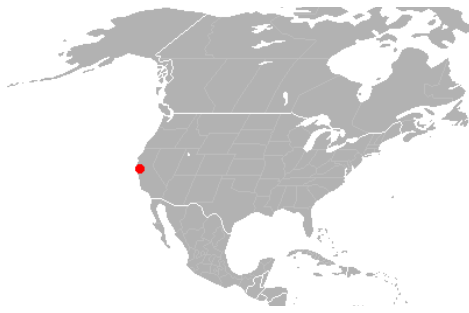
Tremella sp. 8 on *Evernia prunastri*

Basidiomata inducing superficial galls, brown, slightly convex, basally not constricted, up to 1 mm diam. or larger when confluent. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3–4 μ m thick; haustoria not observed. *Hymenium* containing a few indistinct probasidia; basal clamp not observed. *Basidia*, when mature, ellipsoid, 2-celled, with a longitudinal or slightly oblique septum, 14–24 \times 10–13 μ m; epibasidia cylindrical, 2–4 μ m thick, at least 28 μ m long. *Basidiospores* not observed. *Asexual stage* unknown. *Yeast* cells subspherical to broadly ellipsoid, 1.5–2.5 \times 1.5–2 μ m.

Notes. Although the specimen looks healthy and basidiomata are abundant, the hymenium is in a poor condition. Basidia cannot easily be separated after pressure on the cover glass, and no basidiospores have been seen.



Tremella sp. 8 on *Evernia prunastri*, USA, California, Robertson 5388. Basidiomata on the thallus of *Evernia prunastri*. Scale bar: 500 μ m.



Tremella sp. 8 on *Evernia prunastri*

While the host, *Evernia prunastri*, is extremely abundant, especially in Europe, this *Tremella* species has never been found in the past, suggesting that it almost always stays in the host in the yeast stage, and basidiomata are only formed under very special environmental conditions. *Tremella everniae* seems to be confined to *Evernia mesomorpha* and is distinguished by the induction of large bullate, cerebriform, gall-like deformations of 3–15 mm diam., and by the 4-celled basidia. The species on *Evernia prunastri* will hardly be confused with galls induced by *Unguiculariopsis lettaui* (Grumann) Coppins, as these are typically covered by ascomata. Minuscule, medium to dark brown dots or convex galls are frequently encountered on *E. prunastri* in Europe, but they do not appear to be related to the presence of any lichenicolous fungus.

Ecology and host. On the thallus of *Evernia prunastri*.

Distribution. North America (USA: California).

Specimen examined. USA: California: Marin Co., Mt. Tamalpais State Park, along Verna Dunshee trail, north side of East Peak, 700 m (2300 ft), on *Evernia prunastri*, 2000, Robertson 5388 (NY).

Tremella sp. 9 on cf. *Lecanora appalachensis*

Basidiomata superficial, pulvinate, subspherical, slightly flattened, occasionally lobed or subtuberculate, often irregular in form, gelatinous, pale brown, 0.2–1.3 mm diam. **Context hyphae** not observed; subbasidial hyphae thick-walled, 1.5–3.5 µm diam.; haustoria present, with a basal clamp. **Hymenium** containing numerous subspherical to ellipsoid probasidia with a basal clamp. **Basidia**, when mature, ellipsoid, 4-celled, with longitudinal or oblique septa, 12–19.5 × 8.5–13.5 µm; epibasidia not observed. **Basidiospores** not observed. **Asexual stage** unknown.

Notes. This seems to be a distinct species, characterized by the large, pale brown basidiomata developing over the thallus of cf. *Lecanora appalachensis*, and the 4-celled basidia. As no basidiospores were found, as the genus *Lecanora* seems to harbour a large number of *Tremella* species, and as no molecular data are available, we do not formally describe the species.



Tremella sp. 9, USA, North Carolina, Buck 35130. Basidiomata on the thallus of cf. *Lecanora appalachensis*. Scale bar: 500 µm.



Tremella sp. 9 on *Lecanora appalachensis*

Ecology and host. On the sterile thallus of cf. *Lecanora appalachensis* (TLC: atranorin, zeorin, terpenoid) on a dead tree trunk in moist mixed hardwoods.

Distribution. North America (USA: North Carolina).

Specimen examined. USA: North Carolina: Macon Co., Nantahala National Forest, N slope of Wayah Bald along Appalachian Trail, 35°11'N, 83°34'W, 1535 m, on dead tree trunk, on cf. *Lecanora appalachensis*, 1998, Buck 35130 (NY).

Tremella sp. 10 on *Letrouitia domingensis*

Basidiomata reduced, intrahymenial; infected host hymenium not or slightly swollen. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2–3.5 µm diam.; haustoria present, with a basal clamp. **Hymenium** reduced, mixed with the host hymenium; probasidia narrowly ellipsoid, with a basal clamp. **Basidia**, when mature, elongate ellipsoid to claviform, 2-celled, with one transverse septum, the upper cell shorter, sometimes almost subspherical, the lower cell elongate, sometimes distinctly stalked, 21–40 × 5.5–9 µm; epibasidia cylindrical, at least 35 µm long, 3–3.5 µm thick. **Basidiospores** not seen. **Asexual stage** unknown.

Notes. This species can hardly be recognized macroscopically. As many specimens of this host are frequently lack-



Tremella sp. 10 on *Letrouitia domingensis*, Dominican Republic, Harris 26762. Infected apothecia. Scale bar: 500 μ m.



Tremella sp. 10 on *Letrouitia domingensis*

ing well developed ascospores, the *Tremella* may be more frequent than these two specimens suggest.

Ecology and host. In the hymenium of *Letrouitia domingensis*, probably damaging the host, as the production of asci and ascospores is reduced.

Distribution. Caribbean (Dominican Republic).

Specimens examined (both in the hymenium of corticolous *Letrouitia domingensis*). **Dominican Republic:** Prov., Espaillat, 7.5 km E of Gaspar Hernández, 19°38'N, 70°14'W, 50 m, dry scrub forest over serpentine, 1991, Buck 19401 (NY). Prov. Puerto Plata, 4.5 km S of Sosúa-Puerto Plata Hwy at Sosúa just W of Río Sosúa, near source of Río Sosúa, 19°41'N, 70°31'W, moist primary forest near sea level, 1991, Harris 26762 (NY).

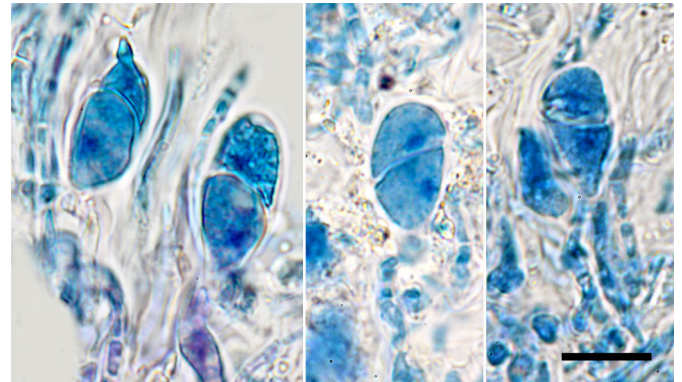
Tremella sp. 11 on *Pyrenodesmia chalybaea*

Basidiomata reduced, intrahymenial. **Basidia**, when mature, ellipsoid, 1-transseptate, 12–18 \times 7–9 μ m. **Basidiospores** not observed. **Asexual stage** unknown.

Notes. Photos of basidia have been published by Schumm & Aptroot (2019, as *Lindauopsis caloplacae*). We have examined the corresponding specimen, sectioned a number of apothecia, but failed to observe the *Tremella*. Our description above is based on the published photos.



Tremella sp. 11 on *Pyrenodesmia chalybaea*



Tremella sp. 11 on *Pyrenodesmia chalybaea*, Slovakia, Vězda *Lichenes Selecti Exsiccati* 1145. Basidia. Scale bar: 10 μ m. Photos: F. Schumm.

Ecology and host. Intrahymenial in the apothecia of *Pyrenodesmia chalybaea*.

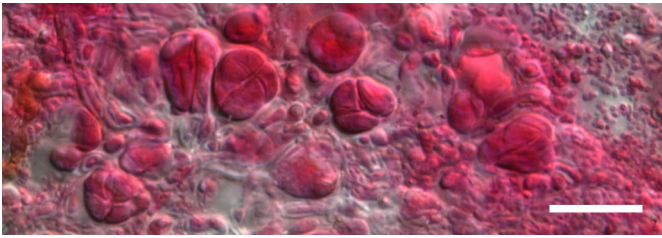
Distribution. Europe (Slovakia).

Specimen examined. **Slovakia:** Iugum Carpatorum “Bílé Karpaty” dictum, in monte Vršatec, 850 m, ad saxa calcarey, on *Pyrenodesmia chalybaea*, 31 May 1971, Pišút & Vězda, Vězda *Lichenes Selecti Exsiccati* 1145 (herb. Schumm, as *Caloplaca chalybaea*).

Tremella sp. 12 on *Tetramelas* aff. *graminicola*

Basidiomata absent, basidia endolichenic. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2–3.5 μ m diam.; haustoria not observed. **Hymenium** reduced to fertile loci immersed in the host thallus, containing probasidia and mature basidia; probasidial initials subspherical to ellipsoid, basal clamps not seen. **Basidia**, when mature, subspherical to ellipsoid, 4-celled, longitudinally cruciately septate, 11–14.5 \times 10–16 μ m; epibasidia not seen. **Basidiospores** absent. **Asexual stage** unknown.

Notes. This species has been observed by chance in a specimen of *Kriegeriopsis livingstonensis*, is asymptomatic and not visible macroscopically.



Tremella sp. 12 on *Tetramelas* aff. *graminicola*, Antarctica, Etayo 31367. A–B, Endolichenic basidia. In phloxine. Scale bar: 10 µm.



Tremella sp. 12 on *Tetramelas* aff. *graminicola*

Ecology and host. Endolichenic in the thallus of *Tetramelas* aff. *graminicola* that is also parasitized by *Kriegeriopsis livingstonensis*.

Distribution. Antarctica (South Shetland Islands: Livingston Island).

Specimen examined. **Antarctica:** South Shetland Islands, Livingston Island, 2018, on *Tetramelas* aff. *graminicola*: Caleta Alemana, rocky place E of the beach, 62°40'11"S, 60°24'09"W, 0–10 m, Etayo 31367 (herb. Etayo).

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *AGARICOSTILBOMYCETES*

Order *AGARICOSTILBALES*

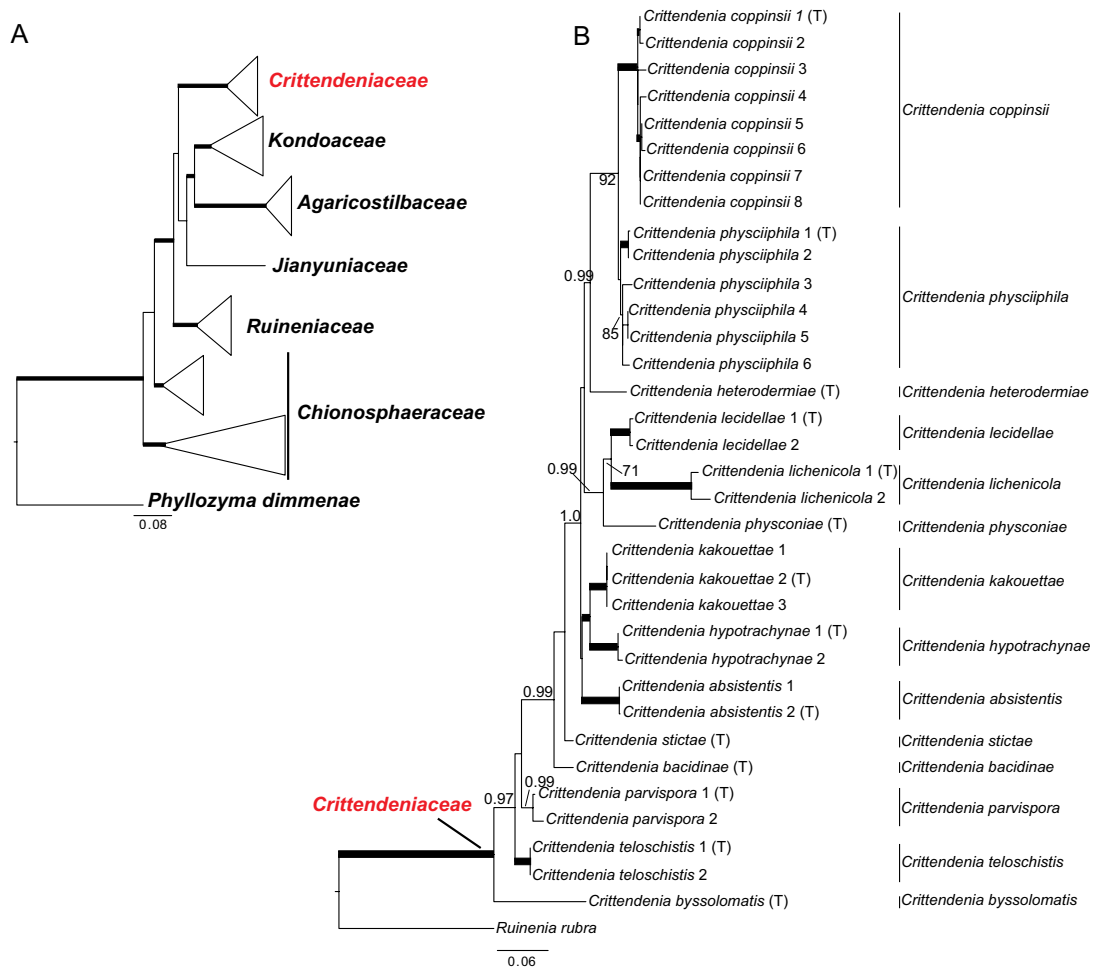
by P. Diederich, A. M. Millanes, J. Etayo, P. P. G. van den Boom & M. Wedin

Diederich, P., A. M. Millanes, J. Etayo, P. P. G. van den Boom & M. Wedin. 2022. Class *Agaricostilbomycetes*, order *Agaricostilbales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 283–303.

Introduction and phylogeny

The *Agaricostilbomycetes* includes only the order *Agaricostilbales*, which Bauer et al. (2006) referred to as dimorphic fungi without haustorial cells, and septal pores without microbodies. The *Agaricostilbales* contains taxa with auricularioid basidia

(e.g. *Agaricostilbum*) and holobasidia (e.g. *Chionosphaera*), and also yeasts that form ballistosporic phragmobasidia in culture (e.g., *Kondoa*) (Aime et al. 2006, Bauer et al. 2006, Wang et al. 2015a, Wang et al. 2015b). There are currently



A, Phylogeny based on ITS and nuLSU sequences, representing the *Agaricostilbomycetes* (modified from Fig. 1 in Diederich et al. 2022). Branches in boldface indicate nodes supported both by Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . **B**, Phylogeny based on ITS and nuLSU sequences, modified from Fig. 2 in Diederich et al. (2022), and used to place only *Crittendenia* species. Branches in boldface indicate nodes supported both by Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . When nodes received support from only one of the two methods, Bayesian posterior probabilities values ≥ 0.95 are indicated over branches and ML-BS values ≥ 70 , below branches. Type specimens are indicated with '(T)'. Branch lengths are scaled to the expected number of substitutions per site. See Diederich et al. (2022) for more details.

six accepted families viz., *Agaricostilbaceae* (teleomorphic), *Chionosphaeraceae* (teleomorphic), *Crittendeniaceae* (teleomorphic, lichenicolous fungi), *Jianyuniaceae* (yeasts), *Kondoaceae* (yeasts) and *Ruineniaceae* (yeasts forming salmon-orange to red colonies, which are a unique feature in the *Agaricostilbomycetes*) (Wang et al. 2015b; Li et al. 2020, Diederich et al. 2022).

The lichenicolous taxa in the group were at first only tentatively assigned to the genus *Chionosphaera* by Diederich (1996). Posterior molecular studies revealed that the lichenicolous ‘*Chionosphaera*’ species formed a distinct clade outside the *Chionosphaeraceae* and therefore the new genus *Crittendenia* was described to accommodate the lichen-inhabiting taxa in the *Agaricostilbales* (Millanes et al. 2021). Diederich et al.

(2022) later achieved a thorough taxonomic revision of the group, describing sixteen new species in *Crittendenia*. They also confirmed the monophyly of the genus – and that it could not be included in any of the existing families in the *Agaricostilbomycetes* – and proposed the new family *Crittendeniaceae* (see phylogenetic tree A). *Crittendenia* currently includes 18 species of lichenicolous fungi with minuscule needle-like synnematos basidiomata. All species are confined to a single host genus or to several closely related host genera. Published molecular phylogenies (Diederich et al. 2022) include 14 of these species, and species delimitation methods suggested that 2 of them (viz., *C. physciophila* and *C. lichenicola*) could represent species complexes deserving further studies (see phylogenetic tree B).

Key to the lichenicolous species of *Agaricostilbales*

The identification of *Crittendenia* specimens without molecular data may be difficult, and the assumed host-specificity should be used in case of specimens with deviant morphological characters.

For the microscopical study, we recommend a preparation of a mature basidioma, without pressure on the cover glass, allowing the observation of free-swimming groups of basidiospores originating from one basidium, to identify the number of spores per basidium. Subsequent pressure on the cover glass and removal of excessive liquid with tissue paper will allow the measurement of a larger number of spores. Additional pressure on the cover glass with lateral movement will separate basidia and may allow, in mature specimens, to observe and measure entire basidia. Staining of microscopical preparations is recommended, e.g., in a mixture of phloxine B and 5% KOH.

The following abbreviations are used in the key: StH (stipe height, including capitulum), StD (stipe diameter), CaD (capitulum diameter), these three measured under a binocular microscope, BaL (basidial length), SpL (spore length), SpB (spore breadth) and Q (ratio SpL/SpB).

Measurements from a specimen are given as $x\text{-}sd - x\text{+}sd$, where x represents the mean and sd the standard deviation. This represents the 69% probability interval, thus excluding the smallest and the largest 15.5%. Measurements from a species are given as $[\min x\text{-}sd]x\text{-}sd - x\text{+}sd[\max x\text{+}sd]$, where ‘ $\min x\text{-}sd$ ’ represents the smallest ‘ $x\text{-}sd$ ’ value obtained within the specimens examined and ‘ $\max x\text{+}sd$ ’ the largest ‘ $x\text{+}sd$ ’ value obtained within these specimens. E. g., if the basidial length from three specimens is 30–60 μm , 40–50 μm and 40–70 μm , and that of the species (including the three specimens) is 35–60 μm , then the resulting measurements will be given as [30]35–60[70] μm . Values between square brackets are omitted when a species is known from a single specimen.

- 1 Basidia (5)7–8-sterigmate; basidiospores, when liberated from the basidia, typically remaining together and arranged in form of a hexagon or heptagon with an additional central spore, recalling a daisy flower when observed from above, relatively small, < 6.8[8.5] μm long; basidiomata slender, StD < 49[80] μm , StH/StD > 3.1[2.3]
 - 2 Basidia [16]16–23[25] μm long; basidiospores [3.5]4.1–5.5[5.7] \times [2.2]2.3–3.3[3.6] μm ; basidiomata [127]140–244[296] μm tall; stipe [17]17–35[36] μm diam.; capitulum [31]33–76[97] μm diam.; on *Byssoloma kakouettae* ***Crittendenia kakouettae*** (293)
[if on *Fellhanera* species ***Crittendenia* aff. *kakouettae***]
 - 2’ Basidia longer, BaL > 21 μm ; stipe and capitulum often wider
 - 3 Basidiomata slender, StD [15]16–27[27] μm , StH/StD = [4.5]4.6–8.2[8.4]; basidiospores [4.9]5.0–6.9[7.0] \times [2.7]2.7–3.7[3.8] μm ; on *Micareia* gr. *prasina* ***Crittendenia lichenicola*** (296)
 - 3’ Basidiomata more robust, StD frequently > 27 μm , StH/StD in some species smaller; basidiospores in some species shorter
 - 4 Basidiospores [4.1]4.9–8.0[8.5] \times [2.4]2.6–3.9[4.2] μm , Q = [1.2]1.4–2.8[3.3]; on *Bacidia absistens* ***Crittendenia absistentis*** (286)
 - 4’ Basidiospores smaller, SpL mostly < 6.3 μm , Q usually < 1.7

- 5 Basidiospores relatively narrow, $[3.7]3.7\text{--}5.2[5.9] \times [2.1]2.3\text{--}3.2[3.4] \mu\text{m}$; $Q = [1.3]1.3\text{--}2.0[2.3]$; on corticolous *Bacidia* ***Crittendenia parvispora*** (297)
- 5' Basidiospores broadly ellipsoid, SpB mostly $> 3.0 \mu\text{m}$; $Q < 1.8$
- 6 Basidiospores subspherical to broadly ellipsoid, SpL $[3.5]3.6\text{--}4.8[5.1] \mu\text{m}$, $Q = [1.0]1.1\text{--}1.4[1.4]$; capitulum relatively broad, compared to stipe height, $\text{CaD/StH} = [0.4]0.4\text{--}1.1[1.3]$; basidia $31\text{--}42 \mu\text{m}$ long; on *Teloschistes* ***Crittendenia teloschistis*** (301)
- 6' Basidiospores broadly ellipsoid, SpP/SpB frequently > 1.3 ; capitulum relatively narrow, compared to stipe height, $\text{CaD/StH} < 0.8$
- 7 Basidiospores relatively short, $4.0\text{--}5.1 \times 3.0\text{--}3.9 \mu\text{m}$; basidia relatively short, $24\text{--}39 \mu\text{m}$ long; on *Bryostigma muscigenum*..... ***Crittendenia bryostigmatis*** (288)
- 7' Basidiospores frequently over $5 \mu\text{m}$ in length, $[4.1]4.2\text{--}6.3[7.2] \times [3.0]3.1\text{--}4.2[4.2] \mu\text{m}$; basidia frequently longer, $[29]30\text{--}50[59] \mu\text{m}$ long; on *Lopadium disciforme*..... ***Crittendenia lopadii*** (296)
- 1' Basidia (1)3–4-sterigmate (on *Lecidella* up to 6-sterigmate); basidiospores often larger, never arranged in form of a daisy flower with a central spore; basidiomatal stipe in most species thicker
- 2 Basidia $< 31 \mu\text{m}$ long
- 3 Basidiomata very small and slender, StH $69\text{--}116 \mu\text{m}$, StD $16\text{--}27 \mu\text{m}$, CaD $24\text{--}54 \mu\text{m}$; basidia very short; basidiospores $4.0\text{--}6.3 \times 2.2\text{--}2.9 \mu\text{m}$, $Q = [1.2]1.4\text{--}2.8[3.3]$; on *Bacidina apiatica*..... ***Crittendenia bacidinae*** (287)
- 3' Basidiomata taller and more robust, with a broader capitulum, StH $112\text{--}165 \mu\text{m}$, StD $23\text{--}43 \mu\text{m}$, CaD $59\text{--}96 \mu\text{m}$; basidiospores shorter, $3.8\text{--}5.0 \times 2.4\text{--}3.0 \mu\text{m}$, $Q = [1.2]1.3\text{--}1.9[2.4]$; on *Byssoloma maderense* ***Crittendenia byssolomatis*** (289)
- 2' Basidia $> 29 \mu\text{m}$ long
- 3 Basidiospores relatively long and narrow, $Q > 1.6$; on *Parmeliaceae*
- 4 Basidiomata very short and broad, StH c. $70\text{--}200 \mu\text{m}$, StD c. $50\text{--}200 \mu\text{m}$; basidiospores $8.4\text{--}9.7 \times 4.0\text{--}5.4 \mu\text{m}$, $Q = (1.5)1.7\text{--}2.3(2.4)$; on *Parmelina quercina* ***Crittendenia sp. 1*** (302)
- 4' Basidiomata more slender, $\text{StH/StD} > 1.3$
- 5 Basidia very long, BaL $[47]66\text{--}99[109] \mu\text{m}$; basidiomatal stipe relatively thick, $\text{StH/StD} = [0.7]1.3\text{--}3.2[4.4]$; capitulum only slightly wider than the stipe, $\text{CaD/StD} = [0.8]1.0\text{--}1.6[2.0]$; StH $[79]85\text{--}163[233] \mu\text{m}$, StD $[36]37\text{--}87[139] \mu\text{m}$, CaD $[42]48\text{--}105[146] \mu\text{m}$; basidiospores mostly with an evenly thickened wall, $[6.2]7.0\text{--}9.5[10.5] \times [3.1]3.3\text{--}4.3[4.7] \mu\text{m}$, $Q = [1.7]1.9\text{--}2.5[2.7]$; on *Melanelixia* and *Melanohalea* ***Crittendenia coppinsii*** (289)
- 5' Basidia shorter, BaL $< 53 \mu\text{m}$; basidiomata more slender, $\text{StH/StD} > 3.2$; capitulum at maturity often much wider than the stipe, $\text{CaD/StD} > 1.5$; basidiospores often with an unevenly thickened wall
- 6 Basidiospores very large, $8.6\text{--}13.1 \times 3.5\text{--}4.7 \mu\text{m}$, $Q = 2.1\text{--}3.3$; basidiomata very large, StH $218\text{--}353 \mu\text{m}$, StD $37\text{--}63 \mu\text{m}$, CaD $69\text{--}157 \mu\text{m}$; basidia $39\text{--}53 \mu\text{m}$ long; on *Melanohalea ushuaiensis* ***Crittendenia crassitunicata*** (290)
- 6' Basidiospores smaller, $[5.5]5.7\text{--}9.4[9.8] \times [2.9]3.0\text{--}4.3[4.5] \mu\text{m}$, $Q = [1.5]1.6\text{--}2.7[2.8]$; basidiomata smaller, StH $[110]116\text{--}232[237] \mu\text{m}$, StD $[17]24\text{--}55[68] \mu\text{m}$, CaD $[52]58\text{--}127[137] \mu\text{m}$; basidia shorter, $[26]29\text{--}43[46] \mu\text{m}$ long; on *Hypotrachyna* ***Crittendenia hypotrachynae*** (292)
- 3' Basidiospores ratio Q mostly < 1.8 (on *Lecidella* exceptionally longer); on other hosts
- 4 Basidiomata reduced to a very large capitulum, $147\text{--}390 \mu\text{m}$ diam.; stipe reduced, not visible macroscopically; basidiospores $5.8\text{--}8.0 \times 4.7\text{--}6.1 \mu\text{m}$; on *Physconia* ***Crittendenia physconiae*** (299)
- 4' Stipe present, but sometimes short, always visible; capitulum rarely $> 180 \mu\text{m}$ diam.
- 5 Basidiomata arising singly, rarely agglomerated, not over galls or conspicuous differently coloured own thalli; on *Physciaceae*

- 6 Basidiomata short and broad, StH [47]75–157[198] µm, StD [33]51–153[191] µm, StH/StD = [0.5]0.7–2.0[3.4]; capitulum often poorly developed, CaD/StD = [0.6]0.9–1.4[1.7]; basidiospores [4.8]5.2–7.0[7.6] × [3.0]3.5–4.9[5.6] µm; on *Phaeophyscia*, *Physcia* and *Physciella* *Crittendenia physciophila* (298)
- 6' Basidiomata long and slender, StH 171–280 µm, StD 21–43 µm, StH/StD = 5.1–10.1; capitulum well developed, often very broad, CaD/StD = 2.0–3.6; basidiospores narrower, 4.7–6.5 × 3.0–4.1 µm; on *Heterodermia comosa* *Crittendenia heterodermiae* (291)
- 5' Basidiomata often grouped, over galls or brownish to olivaceous own thalli; on other hosts
 - 6 Basidiomata developing over strongly convex galls that are often paler than the host thallus; basidiomata with a relatively large capitulum, CaD 61–172 µm, CaD/StH = 0.4–1.1; basidiospores relatively broad, 4.7–7.1 × 3.8–5.4 µm; on *Sticta* *Crittendenia stictae* (300)
 - 6' Basidiomata not over galls, frequently over slightly convex, gelatinous and translucent, brownish to olivaceous thalli that may contain algal cells; capitulum often smaller; basidiospores often narrower
 - 7 Basidiomatal stipe becoming relatively thick when mature, StD [26]22–102[175] µm, StH/StD = [0.6]1.2–5.3[7.8]; capitulum relatively large, CaD [26]39–125[201] µm, CaD/StH = [0.1]0.2–1.2[1.9]; basidiospores [3.4]4.2–6.8[8.0] × [2.5]3.1 × 4.9[5.7] µm, Q = [0.9]1.1–1.7[2.6]; on *Lecidella elaeochroma* *Crittendenia lecidellae* (295)
 - 7' Basidiomata more slender, StD [21]22–43[44] µm, StH/StD = [3.0]2.8–7.5[10.9]; capitulum smaller, CaD [32]32–79[108] µm, CaD/StH = [0.2]0.3–0.5[0.5]; basidiospores [5.1]5.4–6.9[6.9] × [3.0]3.3–4.5[4.6] µm, Q = [1.4]1.4–1.8[2.1]; on *Lecanora* *Crittendenia lecanorae* (294)

AGARICOSTILBOMYCETES R. Bauer, Begerow,
J. P. Samp., M. Weiß & Oberw.

Mycological Progress 5: 45 (2006). *Type*: *Agaricostilbum* J. E. Wright

AGARICOSTILBALES Oberw. & R. Bauer

Sydowia 41: 240 (1989). *Type*: *Agaricostilbum* J. E. Wright

Crittendeniaceae Millanes, Diederich & Wedin

in Diederich et al., *Bryologist* 125: 260 (2022). *Type*: *Crittendenia*
Diederich, Millanes, M. Westb., Etayo, J. C. Zamora & Wedin

CRITTENDENIA Diederich, Millanes, M. Westb.,
Etayo, J. C. Zamora & Wedin

in Millanes et al., *Lichenologist* 53: 111 (2021). *Type*: *Crittendenia*
coppinsii (P. Roberts) Diederich, M. Westb., Millanes & Wedin

Molecular data: yes (T, L). *Number of species*: 18[1]–0–0.

Own thallus often present, either reduced or spreading over the host thallus, flat or swollen to subspherical, hyaline to brownish, strongly gelatinous, translucent. *Basidiomata* stipitate-capitate, synnemata-like, fleshy waxy, whitish, pale brownish, pinkish, or orangish, slightly translucent; capitulum slightly to strongly differentiated and enlarged. *Stipe* composed of subparallel, rarely branched hyphae with few septa; primary septa thick, with clamps, sec-

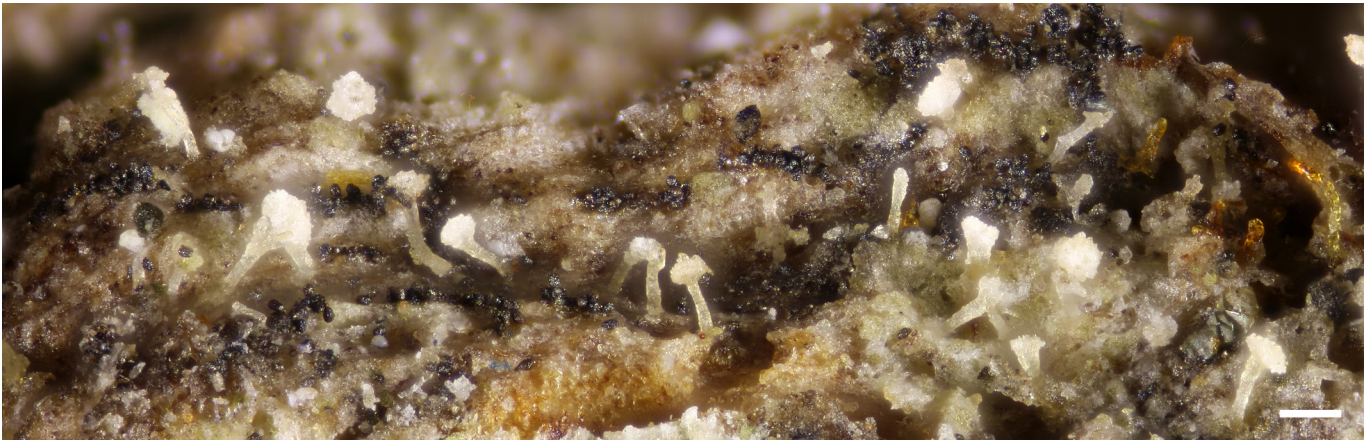
ondary septa thin, without clamps; these hyphae apically giving rise to one or several basidia; haustorial branches unknown. *Hymenium* amphigenous, entirely composed of basidia, without sterile elements or rarely with abnormal basidia-like elements of unknown function, not surrounded by an excipular layer. *Basidia* apical, tubular, with the largest diameter close to the apex, aseptate, thin- or rarely thick-walled, usually with basal clamps that may proliferate to produce further basidia, when immature apically rounded, when mature with (1–)4–8 apical, short, inconspicuous, sterigmata collapsing after spore detachment. *Basidiospores* hyaline, aseptate, shortly to elongate ellipsoid or fusiform, without a distinct basal apiculus, not forcibly discharged, often liberating together as a cluster of 3–8 spores, wall usually smooth and relatively thin, sometimes becoming thicker and rough, developing into a loose perispore sac that eventually detaches, leaving a smaller, smooth-walled spore. *Asexual stage* unknown.

Ecology. Lichenicolous, associated to a large variety of lichens belonging to different phylogenetic lineages.

Crittendenia absistentis Diederich, Coppins & Millanes

in Diederich et al., *Bryologist* 125: 262 (2022). *Type*: UK, Scotland, VC 103, Mid Ebudes, Ulva, 0.5 km S of Aird Glass, 60 m, on *Corylus*, on *Bacidia absistens*, 10 May 2017, B. J. Coppins 25367 (E – holotype).

Basidiomata dispersed, [108]121–209[234] µm tall, stipe relatively long and slender, pale brown, [21]21–35[40] µm diam.,



Crittendenia absistentis, UK, Scotland, Coppins 19800. Basidiomata on the thallus of *Bacidia absistens*. Scale bar: 100 μ m.



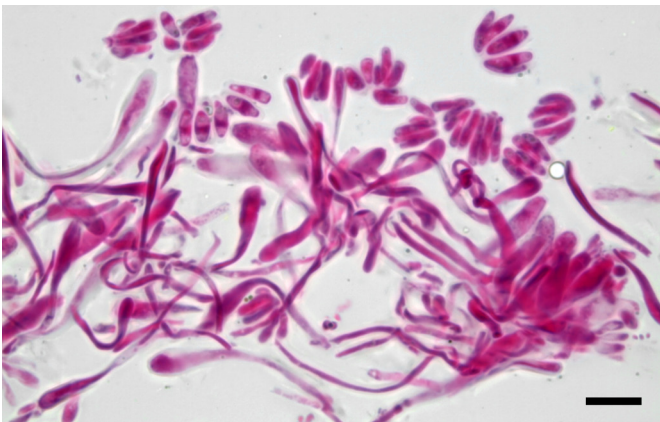
Crittendenia absistentis

capitulum whitish, [41]49–90[98] μ m diam. Own thallus reduced. Basidia 5–8-sterigmate, [28]30–44[49] μ m long. Basidiospores often elongate ellipsoid, occasionally mixed with broadly ellipsoid basidiospores within the same basidioma, thin- to irregularly thick-walled, smooth, [4.1]4.9–8.0[8.5] \times [2.4]2.6–3.9[4.2] μ m, $Q = [1.2]1.4–2.8[3.3]$.

Ecology and host. On the corticolous thallus of *Bacidia absistens*.

Distribution. Europe (UK: Scotland), known from three localities.

Reference. Diederich et al. 2022.



Crittendenia absistentis, UK, Scotland, holotype. Basidia and basidiospores, in phloxine. Scale bar: 10 μ m.

Crittendenia bacidinae Diederich, van den Boom & Millanes

in Diederich et al., *Bryologist* 125: 263 (2022). **Type:** Portugal, Azores, Pico, S of São Roque, secondary road on mountain range, in direction of Arrife, 38°26.95'N, 28°18.36'W, 555 m, on leaf of *Laurus*, on *Bacidina apiahica*, 31 Aug. 2017, P. & B. van den Boom 56783 (BR – holotype).

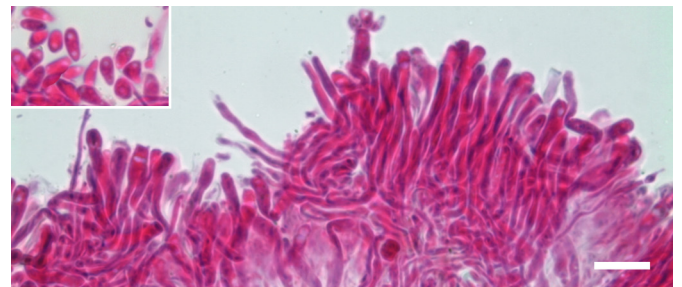
Basidiomata dispersed or in small groups, 69–116 μ m tall, stipe relatively short and very slender, pale brown, 16–27 μ m diam., capitulum whitish, 24–54 μ m diam. Own thallus reduced, hyaline to brownish, gelatinous, subspherical. Basidia 3–4-sterigmate, 19–25 μ m long. Basidiospores ellipsoid, relatively small, thin-walled, smooth, 4.0–6.3 \times 2.2–2.9 μ m, $Q = 1.5–2.6$.

Notes. This is the *Crittendenia* species with the smallest basidiomata, and possibly even the basidiomycete species with the smallest basidiomata known worldwide. The smallest mature basidioma measured by us was just 35 μ m tall, the stipe 17 μ m in diam., and the capitulum 20 μ m in diam.

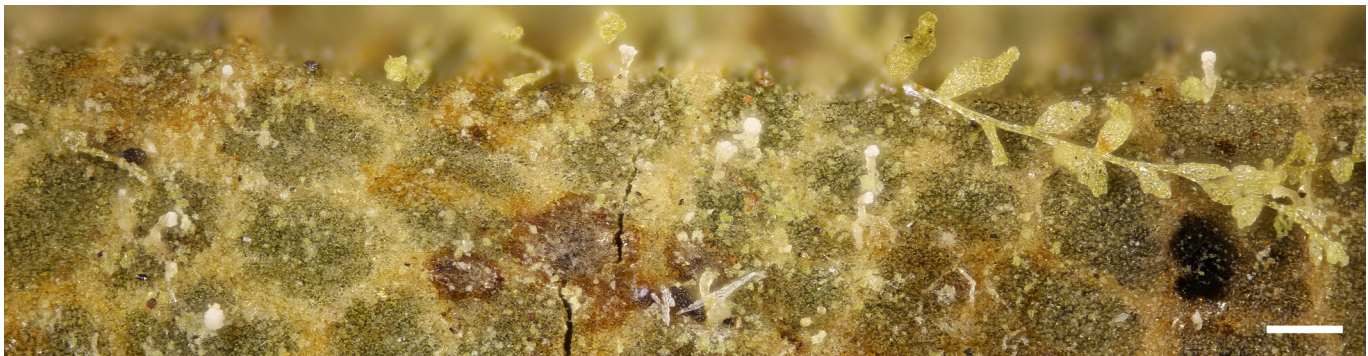
Ecology and host. On foliicolous *Bacidina apiahica*.

Distribution. Macaronesia (Azores: Pico), known only from the type locality.

Reference. Diederich et al. 2022.



Crittendenia bacidinae, Azores, holotype. Basidia and basidiospores, in phloxine. Scale bar: 10 μ m.



Crittendenia bacidinae, Azores, holotype. Basidiomata on the thallus of *Bacidina apiahica*. Scale bar: 200 μ m.



Crittendenia bacidinae

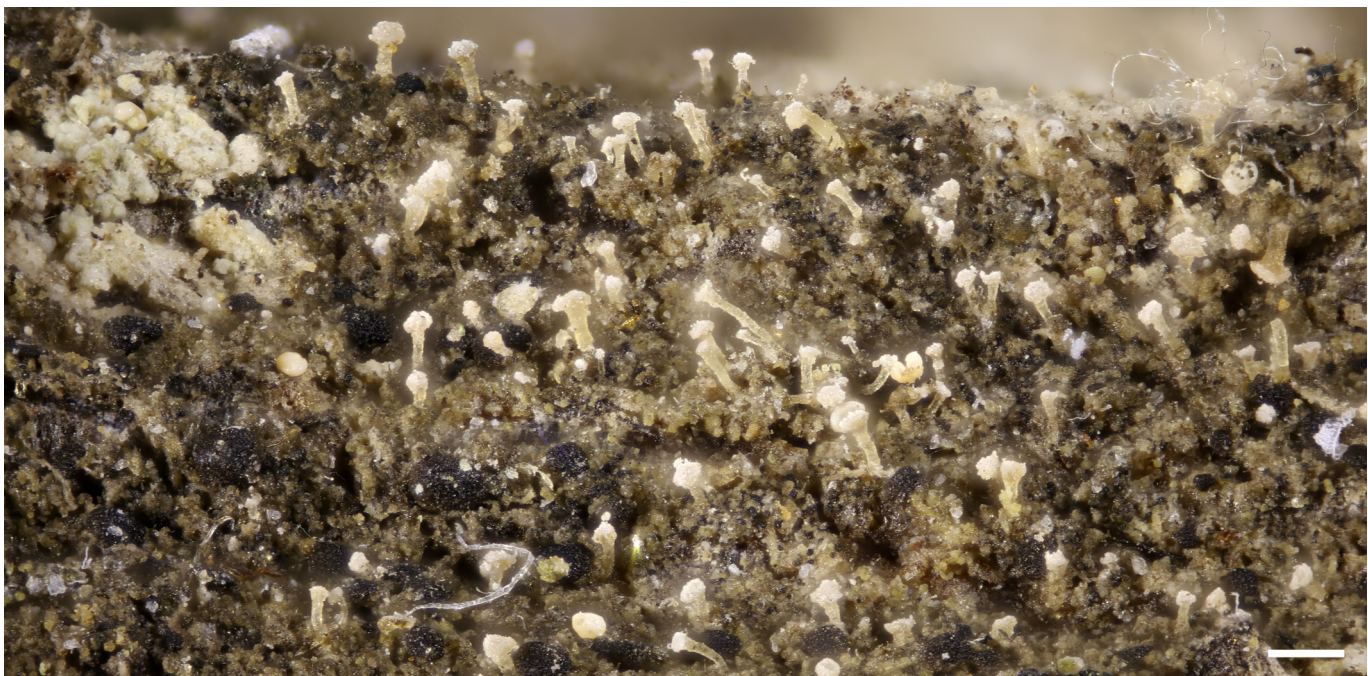
Basidiomata dispersed, 106–228 μ m tall, stipe relatively robust, pale brown, 24–47 μ m diam., capitulum much broader, whitish to pale brownish, 49–101 μ m diam. Own thallus indistinct. Basidia 7-sterigmate, 24–39 μ m long.



Crittendenia bryostigmatis, Canada, British Columbia, holotype. Basidia and basidiospores, in Melzer. Scale bar: 10 μ m.

***Crittendenia bryostigmatis* Diederich & Tønsberg**

in Diederich et al., *Bryologist* 125: 264 (2022). *Type*: Canada, British Columbia, Haida Gwaii (Queen Charlotte Islands), Graham Island, Queen Charlotte, 53°15.09'N, 132°07.24'W, 0–5 m, corticolous on twigs of *Salix* cf. *scouleriana* overhanging upper part of beach, on *Bryostigma muscigenum*, 22 July 2003, T. Tønsberg 32070 (BG – holotype).



Crittendenia bryostigmatis, Canada, British Columbia, holotype. Basidiomata on the thallus of *Bryostigma muscigenum*. Scale bar: 200 μ m.



Crittendenia bryostigmatis

Basidiospores broadly ellipsoid, thin-walled, smooth, $4.0\text{--}5.1 \times 3.0\text{--}3.9 \mu\text{m}$, $Q = 1.1\text{--}1.6$.

Notes. No sequences are yet available from this species.

Ecology and host. On the corticolous thallus of *Bryostigma muscigenum*.

Distribution. North America (Canada: British Columbia), known only from the type locality.

Reference. Diederich et al. 2022.

***Crittendenia byssolomatis* Diederich, van den Boom & Millanes**

in Diederich et al., *Bryologist* 125: 265 (2022). *Type:* Portugal, Azores, Graciosa, S of Ribeirinha, along road R1-2, W of Serra Branca, $39^{\circ}01.92'N$, $28^{\circ}02.22'W$, 285 m, on twigs of *Erica azorica*, on *Byssoloma maderense*, 15 Sept. 2021, P. & B. van den Boom 60700 (BR – holotype).

Basidiomata dispersed or in small groups, $112\text{--}165 \mu\text{m}$ tall, stipe pale brown, $23\text{--}43 \mu\text{m}$ diam., capitulum whitish, $59\text{--}96 \mu\text{m}$ diam. Own thallus reduced. Basidia 4-sterigmate, $19\text{--}31 \mu\text{m}$ long. Basidiospores ellipsoid, relatively small, thin-walled, smooth, $3.8\text{--}5.0 \times 2.4\text{--}3.0 \mu\text{m}$, $Q = 1.3\text{--}1.9$.

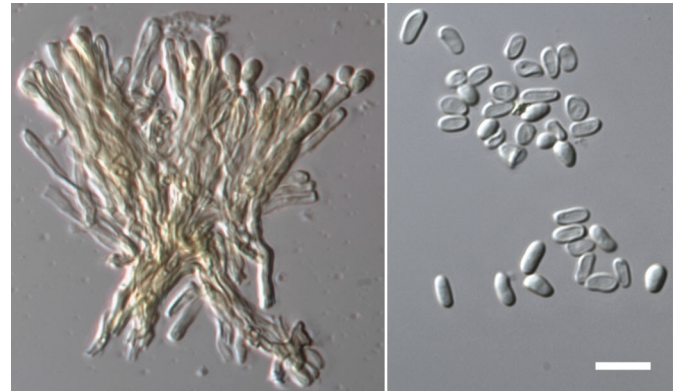
Ecology and host. On the thallus of *Byssoloma maderense* over twigs of *Erica azorica*.

Distribution. Macaronesia (Azores: Graciosa), known only from the type locality.

Reference. Diederich et al. 2022.



Crittendenia byssolomatis



Crittendenia byssolomatis, Azores, holotype. Basidia and basidiospores, in Melzer. Scale bar: $5 \mu\text{m}$.

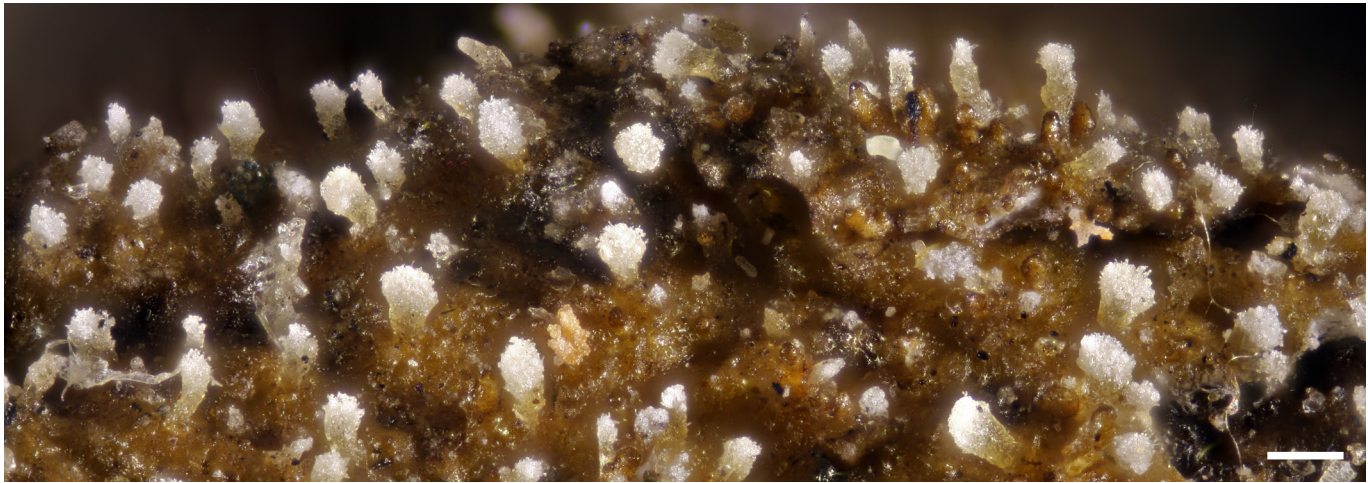
***Crittendenia coppinsii* (P. Roberts) Diederich, M. Westb., Millanes & Wedin**

in Millanes et al., *Lichenologist* 53: 113 (2021); *Chionosphaera coppinsii* P. Roberts, *Mycotaxon* 63: 195 (1997). *Type:* UK, Scotland, Wester Ross, Torridon, Inveralligan, wood & gorge of Abhainn Alligin, on *Melanelixia glabrata*, 21 June 1994, B. J. Coppins 16400 & A. M. O'Dare (E – holotype!; K 39188 – isotype!).

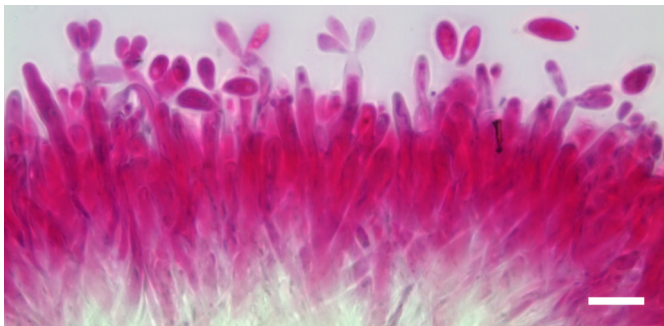
Basidiomata initially aggregated in small groups, later invading the entire host thallus, $[79]85\text{--}163[233] \mu\text{m}$ tall, stipe relatively robust, pale to medium brown, $[36]37\text{--}87[139] \mu\text{m}$ diam., capitulum whitish to pale brown or slightly pinkish, $[42]48\text{--}105[146] \mu\text{m}$ diam. Own thallus brownish, gelatinous, forming delimited patches or spread-



Crittendenia byssolomatis, Azores, holotype. Basidiomata on the thallus of *Byssoloma maderense*. Scale bar: $200 \mu\text{m}$.



Crittendenia coppinsii, Scotland, holotype. Basidiomata on the thallus of *Melanelixia glabratula*. Scale bar: 200 µm.



Crittendenia coppinsii, Norway, Westberg s. n. (DNA: AM1045). Basidia and basidiospores, in phloxine. Scale bar: 10 µm.



Crittendenia coppinsii

ing over large areas of the host thallus. Basidia (1–)4-sterigmate, [47]66–99[109] µm long. Basidiospores ellipsoid to elongate ellipsoid, wall medium thick, smooth, [6.2]7.0–9.5[10.5] × [3.1]3.3–4.3[4.7] µm, $Q = [1.7]1.9–2.5[2.7]$.

Ecology and hosts. On the thallus of corticolous *Melanelixia glabratula*, *M. subaurifera*, *Melanohalea exasperata*, *M. exasperatula* and *M. olivacea*.

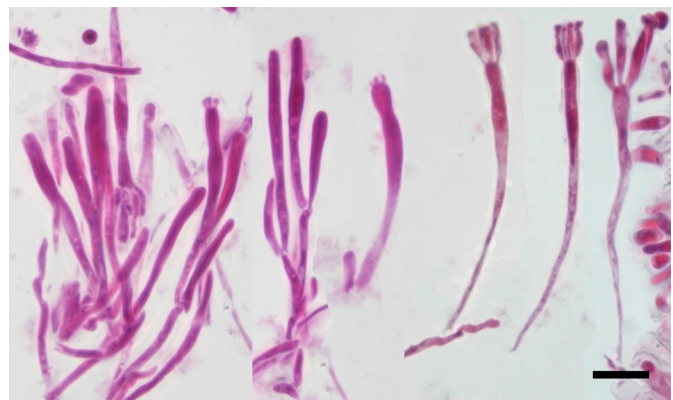
Distribution. Europe (Austria; Belgium; France; Norway; Russia; Spain; Sweden; Switzerland; **UK: Scotland**).

References. Diederich et al. 2022, Millanes et al. 2021, Roberts 1997 [Hitch 2009, Zimmermann & Feusi 2018 as *Chionosphaera* sp.].

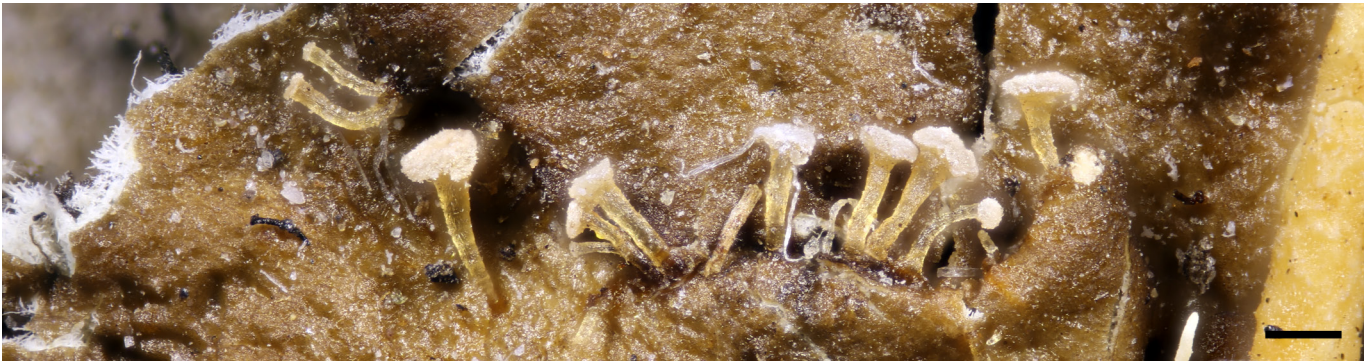
Crittendenia crassitunicata Diederich & Etayo

in Diederich et al., *Bryologist* 125: 269 (2022). **Type.** Argentina, Chubut, P. N. Los Alerces, on *Nothofagus*, on *Melanohalea ushuaiensis*, 4 Nov. 2006, J. Etayo 23715 (MAF – holotype).

Basidiomata in rather dense groups, 218–353 µm tall, stipe very long and robust, brown, 37–63 µm diam., capitulum whitish, 69–157 µm diam. Own thallus brownish, gelatinous, spreading over large areas of the host thallus. Basidia (3–)4-sterigmate, 39–53 µm long. Basidiospores elongate ellipsoid, very large, wall irregularly thickened, especially near the apices, initially smooth, later with a rough, enlarg-



Crittendenia crassitunicata, Argentina, holotype. Basidia with basidiospores, in phloxine. Scale bar: 10 µm.



Crittendenia crassitunicata, Argentina, holotype. Basidiomata on the thallus of *Melanohalea ushuaiensis*. Scale bar: 200 μm .



Crittendenia crassitunicata



Crittendenia heterodermiae

ing and eventually separating perispore sac, $8.6\text{--}13.1 \times 3.5\text{--}4.7 \mu\text{m}$, $Q = 2.1\text{--}3.3$.

Notes. This species is remarkable by the particularly large basidiomata, and by the large basidiospores having an irregularly thickened wall (cf. epithet), the lumen sometimes becoming almost rectangular. No sequences are yet available from this species.

Ecology and host. On the corticolous thallus of *Melanohalea ushuaiensis*.

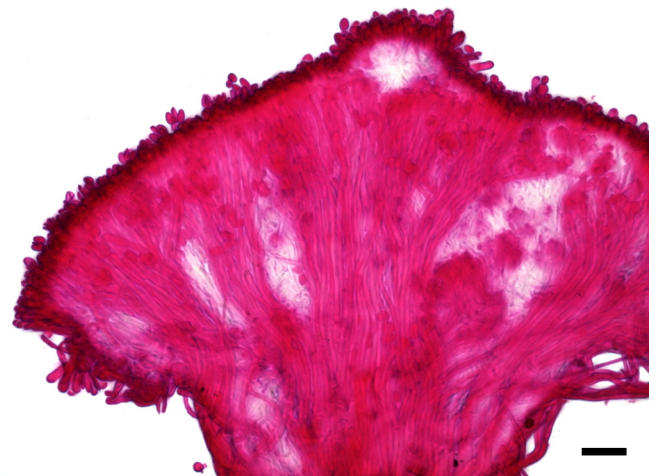
Distribution. South America (Argentina), known only from the type locality.

Reference. Diederich et al. 2022.

Crittendenia heterodermiae Diederich, Etayo & Millanes

in Diederich et al., *Bryologist* 125: 270 (2022). *Type:* Bolivia, Dept. Chuquisaca, Prov. Luis Calvo, P. N. y Á. N. M. I, Seranía de Iñao, close to Ticucha, Monteagudo, $19^{\circ}39'50''\text{S}$, $63^{\circ}49'14''\text{W}$, 1022 m, on thin branches, on *Heterodermia comosa*, 15 July 2015, J. Etayo 32711 (LPB – holotype).

Basidiomata dispersed, 171–280 μm tall, stipe relatively robust, whitish to pale brown, 21–43 μm diam., capitulum much broader, whitish to pale brown, 59–114 μm diam. Own thallus hyaline to brownish, gelatinous, spreading over small areas of the host thallus. Basidia 4-sterigmate,



Crittendenia heterodermiae, Bolivia, holotype. Squash preparation of basidioma, in phloxine. Scale bar: 20 μm .

57–74 μm long. Basidiospores ellipsoid, thin-walled, smooth, $4.7\text{--}6.5 \times 3.0\text{--}4.1 \mu\text{m}$, $Q = 1.4\text{--}2.8$.

Ecology and host. On the thallus of *Heterodermia comosa* on thin branches of a tree.

Distribution. South America (Bolivia), known only from the type locality.

Reference. Diederich et al. 2022.

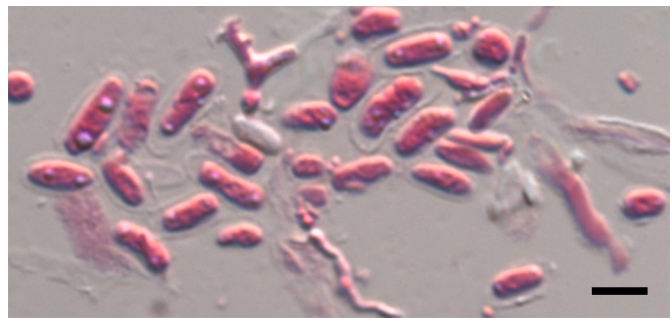


Crittendenia heterodermiae, Bolivia, holotype. Basidiomata on the thallus of *Heterodermia comosa*. Scale bar: 200 μ m.

Crittendenia hypotrachynae Diederich, Etayo, van den Boom & Millanes

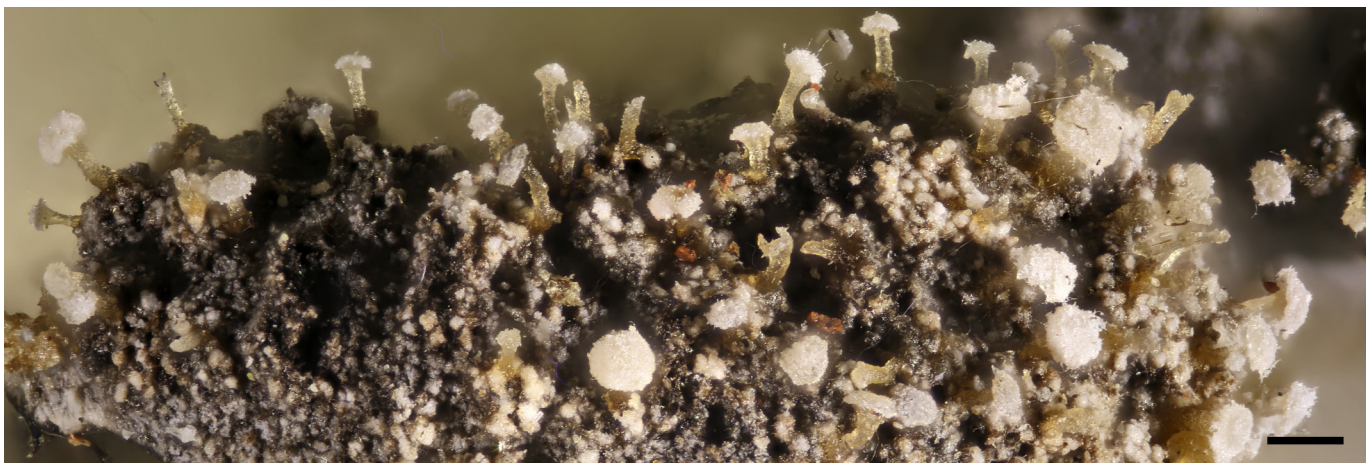
in Diederich et al., *Bryologist* 125: 271 (2022). *Type*. Portugal, Azores, Terceira, Camino de Algar do Carvao a Aqualva, 38°44'01"N, 27°12'35"W, 630 m, in laurisilva, on *Hypotrachyna endochlora*, 26 July 2017, J. Etayo 31093 (MAF – holotype).

Basidiomata dispersed over the host thallus or confined to host soralia, [110]116–232[237] μ m tall, stipe relatively robust, pale brown to orange brown, [17]24–55[68] μ m diam., capitulum frequently much broader, whitish, [52]58–127[137] μ m diam. Own thallus brownish, gelatinous, present around basidiomata or spreading over large areas of the host thallus. Basidia 3–4-sterigmate, [26]29–43[46] μ m long. Basidiospores elongate ellipsoid, relative-



Crittendenia hypotrachynae, Azores, holotype. Basidiospores, most surrounded by a perispore, in phloxine. Scale bar: 10 μ m.

ly long, wall often unevenly thickened, often with a perispore that may eventually detach, [5.5]5.7–9.4[9.8] \times [2.9]3.0–4.3[4.5] μ m, $Q = [1.5]1.6–2.7[2.8]$.



Crittendenia hypotrachynae, Azores, holotype. Basidiomata on the thallus of *Hypotrachyna endochlora*. Scale bar: 200 μ m.



Crittendenia hypotrachynae

Ecology and hosts. On the thallus of *Hypotrachyna endochlora*, *H. laevigata* and *H. sp.*, sometimes in necrosed parts of the host thallus or in soralia.

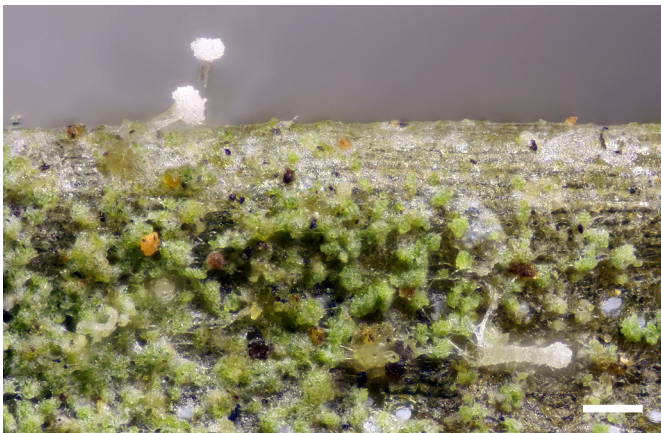
Distribution. Macaronesia (Azores: Terceira; Madeira).

References. Diederich et al. 2022 [Etayo 2018 as *Chionosphaera apobasidialis*].

***Crittendenia kakouettiae* Diederich, van den Boom & Millanes**

in Diederich et al., *Bryologist* 125: 273 (2022). **Type:** Portugal, Azores, Santa Maria, E of Almagreira, along road ER-1-2 to Santo Espírito, Reserva Florestal das Fontinhas, picnic area, 36°57.61'N, 25°04.40'W, 335 m, on needles of *Cryptomeria*, on *Byssoloma kakouettiae*, 16 Sept. 2019, P. van den Boom 58956 (BR – holotype).

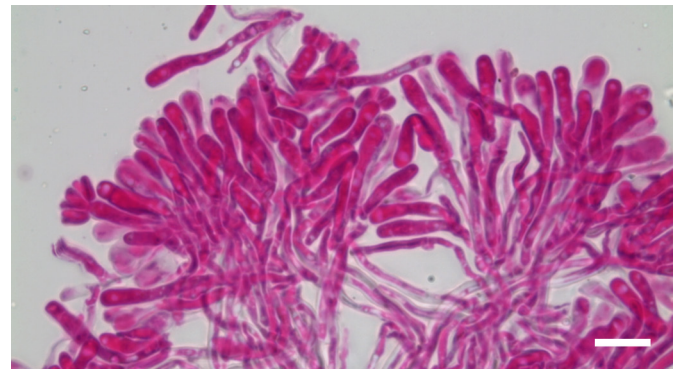
Basidiomata dispersed or in small groups, [127]140–244[296] µm tall, stipe very long and slender, pale brown, [18]20–33[42] µm diam., capitulum whitish, relatively broad, [31]33–76[97] µm diam. Own thallus reduced. Basidia 7–8-sterigmate, [16]16–23[25] µm long. Basidiospores ellipsoid, relatively small, thin-walled, smooth, [3.5]4.1–5.5[5.7] × [2.2]2.3–3.3[3.6] µm, Q = [1.3]1.4–2.1[2.2].



Crittendenia kakouettiae, Azores, holotype. Basidiomata on the thallus of *Byssoloma kakouettiae*. Scale bar: 100 µm.



Crittendenia kakouettiae, Azores, holotype. Entire basidioma with capitulum covered by basidiospores, in phloxine. Scale bar: 20 µm.



Crittendenia kakouettiae, Azores, holotype. Basidia with basidiospores, in phloxine. Scale bar: 10 µm.



Crittendenia kakouettiae, Azores, van den Boom 58880. Basidiomata on the thallus of *Byssoloma kakouettiae*. Scale bar: 100 µm.



Crittendenia kakouettae

Notes. Although this species has been collected several times on *Byssoloma kakouettae* and seems to be rather common on this host, all known specimens are reduced, with just a few basidiomata present.

Ecology and host. On the foliicolous thallus of *Byssoloma kakouettae*.

Distribution. Macaronesia (Azores: Santa Maria; Canary Islands: Tenerife; Madeira).

Reference. Diederich et al. 2022.

Crittendenia aff. *kakouettae*

Basidiomata dispersed or in small groups, [98]131–238[242] μm tall, stipe very long and slender, pale brown, [17]17–35[36] μm diam., capitulum whitish, relatively broad, [34]38–76[81] μm diam. Own thallus reduced. Basidia 7-sterigmate, [14]15–20[20] μm long. Basidiospores ellipsoid, relatively small, thin-walled, smooth, [4.1]4.1–5.5[5.7] \times [2.3]2.3–3.0[3.0] μm , $Q = [1.5]1.5–2.2[2.3]$.

Notes. While the host choice of populations on *Fellhanera* suggests a distinct species, both known specimens are mor-

phologically indistinguishable from *C. kakouettae*. As no sequences are yet available from them, we provisionally treat them as *C. aff. kakouettae*.

Ecology and host. On the foliicolous thallus of *Fellhanera azorica* and *F. bouteillei*.

Distribution. Macaronesia (Azores: Pico, Santa Maria).

Reference. Diederich et al. 2022.

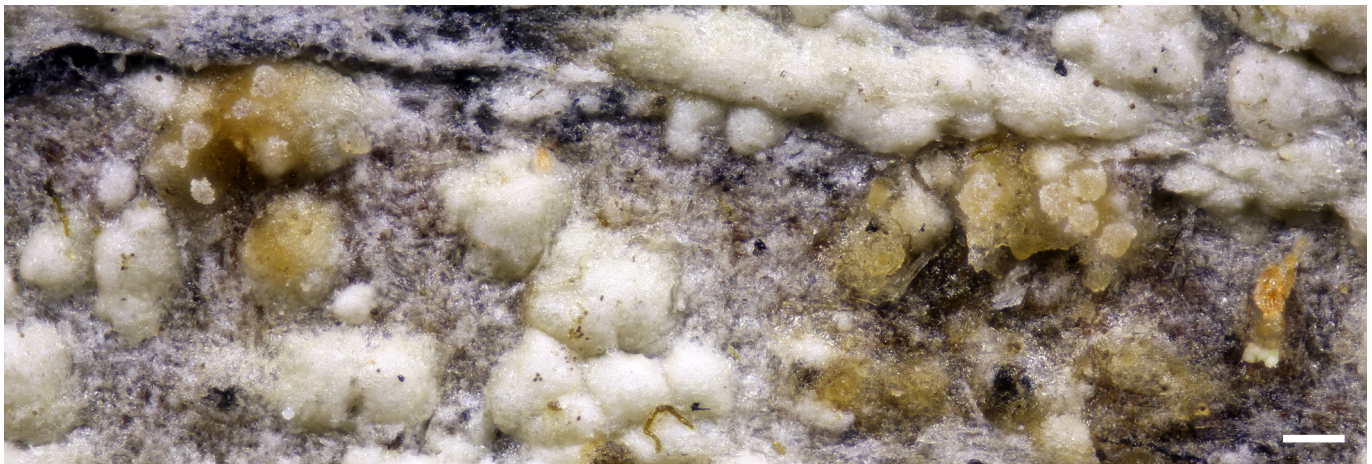
Crittendenia lecanorae Diederich & Etayo

in Diederich et al., *Bryologist* 125: 275 (2022). **Type:** Brazil, Alagoas, c. 35 km N of Maceió, 9°30'S, 35°32'W, 1 m, in a mangrove with *Rhizophora* mangle and *Avicennia*, on *Lecanora*, 1. Aug. 1993, K. & A. Kalb 27958 (WIS – holotype).

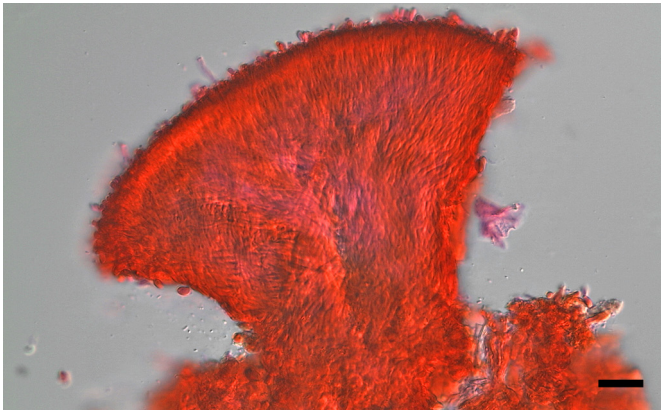
Basidiomata aggregated, [104]92–219[308] μm tall, stipe relatively slender, pale brown, [21]22–43[44] μm diam., capitulum whitish to brownish, [32]32–79[108] μm diam. Own thallus brownish, gelatinous, spreading over small areas of the host thallus. Basidia 3–4-sterigmate, 45–65 μm long. Basidiospores ellipsoid to broadly ellipsoid, wall me-



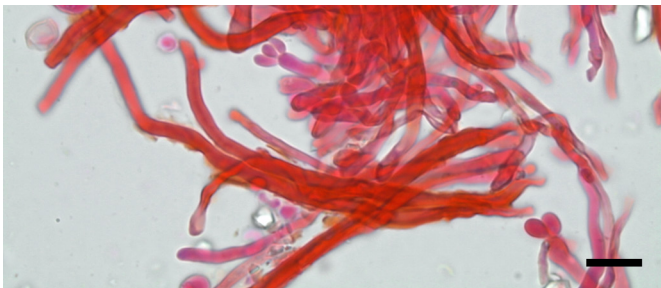
Crittendenia lecanorae



Crittendenia lecanorae, Brazil, holotype. Basidiomata emerging from brownish own thalli, on the thallus of a corticolous *Lecanora* species. Scale bar: 100 μm .



Crittendenia lecanorae, Brazil, holotype. Squash preparation of basidioma, in phloxine + Congo red. Scale bar: 20 µm.



Crittendenia lecanorae, Brazil, holotype. Squash preparation of hymenium, with basidia, basidiospores and stipe hyphae, in phloxine + Congo red. Scale bar: 10 µm.

dium thick, smooth, $[5.1]5.4-6.9[6.9] \times [3.0]3.3-4.5[4.6]$ µm, $Q = [1.4]1.4-1.8[2.1]$.

Notes. No sequences are yet available from this species.

Ecology and hosts. On the thallus of corticolous *Lecanora* species.

Distribution. South America (Argentina; [Brazil](#)).

References. Diederich et al. 2022 [Etayo & Breuss 1998 as *Chionosphaera* cf. *apobasidialis*].

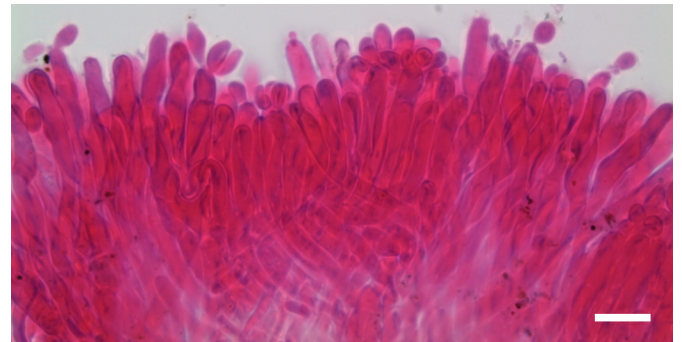
Crittendenia lecidellae Diederich, Etayo & Millanes

in Diederich et al., *Bryologist* 125: 276 (2022). *Type:* Canada, British Columbia, Bridge at Boston Bar, on *Acer macrophyllum*, on *Lecidella elaeochroma*, 7 May 2009, C. Björk 17999 (UBC – holotype).

Basidiomata dispersed or aggregated in small groups, $[67]88-212[295]$ µm tall, stipe extremely variable, from relatively slender to short and broad, pale brown, $[26]22-102[175]$ µm diam., capitulum whitish to pinkish, $[26]39-125[201]$ µm diam. Own thallus brownish to olivaceous, gelatinous, spreading over small or larger areas of the host thallus, frequently including algal cells and then representing simple lichen thalli. Basidia (1?–)4(–)6-sterigmate, $[31]40-71[88]$ µm long. Basidiospores ellipsoid to broadly ellipsoid, relatively thick-walled, smooth to rough, $[3.4]4.2-6.8[8.0] \times [2.5]3.1-4.9[5.7]$ µm, $Q = [0.9]1.1-1.7[2.6]$.

Notes. Some specimens examined possess a small thallus containing algal cells, which may be considered as an own lichenized thallus.

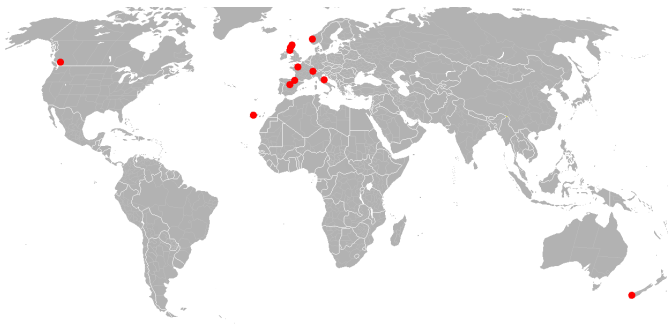
Ecology and host. On the corticolous thallus of *Lecidella elaeochroma*.



Crittendenia lecidellae, Canada, British Columbia, holotype. Hymenium with basidia and basidiospores, in phloxine. Scale bar: 10 µm.



Crittendenia lecidellae, Canada, British Columbia, holotype. Basidiomata on the thallus of *Lecidella elaeochroma*. Scale bar: 200 µm.



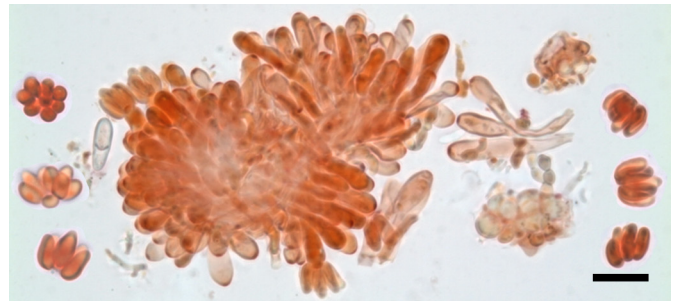
Crittendenia lecidellae

Distribution. Europe (France; Italy; Norway; Spain; Switzerland; UK: Scotland), Macaronesia (Canary Islands: La Gomera), North America (Canada: British Columbia) and Oceania (New Zealand).

References. Diederich et al. 2022, Etayo 1996 as *C. cf. apobasidialis* [Brackel 2015 as *Chionosphaera cf. apobasidialis*, Diederich 1996 as *C. cf. apobasidialis*, Kirschner et al. 2001 as *C. lichenicola*, Roberts 1997 as *C. coppinsii*].



Crittendenia lichenicola



Crittendenia lichenicola, Norway, holotype. Basidia and groups of basidiospores, in ammoniacal Congo red. Scale bar: 10 µm.

***Crittendenia lichenicola* (Alstrup, B. Sutton & Tønsberg)
Diederich, Millanes & Wedin**

in Millanes et al., *Lichenologist* 53: 113 (2021); *Chionosphaera lichenicola* Alstrup, B. Sutton & Tønsberg, *Graphis Scripta* 5: 97 (1993). **Type.** Norway, Hordaland, Fjell, Lokøy, the peninsula S of Storafjellet, alt. 10 m, on *Sorbus aucuparia*, on *Micarea prasina* s. lat., 27 Aug. 1989, T. Tønsberg 12000 (BG – holotype; C, IMI – isotypes).

Basidiomata dispersed, [93]96–165[166] µm tall, stipe long and slender, pale brown, [15]16–27[27] µm diam., capitulum whitish, [30]32–65[72] µm diam. Own thallus reduced. Basidia 5–8-sterigmate, [23]21–39[55] µm long. Basidiospores elongate ellipsoid, rather long, thin-walled, smooth, [4.9]5.0–6.9[7.0] × [2.7]2.7–3.7[3.8] µm, $Q = [1.4]1.5–2.4[2.4]$.

Ecology and hosts. On the thallus of *Micarea* gr. *prasina* (incl. *M. micrococca*).

Distribution. Europe (Norway; UK: Scotland).

References. Diederich 1996; Kirschner et al. 2001 [Aguirre-Hudson & Spooner 2005].

***Crittendenia lopadii* Diederich, Holien & Tønsberg**

in Diederich et al., *Bryologist* 125: 280 (2022). **Type:** USA, Alaska, Kodiak Island Borough, Kodiak Island E, along road to Anton Larsen Bay, bank of Red Cloud River, 57°49.0'N, 152°37.6'W, 20 m, on trunk of *Alnus*, on *Lopadium disciforme*, 15 May 1991, T. Tønsberg 15250 (BG L-69060 – holotype).

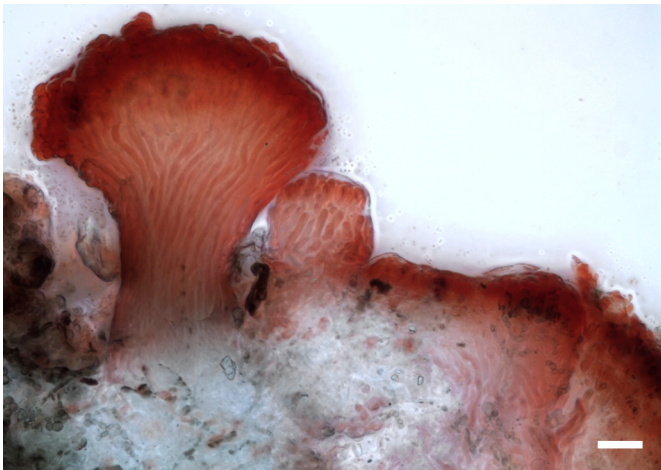
Basidiomata dispersed, [95]104–205[213] µm tall, stipe relatively slender, pale brown, [20]24–58[80] µm diam., capitulum whitish to brownish, [40]55–115[120] µm diam. Own thallus brownish, gelatinous, spreading over small areas around basidiomata, often swollen. Basidia 7-sterigmate, [29]30–50[59] µm long. Basidiospores ellipsoid to broadly ellipsoid, wall thin to thick, some with a distinct perispore sac, [4.1]4.2–6.3[7.2] × [3.0]3.1–4.2[4.2] µm, $Q = [1.1]1.1–1.8[2.1]$.



Crittendenia lichenicola, Norway, holotype. Basidiomata on the thallus of *Micarea prasina* s. lat. Scale bar: 200 µm.



Crittendenia lopadii, USA, Alaska, holotype. Basidiomata on the thallus of *Lopadium disciforme*. Scale bar: 200 µm.



Crittendenia lopadii, USA, Alaska, holotype. Young basidiomata developing from the thallus of *Lopadium disciforme*, in ammoniacal Congo red. Scale bar: 20 µm.

Notes. Most infected host thalli are sterile and reduced, making their identification difficult. No sequences are yet available from this species.

Ecology and host. On the thallus of *Lopadium disciforme*, on the bark of *Alnus* and on twigs of *Picea abies*.

Distribution. Europe (Norway) and North America (USA: Alaska).

Reference. Diederich et al. 2022.



Crittendenia lopadii

Crittendenia parvispora Diederich, van den Boom & Millanes

in Diederich et al., *Bryologist* 125: 281 (2022). *Type.* France, Finistère, Quimperlé, forêt de Toulfoën (= forêt de Carnoët), in a mixed forest with mainly *Fagus* and *Quercus*, on a thin branch of *Abies grandis*, on *Bacidia laurocerasi*, 13 April 2021, Y. Quelen s. n. (BR – holotype).

Basidiomata aggregated in small or larger groups, [108]120–193[198] µm tall, stipe slender to sometimes relatively robust, pale brown, [22]23–46[52] µm diam., capitulum pinkish white, much broader than the stipe, [31]38–116[150] µm diam. Own thallus brownish, gelatinous, developed around basidiomata. Basidia 7–8-sterigmate, [19]22–36[39] µm long. Basidiospores small, subspherical to broadly ellipsoid, thin-walled, smooth, [3.7]3.7–5.2[5.9] × [2.1]2.3–3.2[3.4] µm, Q = [1.3]1.3–2.0[2.3].

Notes. This is the *Crittendenia* species with the smallest basidiospores (cf. epithet).

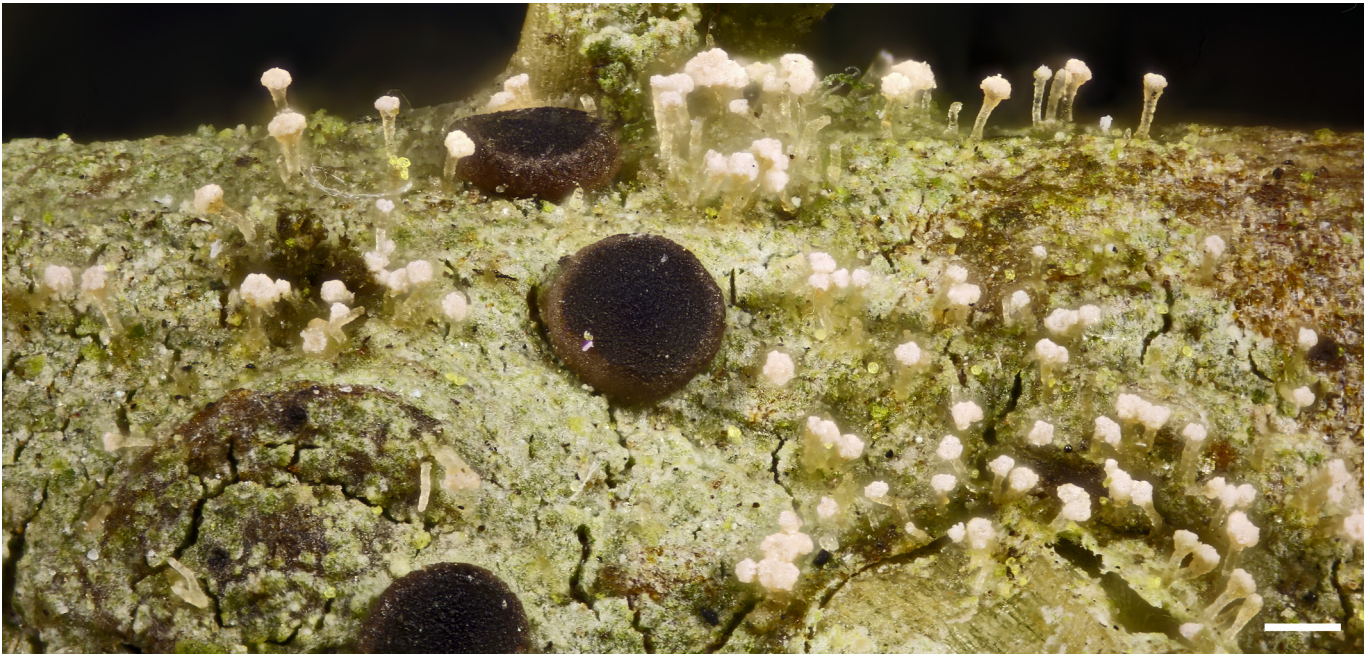
Ecology and hosts. On the thallus of corticolous *Bacidia* species, incl. *B. laurocerasi* and *B. polychroa*.

Distribution. Europe (France), Macaronesia (Cape Verde: São Vicente) and South America (Venezuela).

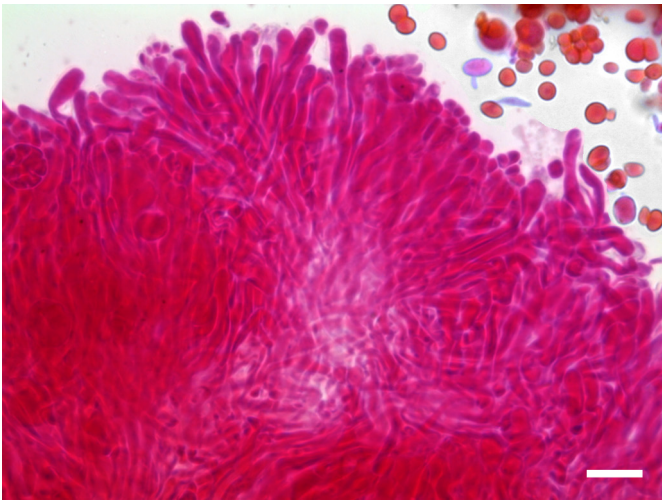
References. Diederich et al. 2022 [van den Boom 2012 as *Chionosphaera* cf. *apobasidialis*].



Crittendenia parvispora



Crittendenia parvispora, France, holotype. Basidiomata on the thallus of *Bacidia laurocerasi*. Scale bar: 200 µm.



Crittendenia parvispora, Venezuela, Kalb 26946. Hymenium with basidia and young basidiospores, in KOH + phloxine; top right: basidiospores, in phloxine + Congo red. Scale bar: 10 µm.

Crittendenia physciiphila Diederich, P. Pinault, Etayo & Millanes

in Diederich et al., *Bryologist* 125: 283 (2022). *Type*. France, Puy-de-Dôme, Châteaugay, 45.8504°N, 3.0855°E, 500 m, on *Physcia adscendens*, 26 March 2020, P. Pinault s.n. (BR – holotype and isotype).

Basidiomata dispersed or aggregated in small groups, [47]75–157[198] µm tall, stipe rarely slender to most often rather robust, relatively short, often irregular in form, pale to orange brown, often with a rough or irregular surface,

[33]51–153[191] µm diam., capitulum whitish to pinkish or orange brown, often not well developed and then narrower than the stipe, [31]54–185[243] µm diam. Own thallus brownish, gelatinous, reduced or immersed in the host thallus, or well developed and swollen. Basidia 3–4-sterigmate, [38]42–72[93] µm long. Basidiospores ellipsoid, wall thin or slightly thickened, smooth, [4.8]5.2–7.0[7.6] × [3.0]3.5–4.9[5.6] µm, $Q = [1.1]1.2–1.7[1.9]$.

Notes. Although this species has been collected on many different hosts from three closely related genera, most specimens are rather reduced, with often just a few basidiomata present on each host thallus. More molecular data are necessary to determine whether this is a species complex, comprising several species each being confined to a single host genus.

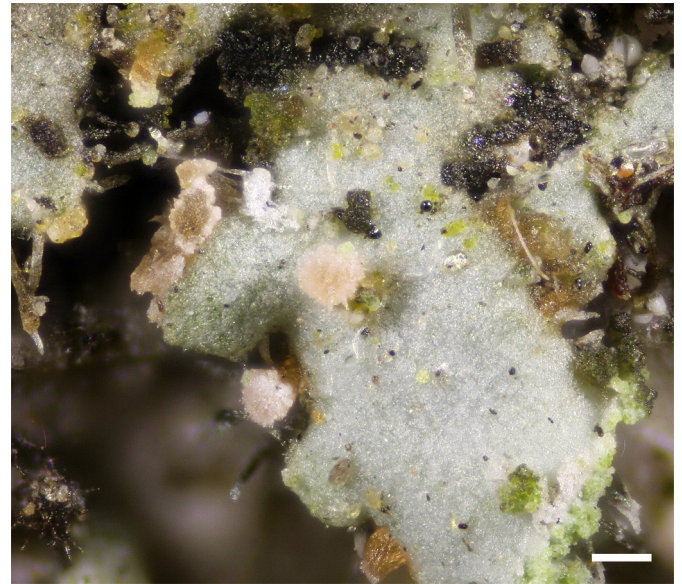
Ecology and hosts. On the thallus of corticolous or rarely foliicolous *Phaeophyscia orbicularis*, *P. rubropulchra*, *Physcia adscendens*, *P. leptalea*, *P. tenella* and *Physciella chloantha*.



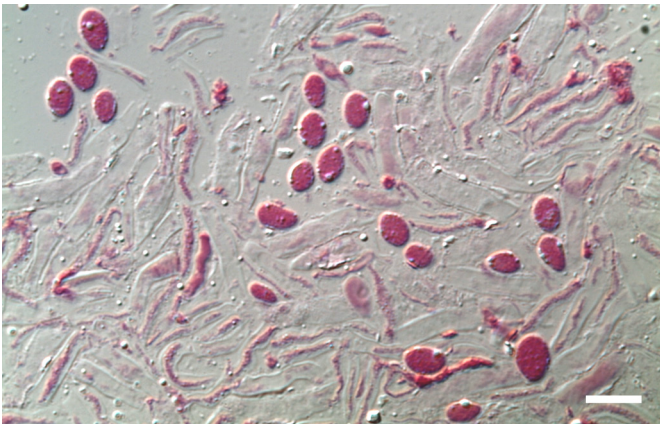
Crittendenia physciiphila



Crittendenia physciiphila, France, holotype. Basidiomata on the thallus of *Physcia adscendens*. Scale bar: 100 µm.



Crittendenia physciiphila, France, Pinault s. n. Basidiomata on the thallus of *Phaeophyscia orbicularis*. Scale bar: 100 µm.



Crittendenia physciiphila, France, holotype. Basidiospores, in phloxine. Scale bar: 10 µm.

Distribution. Europe ([France](#); Italy; Luxembourg; Spain) and North America (USA: Massachusetts).

References. Diederich et al. 2022 [Brackel 2015, Etayo 2004, 2009, van den Boom 2021, all four as *C. apobasidialis*, Roux 2020 as *C. cf. coppinsii*].

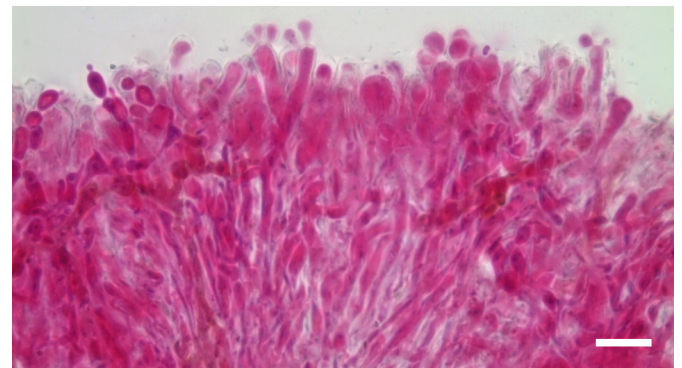
Crittendenia physconiae Diederich, Zamora & Millanes

in Diederich et al., *Bryologist* 125: 285 (2022). *Type*. Spain, Madrid, San Lorenzo de El Escorial, alrededores de la Silla de Felipe II, on *Crataegus monogyna*, on *Physconia distorta*, 3 June 2010, J. C. Zamora s. n. (G – holotype).

Basidiomata dispersed, 57–187 µm tall, stipe reduced, immersed, macroscopically not visible, capitulum pale pinkish brown, 147–390 µm diam. Own thallus indistinct. Basidia 1–3-sterigmate, 47–56 µm long. Basidiospores el-

lipsoïd, at the beginning surrounded by a thick perispore that becomes more and more loose and wrinkled, and eventually separates as a perisporeal sac, leaving a smooth- and thin-walled spore, $5.8\text{--}8.0 \times 4.7\text{--}6.1$ µm, $Q = 1.1\text{--}1.5$.

Notes. This species is remarkable by the completely reduced and macroscopically invisible stipe.



Crittendenia physconiae, Spain, holotype. Hymenium with basidia and basidiospores, in phloxine. Scale bar: 10 µm.



Crittendenia physconiae



Crittendenia physconiae, Spain, holotype. Basidiomata on the thallus of *Physconia distorta*. Photo: J. C. Zamora.

Ecology and host. On the thallus or apothecial margin of corticolous *Physconia distorta*.

Distribution. Europe (Spain), known only from the type locality.

Reference. Diederich et al. 2022.

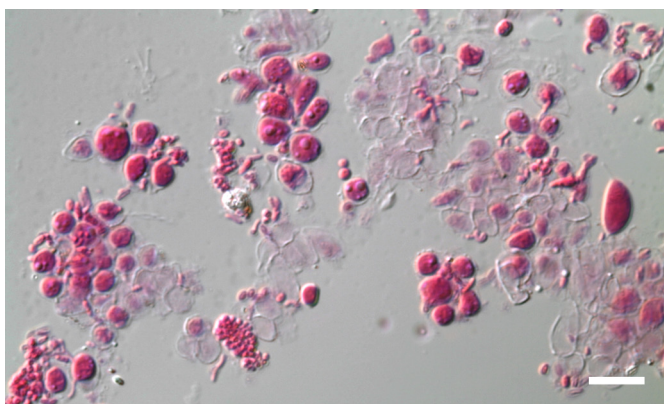
***Crittendenia stictae* Diederich, Etayo & Millanes**

in Diederich et al., *Bryologist* 125: 286 (2022). *Type*. Bolivia, Laguna Vizcachani, camino de La Paz a Zongo, 16°11'45"S, 68°07'33"W, 3675–3860 m, on *Sticta fuliginosa* s. lat. on bushes, 30 May 2011, J. Etayo 26611 (LPB – holotype, herb. Etayo – isotype).

Basidiomata densely covering galls on the host thallus, 118–191 μm tall, stipe relatively robust, pale brown,

39–74 μm diam., capitulum whitish to brownish, 61–172 μm diam. Own thallus brownish, gelatinous, abundantly developed and often thick around basidiomata, developing over large, superficial, subspherical, pale to medium brown, smooth galls, 0.2–1 mm diam. Basidia 3–4-sterigmate, c. 44–49 μm long. Basidiospores broadly ellipsoid, more rarely elongate ellipsoid, thick-walled, some with indistinct apical appendages, eventually with a perisporal sac, $4.7\text{--}7.1 \times 3.8\text{--}5.4 \mu\text{m}$, $Q = 1.1\text{--}1.5$.

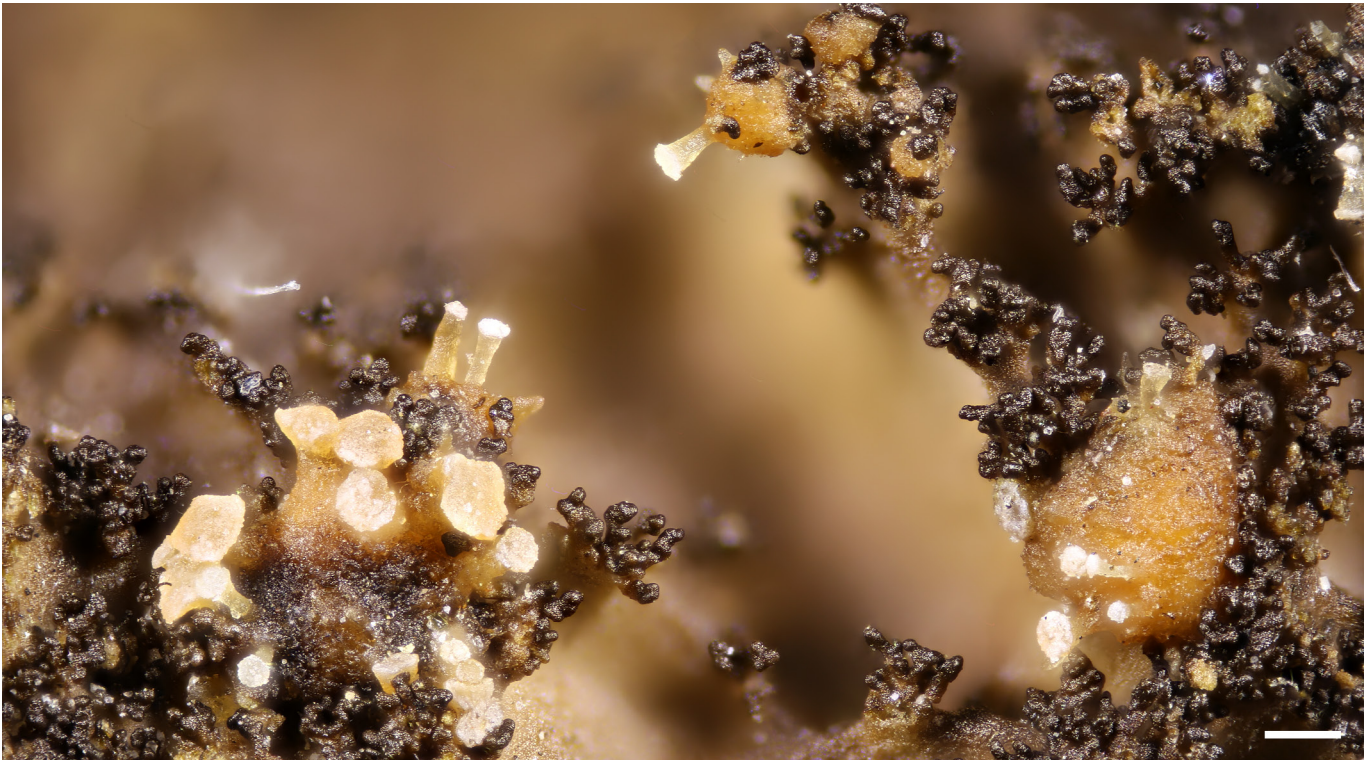
Notes. This is the only *Crittendenia* species known to develop over galls of the host. However, it is not certain whether these galls are induced by *Crittendenia*,



Crittendenia stictae, Bolivia, holotype. Basidiospores surrounded by a perisporal sac and empty perisporal sacs, in phloxine. Scale bar: 10 μm .



Crittendenia stictae



Crittendenia stictae, Bolivia, holotype. Basidiomata over galls on the thallus of *Sticta fuliginosa* s. lat. Scale bar: 200 µm.

or perhaps by another fungus devoid of fruiting bodies. Two reduced specimens from Bolivia and Ecuador on *Sticta* with deviant morphological characters were provisionally excluded from *C. stictae* by Diederich et al. (2022).

Ecology and host. On the thallus of *Sticta fuliginosa* s. lat.

Distribution. South America (Bolivia), known only from the type locality.

Reference. Diederich et al. 2022.

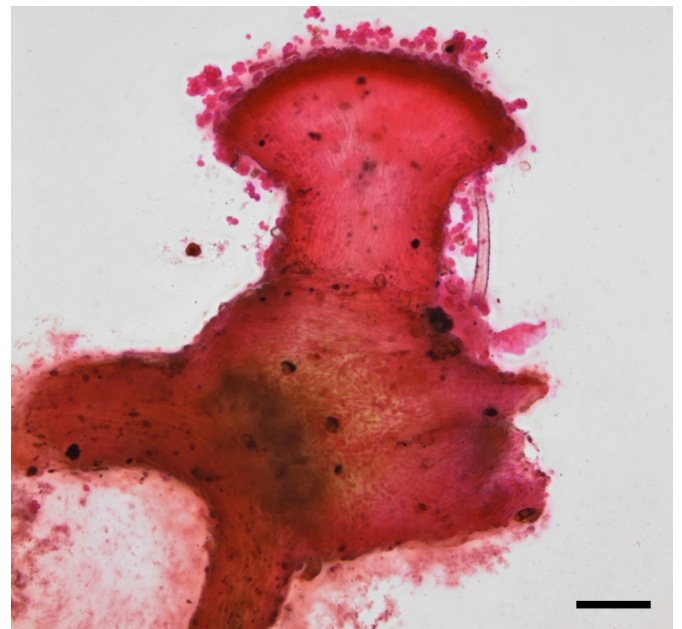
***Crittendenia teloschistis* Diederich, Etayo, F. Berger & Millanes**

in Diederich et al., *Bryologist* 125: 288 (2022). *Type:* Spain, Canary Islands, La Gomera, NP Garajonay, on *Teloschistes flavicans*, July 2012, M. Koller s. n. (BR [ex herb. Berger 26836] – holotype).

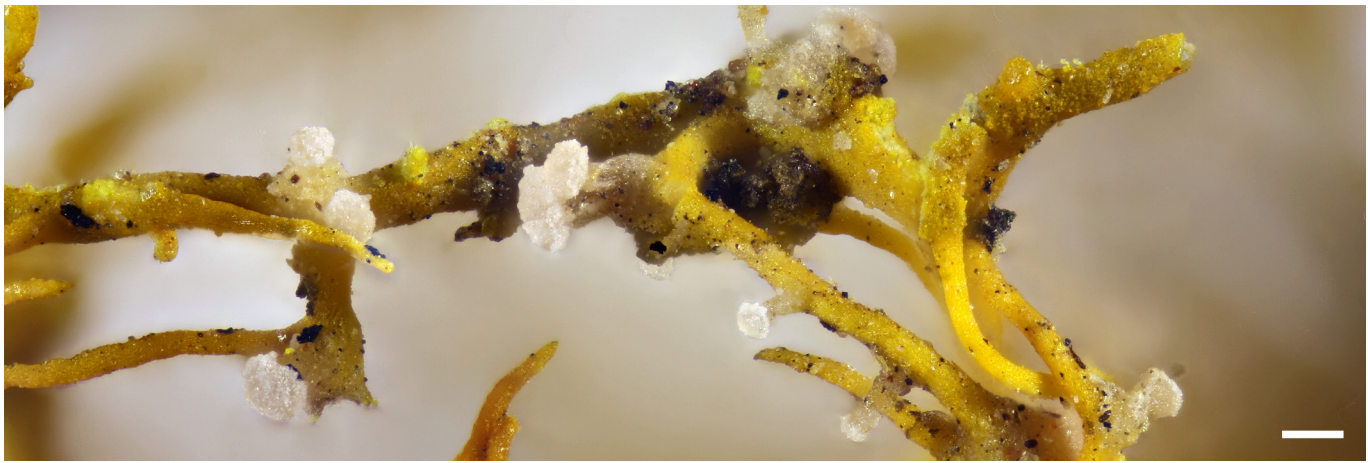
Basidiomata dispersed, [98]116–198[212] µm tall, stipe relatively narrow to robust, pale brown, [26]31–70[81] µm diam., capitulum whitish to pale brownish, much broader, [62]62–153[180] µm diam. Own thallus hyaline to brownish, gelatinous, developed around basidiomata, in the type specimen strongly swollen. Basidia 6–8-sterigmate, 31–42 µm long. Basidiospores subspherical to shortly ellipsoid, thin-walled, smooth, [3.5]3.6–4.8[5.1] × [2.9]3.0–4.0[4.2] µm, Q = [1.0]1.1–1.4[1.4].

Ecology and hosts. On the thallus of *Teloschistes flavicans* and *T. exilis*.

Distribution. Macaronesia (Canary Islands: La Gomera) and South America (Bolivia).



Crittendenia teloschistis, Canary Islands, holotype. Basidioma developing over a subpherical own thallus (centre), arising from the thallus of *Teloschistes flavicans* (bottom left), in phloxine. Scale bar: 50 µm.



Crittendenia teloschistis, Canary Islands, holotype. Basidiomata on the thallus of *Teloschistes flavicans*. Scale bar: 100 μ m.



Crittendenia teloschistis

Additional specimen (examined and communicated by the collector). **Spain:** Canary Islands, La Gomera, NP Garajonay, Mirador “El Bailadero”, 28°07’22”N, 17°12’17”W, 1035 m, on *Teloschistes flavicans*, 2016, Berger 30711 (herb. Berger).

Reference. Diederich 1996 as *Crittendenia* cf. *apobasidialis*, Diederich et al. 2022, Etayo 1996 as *C. cf. apobasidialis*.

Crittendenia sp. 1 on *Parmelina quercina*

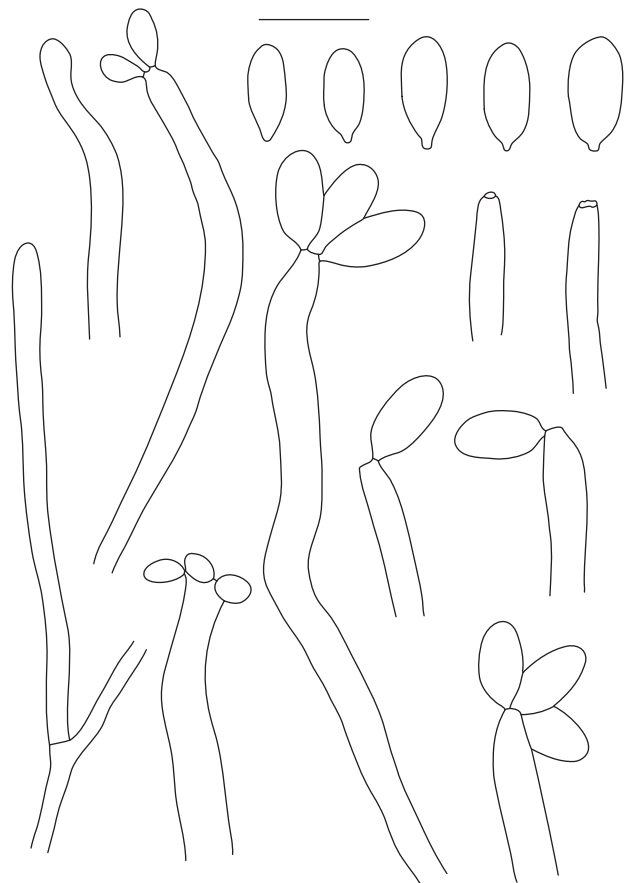
Basidiomata c. 70–200 μ m tall, stipe short, pinkish brown, c. 50–200 μ m diam., capitulum c. 50–400 μ m diam. Basidia 4-sterigmate, c. 38–63 μ m long. Basidiospores ellipsoid, wall thin to thick, some with a distinct perispore sac, $8.4\text{--}9.7 \times 4.0\text{--}5.4 \mu\text{m}$, $Q = 1.7\text{--}2.3$.

Notes. No specimens of this species are currently available, one having been lost, the other having no basidiomata anymore. The short description is based on older notes. No sequences are yet available from this species.

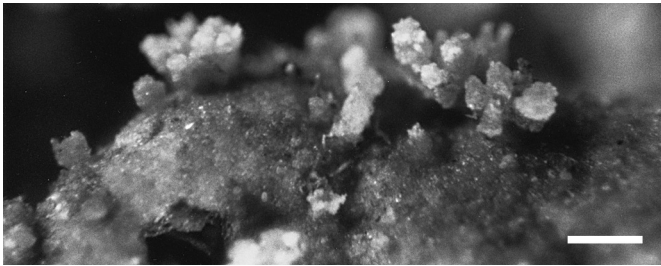
Ecology and host. On the corticolous thallus of *Parmelina quercina*.

Distribution. Europe (Spain: Mallorca, Tarragona).

Reference. Diederich et al. 2022 [Diederich 1996 as *Crittendenia* cf. *apobasidialis*].



Crittendenia sp. 1 on *Parmelina quercina*, Mallorca, Etayo 12503 (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 μ m.



Crittendenia sp. 1, Mallorca, Etayo 12503 (modified from Diederich 1996). Basidiomata on the thallus of *Parmelina quercina*. Scale bar: 200 µm.



Crittendenia sp. 1 on *Parmelina quercina*

Acknowledgments

J. C. Zamora (photo of *Crittendenia physconiae*).

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *CYSTOBASIDIOMYCETES*

Order *CYPHOBASIDIALES*

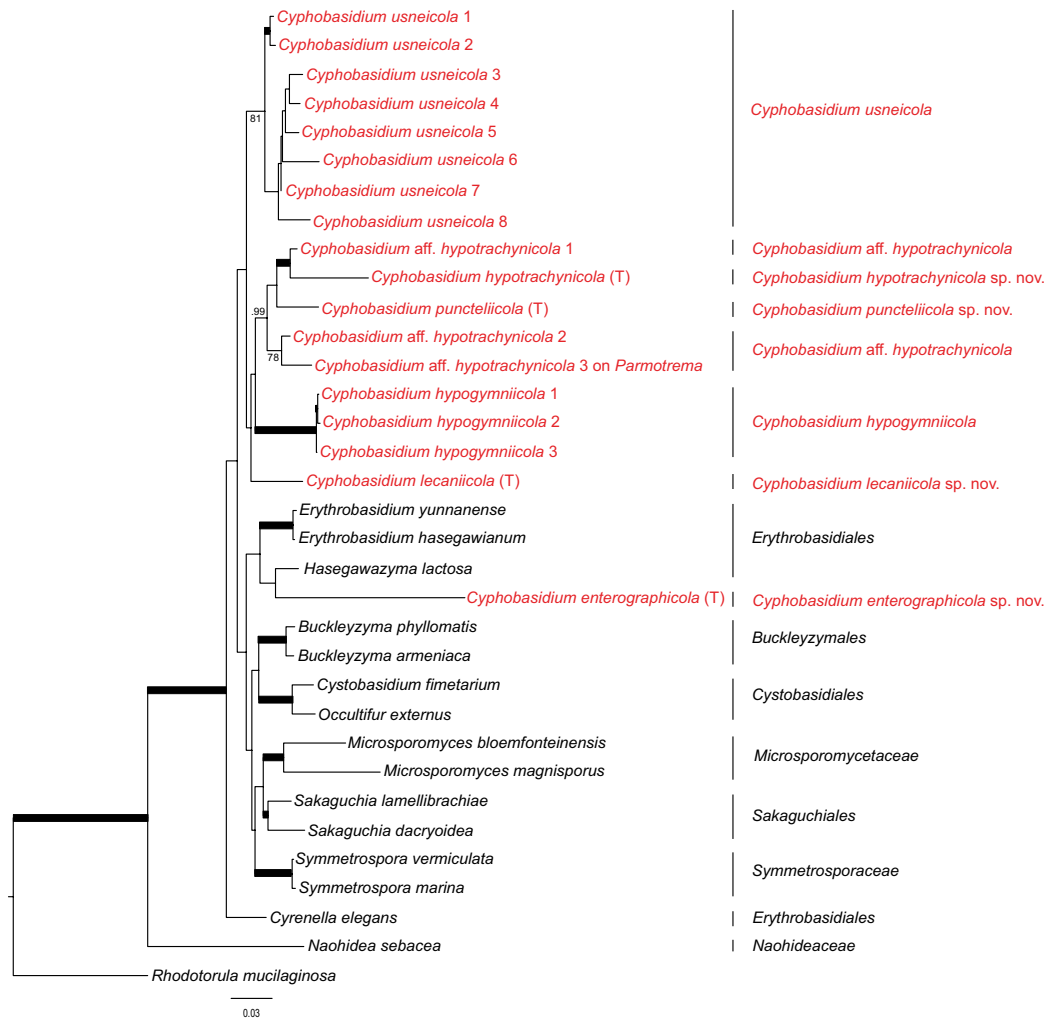
by P. Diederich, A. M. Millanes, A. Flakus, P. Rodriguez-Flakus, J. Etayo & M. Wedin

Diederich, P., A. M. Millanes, A. Flakus, P. Rodriguez-Flakus, J. Etayo & M. Wedin. 2022. Class *Cystobasidiomycetes*, order *Cyphobasidiales*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 305–324.

Introduction and phylogeny

The *Cystobasidiomycetes* was established by Bauer et al. (2006), as fungi characterized by the absence of fucose in their cell walls, and the presence of intranuclear spindle pole bodies during the metaphase. Recent phylogenetic stud-

ies have suggested the recognition of six orders within the group: *Buckleyziales*, *Cyphobasidiales*, *Cystobasidiales*, *Erythrobasidiales*, *Naohideales* and *Sakaguchiales* (Spribille et al. 2016, Wang et al. 2015b, Zhao et al. 2017). Two fami-



Phylogeny based on nuSSU, ITS and nuLSU sequences, representing the *Cystobasidiomycetes*. Branches in boldface indicate nodes supported by both Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70. When nodes received support only from one of the two methods, Bayesian posterior probabilities values ≥ 0.95 are indicated over branches and ML-BS values ≥ 70, below branches. Branch lengths are scaled to the expected number of substitutions per site. Taxonomic assignments are indicated in the right margin. Red font used for *Cyphobasidium* indicates that this genus includes only lichenicolous species. The type specimen of each new species is indicated with '(T)'.
0.03

lies (*Microsporomycetaceae* and *Symmetrosporaceae*) are not included in any of these (Wijayawardene et al. 2020), and three genera, *Cyrenella* (*Erythrobasidiales*), *Hasegawazyma* (*Erythrobasidiales*) and *Queiroziella* (*Cystobasidiales*), do not yet have a family assignment in their respective orders (Crous et al. 2018, Wijayawardene et al. 2020). Kachalkin et al. (2019) and Wijayawardene et al. (2020) proposed to synonymize *Cyphobasidiales* under *Erythrobasidiales*. Kachalkin et al. (2019) based this decision on the unsupported phylogenetic affinity of the nuLSU sequences of *Cyphobasidium* to *Cyrenella* (*Erythrobasidiales*) and the uncertainty regarding the phylogenetic position of *Cyphobasidium* within the *Cystobasidiomycetes*. Although this reasoning is well based, their and our phylogenetic results also do not support the close relationship of *Cyrenella* and *Cyphobasidium* (see also single marker trees in Supplementary material). The analyses by Černajová & Škaloud (2019), based on seven genes, clearly separate *Cyphobasidiales* from *Cyrenella* although only three ribosomal markers were used for *Cyphobasidium*. Additional multigene phylogenies will be necessary to ascertain the systematics of *Cyphobasidium* and *Cyphobasidiales*. In this Flora, considering the phylogenetic results of Černajová & Škaloud (2019) and the lichen-inhabiting ecology of *Cyphobasidium*, we accept *Cyphobasidiaceae* and *Cyphobasidiales* to accommodate *Cyphobasidium*. The *Cystobasidiomycetes* comprise both sexual and asexual yeast forming taxa. As it is also the case in other ‘heterobasidiomycete’ groups, dimorphism is frequent in the group, and yeasts are a natural and expected part of the life cycle of these fungi. Examples in which both the yeast stage and the basidia-producing mycelial phase are known in nature are *Nahoidea* and *Oc-cultifur* (Oberwinkler 1990). In some teleomorphs, including species in *Bannoa*, *Erythrobasidium* and *Sakaguchia*, basidia have been interpreted as conidial stages by some authors (Sampaio et al. 1999, Aime et al. 2006, Bauer et al. 2006). In other species, basidia have never been observed or are only found in culture (Hamamoto et al. 2002, Sampaio 2011, Fell 2011, Wang et al. 2015a, 2015b). Two genera with lichenicolous species are known in the *Cystobasidiomycetes*, *Cyphobasidium* (sexual and yeasts) and *Lichenozyma* (yeasts), while sequences related to *Symmetrospora* need further studies (Millanes et al. 2016, Spribille et al. 2016, Černajová & Škaloud 2019). The genus *Cyphobasidium* was described to accommodate lichen-inhabiting species in the *Pucciniomycotina* known to induce conspicuous galls on the host lichen thalli (Millanes et al. 2016). Spribille et al. (2016) discovered numerous yeast lineages from this genus that are

widespread in lichens – especially in the cortex of species of the family *Parmeliaceae*. They also suggested that cystobasidiomycete yeasts could constitute a third component of the lichen symbiosis, being an essential partner in the formation of the lichen cortex. This is an interesting hypothesis that has since then received much attention from lichenologists and mycologists. Lücking et al. (2016) even introduced the new term ‘Hyperlichenized Fungi’ for *Cyphobasidium*. However, Černajová & Škaloud (2019) also sequenced these yeasts from ecorticate species, showing that the yeasts are not restricted to grow in the cortex, although they could still be part of a superficial lichen biofilm (Spribille 2018, Spribille et al. 2020). Recent genomic investigations have revealed enzymatic profiles in the basidiomycete yeast genomes not found in the lichen mycobiont (Tagirdzhanova et al. 2021), but the hypothetical role of the yeasts in the lichen symbiosis still remains to be tested. Oberwinkler (2017) considered that the basidiomycete yeasts in lichen thalli are simply the typical yeast colonies propagating mitotically, frequently produced by other dimorphic mycoparasites. We, for the time being, consider this explanation more plausible. Nevertheless, future investigations will surely shed light on these questions. Other authors have confirmed the presence of *Cyphobasidium* yeasts in *Parmeliaceae* and in other lichen families, such as *Cladoniaceae*, *Lecanoraceae* and *Physciaceae* (Černajová & Škaloud 2019, Mark et al. 2020). All this has nevertheless raised new challenges for the taxonomic characterization of this diversity, since *Cyphobasidium* yeasts have not yet been obtained in culture. Černajová & Škaloud (2019) described the monotypic genus *Lichenozyma* for a lineage of yeasts isolated from *Cladonia*, which Li et al. (2020) suggested to be synonymized under *Microsporomyces*. We still consider that the distinction of a different genus is justified. In the context of this Flora, however, we are not treating the yeast species individually, because we consider that a Flora should be a tool for knowing and identifying species, macroscopically and microscopically, in rare cases using molecular data (cryptic species). Therefore, both the yeast lineages in *Cyphobasidium* and also *Lichenozyma pisutiana* have been excluded. In the phylogenies reconstructed for the filamentous taxa in this Flora, neither *Cyphobasidium*, nor its phylogenetic position within the *Cystobasidiomycetes* get support. Additional specimens and molecular markers are needed to clarify the generic and species delimitation in *Cyphobasidium*. However, with the data at hand, we prefer to use conservatively wide concepts both for the genus and the species included.

Key to the lichenicolous species of *Cystobasidiomycetes*

- 1 On macrolichens
 - 2 Basidiomata resupinate over the host thallus or over applanate gall-like deformations, not or only slightly convex
 - 3 Probasidia shortly ellipsoid to pyriform, $10\text{--}14 \times 7\text{--}9.5\ \mu\text{m}$; meiosporangia 3-septate, $35\text{--}55 \times 4\text{--}6.5\ \mu\text{m}$; basidiospores $6\text{--}8.5 \times 4.5\text{--}6\ \mu\text{m}$; basidiomata pale orange brown; on *Ramalina fraxinea* *Cyphobasidium ramalinicola* (319)
 - 3' Probasidia claviform, ellipsoid, $12\text{--}23 \times 3.5\text{--}8\ \mu\text{m}$; basidiospores $8\text{--}9.5 \times 4.5\text{--}6\ \mu\text{m}$; meiosporangia 1–3-septate, $20\text{--}34 \times 2.5\text{--}6\ \mu\text{m}$; basidiomata medium to dark brown; on *Hypotrachyna* *Cyphobasidium hypotrachynicola* (314)
 - 2' Basidiomata inducing convex galls
 - 3 Meiosporangia (= upper part of basidium) $50\text{--}80\ \mu\text{m}$ long
 - 4 Probasidia claviform, $20\text{--}35 \times 5.5\text{--}6\ \mu\text{m}$; epibasidia $4\text{--}7\ \mu\text{m}$ long; basidiomatal galls subspherical, with a constricted base, often with a slightly cerebriform surface; on *Usnea* *Cyphobasidium usneicola* (321)
 - 4' Probasidia elongate ellipsoid, $14\text{--}22 \times 5.5\text{--}10\ \mu\text{m}$; epibasidia $2.5\text{--}4.5\ \mu\text{m}$ long; basidiomatal galls convex, with a constricted base, irregular in form, rarely subspherical; on *Crocodia rubella* *Cyphobasidium crocodiicola* (309)
 - 3' Meiosporangia $22\text{--}40\ \mu\text{m}$ long; probasidia elongate ellipsoid, $9\text{--}22 \times 4\text{--}11\ \mu\text{m}$
 - 4 Basidiomatal galls very large, up to 17 mm diam., with a constricted base, becoming bullate; probasidia ellipsoid, $11\text{--}22 \times 4\text{--}11\ \mu\text{m}$; meiosporangia $29\text{--}38 \times 3\text{--}5\ \mu\text{m}$; basidiospores $7\text{--}12 \times 4\text{--}7\ \mu\text{m}$; on *Hypogymnia* *Cyphobasidium hypogymniicola* (312)
 - 4' Basidiomatal galls smaller, less than 3 mm diam.
 - 5 Basidiomatal galls pale brown, concolorous to the host thallus, strongly convex, mostly subspherical, $0.1\text{--}1.2\ \text{mm}$ diam.; probasidia elongate ellipsoid, $12\text{--}22 \times 4\text{--}6.5\ \mu\text{m}$; meiosporangia at least $30 \times 3\text{--}5\ \mu\text{m}$; basidiospores $7\text{--}9.5 \times 4\text{--}7\ \mu\text{m}$; on *Hypogymnia hultenii* *Cyphobasidium* aff. *hypogymniicola* (313)
 - 5' Basidiomatal galls first simple, subspherical, with a constricted base, often irregular in form, rapidly becoming larger and medium to dark brown, upper surface often partly flat or concave, or galls becoming bullate
 - 6 Basidiomatal galls initially $0.2\text{--}0.6\ \text{mm}$ diam., later becoming bullate, up to 3 mm diam.; probasidia claviform, $12\text{--}23 \times 3.5\text{--}8\ \mu\text{m}$; meiosporangia $20\text{--}34 \times 2.5\text{--}6\ \mu\text{m}$; basidiospores $8\text{--}9.5 \times 4.5\text{--}6\ \mu\text{m}$
 - 7 On *Hypotrachyna* *Cyphobasidium hypotrachynicola* (314)
 - 7' On *Parmotrema reticulatum*, resembling *Tremella parmeliarum* *Cyphobasidium* aff. *hypotrachynicola* (317)
 - 6 Basidiomatal galls initially $0.3\text{--}0.4\ \text{mm}$ diam., later becoming lobiform, often with a concave to foveolate upper surface and up to 1 mm diam.; probasidia $9\text{--}17 \times 5.5\text{--}11\ \mu\text{m}$; meiosporangia $25\text{--}40 \times 4\text{--}5\ \mu\text{m}$; basidiospores $5\text{--}9 \times 4\text{--}6.5\ \mu\text{m}$; on *Punctelia graminicola* *Cyphobasidium puncteliicola* (318)
 - 6' Basidiomatal galls initially $0.3\text{--}1\ \text{mm}$ diam., very irregular, weakly bullate, later more flattened, up to 2.5 mm diam., sometimes with brown, bullate outgrowths; on *Menegazzia* *Cyphobasidium* sp. 1 (322)
 - 1' On lichens with a crustose thallus
 - 2 Basidiomata immersed to superficial, pulvinate, subspherical or irregular, not gelatinous, whitish to pale brown, concolorous with the host thallus, matt, $0.2\text{--}0.35\ \text{mm}$ diam.; probasidia $11\text{--}19.5 \times 7.5\text{--}12\ \mu\text{m}$; on the apothecial margin of *Enterographa pallidella* *Cyphobasidium enterographicola* (311)
 - 2' Basidiomata superficial, convex, waxy-gelatinous, pinkish to orange-brown, $0.2\text{--}0.45\ \text{mm}$ diam.
 - 3 Probasidia ellipsoid, $10\text{--}19 \times 6\text{--}8\ \mu\text{m}$; epibasidia $3\text{--}4\ \mu\text{m}$ thick, $13.5\text{--}22.5\ \mu\text{m}$ long; on *Lecania naegelii* *Cyphobasidium lecaniicola* (317)
 - 3' Probasidia elongate ellipsoid to claviform, often with a stalk-like base, $18\text{--}32 \times 5\text{--}8\ \mu\text{m}$; epibasidia much smaller, $1.5\text{--}2.5\ \mu\text{m}$ thick, $5\text{--}7.5\ \mu\text{m}$ long; on *Buellia stillingiana* *Cyphobasidium buelliicola* (308)

CYSTOBASIDIOMYCETES R. Bauer, Begerow,
J. P. Samp., M. Weiß & Oberw.

Mycological Progress 5: 46 (2006). Type: *Cystobasidium* (Lagerg.) Neuhoff

CYPHOBASIDIALES T. Sprib. & H. Mayrhofer

Index Fungorum 309: 1 (2016); *Cyphobasidiales* T. Sprib. & H. Mayrhofer, in Spribille et al., *Science* 353 (6298): 491 (2016), nom. inval., Art. 32.1 (c). Type: *Cyphobasidium* Millanes, Diederich & Wedin

Cyphobasidiaceae T. Sprib. & H. Mayrhofer

Index Fungorum 309: 1 (2016); *Cyphobasidiaceae* T. Sprib. & H. Mayrhofer, in Spribille et al., *Science* 353 (6298): 491 (2016), nom. inval., Art. 32.1 (c). Type: *Cyphobasidium* Millanes, Diederich & Wedin

Notes. The genus *Cyphobasidium* introduced in Millanes et al. (2016) has been effectively and validly published in *Fungal Biology* in Nov. 2016 (although available online on 31 Dec. 2015 as ‘Article in press’ with a different pagination and layout). The names of the order *Cyphobasidiales* and of the family *Cyphobasidiaceae* were published in *Science* online on 21 July 2016 (with a provisional pagination and layout) and in print on 29 July 2016, thus before Nov. 2016, and are therefore invalid. Both names were validated in *Index Fungorum* on 13 Dec. 2016.

CYPHOBASIDIUM Millanes, Diederich & Wedin

Fungal Biology 120: 1473 (2016). Type: *C. hypogymniicola* (Diederich & Ahti) Millanes, Diederich & Wedin

Molecular data: yes (T, L). **Number of species:** 9[1]–0–0.

Basidiomata inducing conspicuous galls on the host lichen thalli; galls convex, with a constricted base, often becoming irregular in form. **Context hyphae** with or without clamps; haustoria unknown. **Basidia**, when mature, consisting of a thick-walled, ellipsoid to elongate lower part (the probasidium) and a thin-walled, cylindrical, often bent, transversely 3-septate, upper part (the meiosporangium); epibasidia short, more or less perpendicular to the basidium. **Basidiospores** ellipsoid to broadly fusiform, sometimes slightly curved, with a distinct refractive apiculus at the lower end and a rounded upper end. **Asexual stage:** lunate conidia observed in one species. **Yeast stage** usually present, but difficult to observe by light microscopy.

Notes. Sexual stages induce conspicuous galls, while yeast stages are asymptomatic, mainly in the lichen cortex. DNA sequences of many unnamed species have been obtained by Spribille et al. (2016) from the cortex of macrolichens, espe-

cially in *Parmeliaceae*. Lendemer et al. (2019) found *Cyphobasidium* yeasts in 9 species out of 339, belonging to *Bryoria*, *Lecidea*, *Leucodermia*, *Opegrapha*, *Parmotrema* and *Usnea*.

Spribille et al. (2016) included the generic type *Cyphobasidium hypogymniicola* in their studies and documented that this species is able to complete the whole life cycle within the thallus of the host, including yeasts, mycelium and basidiomata.

Ecology. All known species are lichenicolous.

Cyphobasidium buelliicola Diederich & W. R. Buck,
sp. nov.

Diagnosis: Characterized by the waxy-gelatinous, orange-brown, pulvinate basidiomata, 0.2–0.45 mm diam., developing on *Buellia stillingiana*, the elongate ellipsoid probasidia, often with a stalk-like base, 18–32 × 5–8 µm, the cylindrical, 3-septate meiosporangia, 30–40 × 4–6 µm, the cylindrical to subuliform, 1.5–2.5 µm thick and 5–7.5 µm long epibasidia, and the ellipsoid basidiospores, 5–6 × 3.5–4.5 µm.

Etymology: From *Buellia*, the host lichen, and *icola*, dweller.

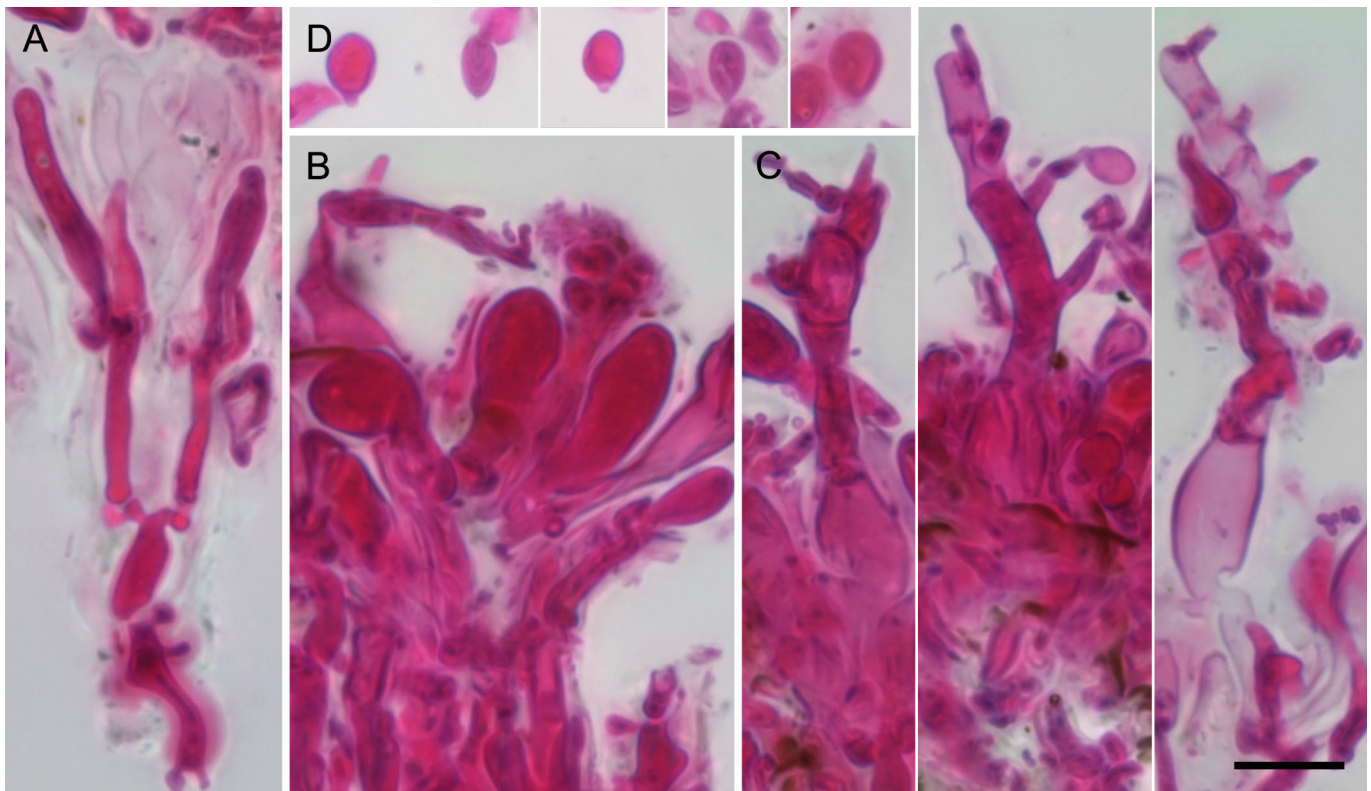
Type: USA, Arkansas, Madison Co., Madison County Wildlife Management Area, along CR 30, 3.2 mi E of AR 23, 36°14'N, 93°41'W, mesic *Quercus*-dominated forest, on *Buellia stillingiana*, 2 Nov. 2000, W. R. Buck 38765 (NY – holotype).

MycoBank: MB844626

Basidiomata superficial, pulvinate, waxy-gelatinous, orange-brown, smooth, 0.2–0.45 mm diam., dispersed, sometimes fusing. **Context hyphae** not observed; subbasidial hyphae thick-walled, 2.5–3.5 µm diam., septa with clamps; haustoria absent. **Hymenium** containing numerous probasidia; probasidial initials elongate ellipsoid, often with a narrower stalk-like base, proliferations occurring through the basal clamp. **Basidia**, when mature, composed of an elongate ellipsoid to claviform, thick-walled probasidium, often with a stalk-like base, 18–32 × 5–8 µm, and a



Cyphobasidium buelliicola, USA, Arkansas, holotype. Basidiomata on the thallus of *Buellia stillingiana*. Scale bar: 500 µm.



Cyphobasidium buelliicola, USA, Arkansas, holotype. A, Subbasidial hyphae and probasidial initials, proliferations occurring through the basal clamp. B, Probasidia and collapsed meiosporangium with epibasidia (upper left). C, Mature meiosporangia emerging from thick-walled probasidia, epibasidia, and one basidiospore. D, Basidiospores. In phloxine. Scale bar: 10 μ m.

cylindrical, thin-walled, often deciduous meiosporangium (upper part), $30\text{--}40 \times 4\text{--}6$ μ m; upper part with 3 transverse septa, each cell with an epibasidium; epibasidia more or less perpendicular to the basidium or slightly directed upwards, cylindrical to subuliform, $1.5\text{--}2.5$ μ m thick, $5\text{--}7.5$ μ m long. *Basidiospores* ellipsoid, more or less symmetrical, with a distinct apiculus at the lower end, $5\text{--}6 \times 3.5\text{--}4.5$ μ m (apiculus not included). *Asexual stage* unknown.

Notes. This taxon is distinguished from most other *Cyphobasidium* species by the small, waxy-gelatinous basidiomata. The only macroscopically similar species, *C. lecaniicola*, differs by the shorter probasidia, $10\text{--}19 \times 6\text{--}8$ μ m, and the much larger epibasidia, $3\text{--}4$ μ m thick and $13.5\text{--}22.5$ μ m long.



Cyphobasidium buelliicola

Ecology and host. On the corticolous thallus and apothecial margin of *Buellia stillingiana*.

Distribution. North America (USA: Arkansas), known only from the type locality.

***Cyphobasidium crocodiicola* Diederich & W. R. Buck, sp. nov.**

Diagnosis: Characterized by the basidiomata inducing brown, convex, irregular galls with a strongly constricted base, $0.2\text{--}5$ mm diam., on the thallus of *Crocodia rubella*, with ellipsoid probasidia, $14\text{--}22 \times 5.5\text{--}10$ μ m, cylindrical, 3-transseptate meiosporangia, $50\text{--}70$ μ m long, $2.5\text{--}6.5$ μ m wide, short epibasidia, $1.5\text{--}2$ μ m thick and $2.5\text{--}4.5$ μ m long, and pyriform to ellipsoid basidiospores, up to at least 10×4.5 μ m.

Etymology: From *Crocodia*, the host lichen, and *incola*, dweller.

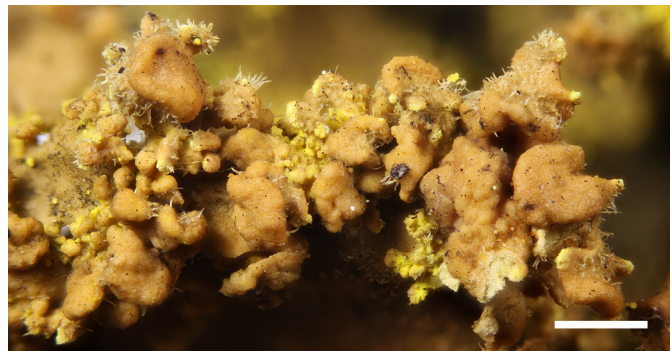
Type: New Zealand, South Island, Boyle River Lodge, $42^{\circ}31'S$, $172^{\circ}23'E$, *Discaria toumatou* groves on river-flat, *Leptospermum ericoides* and *L. scoparium* shrubland on terrace behind lodge and *Nothofagus*, on *Leptospermum* scrub, on *Crocodia rubella*, 13 Sept. 1981, W. R. Buck 7000 (NY – holotype; BR – isotype).

Mycobank: MB844627

Basidiomata inducing the formation of brown, convex, often irregular galls on the host thallus, with a smooth, often partly

concave surface and a strongly constricted base, 0.2–5 mm diam. *Context hyphae*, subbasidial hyphae and clamps not observed; haustoria absent. *Hymenium* containing numerous probasidia that are rather indistinct in thin sections (in phloxine), and are still difficult to observe in squash preparations using DIC optics, usually ellipsoid to elongate ellipsoid, sometimes irregular in form with apparent outgrowths, without a stalk-like base; basal clamp not observed. *Basidia*, when mature, composed of an elongate ellipsoid, thin- to thick-walled probasidium, $14\text{--}22 \times 5.5\text{--}10\text{ }\mu\text{m}$, often collapsing after meiosporangium-production, and a cylindrical, thin-walled, frequently deciduous meiosporangium (upper part), $50\text{--}70 \times 2.5\text{--}6.5\text{ }\mu\text{m}$; upper part with 3 transverse septa, each cell with a median epibasidium; epibasidia more or less perpendicular to the basidium, subulate, $1.5\text{--}2\text{--}(2.5)\text{ }\mu\text{m}$ thick, $2.5\text{--}4.5\text{ }\mu\text{m}$ long, poorly to distinctively refractive at the apex. *Basidiospores* pyriform to ellipsoid, with no or an indistinct apiculus at the lower end, only observed when fixed at the basidium and then mostly immature, the largest observed $10 \times 4.5\text{ }\mu\text{m}$; morphologically similar free-swimming cells could not be identified with certainty as basidiospores. *Asexual stage*: lunate conidia abundant, but conidiogenesis not observed and thus not certainly belonging to this species, $2.5\text{--}3.5\text{ }\mu\text{m}$ thick, the entire conidia (considered as an open ellipse) c. $8\text{--}10 \times 7\text{--}8\text{ }\mu\text{m}$.

Notes. This taxon is distinguished from the other gall-inducing *Cyphobasidium* species developing on macroli-



Cyphobasidium crocodiicola, New Zealand, holotype. Basidiomatal galls on the thallus of *Crocodia rubella*. Scale bar: 1 mm.

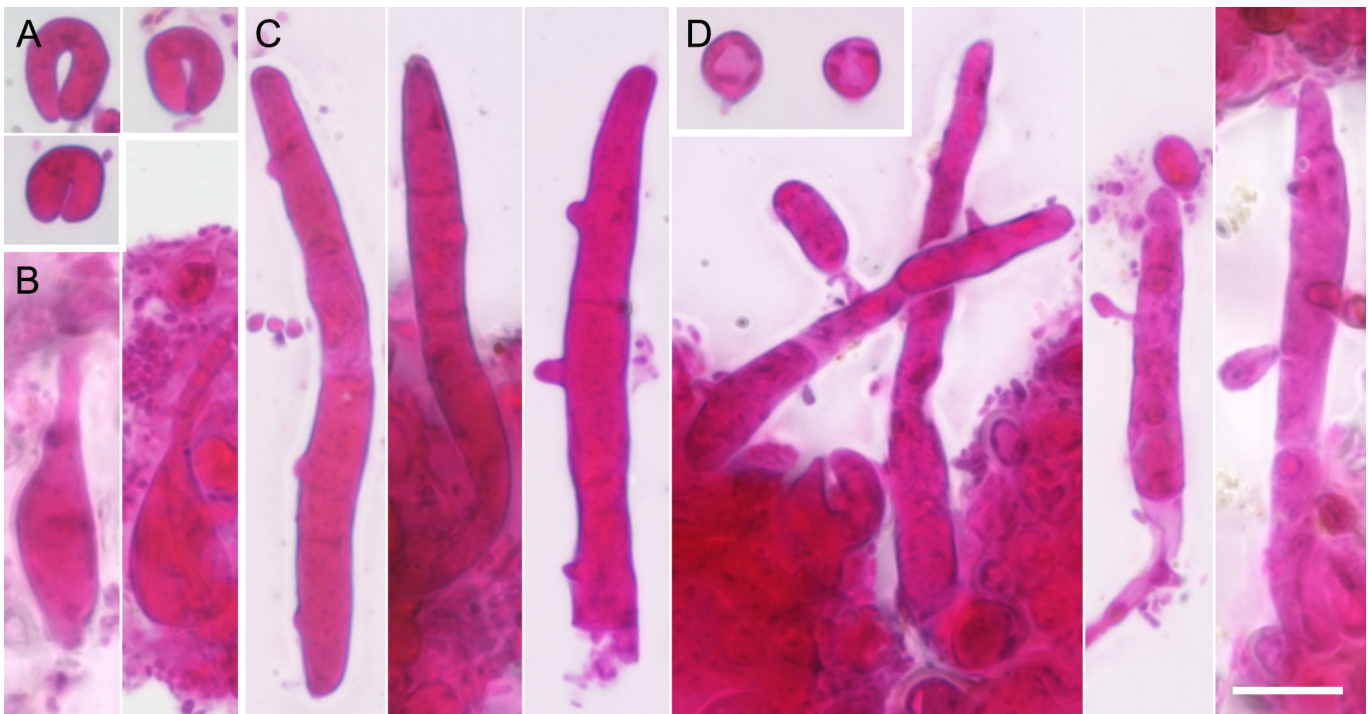
chens by the very small epibasidia, and the particularly long meiosporangia (only *C. usneicola* has similar ones).

Ecology and host. On the thallus of *Crocodia rubella*.

Distribution. Oceania (New Zealand: South Island), known only from the type locality.



Cyphobasidium crocodiicola



Cyphobasidium crocodiicola, New Zealand, holotype. A, Lunate conidia. B, Thick-walled probasidia with emerging meiosporangia. C, Meiosporangia with epibasidia and basidiospores. D, Basidiospores. In phloxine. Scale bar: 10 μm .

Cyphobasidium enterographicola Diederich, Ertz & Millanes, sp. nov.

Diagnosis: Characterized by the non-gelatinous, whitish to pale brown, pulvinate basidiomata, 0.2–0.35 mm diam., developing on *Enterographa pallidella*, the ellipsoid to elongate probasidia, $11\text{--}19.5 \times 7.5\text{--}12\ \mu\text{m}$, and a $3.5\text{--}4.5\ \mu\text{m}$ thick meiosporangium.

Etymology: From *Enterographa*, the host lichen, and *incola*, dweller.

Type: Réunion, entre Saint-Joseph et Saint-Philippe, le Cap Méchant et Puits des Français, $21^{\circ}22'30''\text{S}$, $55^{\circ}42'36''\text{E}$, 18 m, trunc of *Pandanus utilis*, on *Enterographa pallidella*, 7 Dec. 2012, D. Ertz 17902 (BR – holotype).

Mycobank: MB844628

Basidiomata immersed to superficial, pulvinate, subspherical or irregular, not gelatinous, whitish to pale brown, concolorous with host thallus, paler than host hymenium, matt, 0.2–0.35 mm diam. **Context hyphae** not observed; subbasidial hyphae thick-walled, $2.5\text{--}4\ \mu\text{m}$ diam., septa with clamp connections; haustoria absent. **Hymenium** containing numerous probasidia intermixed with subbasidial hyphae; probasidial initials subspherical to ellipsoid, proliferations occurring through the basal clamp. **Basidia**, when mature, composed of an ellipsoid to elongate probasidium, $11\text{--}19.5 \times 7.5\text{--}12\ \mu\text{m}$, from which a $3.5\text{--}4.5\ \mu\text{m}$ thick meiosporangium emerges; mature meiosporangia, epibasidia and basidiospores not observed. **Asexual stage** unknown. **Yeast** cells abundant in infected host portions, subspherical to ellipsoid, $3.2\text{--}5.4(-7) \times 2.6\text{--}4.8\ \mu\text{m}$, wall

$0.5\text{--}0.8\ \mu\text{m}$ thick, occasionally germinating into hyphae with conspicuous clamp connections, these acting as subbasidial hyphae.

Notes. This species has not been observed in the mature stage, and no epibasidia and basidiospores have been seen. Nevertheless, the species is well distinguished from the gall-inducing *C. hypogymnicola* and *C. puncteliicola* by the formation of true basidiomata, from *C. usneicola* by the much smaller basidiomata, and from *C. lecaniicola*, which has basidiomata with a smoother surface and a pinkish to orange tinge, and narrower probasidia, $10\text{--}19 \times 6\text{--}8\ \mu\text{m}$. Phylogenetically, it is only distantly related to these species.

Ecology and host. On corticolous *Enterographa pallidella*, mainly in the apothecia, but also in the thallus.

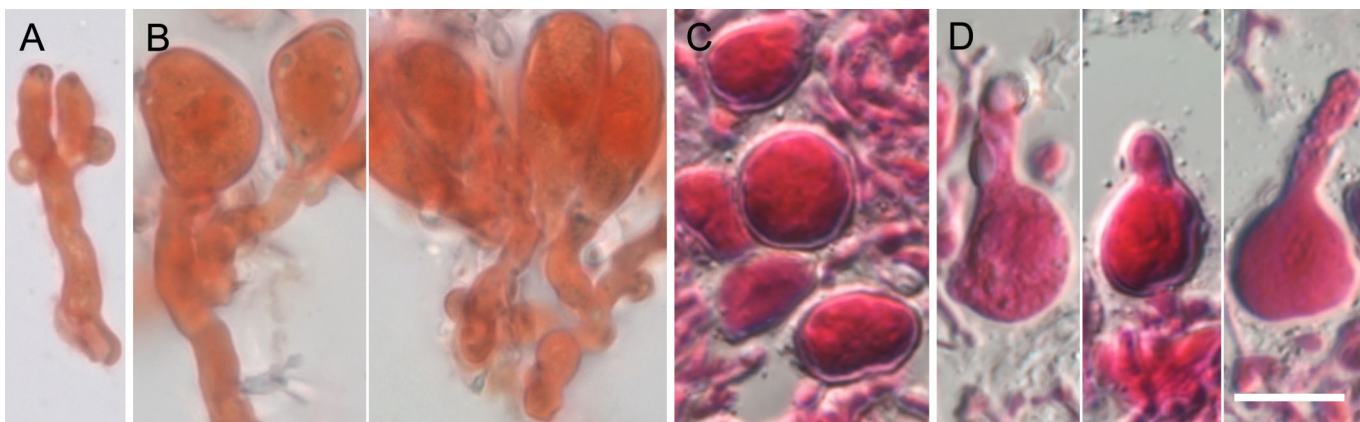
Distribution. Indian Ocean (Réunion), known only from the type locality.



Cyphobasidium enterographicola



Cyphobasidium enterographicola, Réunion, holotype. Basidiomata (arrows) on the thallus and apothecia of *Enterographa pallidella*. Scale bar: 200 μm .



Cyphobasidium enterographicola, Réunion, holotype. A, Fertile hypha with probasidial initials, proliferations occurring through the basal clamp. B, Subbasidial hyphae with probasidia. C, Thick-walled probasidia. D, Probasidia with young meiosporangia. A–B, in Congo red, C–D, in phloxine. Scale bar: 10 µm.

***Cyphobasidium hypogymniicola* (Diederich & Ahti)**
Millanes, Diederich & Wedin

Fungal Biology 120: 1474 (2016); *Cystobasidium hypogymniicola* Diederich & Ahti, in Diederich, *Bibl. Lichenol.* 61: 21 (1996). *Type*: Canada, Newfoundland, Gander District, 1 mile SE of Mount Peyton, on *Betula papyrifera* in forest, on *Hypogymnia physodes*, 1 Aug. 1956, T. Ahti 8948 (H – holotype; BR – isotype).

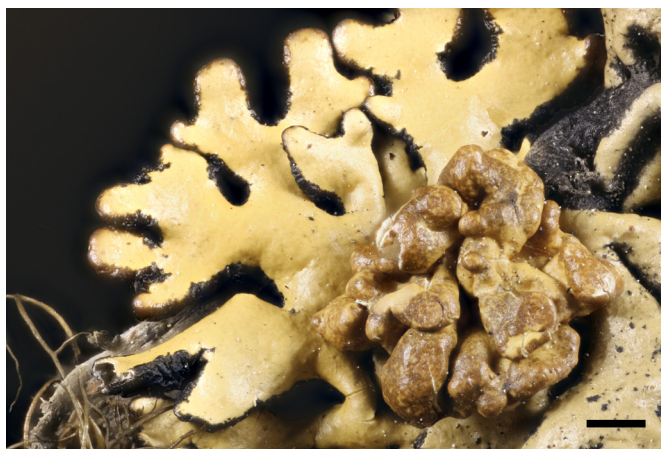
Basidiomata brownish, resupinate, forming a thin subgelatinous hymenium over galls of the host lichen; galls initially simple, with a constricted base, often irregular in form, 0.1–3 mm diam., later bullate and reaching 17 mm diam., initially concolorous with the thallus, becoming brownish in the upper part. *Context hyphae* difficult to study, c. 1–1.5 µm diam., clamp connections not observed; subbasidial hyphae thick-walled, 2.5–4 µm diam.; haustoria unknown. *Hymenium* containing numerous probasidia, intermixed with some subbasidial hyphae, embedded in a

dense gel, 30–40 µm tall; probasidial initials subspherical to ellipsoid, thick-walled, with a basal clamp connection, situated in or below the cortex of the galls. *Basidia*, when mature, composed of an ellipsoid, thick-walled probasidium, 11–22 × 4–11 µm, and a cylindrical, generally bent, thin-walled, often deciduous meiosporangium (upper part), 29–38 × 3–5 µm; upper part with 3 transverse septa, individual cells collapsing after spore production, with 4 epibasidia; epibasidia more or less perpendicular to the basidium, subulate, 1–2 µm thick, 3.5–8.5 µm long, poorly to distinctively refractive at the apex. *Basidiospores* ellipsoid to fusiform, more or less symmetrical, with a more or less distinct refractive apiculus at the lower end, 7–12 × 4–7 µm. *Asexual stage* unknown.

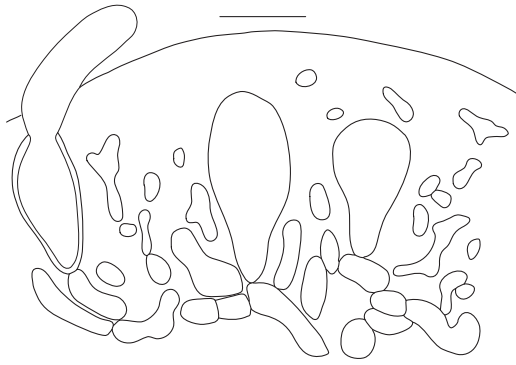
Notes. In most specimens, only probasidia have been observed, sometimes with the developing, but immature septate meiosporangium. The mature, spore-producing meiosporangium in *C. hypogymniicola* easily becomes detached



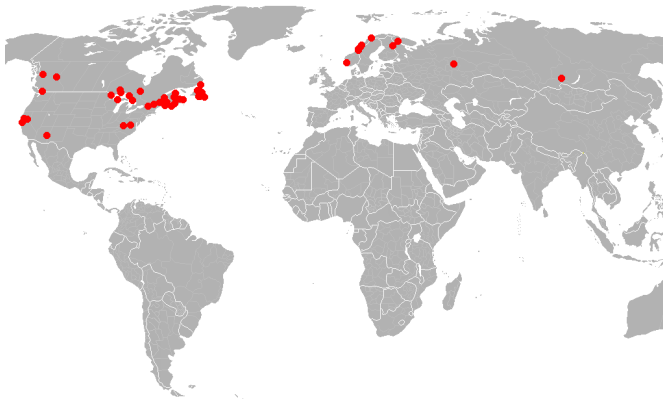
Cyphobasidium hypogymniicola, Canada, Newfoundland, isotype. Basidiomatal galls on the thallus of *Hypogymnia physodes*. Scale bar: 2 mm.



Cyphobasidium hypogymniicola, Canada, Ontario, Ahti 4260a. Basidiomatal gall on the thallus of *Hypogymnia physodes*. Scale bar: 1 mm.



Cyphobasidium hypogymniicola, Canada, Ahti 2763 (modified from Diederich 1996). Section through a basidioma, showing three basidia and basidiospores. Scale bar: 10 µm.



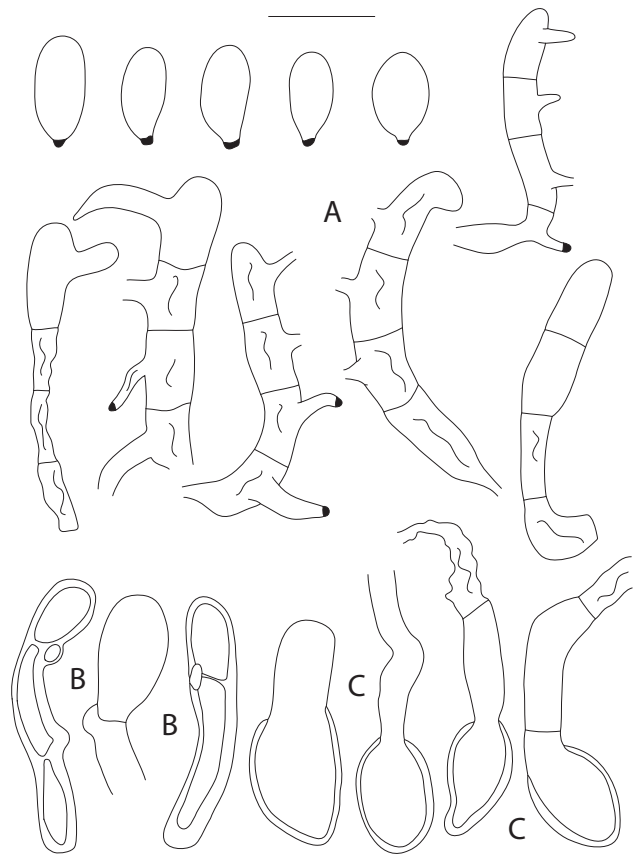
Cyphobasidium hypogymniicola

from the probasidium in microscopic preparations when the lower cell has already collapsed after spore-production.

The galls induced by *C. hypogymniicola* on *Hypogymnia physodes* are very distinct from those of *Tremella hypogymniae*. In *T. hypogymniae*, the galls are always simple, with a broad, non-constricted base, and they are pinkish when young (but blackish, when attacked by parasitic fungi). The galls of *C. hypogymniicola* are concolorous with the thallus when young, have a distinctly constricted base, and they develop into larger bullate galls reaching almost 2 cm in some specimens. The report from South America (Chile, Isla Navarino, on *Hypogymnia antarctica*, Etayo 22668, Etayo & Sancho 2008) is not accepted here as the galls look different, and as no typical basidia could be seen.

Ecology and hosts. Mostly on the thallus of *Hypogymnia physodes*, more rarely on *H. imshaugii*, *H. incurvoides*, *H. krogiae* and *H. vittata*.

Distribution. Europe (Finland; Norway; Russia), North America (Canada: British Columbia, New Brunswick, Newfoundland, Nova Scotia, Ontario; USA: Arizona, Cali-



Cyphobasidium hypogymniicola, Canada (A–B) and Finland (C), holotype (A), Ahti 7777 (B) and Ahti 363 (C) (modified from Diederich 1996). Probasidia, basidia and basidiospores. Scale bar: 10 µm.

fornia, Maine, Minnesota, New York, North Carolina, Vermont, Virginia) and Asia (Russia).

Additional specimens examined. **USA:** California: Napa Co., on Cal. Hwy 28, 2 mi W of Moscowitz Corner, 38°27'N, 122°36'02"W, on *Hypogymnia imshaugii*, 2001, Tucker 37427 (BR, SBBG). Minnesota: Lake Co., Superior National Forest, c. 6.47 km W of Isabella and 12.87 km NW of Murphy city, 47.5976°N, 91.4360°W, on *Abies balsamea* branches, on *H. physodes*, 2018, Gockman 5673 (BR).

References. Diederich 1996, Millanes et al. 2016, Spribille et al. 2016 [Brinker 2020, Diederich 2003, Etayo & Sancho 2008, Hodgkinson et al. 2009, Holien 2001, Kocourková et al. 2012, Shiryayev et al. 2010, Urbanavichene & Urbanavichus 2005, Urbanavichus & Urbanavichene 2008, Zhurbenko & Vershinina 2014].

Cyphobasidium aff. *hypogymniicola*

Basidiomata inducing the formation of pale, rarely medium brown, convex, subspherical, sometimes irregular galls on the host thallus, with a smooth surface and a slightly constricted base, 0.1–1.2 mm diam. **Context hyphae** and subbasidial hyphae indistinct; clamp connections and haustorial branches not observed. **Hymenium** gelatinous,



Cyphobasidium aff. *hypogymniicola*, Norway, Haugan 151236. Basidiomatal galls on the thallus of *Hypogymnia hultenii*. Scale bar: 1 mm.



Cyphobasidium aff. *hypogymniicola*, Norway, Tønsberg 30510. Basidiomatal galls on the thallus of *Hypogymnia hultenii*. Scale bar: 200 μ m.

containing numerous probasidia; probasidial initials subspherical to ellipsoid, thick-walled, basal clamp not observed. *Basidia*, when mature, composed of an elongate ellipsoid, thick-walled probasidium, $12\text{--}22 \times 4\text{--}6.5 \mu\text{m}$, and a cylindrical, generally bent, thin-walled, often deciduous meiosporangium, at least $30 \mu\text{m}$ long and $3\text{--}5 \mu\text{m}$ diam.; upper part with up to 3 transverse septa, individual cells collapsing after spore production, each with one epibasidium; epibasidia more or less perpendicular to the basidium, subulate, $1\text{--}2 \mu\text{m}$ thick, at least $2 \mu\text{m}$ long, not or poorly refractive at the apex. *Basidiospores* ellipsoid to fusiform, more or less symmetrical, with a distinct, not or poorly refractive apiculus at the lower end, $7\text{--}9.5 \times 4\text{--}7 \mu\text{m}$. *Asexual stage* unknown.

Notes. The populations on *Hypogymnia hultenii* differ from *Cyphobasidium hypogymniicola* s. str. by the much smaller, subspherical, never bullate or lobate basidiomatal galls. Microscopically, the observed probasidia were narrower than those of *C. hypogymniicola* s. str., $4\text{--}6.5$ vs $4\text{--}11 \mu\text{m}$ wide. We prefer to await for additional specimens and molecular data before taking a decision about their taxonomic status.

Ecology and host. On the thallus of *Hypogymnia hultenii* on twigs of *Picea abies*.

Distribution. Europe (Norway).

Specimens examined (all on *Hypogymnia hultenii*). **Norway:** Trøndelag: Overhalla, farm Grande, $64^{\circ}29'N$, $12^{\circ}00'E$, 50 m, 2001, Tønsberg 30510 (BG-L70660); Snåsa, N of Jørstadmoen, W of Finnsås, Finnsåsmarka, $64^{\circ}13'N$, $12^{\circ}13'E$, 60 m, 2001, Tønsberg 30481 (BG-L70643); Meråker hd, Tevldalen, 1950, Santesson s.n. (UPS); Lånke hd, 1938, Ahlner s.n. (UPS); Flåtanger, Dale Nature Reserve, Stordalen, $64.4434^{\circ}N$, $10.9699^{\circ}E$, 45 m, 2015, Haugan 151236 (BR).

Reference. Diederich 2007 as *Cystobasidium hypogymniicola*.

***Cyphobasidium hypotrachynicola* Diederich, Flakus, Etayo & Rodr. Flakus, sp. nov.**

Diagnosis: Characterized by the medium to dark brown, waxy-gelatinous basidiomata becoming resupinate over the thallus or rarely galls of *Hypotrachyna* spp., claviform probasidia, $12\text{--}23 \times 3.5\text{--}8 \mu\text{m}$, and relatively short, cylindrical, $1\text{--}3$ -transseptate meiosporangia, $20\text{--}34 \times 2.5\text{--}6 \mu\text{m}$.

Etymology: From *Hypotrachyna*, the host lichen, and *incola*, dweller.

Type: Bolivia, Dept. La Paz, Prov. Larecaja, near Chumisa, close to Sorata-Consata road, $15^{\circ}36'23''S$, $68^{\circ}39'28''W$, 3300 m, open area with shrubs, piso Ceja da Monte Inferior (Altimontano), rama de árbol selvático, on *Hypotrachyna* sp., 22 Nov. 2015, J. Etayo 33322 (LPB – holotype; herb. Etayo – isotype).

Mycobank: MB844629

Basidiomata medium to dark brown, waxy-gelatinous, applanate, irregularly delimited, soon fusing with neighbouring basidiomata to become resupinate. *Context hyphae* and subbasidial hyphae thick-walled, $2\text{--}4 \mu\text{m}$ diam., with



Cyphobasidium hypotrachynicola, Bolivia, holotype. Basidiomata on the thallus of *Hypotrachyna* sp. Scale bar: 500 μ m.



Cyphobasidium hypotrachynicola, Bolivia, Etayo 33315. Basidiomata on the thallus of *Hypotrachyna* subgen. *Everniastrum*. Scale bar: 500 μ m.



Cyphobasidium hypotrachynicola, Ecuador, Etayo 25386. Basidiomata on the thallus of *Hypotrachyna* sp. Scale bar: 500 μ m.



Cyphobasidium hypotrachynicola, Bolivia, Flakus 25637. Young basidiomatal galls on the thallus of *Hypotrachyna* sp. Scale bar: 1 mm.



Cyphobasidium hypotrachynicola, Bolivia, Flakus 25637. Mature basidiomatal galls on the thallus of *Hypotrachyna* sp. Scale bar: 1 mm.

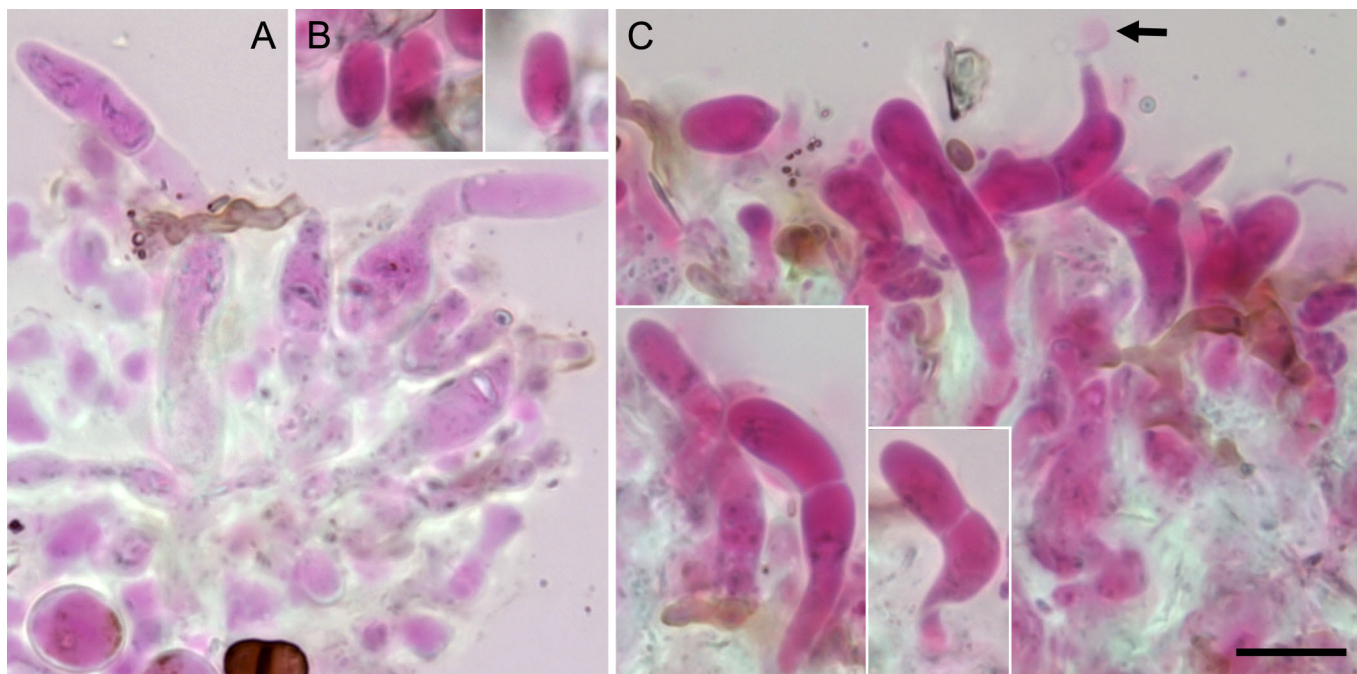
clamp connections; haustoria unknown. *Hymenium* containing numerous probasidia arising from subbasidial hyphae, embedded in a dense gel, 30–50 μ m tall; probasidial initials claviform, thick-walled, with a basal clamp. *Basidia*, when mature, composed of a claviform, thick-walled probasidium, 12–23 \times 3.5–8 μ m, and a cylindrical, generally bent, thin-walled, often deciduous meiosporangium (upper part), 20–34 \times 2.5–6 μ m; upper part with 1–3 transverse septa, with 4 epibasidia; epibasidia more or less perpendicular to the basidium, subulate, 1.5–2 μ m thick, 3–7.5 μ m long. *Basidiospores* ellipsoid to fusiform, more or less symmetrical, with a distinct apiculus at the lower end, 8–9.5 \times 4.5–6 μ m (apiculus not included). *Asexual stage* unknown.

Notes. We have carefully examined many *Cyphobasidium* specimens on *Hypotrachyna*, including from subgen. *Everniastrum*, and wondered whether this material might represent a complex of several distinct species. (1) In most specimens, including the type, no gall-induction could be observed, and meiosporangia were constantly 1-septate. (2) In specimens Flakus 25636, 25637 & Etayo 33977, all from the same locality, small to conspicuous galls are

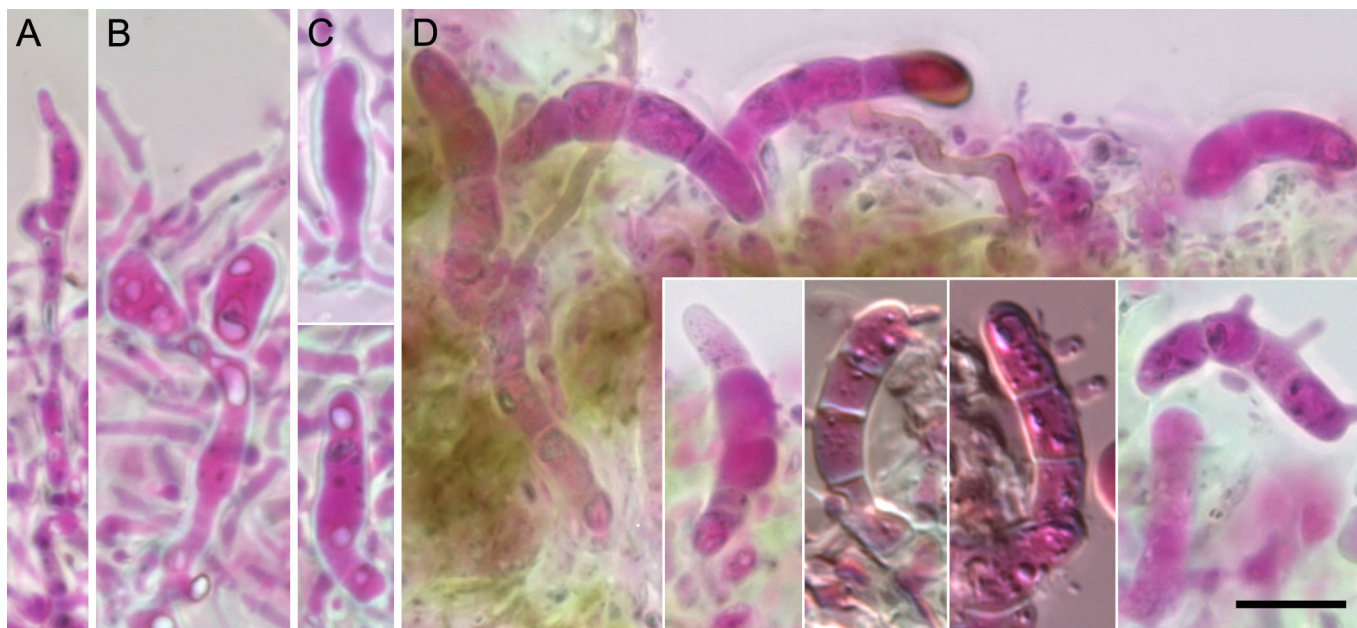
present, and in that material, meiosporangia are constantly 3-septate, but similar in length to 1-septate ones from other specimens; galls are initially simple, with a constricted base, often irregular in form, 0.2–0.6 mm diam., medium to dark brown, but base often concolorous with the host thallus, later bullate and reaching 3 mm diam. (3) Two other specimens (Etayo 33998A and Etayo 34397) were



Cyphobasidium hypotrachynicola



Cyphobasidium hypotrachynicola, specimens with 1-septate meiosporangia devoid of galls, A: Bolivia, Etayo 33315, B–C: Bolivia, holotype. A, Subbasidial hyphae with thick-walled probasidia, of which two with mature, 1-septate meiosporangia. B, Basidiospores. C, Mature meiosporangia, epibasidia, young developing basidiospore (arrow) and mature basidiospore. In phloxine. Scale bar: 10 μ m.



Cyphobasidium hypotrachynicola, specimen with 3-septate meiosporangia and large basidiomatal galls, Bolivia, Flakus 25637. A, Subbasidial hyphae with probasidial initial and basal clamp. B, Subbasidial hyphae with probasidia. C, Thick-walled probasidia. D, Meiosporangia, some with epibasidia. In phloxine. Scale bar: 10 μ m.

intermediate by being devoid of galls, but having 3-septate meiosporangia, these again similar in length.

As sequences from these three morphotypes group together in our phylogenetic tree, without being identical, we provi-

sionally treat the entire material as a single species, but are aware that it might represent a species complex.

Ecology and hosts. On the thallus of *Hypotrachyna* species, including species of subg. *Everniastrum*.

Distribution. South America (Bolivia; Colombia; Ecuador).

Additional specimens examined (all on *Hypotrachyna*). **Bolivia:** Same locality as type, on subg. *Everniastrum*, Etayo 33315 (LPB, herb. Etayo). Dept. Cochabamba, Prov. Carrasco, Parque Nacional Carrasco, between Meruvia and Monte Punku, 17°34'43"S, 65°15'25"W, 3082 m, *Podocarpus* forest, on corticolous *Hypotrachyna*, 2014, Flakus 25636, 25637 (KRAM, LPB) & Etayo 33977 (LPB, herb. Etayo); *ibid.*, 17°34'46"S, 65°15'27"W, 3080 m, Etayo 33998A (LPB, herb. Etayo). Dept. La Paz, Prov. Franz Tamayo, Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo, 14°41'47"S, 69°04'10"W, 3160 m, 2014, Etayo 34397 (LPB, herb. Etayo). Dept. La Paz, Prov. Franz Tamayo, Área Natural de Manejo Integrado Nacional Apolobamba, below Pelechuco, 14°49'08"S, 69°03'50"W, 3560 m, on *H.* (subg. *Everniastrum*) *vexans*, 2014, Flakus 25457 (KRAM, LPB). **Colombia:** Dept. Nariño, munic. Cumbal, subida al volcán Cumbal, 3450–3800 m, on subg. *Everniastrum*, 1998, Etayo 16203, 16943 (herb. Etayo). **Ecuador:** Otavalo, Lagunas de Mojanda, Iadera entre Laguna Grande y Laguna Chiquita, 3700 m, 2003, Etayo 25386 (herb. Etayo). Tulcán, 2 km de Tufiño, en dirección a Maldonada, 3400 m, on subg. *Everniastrum*, 2003, Etayo 26682 (herb. Etayo).

Cyphobasidium aff. *hypotrachynicola*

Notes. We have examined a *Cyphobasidium* specimen on *Parmotrema*, inducing large galls that are macroscopically indistinguishable from those of *Tremella parmeliarum*. Unfortunately, the specimen is immature, with a hymenium containing numerous claviform probasidia, devoid of meiosporangia and basidiospores. Phylogenetically, it is close to *C. hypotrachynicola*, but probably represents a distinct species.

Specimen examined. **Bolivia:** Dept. La Paz, Prov. Franz Tamayo, Área Natural de Manejo Integrado Nacional Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'22"S, 69°00'11"W, 2480 m, lower montane Yungas forest, on *Parmotrema reticulatum*, 2014, Flakus 25091 (KRAM, LPB).



Cyphobasidium aff. *hypotrachynicola*, Bolivia, Flakus 25091. Basidiomatal galls on the thallus of *Parmotrema reticulatum*. Scale bar: 500 µm.

Cyphobasidium lecaniicola Diederich, Ertz & Millanes, sp. nov.

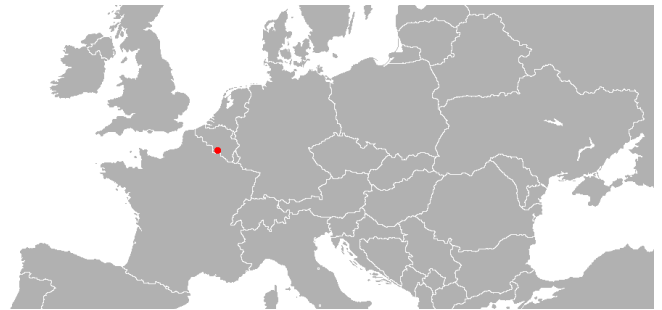
Diagnosis: Characterized by the waxy-gelatinous, pulvinate, pale brown to orange basidiomata, 0.2–0.45 mm diam., developing on *Lecania naegeli*, the ellipsoid probasidia, 10–19 × 6–8 µm, the cylindrical, 1-septate meiosporangia, 32–43 × 3–5 µm, and the large, cylindrical, 3–4 µm thick and 13.5–22.5 µm long epibasidia.

Etymology: From *Lecania*, the host lichen, and *incola*, dweller.

Type: Belgium, 2 km SSE of Olloy-sur-Viroin, rive gauche du ruisseau Nouée, carrière abandonnée entourée d'une forêt de feuillus au lieu-dit 'Bois Noé', 50°03'19"N, 4°35'18"E, 240 m, branche d'un *Quercus* dans la carrière, on *Lecania naegeli*, 21 Febr. 2021, D. Ertz 25890 (BR – holotype).

Mycobank: MB844630

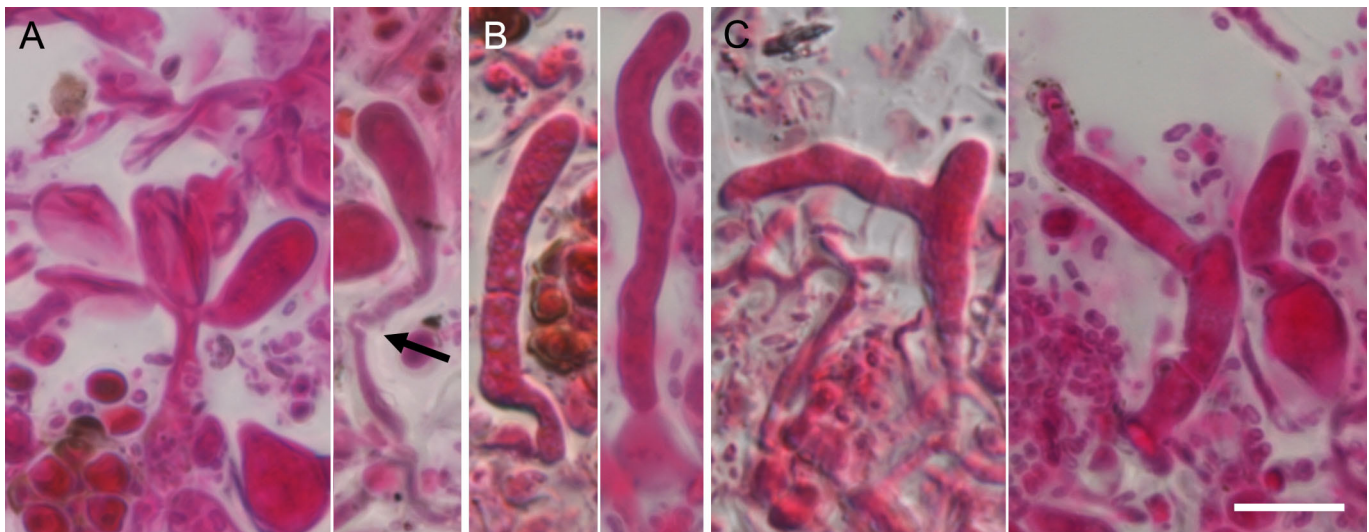
Basidiomata superficial, pulvinate, waxy-gelatinous, pale brown to orange, smooth, 0.2–0.45 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2–3 µm diam.; haustoria absent. *Hymenium* containing numerous probasidia; probasidial initials subspherical to ellipsoid, with a basal clamp. *Basidia*, when mature, composed of an ellipsoid, thick-walled probasidium, 10–19 × 6–8 µm, and a cylindrical, often bent, thin-walled, often deciduous meiosporangium (upper part), 32–43 × 3–5 µm; upper part with 1 transverse



Cyphobasidium lecaniicola



Cyphobasidium lecaniicola, Belgium, holotype. Basidiomata on the thallus of *Lecania naegeli*. Scale bar: 500 µm.



Cyphobasidium lecanicola, Belgium, holotype. A, Subbasidial hyphae with probasidia and basal clamp (arrow). B, Meiosporangia, the right one with basal probasidium. C, Meiosporangia with large epibasidia-like structures, possibly representing secondary meiosporangia. In phloxine. Scale bar: 10 µm.

septum; epibasidia-like structures more or less perpendicular to the basidium or directed upwards, cylindrical, 3–4 µm thick, 13.5–22.5 µm long, possibly representing secondary meiosporangia. *Basidiospores* not observed. *Asexual stage* unknown.

Notes. This species is distinguished from all known lichenicolous *Cyphobasidium* species by the very thick and long epibasidia-like structures that might function as secondary meiosporangia. No basidiospores have been observed.

Ecology and host. On the thallus of *Lecania naegelii* on thin branches of *Quercus*.

Distribution. Europe (Belgium), known only from the type locality.

Cyphobasidium puncteliicola Diederich & Millanes, sp. nov.

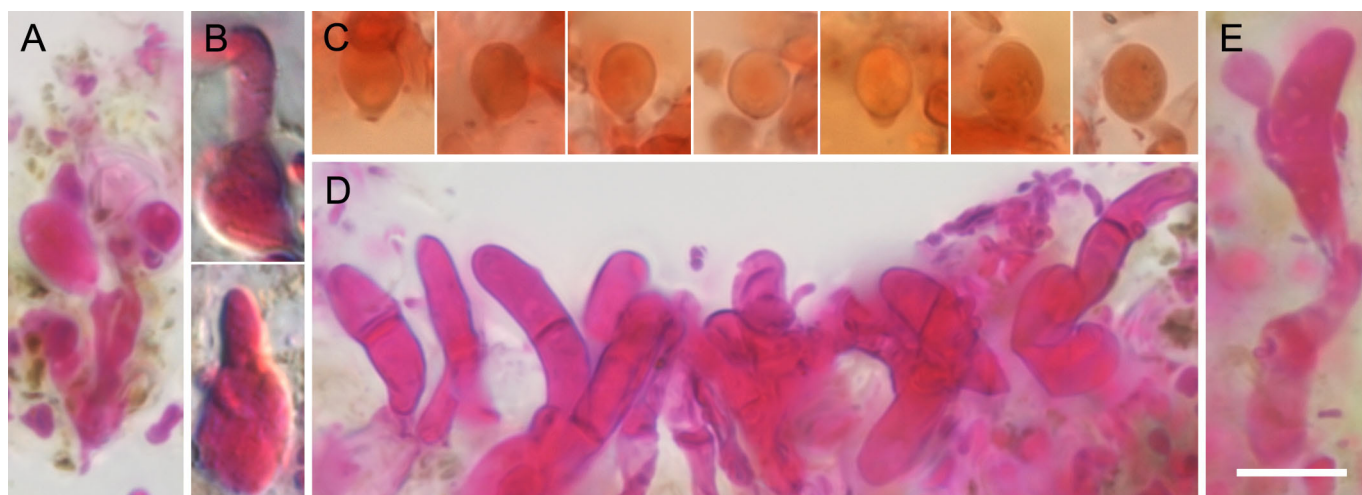
Diagnosis: Characterized by the basidiomata inducing galls with a constricted base, first 0.3–0.4 mm diam., concolorous to the host thallus, soon partly dark brown, eventually lobiform with a concave to foveolate upper surface and up to 1 mm diam., on the thallus of *Punctelia graminicola*, ellipsoid probasidia, 9–17 × 5.5–11 µm, cylindrical, 2–3-transseptate meiosporangia, 25–40 × 4–5 µm, short epibasidia, 1–2 µm thick and 4–5 µm long, and ellipsoid to fusiform basidiospores, 5–9 × 4–6.5 µm.

Etymology: From *Punctelia*, the host lichen, and *incola*, dweller.

Type: USA, Missouri, Dade Co., Bona Glade Natural Area, along MO 215 just E of bridge over Maze Creek Arm of Stockton Lake, 37°32'43"N, 93°41'30"W, channel sandstone glade with



Cyphobasidium puncteliicola, USA, Missouri, holotype. Basidiomatal galls on the thallus of *Punctelia graminicola*. Scale bar: 200 µm.

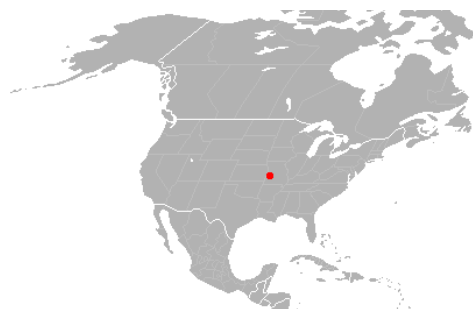


Cyphobasidium puncteliicola, USA, Missouri, holotype. A, Subbasidial hyphae with probasidia. B, Probasidia with young emerging meiosporangia. C, Basidiospores. D, Meiosporangia. E, Meiosporangium with lateral epibasidium and basidiospore. C, in Congo red, all other photos in phloxine. Scale bar: 10 µm.

shaded sandstone bluffs, on corticolous *Punctelia graminicola*, 16 April 2005, R. C. Harris 50901 (NY – holotype).

Mycobank: MB844631

Basidiomata inducing galls on the host thallus; galls initially simple, roundish, with a constricted base, often irregular in form, 0.3–0.4 mm diam., concolorous to the thallus, soon medium to dark brown in delimited areas, later becoming lobiform, often with a concave to foveolate upper surface and up to 1 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 2–3 µm diam.; haustoria unknown. *Hymenium* containing numerous probasidia and some subbasidial hyphae, mixed with the host cortical cells; probasidial initials shortly ellipsoid, thick-walled, basal clamp not observed. *Basidia*, when mature, composed of an ellipsoid, thick-walled probasidium, 9–17 × 5.5–11 µm, and a cylindrical, generally bent, thin-walled, often deciduous meiosporangium (upper part), 25–40 × 4–5 µm; upper part with 2–3 transverse septa, individual cells collapsing after spore production; epibasidia growing upwards, subulate, 1–2 µm thick, 4–5 µm long. *Basidiospores* ellipsoid to fusiform, more or less symmetrical, with a distinct apiculus at the lower end, 5–9 × 4–6.5 µm (apiculus not included).



Cyphobasidium puncteliicola

Asexual stage unknown. *Yeast* cells abundant in some parts of the hymenium, subspherical to shortly ellipsoid, 2–2.5 × 1.7–2.3 µm, budding and germination not observed.

Notes. This species induces the formation of conspicuous galls on the host thallus, resembling somewhat those of *Cyphobasidium hypogymnicola*, which become, however, much larger, up to 17 mm diam., and bullate. Microscopically, *C. hypogymnicola* has larger basidiospores, 7–12 × 4–7 µm.

Ecology and host. On the corticolous thallus of *Punctelia graminicola*.

Distribution. North America (USA: Missouri), known only from the type locality.

Cyphobasidium ramalinicola P. Pinault & Diederich, sp. nov.

Diagnosis: Characterized by the resupinate, poorly delimited, pale orange-brown basidiomata, 1–15 mm diam., on the thallus of *Ramalina fraxinea*, ellipsoid probasidia, 10–14(–18) × 7–9.5 µm, cylindrical, 3-transseptate meiosporangia, 35–55 × 4–6.5 µm, subulate epibasidia, 1.5–2 µm thick and 3–5 µm long, and ellipsoid basidiospores, 6–8.5 × 4.5–6 µm.

Etymology: From *Ramalina*, the host lichen, and *incola*, dweller.

Type: France, Puy-de-Dôme, commune de Saint-Genès-Champagnelle, Chatrat, 45.7301°N, 3.0132°E, 910 m, on *Fraxinus*, on *Ramalina fraxinea*, 9 April 2022, P. Pinault 77 (BR – holotype).

Mycobank: MB844632

Basidiomata resupinate over thin or thick, often irregular, frequently poor delimited gall-like swellings of the host thallus, waxy-gelatinous, pale orange-brown, 1–15 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, 3–3.5 µm diam.; haustoria unknown. *Hyme-*



Cyphobasidium ramalinicola, France, holotype. Resupinate basidiomata on the thallus of *Ramalina fraxinea*. Scale bar: 1 mm.



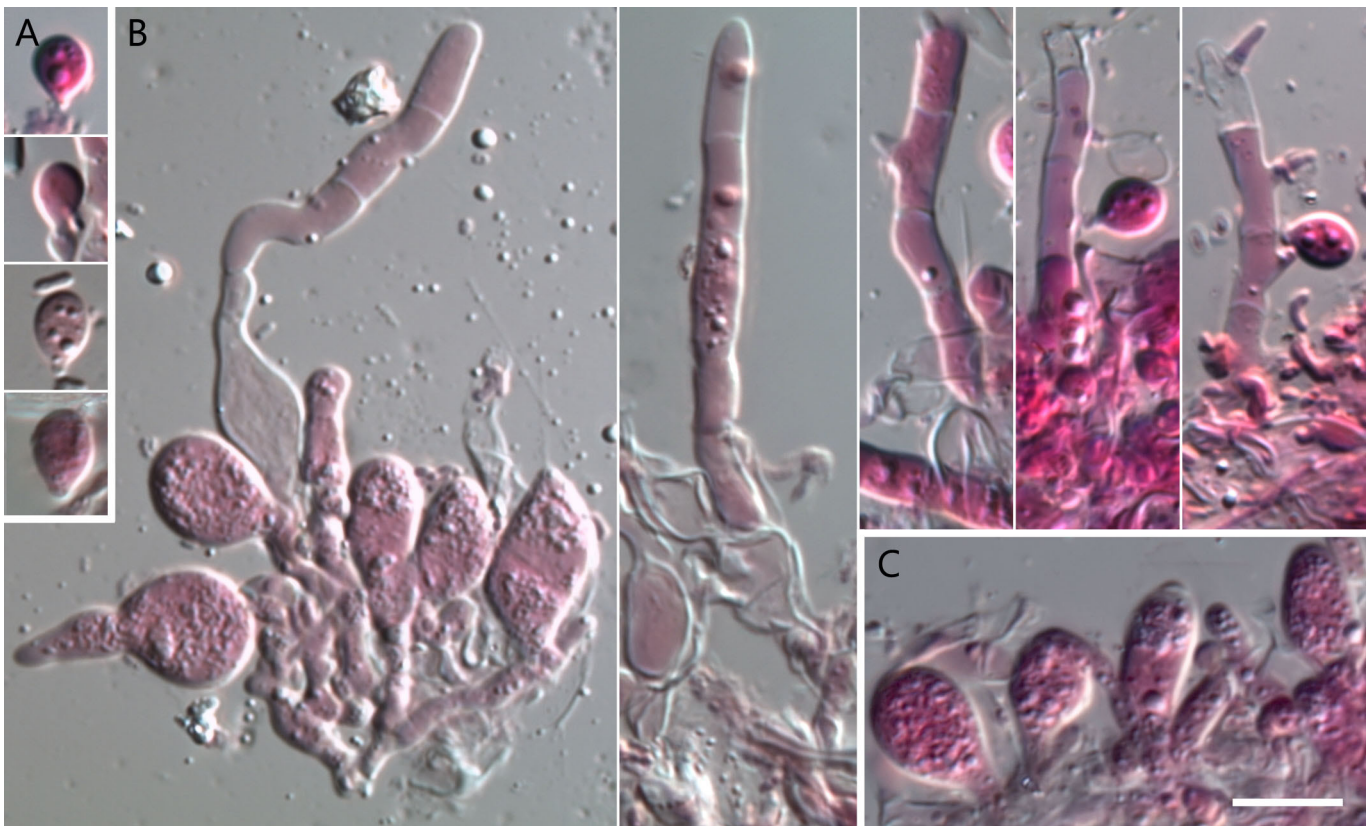
Cyphobasidium ramalinicola

cal, with a distinct apiculus at the lower end, $6\text{--}8.5 \times 4.5\text{--}6\ \mu\text{m}$. *Asexual stage* unknown.

Notes. This species looks very similar to *Tremella celata* and *T. tuckerae* and can hardly be distinguished from them without a microscopical examination. *Tremella ramalinae* is also abundant in the type specimen of *C. ramalinicola*, but is easily distinguished by the convex basidiomata with a constricted base that are pale brown, without an orange tinge. In some basidiomatal sections of the type specimen, basidia of both *C. ramalinicola* and *T. ramalinae* were observed side by side. The new species is distinguished from the other *Cyphobasidium* species by the large resupinate basidiomata, the relatively long meiosporangia and the relatively short probasidia.

Ecology and host. On the thallus of *Ramalina fraxinea*.

Distribution. Europe (France), known only from the type locality.



Cyphobasidium ramalinicola, France, holotype. A, Basidiospores. B, Probasidia and meiosporangia in different stages of development, and basidiospores. C, Probasidia. In phloxine. Scale bar: $10\ \mu\text{m}$.

Cyphobasidium usneicola (Diederich & Alstrup) Milanés, Diederich & Wedin

Fungal Biology 120: 1474 (2016); *Cystobasidium usneicola* Diederich & Alstrup, in Diederich, *Bibl. Lichenol.* 61: 25 (1996). *Type*: Canada, British Columbia, Vancouver Island, Bamfield area, head of fjord S of Bamfield, 48°49' N, 125°08' W, alt. c. 9–15 m, on *Usnea* sp., 30 Aug. 1994, V. Alstrup 22111 (C – holotype; BR – isotype).

Basidiomata subspherical, convex, with a constricted base, waxy-cartilaginous, pale, pinkish, brown or blackish, 0.3–1.5 mm diam. *Context hyphae* thick-walled, 2.5–3.5 µm diam., with clamp connections; subbasidial hyphae thick-walled, 2.5–3 µm diam.; haustoria unknown. *Hymenium* gelatinous, containing numerous probasidia; probasidial initials claviform, thick-walled, with a basal clamp connection. *Basidia*, when mature, composed of an elongate, claviform, thick-walled probasidium, 20–35 × 5.5–6 µm, and a cylindrical, often bent or irregular, thin-walled, 3-septate meiosporangium (upper part), up to 80 µm long and 3.5–4.5 µm diam.; epibasidia more or less perpendicular to the basidium, subulate, 1.5–2 µm thick, 4–7 µm long, distinctively refractive at the apex. *Basidiospores* ellipsoid to fusiform, more or less symmetrical, rarely a little bent, with a distinct refractive apiculus at the lower end, 8.5–10 × 4–5 µm. *Asexual stage* unknown.

Notes. Basidiomata of this taxon are reminiscent of those of *Biatoropsis* species on *Usnea*. As probasidia are also similar, some specimens identified as *B. usnearum* in the past may actually belong to *Cyphobasidium usneicola*. Our phylogenetic results combined with a remarkable macro-morphological variability suggests that *C. usneicola* is a species complex in need of further studies.

Ecology and hosts. On the thallus of *Usnea* sp., *U. articulata*, *U. brasiliensis*, *U. cornuta* s. lat., *U. galapagona*, *U.*



Cyphobasidium usneicola, Tenerife, Diederich 16700. Basidiomata on the thallus of *Usnea articulata*. Scale bar: 2 mm.

hawaiiensis, *U. madeirensis*, *U. cf. praetervisa*, *U. rubicunda*, *U. subfloridana*, *U. subscabrosa* and *U. undulata*.

Distribution. Europe (Finland; France; UK: Scotland), Macaronesia (Canary Islands: Gran Canaria, La Palma, Tenerife; Madeira), North America (Canada: British Columbia; Mexico; USA: Arizona, California, Washington), Central America (Costa Rica), South America (Bolivia; Colombia; Ecuador [incl. Galápagos]) and Oceania (Australia; Hawaii; Papua New Guinea).

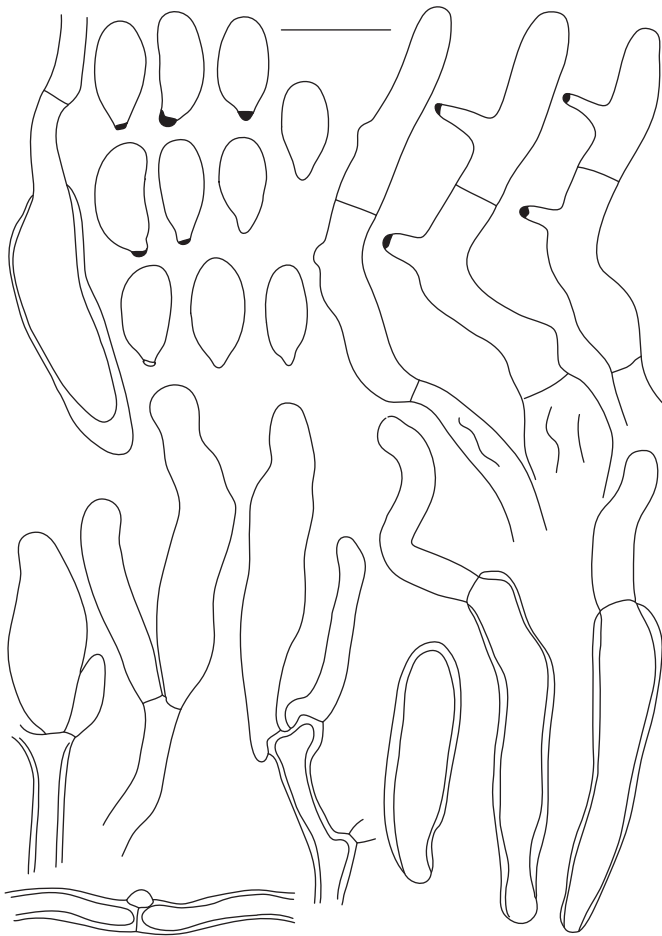
Additional specimens examined (all on *Usnea*). **Australia:** Queensland: Bunya Mts, 26.85°S, 151.5667°E, 800 m, on *U. undulata*, 1974, s. coll. (BR ex HO 55893); Manumbar, Manumbar Mill, 26.4°S, 152.5833°E, 250 m, on *U. rubicunda*, 1991, Stevens 7221 (BR). **Bolivia:** Dept. Chuquisaca, Prov. Belisario Boeto, close to Padilla, between Nuevo Mundo and Santa Rosa, 18°57'12"S, 64°16'36"W, 1830 m, transition between Bolivian-Tucuman forest and dry interandean vegetation, 2015, Etayo 29850 (LPB, herb. Etayo). Dept. Cochabamba, Prov. Carrasco, Parque Nacional Carrasco, Wayra Mayu close to Monte Punku,



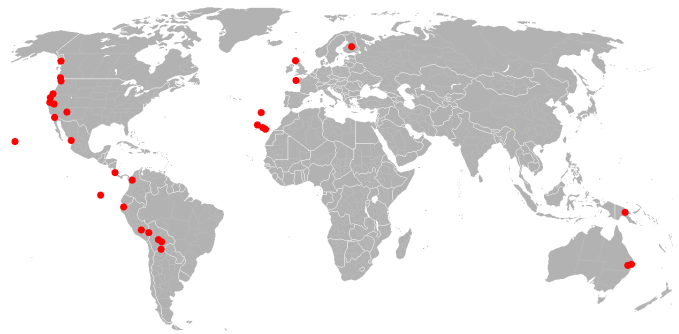
Cyphobasidium usneicola, Canada, British Columbia, isotype. Basidiomata on the thallus of *Usnea* sp. Scale bar: 500 µm.



Cyphobasidium usneicola, Costa Rica, Bandoni 12367. Basidiomata on the thallus of *Usnea* sp. Scale bar: 1 mm.



Cyphobasidium usneicola, Canada, holotype (modified from Diederich 1996). Probasidia, basidia, basidiospores and hypha with clamp connection. Scale bar: 10 µm.



Cyphobasidium usneicola (Hawaiian dot should be more to the west)

16°30'33"W, 1180 m, on *U. articulata*, 2007, Diederich 16700 (BR, S-F102402; also distributed in Hafellner *Lichenicolous Biota* 31, 2008). **Finland**: Savonia borealis, Pielavesi, W-Säviä, Kallioselkä, Rasi, 1949, Huuskonen (BR). **France**: *Finistère*: Saint-Rivoal, mont Saint-Michel de Brasparts, 48.3494°N, 3.9487°W, 330 m, on *U. articulata*, 2022, Bouffinier (BR). **Hawaii**: Hawaii, Volcano Golf Course, on *U. hawaiiensis*, 1992, Smith 920928001 (BR). **Papua New Guinea**: *Simbu Prov.*: Mount Wilhelm, Pindaunde valley, near lake Piunde, 5.78°S, 145.05°E, 3600 m, 1992, Diederich 10113, 10166 (BR); Mount Wilhelm area, Bundi Gap, on road Keglsugl-Bundi, 5.8°S, 145.15°E, 2800 m, 1992, Diederich 11025 (BR). **UK**: *Scotland*: Isle of Skye, Dunvegan, parc around castle, 2003, Diederich 15637 (BR). **USA**: *California*: Del Norte Co., SE of Crescent City, along Redwood Hwy/ U.S. Route 101 just N of Redwood Nat. Park, just E of Enderts Beach, 41°43.7'N, 124°08.6'W, 50 m, 1991, Tønsberg 14724 (BG L-37595). *Washington*: Clallam Co., Olympic Peninsula, Olympic Nat. Park, Ozette Lake N, North End, the S-facing shore of the peninsula S of Deer Bay, 48°08.1'N, 124°38.2'W, 10 m, 1999, Tønsberg 27095 (BG L-66329).

References. Diederich 1996, Millanes et al. 2016 [Diederich 2003, Kocourková et al. 2012, van den Boom & Clerc 2017].

Cyphobasidium sp. 1 on *Menegazzia*

Notes. A specimen on *Menegazzia* from S Chile (Etayo & Sancho 2008) slightly resembles *Cyphobasidium hypogymniicola*. Basidiomatal galls are initially 0.3–1 mm diam., very irregular, weakly bullate, later more flattened,



Cyphobasidium sp. 1 on *Menegazzia*

17°33'30"S, 65°16'08"W, 2750 m, lower montane Yungas cloud forest, 2014, Etayo 34294 (LPB, herb. Etayo). Dept. La Paz, Prov. Franz Tamayo, Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara and Keara Bajo, 14°42'09"S, 69°05'17"W, 3420 m, 2014, Flakus 25336 (KRAM, LPB). Dept. Tarija, Prov. Burnet O'Connor, close to Los Pinos, old road between Entre Ríos and Tarija, 21°25'57"S, 64°19'17"W, 2178 m, Bolivian-Tucuman forest dominated by shrubs, 2015, Etayo 32934 (LPB, herb. Etayo); id., 90 km from Tarija on old road between Entre Ríos and Tarija, 21°25'30"S, 64°19'07"W, 2265 m, 2015, Etayo 30606 (LPB, herb. Etayo). **Canary Islands**: *Gran Canaria*: By the road from Moya to Artenaria, between Las Fontanales and Los Pinos de Galdar, 28°02'N, 15°37'W, 1350 m, on *U. articulata*, 1994, Hafellner 53831, Santesson *Fungi Lichenicoli Exsiccati* 308 (BR), Hafellner *Lichenicolous Biota* 1, 2007 (BR). *La Palma*: Villa de Mazo, 28.6134°N, 17.8034°W, 975 m, on *U. articulata*, 2016, Wagner 16-15, 16-16, 16-17, 16-18, 16-19, 16-20 (BR); *ibid.*, on *Usnea* sp., Wagner 16-5, 16-6, 16-7, 16-8 (BR). *Tenerife*: S of Los Silos, c. 1 km W of Erjos, Monte del Agua, 28°19'N, 16°48'W, 1140 m, on *U. articulata*, 2007, Diederich 16648 (BR); S of Puerto de la Cruz, Valle de la Orotava, along road to Teide, between Aguamansa and Bermeja, 28°21'24"N,



Cyphobasidium sp. 1, Chile, Etayo 24486. Basidiomatal galls (arrows) on the thallus of *Menegazzia* sp. Scale bar: 1 mm.



Cyphobasidium sp. 1, Chile, Etayo 24486. Basidiomatal galls on soralia of *Menegazzia* sp. Scale bar: 1 mm.

up to 2.5 mm diam., sometimes with brown, bullate outgrowths. Microscopically, only immature basidia in a poor condition and remnants of overmature basidia have been observed. The specimen is thus not suitable for a type, and DNA sequencing failed. More material is needed to assess the identity of populations on that host genus.

Interestingly, Spribille et al. (2016, Fig. S3) have obtained sequences from a specimen of *Menegazzia subsimilis* from Japan that belong to *Cyphobasidiales*, but to another clade than *C. hypogymniicola*.

Ecology and host. On the thallus of *Menegazzia* sp. on *Nothofagus*.

Distribution. South America (Chile).

Specimen examined. **Chile:** Punta Arenas, Reserva forestal Magallanes, 53°09'28"S, 71°01'54"W, 350–500 m, on *Nothofagus pumilio*, on *Menegazzia*, 26 Jan. 2008, Etayo 24486 (herb. Etayo).

Reference. Etayo & Sancho 2008 as *Cystobasidium hypogymniicola*.

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Class *MICROBOTRYOMYCETES*

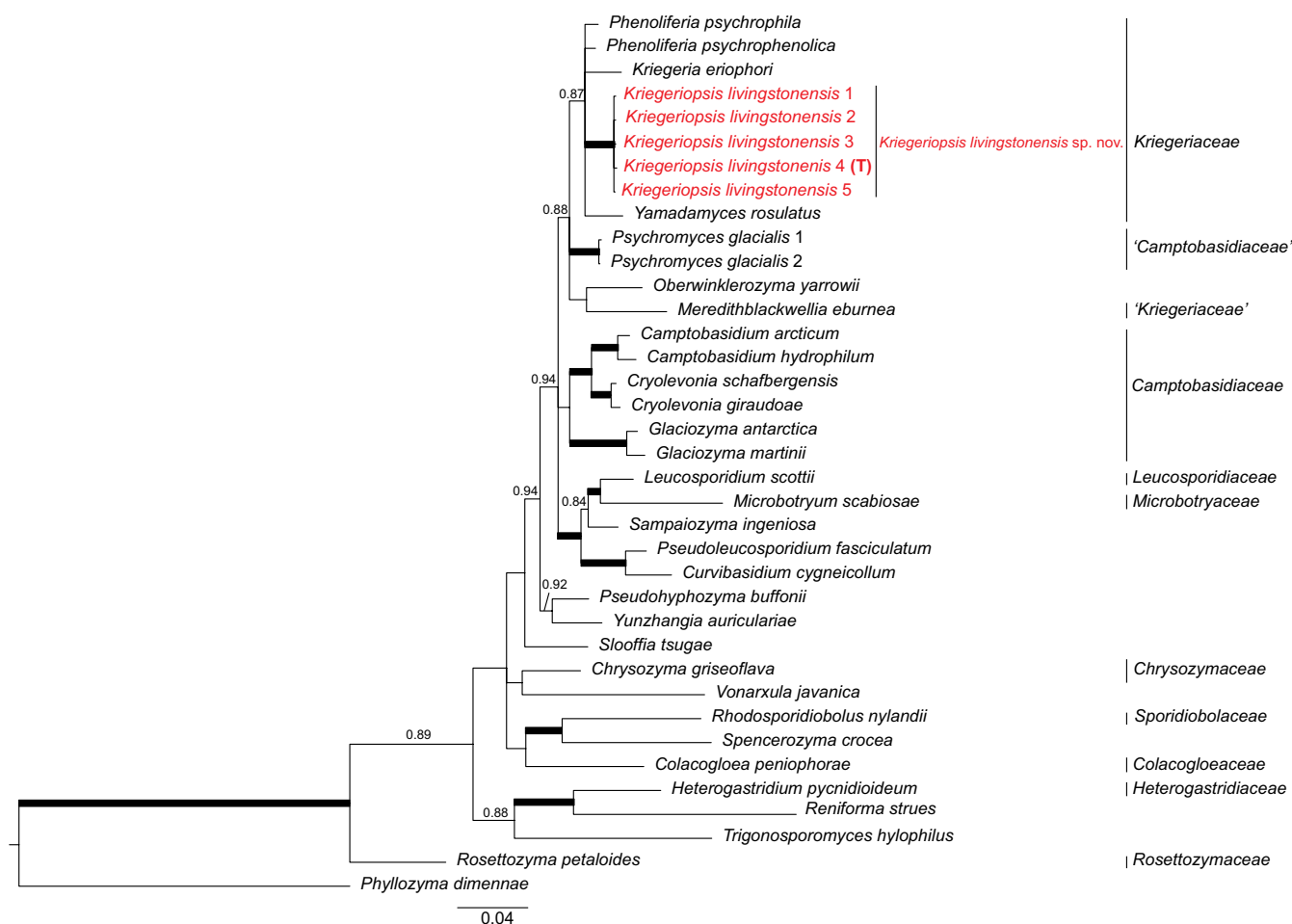
by P. Diederich, A. M. Millanes, J. Etayo & M. Wedin

Diederich, P., A. M. Millanes, J. Etayo & M. Wedin. 2022. Class *Microbotryomycetes*. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 325–330.

Introduction and phylogeny

Microbotryomycetes is a class of *Pucciniomycotina* comprising five orders (Oberwinkler 2017), plus the recently proposed *Heitmaniales* (Li et al. 2021) to accommodate the genus *Heitmania* (Liu et al. 2017). Three of these, *Heterogastridiales*, *Leucosporidiales* and *Sporidiobolales*, mainly include fungal or plant parasites and have specialised organelles, the colacosomes, developed at the contact area with the hosts (Bauer & Oberwinkler 1991). These organelles are missing in the orders

Kriegeriales and *Microbotryales*. *Kriegeriales* was considered to include two families, *Kriegeriaceae* with the genera *Kriegeria* (teleomorphic), *Meredithblackwellia* (yeasts), *Phenolifera* (yeasts) and *Yamadamyces* (yeasts), and *Camptobasidiaceae* with the genera *Camptobasidium* (teleomorphic) and *Glaciozyma* (yeasts) (Toome et al. 2013, Wang et al. 2016). However, Wang et al. (2016) already pointed out that *Camptobasidiaceae* was not supported within the order *Kriegeriales* and proposed



Fifty percent majority-rule Bayesian consensus tree from the analysis including ITS and nuLSU sequences, used to place the only lichenicolous species (*Kriegeriopsis livingstonensis* sp. nov., in red) in the *Microbotryomycetes*. Branches in boldface indicate Bayesian posterior probabilities ≥ 0.95 and ML-BS values ≥ 70 . Bayesian posterior probabilities ≥ 0.80 are indicated over the branches. The type specimen of the new species is indicated with '(T)'. Families representative of all orders included in the *Microbotryomycetes* are indicated to the right. Branch lengths are scaled to the expected number of substitutions per site.

to consider the family as incertae sedis. Perini et al. (2021) definitely considered *Camptobasidiaceae* as incertae sedis – excluded from the *Kriegeriales* – and included the new genus *Phychromyces* in the family. Based on a seven-genes phylogeny, the same authors (Perini et al. 2021) restricted the family *Kriegeriaceae* to *Kriegeria eriophori* because other taxa formerly included in the *Kriegeriaceae*, as *Phenolipheria* and *Yamadamyces*, appeared distantly related to *Kriegeriaceae* s. str. We describe here the first known lichenicolous species in the *Microbotryomycetes*, with an affinity for the family *Kriegeriaceae* s. lat., and confined to the thallus of *Tetramelas* aff. *graminicola* in Antarctica. Phylogenetic analyses and morphological features have shown that the new species cannot be accommodated in any of the known genera, and therefore a new genus *Kriegeriopsis* is described for it. Interestingly, many species closely related to *Kriegeriopsis* have a psychrophilic habit, and particularly all known species of *Glaciozyma* have also been described or reported from Antarctica (Turchetti et al. 2011).

MICROBOTRYOMYCETES R. Bauer et al.

Mycological Progress 5: 47 (2006). Type: *Microbotryum violaceum* (Pers.) G. Deml & Oberw.

Kriegeriaceae Toome & Aime

Mycologia 105: 489 (2013). Type: *Kriegeria* Bres.

KRIEGERIOPSIS LIVINGSTONENSIS Etayo, Diederich, Millanes & Wedin, gen. et sp. nov.

Diagnosis: Characterized by lichenicolous, gall-inducing, blackish basidiomata, the absence of clamps at all septa, claviform to subcylindrical basidia with three transverse septa, sporogenous loci formed in the upper part of the three lower basidial cells, but in the lower part of the apical cell, large, elongate ellipsoid, aseptate basidiospores able to germinate and produce secondary spores, and basidiospores that may eventually become septate and act as secondary basidia.

Etymology: From *Kriegeria* and *-opsis*, denotating a fungus resembling *Kriegeria*, and Livingston Island, where the new species has been collected.

Type: Antarctica, South Shetland Islands, Livingston Island, Caleta Argentina beach and boulders and soil far ahead of the beach, 62°40'20"S, 60°24'43"W, 0–10 m, on terricolous *Tetramelas* aff. *graminicola*, 2 March 2018, J. Etayo 31519 (MAF-Lich – holotype; BR, herb. Etayo – isotypes).

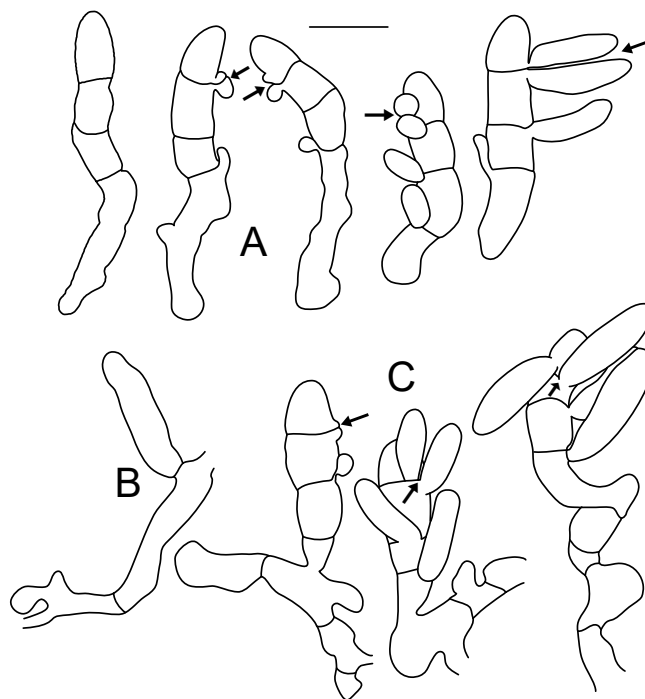
Mycobank: MB844633 (genus) and MB844634 (species)

Molecular data: yes (T, L). Number of species: 1–0–0.

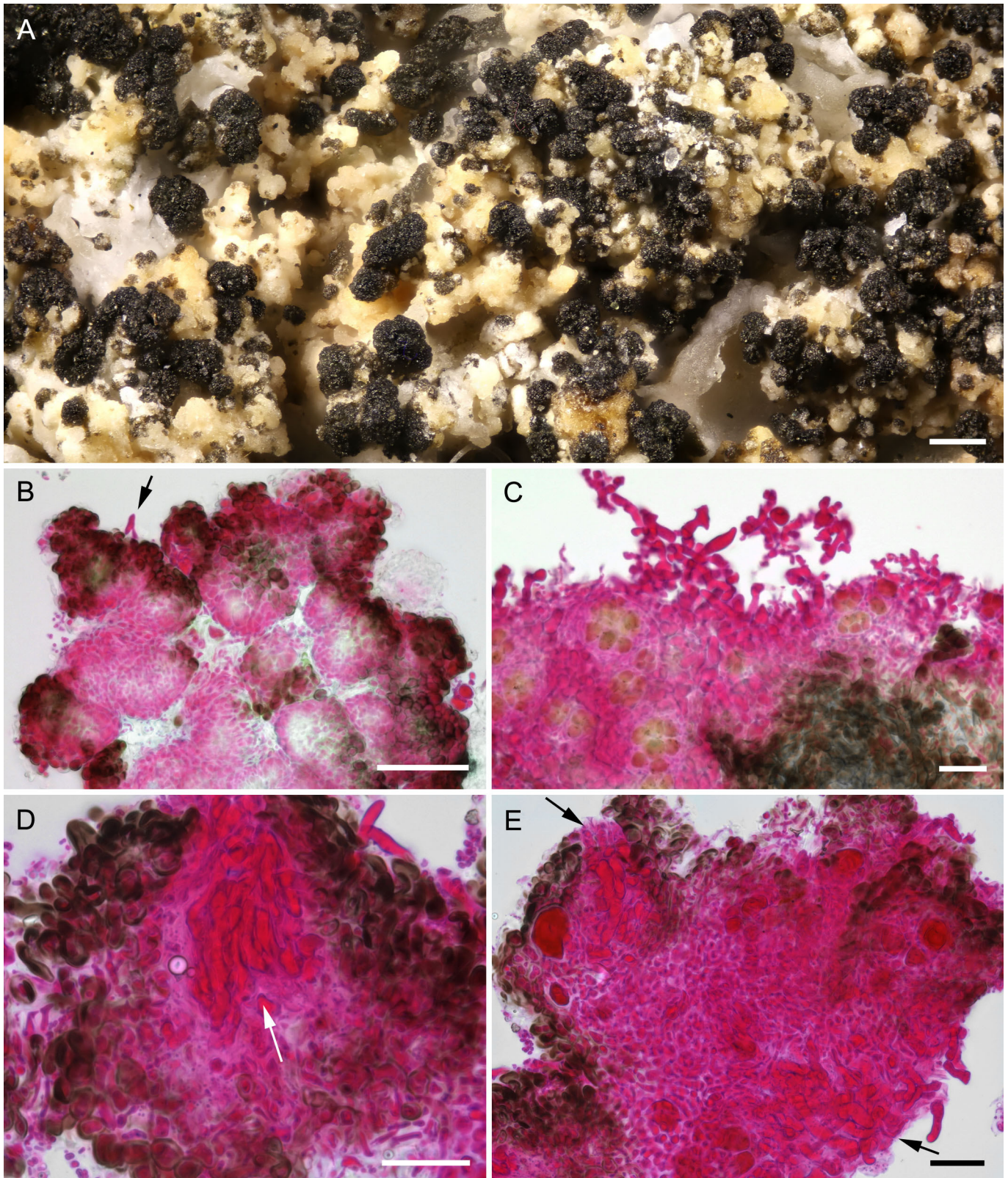
Basidiomatal galls superficial, pulvinate, first subspherical, later slightly tuberculate with a rough or irregular surface, sometimes opening in the centre and then becoming

irregularly concave, not gelatinous, dark brown to blackish, 80–300 µm diam. **Hymenium** developing within agglomerations of infected soredia, either between or inside soredia, composed of a mixture of aseptate basidial initials and thick-walled, frequently branched subhymenial hyphae, c. 1.5–2.5 µm thick; clamps missing; hyphidia absent; haustoria not observed. **Basidia**, when mature, elongate claviform to subcylindrical, with 3 transverse septa, without basal clamp, 30–40 × 4.8–6 µm; upper three cells each c. 5–9 µm long; lower cell elongate, basally narrower, 13–20 µm long; epibasidia and sterigmata missing; sporogenous loci formed laterally at the upper edge of each of the three lower cells (i. e., just below the septum) and at the lower edge of the upper cell (i. e., just above the upper septum), resulting in the two upper spores being adjacent. **Basidiospores** sessile, aseptate, hyaline, elongate ellipsoid, 10–18(–25) × 3.5–5(–5.5) µm, sometimes germinating with secondary spores; old spores still attached to the basidium remnants may in turn become transversely septate and act as secondary basidia producing basidiospores. **Conidial and yeast stages** unknown.

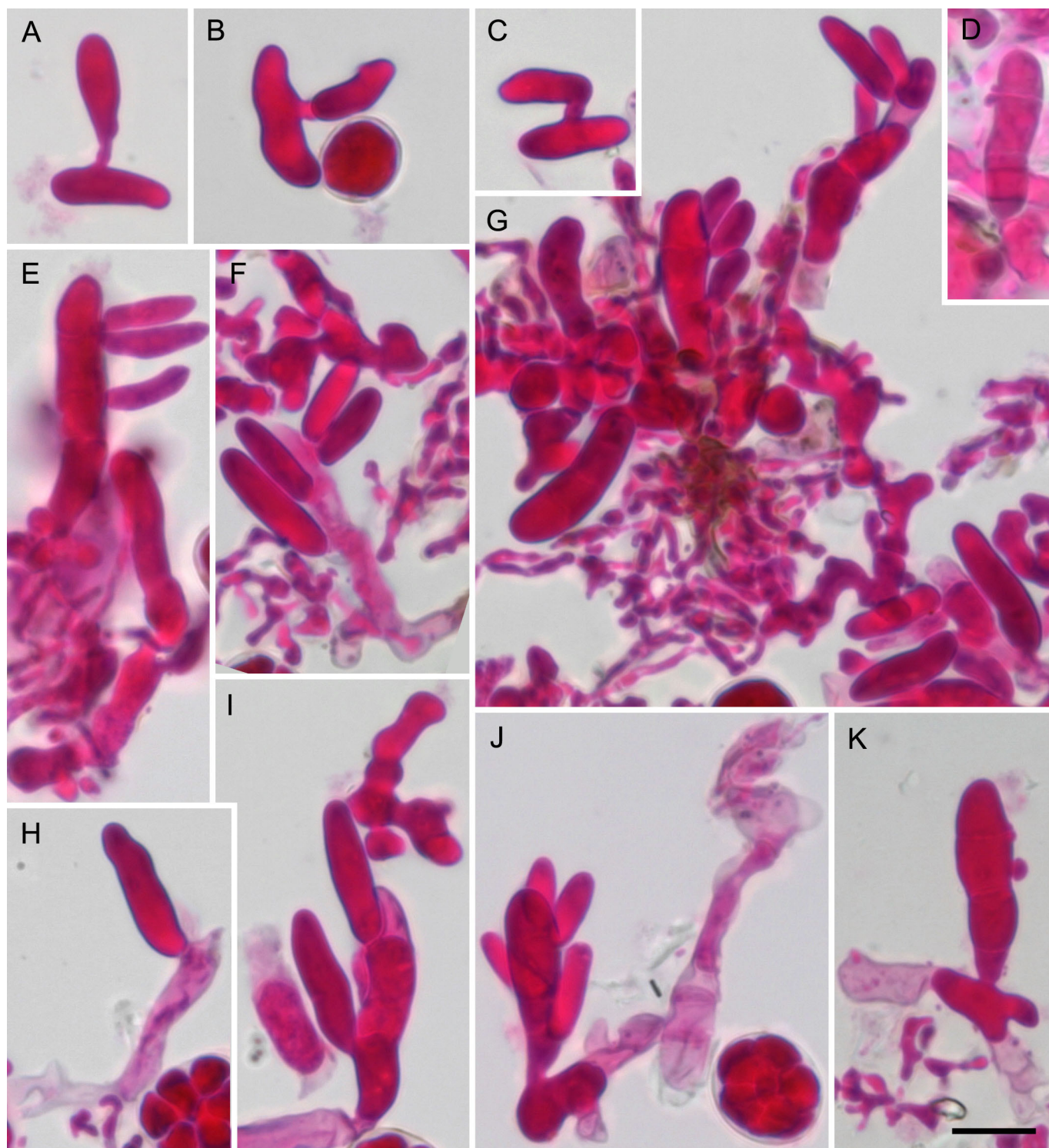
Notes. This is a very conspicuous fungus, with abundant, blackish basidiomatal galls developing over mainly sterile thalli of the host.



Kriegeriopsis livingstonensis, Antarctica, holotype. A, Basidia and basidiospores development; arrows indicate adjacent spores produced from the two apical basidial cells. B, Old basidium remnants (two lower cells) with an enlarged attached basidiospore that may eventually develop into a secondary basidium. C, Old basidium remnants (lower cells) with secondary basidia producing basidiospores. Scale bar: 10 µm.



Kriegeriopsis livingstonensis, Antarctica, A–C, holotype, D–E, Etayo 31367. A, Blackish basidiomatal galls on the sterile thallus of *Tetramelas* aff. *antarctica*. B, Squash preparation through young gall, showing an agglomeration of host soredia, the outer ones strongly pigmented, with a few basidia developed in the upper left part (arrow). C, Fertile hymenium with mature basidia emerging from gall. D, Small gall with almost mature basidia (arrow). E, Large open gall with mature basidia (arrows). B–E in phloxine. Scale bars: A = 200 μ m, B = 50 μ m, C–E = 20 μ m.



Kriegeriopsis livingstonensis, Antarctica, holotype. A–C, Basidiospores germinating with secondary spores. D, Young basidium with adjacent basidiospores initials. E–G, Hymenium with mature basidia originating from subhymenial hyphae, most with four mature basidiospores. H, Old basidium remnants (lower cells) with enlarged attached basidiospore that may eventually develop into a secondary basidium. I–K, Old basidium remnants (lower cells) with secondary basidia producing basidiospores. In phloxine. Scale bar: 10 μ m.



Kriegeriopsis livingstonensis

Phylogenetically, the genus is strongly supported and nested within a group including other genera in *Kriegeriaceae* s. lat., although this relationship has low phylogenetic support. The circumscriptions of the family *Kriegeriaceae* and of the order *Kriegeriales* are still unsettled (Wang et al. 2016, Perini et al. 2016). Our data – based on ITS and nuLSU only – do not allow to ascertain the position of *Kriegeriopsis* within *Kriegeriaceae* s. str. (restricted to *Kriegeria eriophori*, according to Perini et al. 2021) but at the same time would not allow either to assign the new genus to any existing family or to propose a new family for it. Therefore, we tentatively include *Kriegeriopsis* in a wider concept of *Kriegeriaceae* – as considered by Wang et al. (2016) – until further multigene analyses can shed light on its phylogenetic position within the *Microbotryomycetes*.

The new species and genus differ from related sexual taxa by several important morphological characters. (1) Basidiomata are lichenicolous and induce conspicuous blackish galls on host soredia. (2) Clamp connections are missing on all cells. (3) A yeast stage has not been observed. (4) Basidia are transversely 3-septate. (5) Basidiospores are formed at the upper edge of the three lower basidial cells and at the lower edge of the upper cell, resulting in two upper spores developing almost at the same place. (6) Basidiospores frequently germinate to form almost identical secondary spores. (7) Mature basidiospores still attached their basidia may in turn become septate and act as secondary basidia.

The *Kriegeriales* included two sexual species, *Kriegeria eriophori* Bres. in the *Kriegeriaceae* and *Camptobasidium hydrophilum* Marvanová & Suberkropp in the *Camptobasidiaceae*, all other species being known only from the yeast stage. *Kriegeria eriophori*, a parasite of *Scirpus sylvaticus*, differs from our new species by clamped hyphae and basidia, the presence of haustoria, basidiospores budding with yeasts and basidia with all sporogenous loci located at the upper edge of each cell, including the apical cell (Oberwinkler 2017). *Camptobasidium hydrophilum* is an aquatic species, differing from the new species by clamped hyphae, usually bent basidia (devoid of a basal clamp),

the production of numerous (up to 20) basidiospores from each sporogenous locus, the presence of conspicuous chlamydospores and a hyphomycetous asexual stage producing tetradial conidia (Marvanová & Suberkropp 1990); the asexual stage has repeatedly been isolated from leaf litter in streams, while the sexual stage is known exclusively from culture. The authors wrote that sporogenous loci in *C. hydrophilum* are all situated “just below the septa and at the apex”. Their line drawings and photographs (Figs. 1 and 2) clearly show, however, that the apical basidial cell may have two sporogenous loci, one at the base of the cell (thus resulting in spores adjacent to those from the second basidial cell from the top, as in our new species) and one apical. In none of both species are secondary basidia or basidiospores known.

The new taxon may easily be mistaken for a species of *Biatoropsis* or *Cyphobasidium* because of a striking resemblance of the basidia. However, basidia of *Biatoropsis* always develop long epibasidia, and basidiospores are ellipsoid, with a distinct apiculus. Basidia of *Cyphobasidium* are composed of two parts: a thick-walled ellipsoid probasidium and a thin-walled, cylindrical, transversely septate meiosporangium; short epibasidia, perpendicular to the meiosporangium, arise from the central part of each basidial cell.

In one specimen examined (Etayo 31367), basidia of an unknown *Tremella* species have also been observed.

Ecology and host. The new species seems to be confined to thalli of *Tetramelas* aff. *graminicola* growing over soil and plant debris over rocks in antarctic environments, on which it is so common and abundant that it is frequently impossible to find non-infected specimens. Søchting et al. (2004) also collected material of “*Buellia* aff. *graminicola*” in Livingston Island and found it to differ chemically from the holotype, suggesting a distinct species. Non-infected host soredia are pale brown, composed of subspherical to ellipsoid or irregular, thick-walled cells $4\text{--}10 \times 3\text{--}4.5\ \mu\text{m}$, with the exposed cells slightly brownish; when infected, they become larger and strongly convex, the exposed cells dark brown and thick-walled (wall $1\text{--}2\ \mu\text{m}$ thick), while inner cells remain hyaline. Thallus colour and apothecial development do not seem to be influenced by the presence of the fungus.

Distribution. Currently known only from Antarctica (South Shetland Islands: Livingston Island), but possibly widespread in the poorly known distribution area of the host. *Tetramelas graminicola* was previously known only from South Georgia (Giralt & Clerc 2011, Øvstedal & Lewis Smith 2001) and southern Chile, Navarino (Etayo et al. 2021). A photograph of the holotype of the host (Øvstedal & Lewis Smith 2001) does not show any infection by the fungus. Similarly, specimens from Chile are not infected.

Additional specimens examined. **Antarctica:** South Shetland Islands, Livingston Island, 2018, on *Tetramelas* aff. *graminicola* ('h' designates 'herb. Etayo'): Same locality as type, Etayo 31529 (h), 31531 (MAF-Lich, h); Caleta Alemana, rocky place E of the beach, 62°40'11"S, 60°24'09"W, 0–10 m, Etayo 31302 (h), 31367 (h), 31714 (h); Punta Polaca, on rocks near the coast, 62°39'42"S, 60°23'36"W, 0–10 m, Etayo 31382 (h); Sally rocks, large rocky place near the shore at both sides of a small beach, 62°42'07"S, 60°25'44"W, 1–5 m, Etayo 31450 (MAF-Lich); *ibid.*, mountain slope with many large stones between soil ledges, 62°42'04"S, 60°24'59"W, 60–70 m, Etayo 31455 (h), 31456 (h), 31458 (MAF-Lich, h), 31468 (MAF-Lich), 31469 (MAF-Lich, h); Lago Cazadora, track to Reina Sofia mountain from base Juan Carlos I, 62°39'47"S, 60°22'39"W, 70 m, Etayo 31481 (h); rocky place above Punta Polaca, 62°39'49"S, 60°23'40"W, 5–20–50 m, Etayo 31586 (h), Etayo 31591 (MAF-Lich); *ibid.*, 62°39'49"S, 60°23'51"W, 60–70 m, Etayo 31613 (h), 31615 (h); rocks and walls around the laboratory of Base Española, 62°39'45"S, 60°23'09"W, 15 m, Etayo 31633 (h); Base Española Juan Carlos I, rocky place behind zodiac ships hangar, 62°39'40"S, 60°22'57"W, 13–20 m, Etayo 31669 (h), 31679 (MAF-Lich); Punta Barnard, boulders near a great beach and in a near promontory, 62°45'08"S, 60°19'43"W, 0–5 m, Etayo 31697 (h).

Acknowledgments

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Supplementary material

<https://www.mnhn.lu/pub/FloraLichenicolousFungi>

Species incertae sedis

by P. Diederich, A. M. Millanes & J. Etayo

Diederich, P., A. M. Millanes & J. Etayo. 2022. Species incertae sedis. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 331–335.

Introduction

Diederich (1996) described the new *Syzygospora parmeliicola* for a gall-inducing heterobasidiomycete collected on *Hypotrachyna* in Costa Rica. Etayo (2002, 2017) reported several additional specimens of this species from South America, mainly based on similarly looking galls on *Hypotrachyna* hosts. An examination of two Colombian specimens showed that one of these is indeed immature *S. parmeliicola*, while the other is devoid of basidia. An Ecuador specimen has not been re-examined by us, as basidia were not observed by Etayo (2017).

This is an unusual fungus that was only provisionally described in *Syzygospora* by Diederich (1996) because of

the aseptate basidia; it differs from *Syzygospora* and also from the newly described *Zyzygomyces* by the size, form and development of basidia and epibasidia, and by the passively released basidiospores with a non-refractive apiculus. The phylogenetic position is currently unknown, as no sequences have been obtained. Here, we describe a second species, also collected on *Hypotrachyna*, but differing by larger and septate basidia, and differently looking basidiomatal galls. As both species are obviously closely related, and as morphology does not allow identifying their taxonomic position, we provisionally describe the second species also in '*Syzygospora*'.

Key to the lichenicolous species of '*Syzygospora*'

- 1 Basidia usually aseptate, $10\text{--}18 \times 3\text{--}5.5\ \mu\text{m}$; basidiomata inducing subspherical to bullate or lobate brownish galls *Syzygospora parmeliicola* (331)
- 1' Basidia transversely 1–2-septate, $15.5\text{--}27 \times 3.5\text{--}5.5\ \mu\text{m}$; basidiomata inducing dark brown to black galls, 0.3–0.7 mm diam., becoming cerebriform to tuberculate, up to 5 mm diam. *Syzygospora septata* (332)

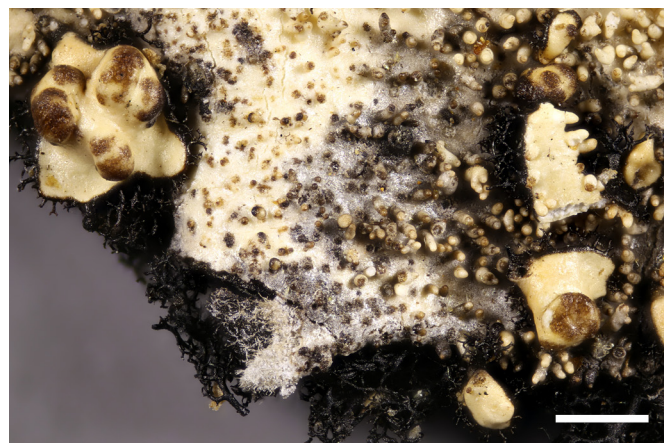
Syzygospora parmeliicola Diederich

Bibl. Lichenol. 61: 164 (1996). *Type*: Costa Rica, prov. San José, Cerro de la Muerte, along Panamerican Highway, 1 km N of Cerro Buenavista, on *Hypotrachyna bogotensis*, 20 March 1985, H. Sipman 20719 & A. Chaverri (B 52875 – holotype; BR – isotype).

Basidiomatal galls lichenicolous, subspherical to bullate or lobate, with a strongly constricted base, surface shiny and smooth, first concolorous with the host thallus, becoming medium to dark brown in fertile regions, 0.3–1.8 mm diam. *Context hyphae* thin-walled, 1–1.5 μm diam.; subbasidial hyphae 2–3 μm diam., clamps not observed; haustoria possibly present (see below). *Hymenium* hyaline, 45–50 μm thick, containing numerous probasidia; probasidial initials ellipsoid, with a basal clamp; hyphidia and cystidia absent. *Basidia*, when mature, ellipsoid, clavate or subcylindrical, aseptate, rarely with a transverse septum close to the apex, $10\text{--}18 \times 3\text{--}5.5\text{--}(7)\ \mu\text{m}$, with 1–2 epibasidia; epibasidia cylindrical to subulate, 1–1.5 μm diam., 1–3(–6) μm long; sterigmata non-refractive. *Basidiospores* ellipsoid, symmetrically attached to sterigmata, passively released, not

refractive at the point of attachment, $4\text{--}5.5 \times 3\text{--}4\ \mu\text{m}$, without a distinct apiculus. *Asexual stage* unknown.

Notes. Diederich (1996) reported tremelloid haustorial branches, with a subspherical mother cell, 2–3 μm diam., and a



Syzygospora parmeliicola, Costa Rica, isotype. Basidiomatal galls on the thallus of *Hypotrachyna bogotensis*. Scale bar: 500 μm .



Syzygospora parmeliicola, Colombia, Etayo 15839. Basidiomata on the thallus of *Hypotrachyna rhabdiformis*. Scale bar: 1 mm.



Syzygospora parmeliicola, Colombia, Etayo 15839. Basidiomata on the thallus of *Hypotrachyna rhabdiformis*. Scale bar: 1 mm.

haustorial filament, 0.5 μm diam., 1–2 μm long, which would represent a good argument to include this species within *Tremellomyces*. No haustoria were observed, however, during a recent re-examination of the isotype, nor in any other specimens of this group.

Ecology and hosts. On the thallus of *Hypotrachyna bogotensis* and *H. rhabdiformis*, inducing the formation of subspherical to bullate or lobate galls.

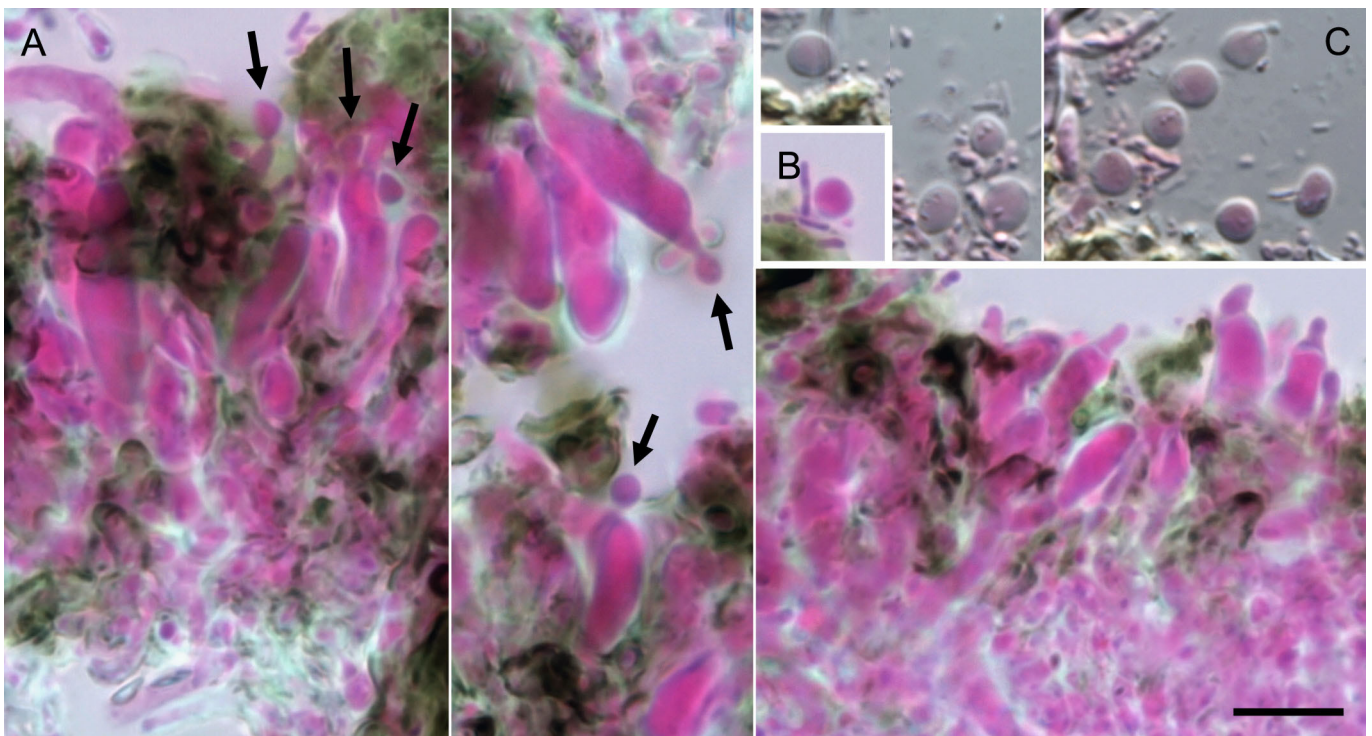
Distribution. Central America (Costa Rica) and South America (Colombia).

Additional specimen examined. Colombia: Nariño, munic. Pasto, corregimiento El Encano, Res. Nat. Tunguragua, SE lago La Cocha (Guanues), 2700 m, páramo azonal sobre turbera con *Espeletia cochensis* y *Blechnum loxense*, on corticolous *Hypotrachyna rhabdiformis*, 1998, Etayo 15839 (herb. Etayo).

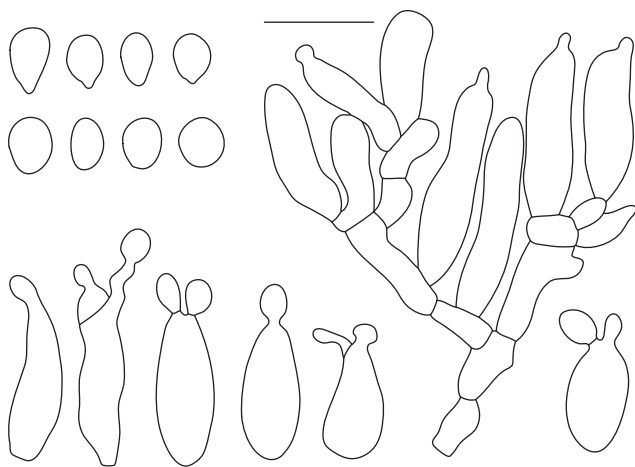
References. Diederich 1996 [Etayo 2002, 2017].

Syzygospora septata Diederich & Etayo, sp. nov.

Diagnosis: Characterized by gall-inducing, later larger, often tuberculate, dark greyish brown to blackish basidiomata, up to 5 mm diam., on the thallus of *Hypotrachyna*, a hymenium



Syzygospora parmeliicola, Costa Rica, isotype. A, Subbasidial hyphae, mature basidia and basidiospores (arrows). B–C, Mature basidiospores (C, using DIC optics). In phloxine. Scale bar: 10 μm .



Syzygospora parmeliicola, Costa Rica, holotype (modified from Diederich 1996). Basidia and basidiospores. Scale bar: 10 μ m.



Syzygospora parmeliicola

made of clavate to subcylindrical, 1–2(–3)-septate basidia, very short, cylindrical to subulate epibasidia, and passively released, ellipsoid, symmetrical basidiospores, $4\text{--}4.5 \times 3.5\text{--}4\text{ }\mu\text{m}$ (apiculus excluded).

Etymology: From *septatus*, septate, referring to the septate basidia.

Type: Mexico, from Refugio de Popocatépetl to repetidor, $19^{\circ}03'39''\text{N}$, $98^{\circ}37'57''\text{W}$, 3950 m, old *Pinus hartwegii* wood, on *P. hartwegii*, on *Hypotrachyna* sp., 2 Nov. 2008, J. Etayo 24890 (MEXU – holotype; BR, herb. Etayo – isotypes).

Mycobank: MB844635

Basidiomata lichenicolous, when young inducing convex galls with a non- or poorly constricted base, lateral part concolorous to the thallus, upper part dark brown to blackish, 0.3–0.7 mm diam., soon developing conspicuous dark greyish brown to blackish basidiomata with a matt, uneven surface, eventually becoming almost cerebriform or tuberculate, up to 5 mm diam. *Context hyphae* not observed; subbasidial hyphae thick-walled, $2.5\text{--}3.5\text{ }\mu\text{m}$ diam., clamps not observed; haustoria not observed. *Hymenium* hyaline,



Syzygospora septata, Mexico, holotype. Young basidiomatal galls (arrows) on the thallus of *Hypotrachyna* sp. Scale bar: 1 μ m.



Syzygospora septata, Mexico, holotype. Mature basidiomata on the thallus of *Hypotrachyna* sp. Scale bar: 1 μ m.

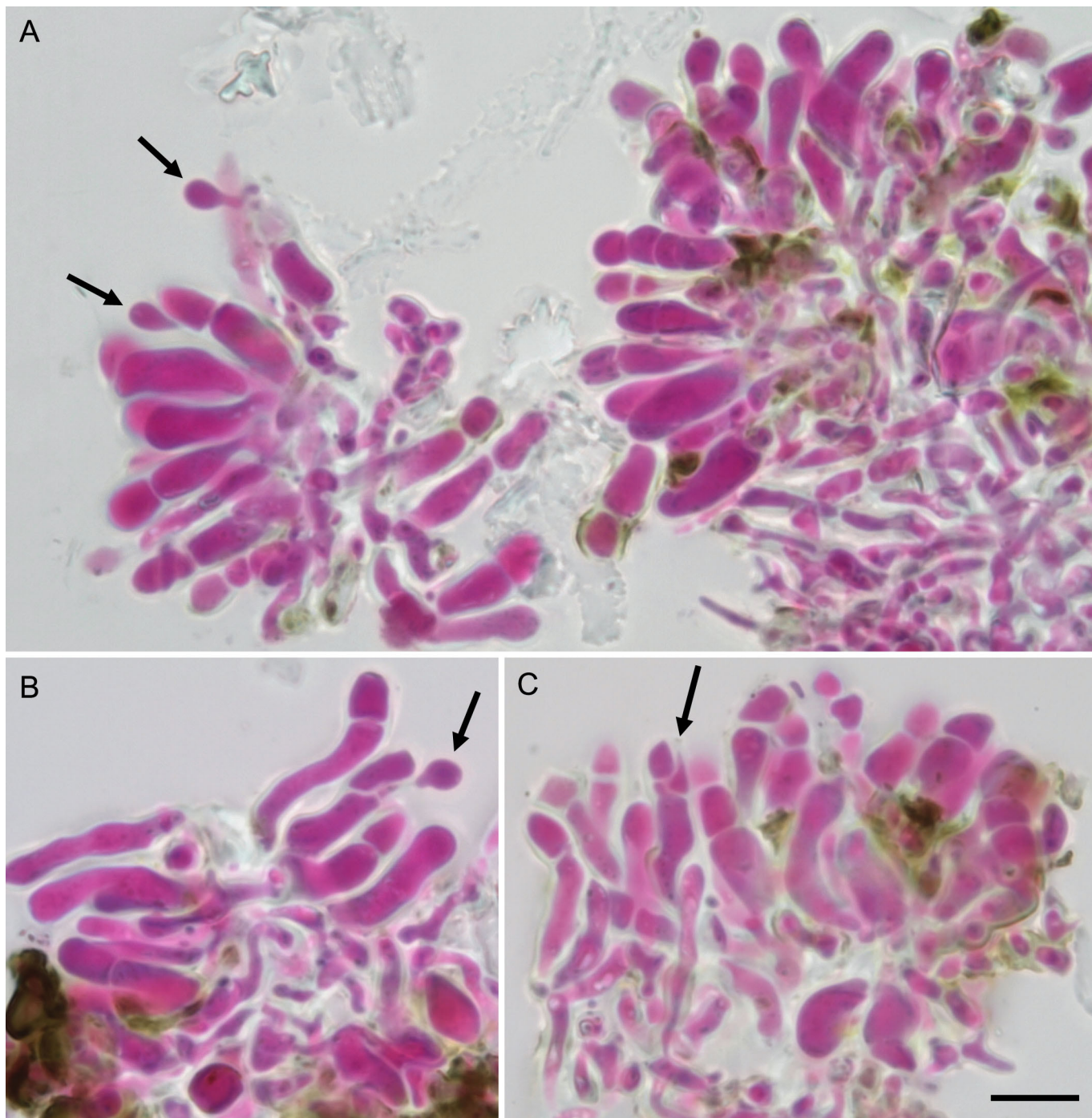


Syzygospora septata, Mexico, holotype. Large, mature, tuberculate basidioma on the thallus of *Hypotrachyna* sp. Scale bar: 1 μ m.

35–55 μ m thick, containing numerous elongate ellipsoid probasidia, basal clamps not observed. *Basidia*, when mature, clavate to subcylindrical, 1–2(–3)-septate, upper cell when 1-septate shorter than lower cell, $15.5\text{--}27 \times 3.5\text{--}5.5$

μm , lower cell(s) with a lateral epibasidium at the upper edge, upper cell with an apical epibasidium; epibasidia cylindrical to subulate, 1–2.5 μm diam., 2–5 μm long; sterigmata non-refractive. *Basidiospores* ellipsoid, symmetrically attached to sterigmata, passively released, with a large basal, non-refractive apiculus c. 1.5 μm long, 4–4.5 \times 3.5–4 μm (apiculus excluded). *Asexual stage* unknown.

Notes. This species cannot be included in any of the known lichenicolous genera of ‘heterobasidiomycetes’. Microscopically, it strongly resembles *Syzygospora parmeliicola*, known from the same host genus, *Hypotrachyna*, from which it is distinguished by the 1–2(–3)-septate (vs aseptate) basidia. Mature basidia are also longer (15.5–27 μm) than those of *S. parmeliicola* (10–18 μm). Macroscopically, both species are



Syzygospora septata, Mexico, holotype. Subbasidial hyphae, mature basidia, epibasidia (arrow in C) and basidiospores (arrows in A and B). In phloxine. Scale bar: 10 μm .



Syzygospora septata

very different: while basidiomata in *S. septata* are conspicuously developed, large, matt, with a rough to tuberculate surface, those of *S. parmeliicola* are reduced to a thin hymenium overgrowing small to bullate, shiny galls that are first con-

colorous to the host thallus, then become reddish brown. Because of the similarities with *S. parmeliicola*, we provisionally describe it here in the same genus, *Syzygospora*.

Ecology and host. On the thallus of an unidentified *Hy-potrachyna* species.

Distribution. North America ([Mexico](#)), known only from the type locality.

References

- Diederich, P. 1996. The lichenicolous heterobasidiomycetes. *Bibliotheca Lichenologica* 61: 1–198.
- Etayo, J. 2002. Aportación al conocimiento de los hongos liquenícolas de Colombia. *Bibliotheca Lichenologica* 84: 1–154.
- Etayo, J. 2017. Hongos liquenícolas de Ecuador. *Opera Lilloana* 50: 1–535.

Tremella-like bacterial galls

by P. Diederich, R. S. Common, J. Etayo, F. Berger & G. Marson

Diederich, P., R. S. Common, J. Etayo, F. Berger & G. Marson. 2022. *Tremella*-like bacterial galls. In: Diederich et al. (eds.), *Flora of Lichenicolous Fungi*, Vol. 1, *Basidiomycota*. National Museum of Natural History, Luxembourg: 337–342.

Introduction

We regularly examined lichenicolous galls that resemble those induced by heterobasidiomycetes, but that are devoid of basidia, hyphae with clamps, haustorial branches, etc. In many of these, abundant bacteria are constantly present, leading to the hypothesis that these galls may be induced by possibly lichen-specific bacteria. The presence of asymptomatic bacteria in lichen thalli has been documented in many papers and summarized by Grimm et al. (2021) who suggested that this microbiome is a ‘structurally integrated element of the classical lichen symbiosis’. However, ours here

seem to be the first report of bacteria confined to particular lichen hosts and forming special gall-like structures. We present a short morphological description of the most common lichenicolous bacterial galls. As it is currently not possible to name bacteria present inside these galls, we use a simple nomenclature, such as ‘Bacterial galls on *Parmelia saxatilis*’, allowing to integrate them in herbaria and to report them in publications. But the main aim of this chapter is to draw the attention to the existence of these fascinating structures and to encourage further research on them.

Bacterial galls on *Canoparmelia cryptochlorophaea*

Galls lichenicolous, dispersed or more rarely confluent, subspherical, base not or slightly constricted, surface shiny and smooth, medium brown when young, rapidly turning dark brown to black, 0.1–0.5(–0.7) mm diam. In section, containing host hyphae intermixed with numerous ellipsoid bacteria, c. $1.2\text{--}1.6 \times 1.0\text{--}1.2 \mu\text{m}$.

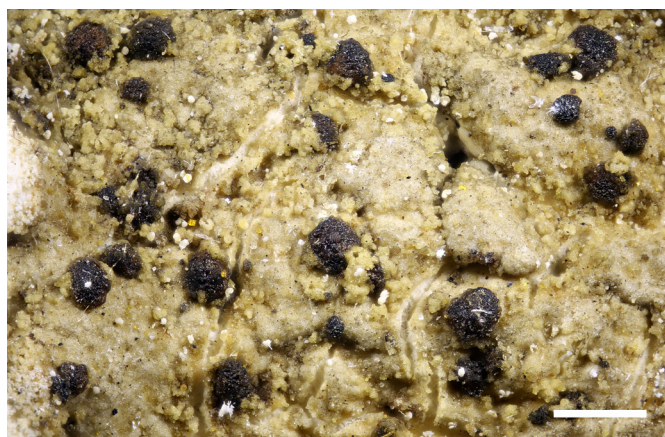
Notes. These galls resemble conidiomata of *Tremella conidiopunctelia* subsp. *parmelinellae* on *Parmelinella amazonica* in Florida, which are distinguished by being flat to slightly convex and distinctly larger, 0.4–1.2 mm diam. As no lichenicolous fungus has been observed in the *Canoparmelia* galls, but instead very abundant bacteria, we suggest that they may be induced by the presence of these bacteria.

Ecology and host. On the thallus of *Canoparmelia cryptochlorophaea*.

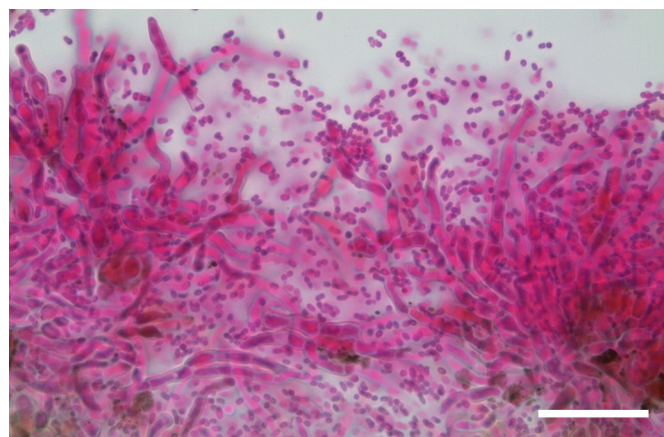
Distribution. North America (USA: Florida, Louisiana).



Bacterial galls on *Canoparmelia cryptochlorophaea*



Bacterial galls on *Canoparmelia cryptochlorophaea*, USA, Tucker 38189. Scale bar: 500 μm .



Bacterial gall on *Canoparmelia cryptochlorophaea*, USA, Tucker 38189. Bacteria and host hyphae in phloxine. Scale bar: 10 μm .

Specimens examined (all on *Canoparmelia cryptochlorophaea*). **USA:** *Florida*: Pasco Co., Zephyrhills, Samuel W. Pasco Recreation Area, 28.213°N, 82.157°W, 25 m, on windfall oak twigs, 2019, Common 10245C, 10245D (BR). *Louisiana*: West Feliciana Parish, between Thompson Creek and Hanmer Creek, Standifer property along La. Hwy 966, Sects. 71, 72, 30°47'30"N, 91°15'30"W, 2004, Tucker 38189 (BR, SBBG).



Bacterial galls on *Graphis scripta*

Bacterial galls on *Graphis scripta*

Galls lichenicolous, aggregated around host apothecia, subspherical to elongate, base not or slightly constricted, surface matt to slightly shiny, rough, orange brown, later dark brown to black, 0.1–0.2 mm diam. In section, containing host hyphae intermixed with numerous ellipsoid bacteria, c. $1.1\text{--}1.6 \times 0.9\text{--}1.1 \mu\text{m}$.

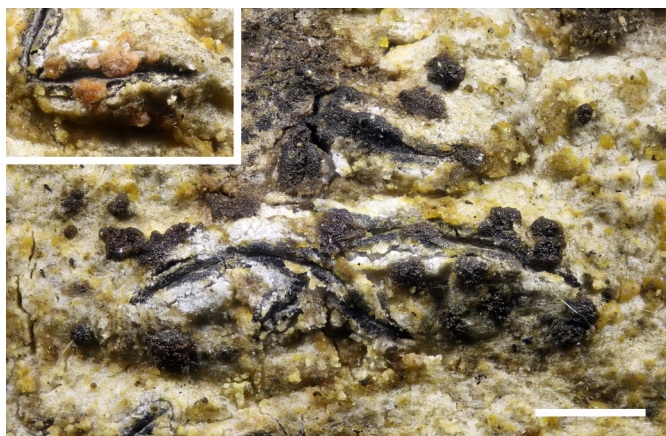
Notes. These galls differ from those on *Canoparmelia cryptochlorophaea* by being orange brown, becoming blackish only when old. Bacterial cells on both hosts have more or less the same size. Galls are entirely filled with bacteria, in addition to

a few host hyphae, while no lichenicolous fungus has been observed, and this indicates that they have probably been induced by these bacteria.

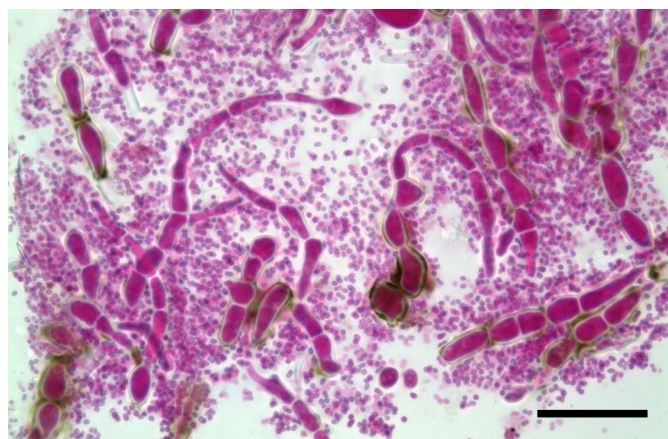
Ecology and host. On the thallus of *Graphis scripta*.

Distribution. Europe (Austria).

Specimen examined. **Austria:** Oberösterreich, Bz. Schärding, Waldkirchen, Ausgang Kl. Keßlbachtal, 48°27'52"N, 13°47'22"E, 290 m, on *Malus*, on *Graphis scripta*, 2016, Berger 31401 (herb. Berger).



Orange brown (upper left) and blackish bacterial galls on apothecia of *Graphis scripta*, Austria, Berger 31401. Scale bar: 500 μm .



Bacterial gall on *Graphis scripta*, Austria, Berger 31401. Bacteria and host hyphae in phloxine. Scale bar: 10 μm .

Bacterial galls on *Hyperphyscia* and *Physcia*

Galls lichenicolous, dispersed, either irregularly subspherical with a constricted base, or pustular to apothecium-like, with a margin formed by the host thallus and a concave apical opening exposing the bacterial layer, surface slightly shiny, orange brown, 0.05–0.4 mm diam. In section, containing numerous ellipsoid bacteria, c. $1.1\text{--}1.7 \times 1.0\text{--}1.2 \mu\text{m}$, mixed with host hyphae.

Notes. These galls are rather variable. While they are more or less subspherical in Diederich 16916, in the other three specimens, they imitate small host apothecia or pycnidia, having a host thallus margin, and a concave apical conical layer. As the bacterial cells, the host hyphae and the gall colour are identical in the four specimens, we consider them as representing the same kind of bacterial galls. They differ from bacterial galls on *Canoparmelia*, *Graphis* and *Phlyctis* by the orange brown galls that never become dark or blackish, while bacterial cells have the same size as on the other hosts. As the galls contain host hyphae and abundant bacteria, while no lichenicolous fungus has been observed, we suggest that they have been induced by these bacteria.

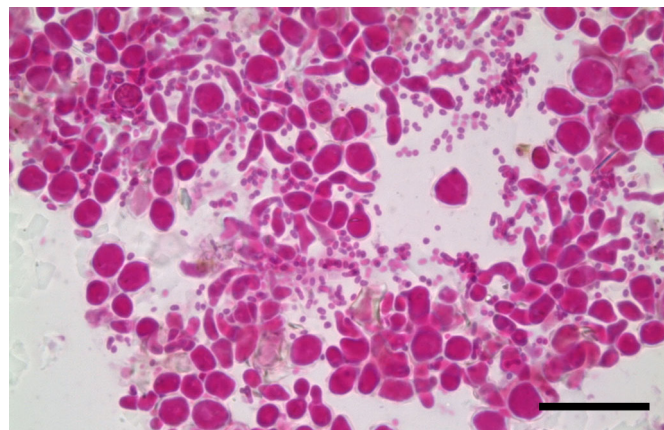
Ecology and hosts. On the thallus of *Hyperphyscia adglutinata*, *Physcia aipolia* and *P. tenella*.

Distribution. Europe (Belgium; Netherlands; Spain: Mallorca).

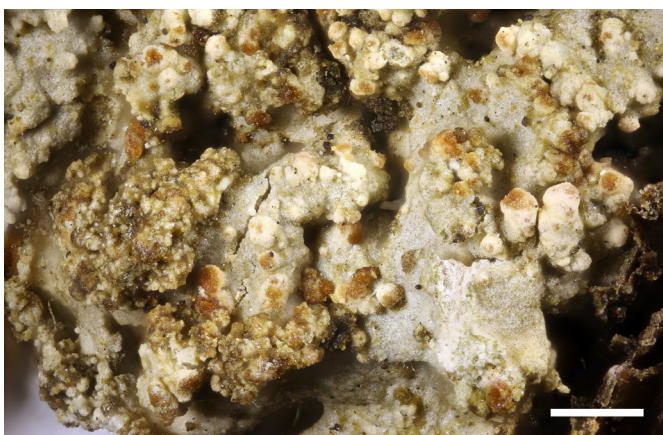
Specimens examined. **Belgium:** Damme, wandelweg van parking naar Kerk, C2.12.42, on *Tilia*, on *Hyperphyscia adglutinata*, 2008, Van den Broeck 2308 (BR). **Netherlands:** Noord-Brabant, SSW of Leende, SE of 't Leenderbos, edge of *Pinus* forest, on twig of *Larix*, on *Physcia tenella*, 2008, van den



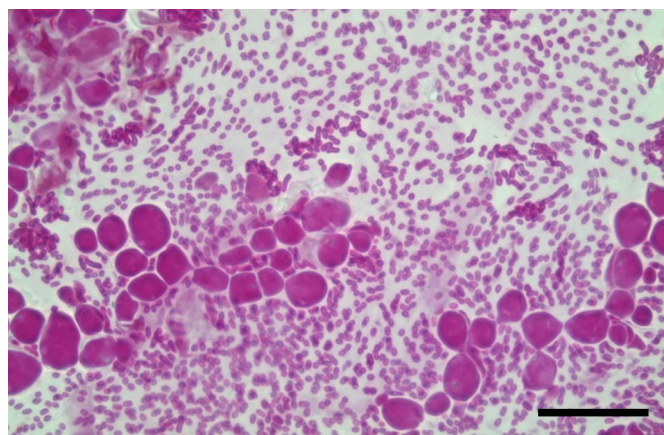
Bacterial galls on *Hyperphyscia adglutinata*, Spain, Mallorca, Diederich 16916. Scale bar: 500 μ m.



Bacterial gall on *Hyperphyscia adglutinata*, Spain, Mallorca, Diederich 16916. Bacteria and host hyphae in phloxine. Scale bar: 10 μ m.



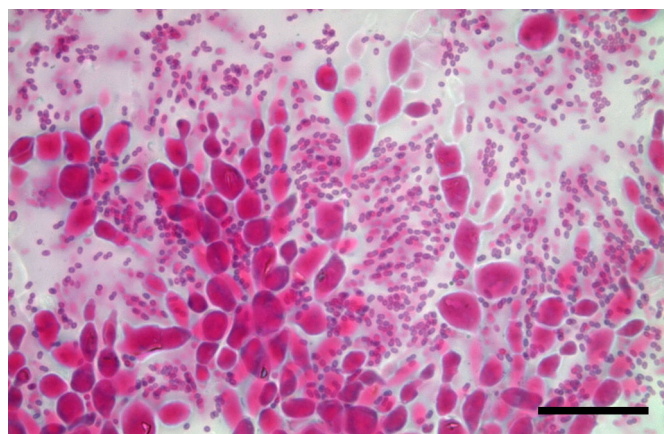
Bacterial galls on *Physcia tenella*, Netherlands, van den Boom. Scale bar: 500 μ m.



Bacterial gall on *Physcia tenella*, Netherlands, van den Boom. Bacteria and host hyphae in phloxine. Scale bar: 10 μ m.



Bacterial galls on *Physcia aipolia*, Netherlands, Van den Broeck 1002. Apothecium of the host on the bottom left. Scale bar: 500 μ m.



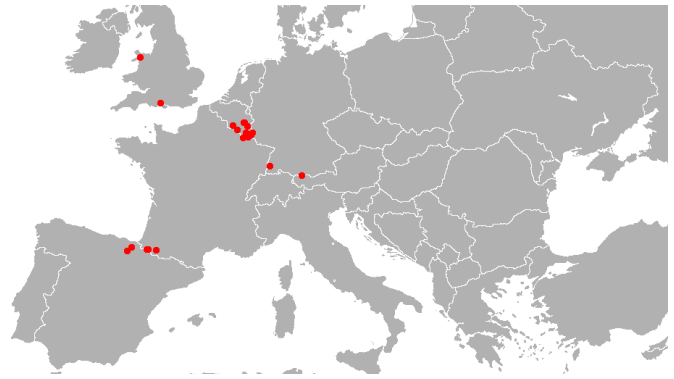
Bacterial gall on *Physcia aipolia*, Netherlands, Van den Broeck 1002. Bacteria and host hyphae in phloxine. Scale bar: 10 μ m.

Boom (herb. van den Boom). Zuid-Limburg, Sittard, Industriepark Noord, on *Quercus*, on *Physcia aipolia*, 2009, Van den Broeck 1002 (BR). **Spain:** Mallorca: NW of Bunyola, 1.5 km

SW of Orient, 39°43'30"N, 2°44'50"E, 430 m, on *Pinus halepensis* in forest, on *H. adglutinata*, 2010, Diederich 16916 (BR).



Bacterial galls on *Hyperphyscia* and *Physcia*



Bacterial galls on *Parmelia saxatilis*

Bacterial galls on *Parmelia saxatilis*

Galls lichenicolous, subspherical, often slightly flattened, when old irregularly formed, mainly made of host hyphae, first pinkish to brownish, rapidly dark brown, eventually black, surface matt, 0.3–0.8 mm diam. In section, containing numerous bacteria-like cells frequently agglomerated in small loculi that may open at maturity and then appear as small depressions of the gall surface; bacterial cells c. $1.2\text{--}1.6 \times 1.0\text{--}1.2\ \mu\text{m}$.

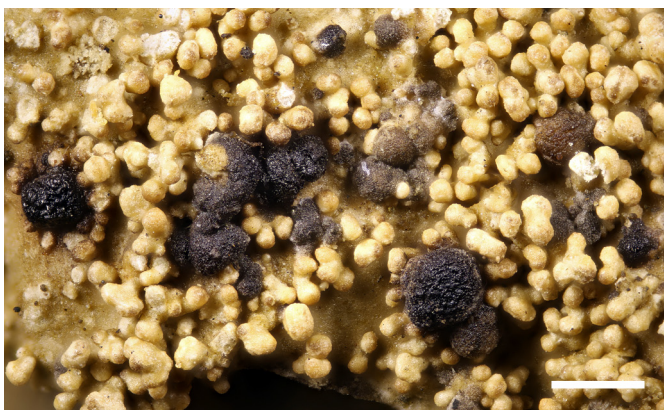
Notes. These galls are particularly common in Europe and are confined to thalli of *Parmelia saxatilis*, suggesting a long evolutionary history between the causal agent and the host. Macroscopically, they are reminiscent of *Tremella* galls, but they are devoid of any tremelloid cells, such as basidia. On the contrary, bacteria-like cells are always abundantly present, and we hypothesise that the galls are induced by these bacteria.

Ecology and host. On the thallus of *Parmelia saxatilis*.

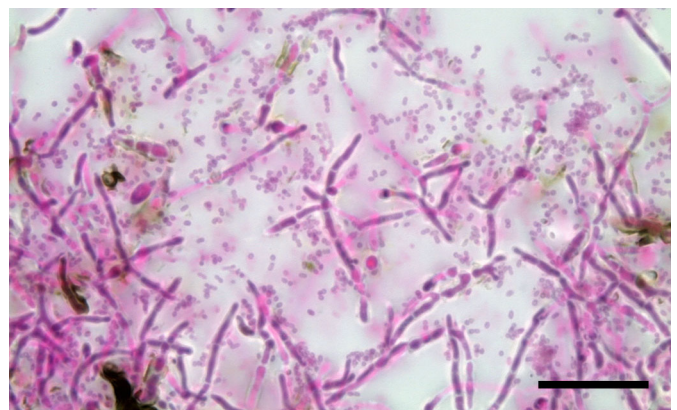
Distribution. Europe (Belgium; France; Germany; Luxembourg; Spain; UK).

Selected specimens examined. **Belgium:** Bomal, Le Calvaire, 2005, van den Boom 34680 (herb. van den Boom). Vallée de l'Hermeton, 2 km N of Gochenée, 2005, Ertz 8838 (BR). Vieuxville, ferme de Palogne, 1993, Sérusiaux (LG). NW of Bouillon, 2 km SSW of Uci-

mont, Moulin du Rivage, 1999, van den Boom 21927 (BR, herb. van den Boom). Lischert, 2001, Diederich 15124 (BR). W of Houffalize, 2 km SW of Nadrin, Le Hérou, 2010, Diederich 17138, 17117 (BR). **France:** *Meurthe-et-Moselle:* S of Colmery, 1980, Diederich 2814 (BR). *Pyrénées-Atlantiques:* S of Pau, E of Bielle, col de Marie-Blanque, 1990, Diederich 9310 (BR); S of Tardets-Sorholus, S^c-Engrâce, 1990, Diederich 9354 (BR); SW of Larrau, 1990, Diederich 9182 (BR); SSW of Oloron-Ste Marie, 1990, Diederich 9252 (BR). **Germany:** *Baden-Württemberg:* Baden, Südschwarzwald, Waldkirch, Kandel, 1985, Wirth 26598 (STU). *Bayern:* Allgäuer Alpen, Bärgründe Tal östlich Oberstdorf, 2003, Dornes & Werth PP-74 (KR). **Luxembourg:** NE of Garnich, 1998 & 2008, Diederich 13566, 16775 (BR). S of Schweich, 1999, Marson (BR). SE of Lasauvage, 1999, Diederich 13862 (BR). Vogelsmühle, Halerbaach valley, 2000, Diederich 14041 (BR). Pétange, Prénzeberg, 2003, Diederich 15602 (BR). Alzingen, 1986–89, Marson s. n., Diederich 8537, 9050 (BR). NE of Lintgen, 1986, Diederich 6855 (BR). SE of Oetrange, Pleitrangle, 1987, Diederich 7757 (BR). Steinsel, Gipsweiher, 2009, Diederich 16796, 16885 (BR). Strassen, 2013–14, Diederich 17494, 17741 (BR). **Spain:** *La Rioja:* Tierra de Cameros, way Villanueva de Cameros to Ortigosa, $42^{\circ}10'36''\text{N}$, $2^{\circ}41'04''\text{W}$, 1010 m, 1996, Etayo 14312 (herb. Etayo). *Navarra:* Entre Roncesvalles y Valcarlos, curva de herradura km 55,5, 1995, Etayo (herb. Etayo); Puerto de Lizarrusti entre Etxarri-Aranaz y Beasain, $42^{\circ}57'\text{N}$, $2^{\circ}05'\text{W}$, 565 m, 2017, Etayo 31126 (herb. Etayo). **UK:** *England:* SW of Southampton, New Forest, 1984, Diederich 5426 (BR). *Wales:* VC 48, Coed Cynevan, Ffestiniog, 1972, Coppins (K-IMI).



Bacterial galls on *Parmelia saxatilis*, Luxembourg, Diederich 13566. Scale bar: 500 μm .



Bacterial gall on *Parmelia saxatilis*, Luxembourg, Diederich 13566. Bacteria and host hyphae in phloxine. Scale bar: 10 μm .

Bacterial galls on *Parmotrema*

Galls lichenicolous, stipitate, mainly made of the medulla and cortex of the host lichen, apically enlarged, becoming pinkish or brownish, rarely blackish; apically 0.1–1 mm diam. In section, almost entirely white (host medulla), often with one or several bacteria-containing loculi that open at maturity and then appear as concave depressions of the gall surface. Squash preparations of galls mainly show host hyphae, while some regions are filled with ellipsoid bacteria, c. $1.2\text{--}1.7 \times 1.0\text{--}1.2\ \mu\text{m}$.

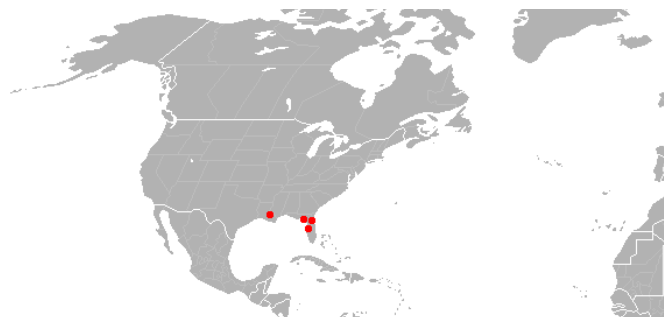
Notes. These galls are relatively common on *Parmotrema* in Florida and Louisiana. They were puzzling us over decades, as they never contain host pycnidia or lichenicolous fungi. Instead, they always contain small loculi filled with bacteria and opening at maturity. Although these galls may have a yet unknown cause and function, we postulate herewith that they are induced by the bacteria observed by us. In one specimen (Harris 41645), galls are developing at the apex of tiny isidia of *P. tinctorum* and are 0.05–0.15 mm wide, the same diameter or a little wider than the isidia; they contain numerous bacteria differing from those on other *Parmotrema* hosts by being imbedded in a gelatinous matrix, and are a little longer, c. $1.4\text{--}1.8 \times 1.0\text{--}1.2\ \mu\text{m}$.

Ecology and hosts. On the thallus of *Parmotrema* species, incl. *P. gardneri*, *P. praesorediosum* and *P. tinctorum*.

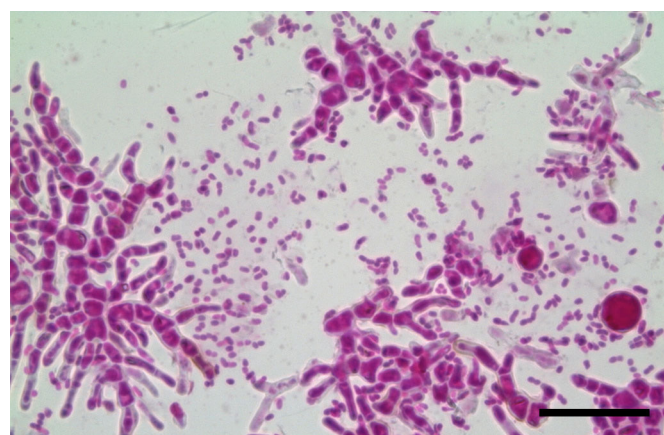
Distribution. North America (USA: Florida, Louisiana).

Specimens examined. **USA: Florida:** Lake Co., Green Swamp Wildlife Management Area, $28^{\circ}21'N$, $81^{\circ}57'W$, on *Parmotrema tinctorum*, 1998, Harris 41645 (NY). Pasco Co., Zephyrhills, Fairlawns Ave., $28.24826^{\circ}N$, $82.19246^{\circ}W$, 30 m, on *P. praesorediosum*, 2014, Common 9652 (BR); id., near post office, $28.24817^{\circ}N$, $82.18633^{\circ}W$, 45 m, on *Parmotrema* sp., 2015, Common 9888B (BR); id., Woodfern Ave., $28.2192^{\circ}W$, 35 m, on *P. praesorediosum*, 2019, Common 10347C (BR); id., Samuel W. Pasco Recreation Area, $28.213^{\circ}N$, $82.157^{\circ}W$, 25 m, on *P. praesorediosum*, 2019, Common 10240C (BR). Putnam Co., 5 mi SW of Palatka and 6

km W of Satsuma, Buckman Locks on the Cross Florida Canal, off the St. Johns River, on *P. gardneri*, 2015, Rosentreter 18757 (herb. Rosentreter). Taylor Co., Big Bend Wildlife Management Area, Tide Swamp Unit, along C. R. 361, 13 mi NW of bridge in Steinhatchee, 6.4 mi SE of Keaton Beach, $29^{\circ}46'N$, $83^{\circ}32'W$, on *P. praesorediosum*, 1996, Harris 39488A (NY). **Louisiana:** East Baton Rouge Par., Baird Drive, south Baton Rouge, $30^{\circ}22'45''N$, $91^{\circ}07'30''W$, on *P. praesorediosum*, 1994, Tucker 33545 (SBBG); ibid., on *P. gardneri*, 1982, Tucker 28697B (SBBG).



Bacterial galls on *Parmotrema*



Bacterial gall on *Parmotrema gardneri*, USA, Louisiana, Tucker 28697B. Bacteria and host hyphae in phloxine. Scale bar: 10 μm .



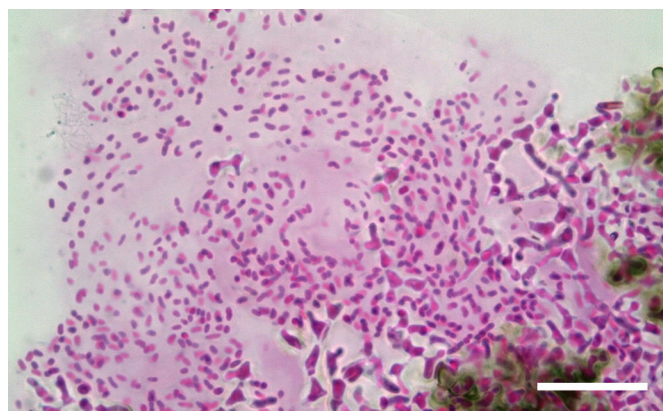
Bacterial gall on *Parmotrema praesorediosum*, USA, Florida, Common 10347C. Scale bar: 500 μm .



Bacterial gall on *Parmotrema praesorediosum*, USA, Florida, Common 10240. Scale bar: 500 μm .



Bacterial galls on isidia of *Parmotrema tinctorum*, USA, Florida, Harris 41645. Scale bar: 500 μ m.



Bacterial gall on *Parmotrema tinctorum*, USA, Florida, Harris 41645. Bacteria and host hyphae in phloxine. Scale bar: 10 μ m.

Bacterial galls on *Phlyctis argena*

Galls lichenicolous, dispersed or more rarely confluent, roundish or irregular in form, often with an undulate margin, with a flat, slightly shiny surface, dark reddish brown to black, 0.1–0.5 mm diam. In section, containing numerous ellipsoid bacteria, c. $1.2\text{--}1.6 \times 1.0\text{--}1.2 \mu\text{m}$.

Notes. The galls differ from those on *Canoparmelia cryptochlorophaea* and *Graphis scripta* by being flat, not subspherical. Bacteria in these hosts have more or less the same size. As the galls are filled with bacteria, while host hyphae are almost absent and no lichenicolous fungus has been observed, we expect that they have been induced by these bacteria.

Ecology and host. On the thallus of *Phlyctis argena*.

Distribution. Europe (Spain).

Specimens examined (on *Phlyctis argena*). **Spain:** País Vasco: Álava, Puerto de Herrera, subida hacia San León, $42^{\circ}35'46''\text{N}$, $2^{\circ}41'03''\text{W}$, 2009, Etayo 25026 (herb. Etayo); Álava, Sierra de Entzía, puerto de Opacua, 1994, Etayo (herb. Etayo); Gipuzkoa, Eibar, alto de Arate, $43^{\circ}12'18''\text{N}$, $2^{\circ}26'47''\text{W}$, 2014, Etayo 28622 (herb. Etayo). Navarra: Viscarret-Guerendiain, hayedo de Sorogáin, $42^{\circ}51'24''\text{N}$,



Bacterial galls on *Phlyctis argena*

$1^{\circ}23'57''\text{W}$, 2020, Etayo 32452 (herb. Etayo); S of Miguel de Aralar, $42^{\circ}58'\text{N}$, $1^{\circ}58'\text{W}$, 940 m, 2018, Etayo 31730 p. p. (herb. Etayo).

Acknowledgments

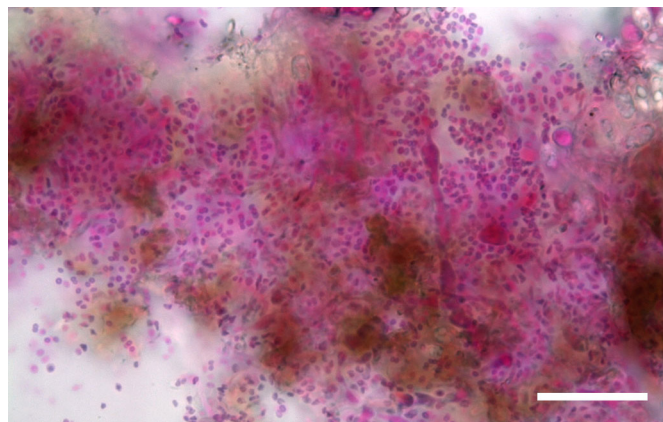
BR, K, KR, LG, NY, SBBG, STU, B. Coppins, P. Dornes, G. Marson, R. Rosentreter, E. Sérusiaux, S. Tucker, D. Van den Broeck, V. Wirth (loan of specimens).

Reference

Grimm, M., M. Grube, U. Schiefelbein, D. Zühlke, J. Bernhardt & K. Riedel. 2021. The lichens' microbiota, still a mystery? *Frontiers in Microbiology* 12: 623839.



Bacterial galls on *Phlyctis argena*, Spain, Etayo 25026. Scale bar: 500 μ m.



Bacterial gall on *Phlyctis argena*, Spain, Etayo 25026. Bacteria in phloxine. Scale bar: 10 μ m.

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Names of *lichenicolous fungi* are given in boldface and italics; **bacterial galls** are given in bold face; pages refer to the main occurrence. *Host names* are given in italics; pages refer to the 'Ecology and hosts' paragraph.

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