

# A peri-reefal brittle-star (Echinodermata, Ophiuroidea) assemblage from the Middle Jurassic of the northeast Paris Basin

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## Zusammenfassung

Disartikulierte Lateralplatten von Schlangensternen liefern, wie bereits mehrfach gezeigt wurde, ein viel vollständigeres Bild der Paläobiodiversität der Gruppe als die seltenen Funde von komplett erhaltenen Skeletten. Nichtsdestotrotz haben Vergesellschaftungen in Form von disartikulierten Lateralplatten bisher nur wenig Beachtung gefunden. Die vorliegende Arbeit stellt die erste umfassende Bearbeitung einer Schlangensternvergesellschaftung aus dem Bajocium (Mittleren Jura) dar, die vollständig auf disartikulierten Lateralplatten basiert. Das untersuchte Material entstammt Schlammresten von zwei Mergelschichten, die an einem Strassenaufschluss nahe Longwy, Frankreich, am nordöstlichen Rand des Pariser Beckens anstehen. Die Mergelschichten werden zur *Laeviuscula* Zone (unteres Bajocium) gestellt und werden als flachmarine, riffnahe Ablagerungen interpretiert. Es wurden insgesamt sieben Arten identifiziert, zwei davon als neu beschrieben: *Ophiotitanos aschmannicor* sp. nov. und *Ophiodoris recon-*

*ciliator* sp. nov. Letztere stellt den bisher ältesten Vertreter der wiedervereinigten Ophionereididae-Ophiochitonidae Gruppe dar. Eine dritte Art wird als neu erfasst, bleibt jedoch unbenannt. Die neue Gattung *Enakomusium* wird für mehrheitlich mesozoische Arten eingeführt, die eine gewisse Ähnlichkeit mit dem heute noch lebenden *Ophiomusium* vorweisen, jedoch die Grenzen der Gattungsdiagnose sprengen. Es wird gezeigt, dass sich die mittelljurassische Vergesellschaftung fundamental auf Familien- und noch stärker auf Gattungsebene von heutigen flachmarinen, riffnahen Äquivalenten unterscheidet. In der Tat wird sie von typischen modernen Tiefseegruppen oder Tiefseevertretern von Flachwassergruppen dominiert. Die hier beschriebene Vergesellschaftung bekräftigt somit die Beobachtung, dass sich flachmarine Schlangensternvergesellschaftungen seit dem Mesozoikum stark in ihrer Zusammensetzung verändert haben müssen.

## Abstract

Dissociated lateral arm plates of ophiuroids have been shown to produce a much more complete picture of the palaeobiodiversity of the group than the assessment of the exceptional finds of articulated skeletons. Yet, ophiuroid assemblages preserved as dissociated lateral arm plates have received only limited attention so far. Here, the first exhaustive survey of an ophiuroid assemblage entirely based on dissociated lateral arm plates is presented for the Bajocian (Middle Jurassic). The studied specimens were retrieved from sieving residues of two marl beds exposed at a roadcut site near Longwy, France, on the northeast margin of the Paris Basin. The marl beds are dated to the Early Bajocian *Laeviuscula* Zone and are interpreted as shallow-water peri-reefal deposits. A total of seven species were identified, two of which are described here as new: *Ophiotitanos aschmannicor* sp. nov.

and *Ophiodoris reconciliator* sp. nov. The latter is the oldest record of the re-united Ophionereididae-Ophiochitonidae group. A third species is recorded as new but left unnamed. The new genus *Enakomusium* gen. nov. is introduced to accommodate mainly Mesozoic species which are superficially similar to extant *Ophiomusium* but fail to match the diagnosis of the latter. The Bajocian ophiuroid assemblage is shown to differ fundamentally from modern shallow-water peri-reefal equivalents on family and, even more, genus level, being dominated by typical extant deep-sea taxa or deep-sea members of otherwise shallow-water groups. The assemblage presented herein thus adds to the growing evidence that shallow-water ophiuroid communities have undergone dramatic changes in composition since the Mesozoic.

## Résumé

Les plaques brachiales latérales dissociées d'ophiures, comme l'a été montré à plusieurs reprises, fournissent un aperçu beaucoup plus complet de la paléobiodiversité du groupe que les rares trouvailles de squelettes intacts. Néanmoins les associations d'ophiures conservées sous forme de plaques brachiales latérales dissociées n'ont reçu que peu d'attention jusqu'à présent. La présente contribution fournit la première étude exhaustive d'une population d'ophiures entièrement basée sur des plaques brachiales dissociées pour le Bajocien (Jurassique Moyen). Les spécimens examinés ont été extraits de résidus de tamisage de deux couches marneuses qui affleurent dans un talus près de Longwy, France, à la bordure nord-est du Bassin de Paris. Les couches marneuses sont datées de la zone à *Laeviuscula* (Bajocien inférieur) et ont été déposées dans un milieu peu profond à proximité de récifs de coraux. Au total sept espèces ont été identifiées, dont deux nouvelles: *Ophiotitanos aschmannicor* sp. nov. et *Ophiodoris reconiliator*

sp. nov.. La dernière représente le plus ancien membre du groupe réunifié Ophionereididae-Ophiochitonidae. Une troisième espèce est décrite comme nouvelle mais reste sans nom formel. Le nouveau genre *Enakomusium* est introduit pour les espèces majoritairement mésozoïques qui ressemblent superficiellement à l'*Ophiomusium* actuel mais qui ne se conforment pas à la diagnose de ce dernier. Il est montré que la population bajocienne diffère fondamentalement des populations actuelles équivalentes au niveau des familles et, surtout, au niveau des genres. En effet, la population comporte principalement des groupes typiques des mers profondes actuelles ou des membres vivant actuellement en mer profonde de groupes majoritairement trouvés dans les mers peu profondes. Ainsi, la présente étude consolide l'hypothèse selon laquelle les populations d'ophiures des mers peu profondes auraient subi de profonds changements au niveau de leur composition depuis le Mésozoïque.

## Introduction

Brittle stars (ophiuroids) are a major component of benthic communities in the modern oceans, abundantly occurring at all latitudes and depths, from the poles to the tropics and from the intertidal to the hadal trenches (Stöhr et al. 2012). Their importance as fossils, however, has long been underestimated. In fact, articulated ophiuroid skeletons, only exceptionally preserved as fossils (Ausich 2001), were commonly considered the only reliable source of evidence for species identifications. Recent systematic morphological analyses of previously neglected ophiuroid skeletal characters, in particular those pertinent to the spine-bearing lateral arm plates (Martynov 2010; Thuy & Stöhr 2011), however, have set a robust fundament to include disarticulated skeletal plates, abundantly occurring as microfossils in most marine sediments, as a promising new source of evidence to explore the fossil record of the group.

As a result, the assessment of ophiuroid palaeobiodiversity is currently witnessing a remarkable ascent, with more than one fifth of the accepted fossil ophiuroid species added during the last three years on the basis of dissociated lateral arm plates (Stöhr & O'Hara 2013). In addition, contributions of a more general scope have begun to explore the potential of ophiuroids as a model organism for

palaeoecological and macroevolutionary studies (e.g. Thuy et al. 2012; Thuy & Meyer 2012; Thuy 2013; Thuy et al. 2013).

Nevertheless, and in spite of fairly numerous taxonomic studies (e.g. Hess 1962, 1963, 1964, 1965a, 1965b, 1966, 1972, 1975a, 1975b; Hess & Meyer 2008; Kutscher & Hary 1991; Kutscher 1996; Kutscher & Jagt 2000; Kutscher & Villier 2003; Thuy 2005; Thuy 2011; Thuy & Kroh 2011; Thuy 2013; Thuy et al. 2013), the ophiuroid fossil record is still only patchily known. For some stages, only very few ophiuroid species have been reported so far. This is particularly the case when no exhaustive survey based on dissociated lateral arm plates is available for a given stage. In fact, inclusion of lateral arm plate evidence has been shown to dramatically expand knowledge on the fossil record of the group (e.g. Thuy 2005, 2013).

The Bajocian is one of these insufficiently explored parts of the ophiuroid fossil records, with, until recently, nine species known on the basis of articulated skeletons (Hess 1964; Thuy & Meyer 2012). In a recent survey of the family Ophiacanthidae, another three species and an unnamed record were added on the basis of dissociated lateral arm plates (Thuy 2013).

This study provides the first exhaustive survey of an ophiuroid assemblage entirely based on dissociated lateral arm plates for the Bajocian,

along with the study by Numberger-Thuy and Thuy in the present volume. The aim of the study is to contribute to a more complete picture of ophiuroid palaeobiodiversity, specifically targeting the species not known from articulated fossils, and thus to expand the alpha-taxonomical basis for further-reaching applications. The study furthermore attempts a comparison with modern equivalents, discussing possible implications for the evolutionary history of shallow-water ophiuroid communities.

## Geological context

The ophiuroid remains described herein were extracted from bulk sediment samples from a roadcut exposure near the southwestern end of the motorway bridge in Piedmont, Longwy, France. The site exposes ferruginous oolites at its base, assigned to the youngest part of the Mont-Saint-Martin-Formation and dated to the earliest Bajocian *Discites* Zone (Boulvain et al. 2001). The oolites are conformably overlain by a succession of marly to sandy limestones, rich in skeletal debris, assignable to the Longwy

Formation and dated to the early Bajocian *Laeviuscula* Zone (Boulvain et al. 2001). The lower part of the limestone succession includes two distinct beds of grey (freshly exposed) to brownish-yellow (weathered), clayey, unconsolidated marls, each approximately 0,4 m in thickness, separated by 1,5 m of coarsely-bedded limestone. The samples yielding the here-described ophiuroid remains were taken from the two marl beds in question.

These marl beds are highly fossiliferous, as evidenced by the abundant fragments of thick-shelled, strongly ribbed limoid and ostreoid bivalves, rhynchonellid and terebratulid brachiopods, cidaroid spines and isocrinid columnals on the weathered surfaces of the marls. Delsate (1993) briefly described elasmobranch teeth retrieved from sieving residues of the two marls beds and highlighted the micropalaeontological potential of the latter. A recent re-assessment of the ophiacanthid fossil record included two species from the assemblage (Thuy 2013) which is now exhaustively described herein.

The marl beds that yielded the ophiuroids were deposited during the early phase of formation of the Burgundy Platform (Boulvain et al. 2001; Brigaud et al. 2009, 2013). This large Bahama-type

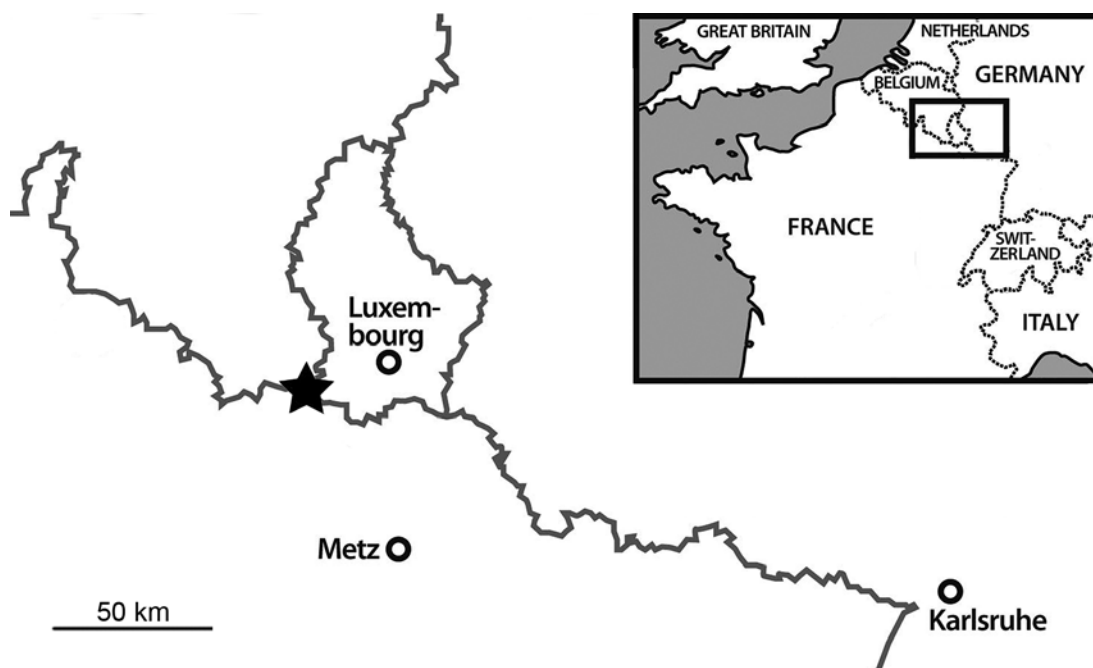


Fig. 1: Locality map showing the position of the studied site (marked by a star).

carbonate platform, at the northeastern margin of which the section was situated, supported widespread hermatypic coral patch reefs during its later development (in particular during the early Bajocian *Humpriesianum* Zone) (Lathuilière 2000). Although reef growth acme postdates the here-described ophiuroid assemblage by one or two ammonite zones, individual patch reefs of the same age as the ophiuroid assemblage are known from nearby sites such as the patch reef exposed between Grandcourt and Tellancourt on the French-Belgian border (Delsate, pers. comm. 2013; Thuy, previously unpublished). The immediate vicinity of coral build-ups therefore qualifies the here-described ophiuroid assemblage as peri-reefal. Sedimentological features of the marl beds, in particular the high clay content and low abrasion grade together with the high disarticulation of the fossils, suggest deposition at or slightly below storm wave base.

## Material and methods

The ophiuroid remains described herein were extracted from the sieving residues of screen-washed bulk sediment samples. No chemical treatment was necessary. The ophiuroid skeletal plates were picked from the > 250 µm residue fraction under a dissecting microscope. A total of 410 dissociated lateral arm plates were extracted. Selected specimens were cleaned in an ultrasonic bath and then mounted on aluminium stubs and gold-coated for scanning electron microscopy (SEM) using a JEOL Neoscope JMC-5000. Lateral arm plates of modern ophiuroids, used for morphological comparison, were extracted from complete specimens using household bleach (NaOCl), as described by Thuy and Stöhr (2011). Identifications, to species level, if possible, were exclusively based on the lateral arm plates (abbreviated in the descriptions as LAPs), following the terminology and guidelines of Thuy and Stöhr (2011). Higher-level classification follows Smith et al. (1995).

All type, figured and additional specimens were deposited in the collection of the Natural History Museum Luxembourg (MnhnL), under series number BU. Specimens previously described and figured by Thuy (2013) are housed at the Geoscientific Museum of the Georg-August-University Göttingen, Germany (GZG.INV.).

## Systematic palaeontology

Class Ophiuroidea Gray, 1840

Order Ophiurida Müller & Troschel, 1840

Family Ophiacanthidae Ljungman, 1867

**Genus *Dermocoma* Hess, 1964**

Type species: *Dermocoma wrighti* Hess, 1964, by original designation.

***Dermocoma longwyensis* Thuy, 2013**

\*2013 *Dermocoma longwyensis* Thuy, p. 147, figs. 26: 9–11.

**Material examined:** GZG.INV.78679; GZG.INV.78680; GZG.INV.78681 and GZG.INV.78682 (94 dissociated LAPs in total).

**Diagnosis:** Species of *Dermocoma* with relatively small LAPs displaying a well-developed, slightly undulose vertical striation; no discernible spurs on outer proximal edge in proximal LAPs; up to two, large, very poorly defined spurs on proximal edge in median to distal LAPs; single moderately well-defined spur on inner distal edge of proximal LAPs, two in median and distal LAPs; up to six large spine articulations; ventral lobe connected with distalwards projecting tip of outer surface stereom separating notches; ridge on inner side long, slender, devoid of thickened dorsal part.

**Remarks:** This species was described and figured in detail by Thuy (2013) on the basis of specimens which are part of the assemblage described herein.

**Genus *Alternacantha* Thuy & Meyer, 2013**

Type species: *Alternacantha occulta* Thuy & Meyer, 2013, by original designation.

***Alternacantha occulta* Thuy & Meyer, 2013**

\*2012 *Alternacantha occulta* Thuy & Meyer, p. 16, figs. 5–6.

2013 *Alternacantha occulta* Thuy, p. 127, figs. 22: 7–8.

**Material examined:** GZG.INV.78648; GZG.INV.78649 and GZG.INV.78650 (50 dissociated LAPs in total).

**Diagnosis (for LAPs):** Species of *Alternacantha* with large LAPs displaying a pointed to tongue-shaped, relatively narrow dorsal edge; outer

surface with a well-developed vertical striation; up to four moderately well-developed spurs on the outer proximal and inner distal edges; up to five spine articulations; distal edge of ventral arm plates evenly convex; distal edge of dorsal arm plates parabolic.

**Remarks:** This species was described and figured in detail by Thuy and Meyer (2013) and complemented by Thuy (2013) on the basis of dissociated LAPs which are part of the assemblage described herein.

Family Ophiidermatidae Ljungman, 1867

Genus *Ophiotitanos* Spencer, 1907

Type species: *Ophiotitanos tenuis* Spencer, 1907, by original designation.

*Ophiotitanos aschmannicor* sp. nov.

Fig. 2h-i

**Derivation of name:** Species named in honour of my longtime friends Nick ("ni") and Corinne ("cor") Aschman.

**Types:** BU 302 (holotype); BU 303, BU 304, BU 304 (paratypes)

**Other material:** BU 306 (79 dissociated LAPs)

**Type locality:** Roadcut at the southwestern end of the motorway bridge in Piedmont, Longwy, France (49° 32' 33.8274" N, 5° 45' 56.3574 E).

**Type horizon:** Marl beds in the lower part of the Longwy Formation, *Laeviuscula* Zone, early Bajocian, Middle Jurassic.

**Diagnosis:** Species of *Ophiotitanos* with large, stout LAPs displaying two well defined, prominent but only weakly, if , protruding spurs on the outer proximal edge, paralleled by two faintly prominent spurs on the inner distal edge; outer surface with finely meshed stereom and trabecular intersections developed into small tubercles; weak horizontal striation around the distal tips of the spurs of the outer proximal edge; five (proximal LAPs) to four (median to distal LAPs) small spine articulations in distinct notches of the distal edge, with strong dorsalward increase in size of the gaps separating the spine articulations. Proximal LAPs with small, prominent knob on inner side of ventro-proximal tip.

**Description of holotype:** BU 302 is a large, dissociated proximal LAP, almost 1.5 times higher than wide; convex dorsal and distal edges; evenly concave proximal edge; two large, prominent, horizontally elongate spurs, with poorly defined distal tip composed of slightly more densely meshed stereom, and sharply defined, pointed proximal tip composed of nearly massive (non-perforate) stereom; dorsal spur non-protruding and located in the centre of the proximal edge, ventral one slightly protruding, more slender than the dorsal one and located in the middle of the ventral half of the proximal edge; ventral seventh of LAP protruding ventro-proximalwards. Outer surface of LAP with finely meshed stereom, with trabecular intersections developed into small tubercles very weakly increasing in size towards the distal edge of the LAP; poorly defined area of slightly more finely meshed stereom encompassing spurs of proximal edge of LAP, with very weak horizontal striation between the distal tips of the spurs and above the distal tip of the dorsal spur. Five small, nearly equal-sized spine articulations sunken in shallow notches of the distal LAP edge, with strong dorsalward increase in size of gap separating the spine articulations, and dorsalmost gap conspicuously larger than remaining ones; notches of the spine articulations tightly encompassed by outer surface stereom and separated by distalward projections of the latter; spine articulations composed of a large, crescent-shaped dorsal lobe and a much smaller ventral lobe mirroring the dorsal one in shape; lobes composed of coarsely meshed stereom and proximally merged by a thin, irregularly denticulate ridge; muscle opening round and slightly larger than nerve opening, separated from the latter by a short, straight to slightly bent ridge.

Inner side of LAP with a large, conspicuous, oblique, prominent and sharply defined ridge, composed of more finely meshed stereom, widest between its dorsal and middle third; dorsal tip of ridge tongue-shaped, not reaching dorsal edge of LAP; ventral tip of ridge slightly less sharply defined but not merged with ventral portion of LAP; small, rounded, protruding knob composed of more densely meshed stereom near the ventro-proximal tip of the LAP. Inner side of distal edge with two large, well defined, weakly prominent, oval spurs composed of very densely meshed stereom; dorsal spur two times as high as ventral one. Ventral edge of LAP

with large, ventralwards to slightly ventro-distalwards pointing tentacle notch, sharply bordered distally and proximally by dorsalwards converging edges. Very weakly defined, shallow vertical furrow dorsalwards projecting from tentacle notch, but no perforations discernible.

**Paratype supplements and variation:** BU 303 is a large dissociated, proximal LAP; generally well in agreement with holotype; more than 1.5 times higher than wide; spurs on outer proximal edge closer to the ventral edge of the LAP; horizontal striation at dorsal edge of dorsal spur more clearly developed; gap between dorsalmost and second dorsalmost spine articulations conspicuously larger than remaining gaps.

Inner side as in holotype, except for less well defined and/or well preserved knob near ventro-proximal tip of LAP; vertical furrow dorsalwards projecting from tentacle notch with very faint, almost indiscernible perforations.

BU 304 is a dissociated median LAP; slightly wider than high; ventral portion only very weakly protruding ventro-proximalwards; irregularly concave proximal edge with two weakly defined, horizontally elongate, prominent but non-protruding ridge composed of slightly more densely meshed stereom than remaining outer surface. Four spine articulations, similar in shape and position to those of holotype; dorsalward increase in size of gaps separating spine articulations but dorsalmost gap not unproportionally larger than remaining ones.

Inner side of LAP with small, sharply defined ridge composed of more finely meshed stereom and with dorso-proximalwards pointing tip. Spurs on inner distal edge slightly less well defined than in holotype. Tentacle notch pointing ventro-distalwards rather than ventralwards. No knob discernible on ventral edge. Single, irregular perforation dorsally bordering tentacle notch, no furrow discernible.

BU 305 is a dissociated distal LAP, almost 1.5 times wider than high, rectangular in outline; dorsal, ventral and distal edges nearly straight; proximal edge irregularly concave, tapered, with two large, hardly recognisable and very weakly prominent spurs on the ventro-distal and dorso-distal tips; outer surface ornamentation as in holotype, including weak horizontal striation between spurs. Four spine articulations of same

shape and position as in holotype but without dorsalward increase in size of gaps between them; ventralmost spine articulation at some distance from distal edge; ventro-distally bordered by perforation.

Inner side with large, conspicuous contact surfaces with opposite LAP; very small, inconspicuous but sharply defined ridge, claw-shaped, with proximalwards bent, pointed dorsal tip; two moderately large, poorly defined and hardly prominent spurs composed of slightly more densely meshed stereom on inner distal edge. Large, round tentacle perforation between the distal and middle third of the inner side, proximally bordering the ventral spur. No other perforation or furrow discernible.

**Remarks:** The above described specimens belong to a LAP type which is commonly found in Mesozoic ophiuroid assemblages and generally placed in the Ophiidermatidae. Formally named types are *Ophiiderma? waliabadensis* Kristan-Tollmann, Tollmann & Hamedani, 1979 from the Rhaetian of Iran, *Ophiiderma? delsatei* Thuy, 2005 from the Hettangian of Belgium, *Ophiiderma? dentata* Kutscher, 1988 from the Pliensbachian of Germany, *Ophiarachna? liasica* Kutscher, 1996 from the Toarcian/Aalenian of Germany, *Ophiiderma? spectabilis* Hess, 1965 from the Oxfordian of France, and the Cretaceous species assigned to *Ophiotitanos* (e.g. Spencer 1907; Hess 1960b; Jagt 2000; Thuy & Kroh 2011). LAPs of the type in question share a relatively large size, stout architecture, conspicuous spurs on the outer proximal and inner distal edges, small to medium-sized spine articulations sunken in notches of the distal edge and a single, conspicuous, generally tongue-shaped ridge on the inner side.

The here described LAPs differ from *Ophiiderma? waliabadensis*, *Ophiiderma? delsatei* and *Ophiiderma? dentata* in displaying only two spurs on the outer proximal and inner distal edges. *Ophiiderma? spectabilis* and the *Ophiotitanos* species lack the knob on the inner side of the ventro-proximal tip and have more numerous spine articulations and a weaker dorsalward increase in size of gaps separating the spine articulations. Closest similarities are shared with *Ophiarachna? liasica*, in particular in terms of number and arrangement of spine articulations. LAPs of the latter, however, differ from the here described specimens in a less strongly ventro-proximalwards protruding ventral portion and a vertical striation on the outer surface.

Another fossil ophiuroid worth mentioning here is an articulated skeleton from the Aalenian of France described as *Ophiuricoma mazenoti* Valette, 1929. Unfortunately, neither the illustrations nor the description provide sufficient details for a robust taxonomic assessment of the specimen in question. The arm skeleton, however, suggests closeness to the Cretaceous *Ophiotitanos* species and allied LAP types. Of relevance here is that the arms of *O. mazenoti*, exposing the ventral side, display four arm spines, which implies a higher number of arm spines than in the here-described LAPs in which the ventral half displays three spine articulations at most.

The above described LAPs are incompatible with any known ophiuroid species and are thus best accommodated in a new species. The highly characteristic spine articulation morphology leaves no doubt as to the ophiidermatid affinities of the new species. On genus level, however, matters are less clear-cut. Previous Mesozoic ophiidermatid records were either preliminarily assigned to extant genera (in particular *Ophioderma*) or placed in the extinct genus *Ophiotitanos*. The ophiidermatid affinities of the latter were recently re-affirmed by Thuy et al. (2013) on the basis of LAP morphology. It should be stressed, however, that a decisive higher taxonomic assignment of *Ophiotitanos* can only be made on the basis of a detailed re-assessment of *O. tenuis*, the type species of the genus.

The LAP morphologies of extant ophiidermatid genera have received only little attention so far, apart from the analysis of Thuy and Stöhr (2011) including three species of *Ophioderma*. Preliminary previously unpublished observations on macerated LAPs, however, suggest that the here described fossil LAPs differ from small-spined modern ophiidermatids in displaying a low number of spine articulations with a strong dorsalward increase in size of the gaps separating them. Since these features are also found in the LAPs of *Ophiotitanos tenuis* (Thuy, previously unpublished), the here described LAPs thus seem best accommodated in this genus, extending its fossil to the Middle Jurassic.

Family Ophiuridae Müller & Troschel, 1840

Subfamily Ophioleucinae Matsumoto, 1915

**Genus *Sinosura* Hess, 1964**

Type species: *Acrourea brodiei* Wright, 1866, by original designation.

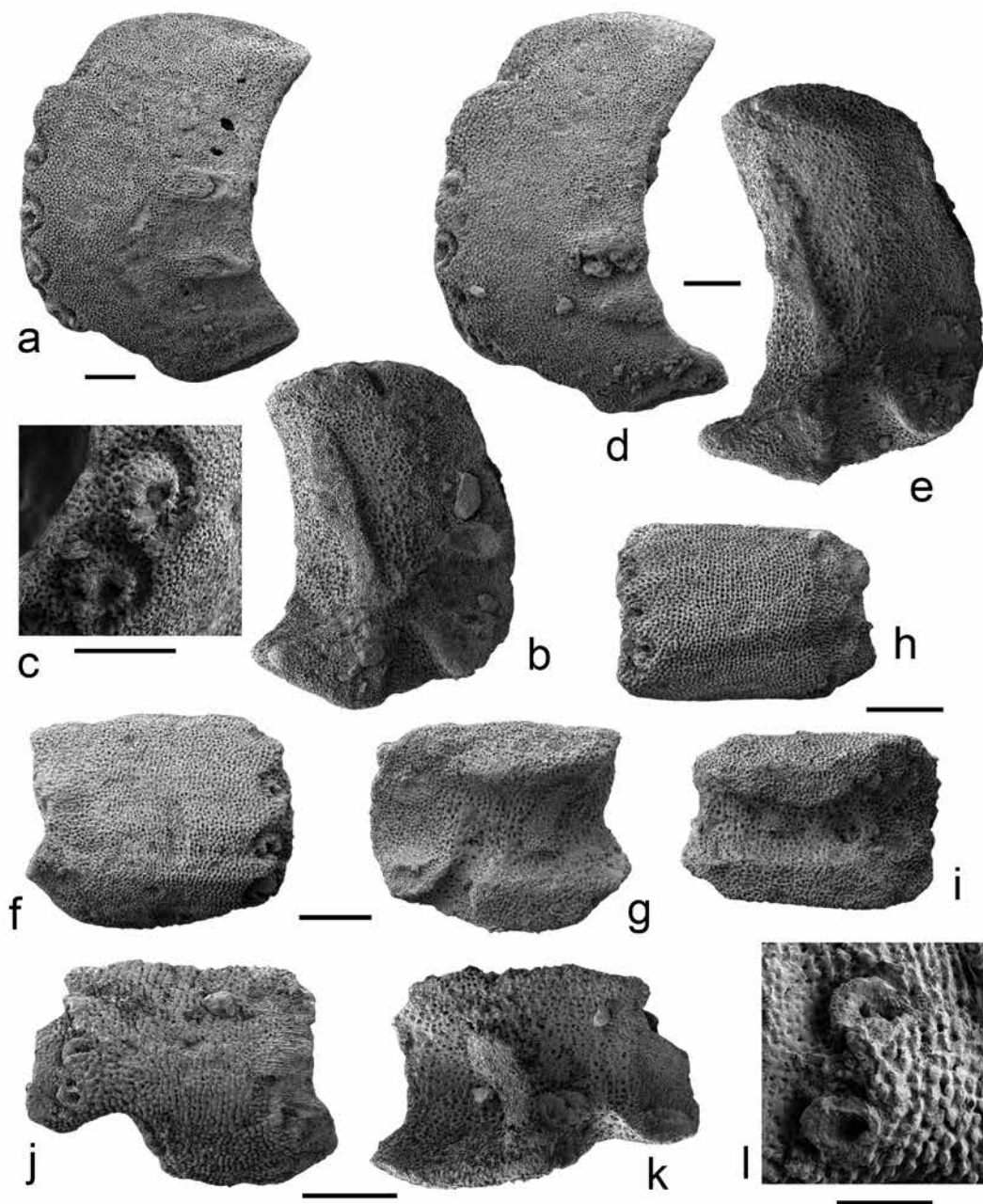
***Sinosura* sp. nov.**

Fig. 2j-l

**Material:** BU 307, a single dissociated LAP.

**Description:** BU 307 is a medium-sized, dissociated median LAP, almost 1.5 times wider than high; dorsal edge nearly straight; distal edge incompletely preserved, probably straight originally; proximal edge irregularly concave, bordered by a broad band of horizontally striated stereom and with two small, poorly defined, horizontally elongate, non-protruding and weakly prominent spurs, one in the middle of the dorsal portion of the proximal edge and the other at the kink between the ventral and dorsal portions of the proximal edge; ventral third of LAP strongly protruding ventro-proximalwards; ventro-distal tip of LAP protruding ventralwards. Outer surface with small, distalwards projecting scale-like tubercles, merged to vertical striation in central and dorsal areas of outer surface. Three moderately large spine articulations near distal edge, integrated to and tightly surrounded by outer surface stereom, with dorsalward increase in size of spine articulations and, to a lesser extent, of the gaps separating them; spine articulations distally bordered by thin projection almost as wide as the spine articulations and composed of densely meshed stereom; spine articulations composed of thin ventral and dorsal lobes merged into oval to slightly rhombic structure encircling round muscle opening and ventro-distally bordered by slightly smaller nerve opening; dorsal and ventral lobes composed of densely meshed to massive stereom.

Inner side of LAP with large, conspicuous, sharply defined and strongly prominent ridge composed of densely meshed stereom, with tongue shaped, proximalwards bent dorsal portion and slightly narrower ventral portion pointing ventralwards and not merged with ventral edge of LAP. Sharply defined, prominent, lens-shaped spur on ventro-distal tip of inner side, composed of densely meshed stereom. Very large, deep tentacle notch pointing ventralwards to slightly ventro-distalwards, with the ventro-proximal edge paralleled by a narrow ridge. No perforations or furrow discernible.



**Fig. 2:** Dissociated ophiuroid lateral arm plates (LAPs) from the Longwy Formation, Laeviuscula Zone, early Bajocian, Middle Jurassic of Longwy, France. *Ophiotitanos aschmanni* sp. nov., a-c: BU 302 (holotype), proximal LAP in external (a) and internal (b) views and with detail of spine articulations (c); d-e: BU 305 (paratype), proximal LAP in external (d) and internal (e) views; f-g: BU 303 (paratype), median LAP in external (f) and internal (g) views; h-i: BU 304 (paratype), distal LAP in external (h) and internal (i) views. *Sinosura* sp. nov., j-l: BU 307, median LAP in external (j) and internal (k) views and with detail of spine articulation (l). Scale bars equal 250 µm in a-k, and 100 µm in l.



**Remarks:** The general plate outline, the outer surface ornamentation, the tentacle notch development and in particular the spine articulation morphology of the above described LAP concurrently suggest an ophioleucin affinity. The fossil record of the subfamily, recently summarised by Thuy et al. (2013), is sparse and patchy, with the exception of the extinct genus *Sinosura* which is known from both articulated skeletons and dissociated LAPs throughout the Jurassic.

The above described LAP adds to the yet poorly documented ophioleucin fossil record. It shares closest similarities with the LAPs of *Sinosura extensa* Kutscher & Villier, 2003 from the Toarcian of France. Differences pertain to details, in particular the slightly wider and less strongly bent ridge on the inner side of the here described LAP as well as its spine articulations oriented approximately perpendicular to the arm axis rather than distalwards tilted. The specimen in question most probably belongs to a yet undescribed species. With only a single LAP at hand, however, no formal description can be proposed.

Family unnamed (see O'Hara et al. 2014)

**Genus *Enakomusium* nov.**

**Type species:** *Ophioderma weymouthiense* Damon, 1880

**Other species included:** *Ophiomusium ferrugineum* Boehm, 1889; *Ophiopsis leckenbyi* Wright, 1880; *Ophiomusium geisingense* Kutscher, 1992; *Ophiomusium mammillatum* Hess, 1966; *Ophiura gagnebini* Thurmman, 1851.

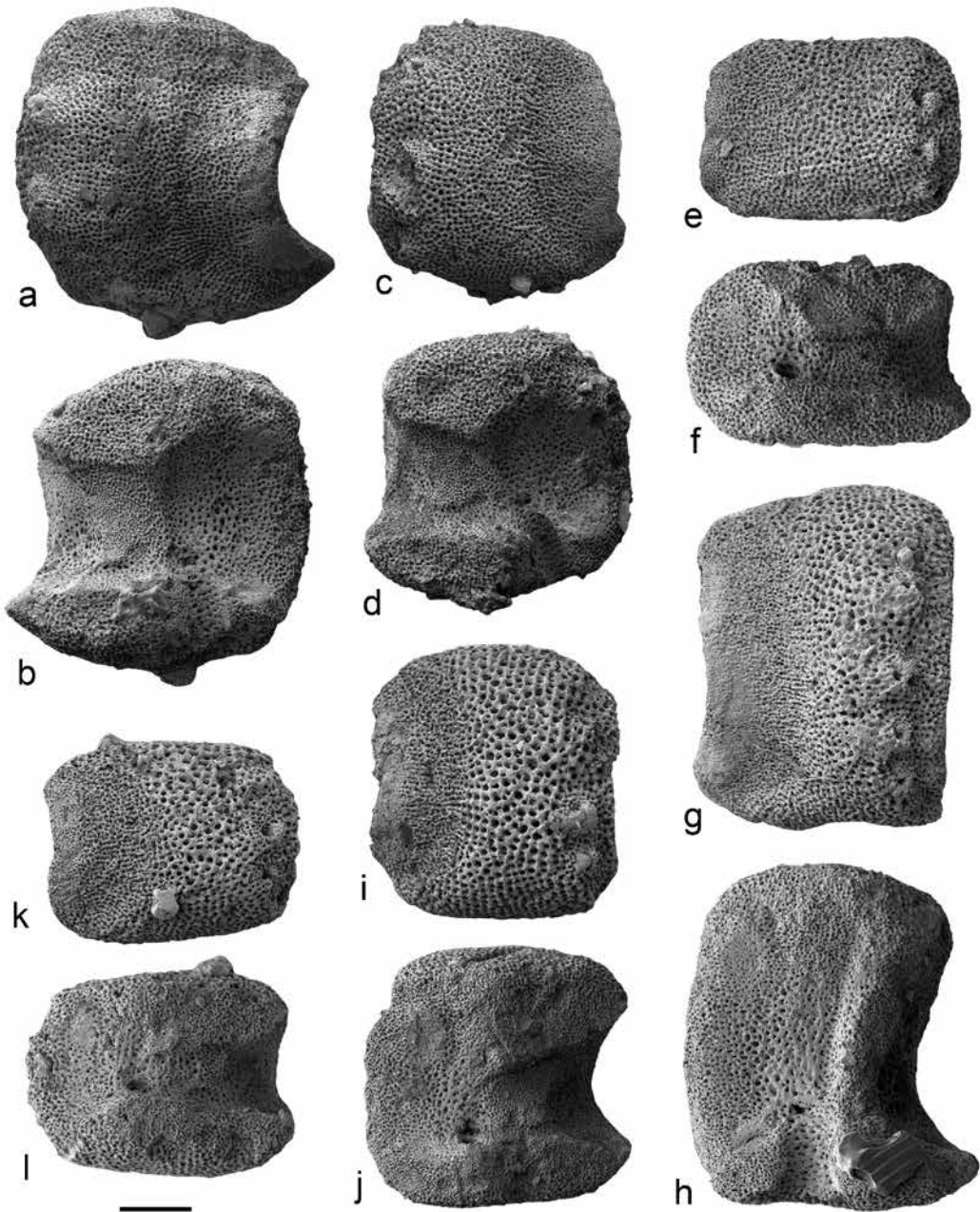
**Diagnosis:** Ophiuroid genus with robust overall skeletal plating; thick disc plates devoid of removable granules; leaf-like oral papillae; arms with small and mostly non-contiguous dorsal and ventral arm plates; lateral arm plates thick, robust, rounded rectangular; outer proximal edge commonly with spurs and paralleled by a conspicuous, deep furrow; spine articulations integrated into outer surface stereom, often slightly prominent, and composed of a round muscle opening proximally tightly encompassed by a small thin, commonly denticulate ridge, and distally separated from a slightly smaller nerve opening by a large, conspicuous vertical ridge; tentacle openings developed as deep, ventralwards pointing notches in proximal to median

arm segments, and as distalwards pointing within-plate perforations in median to distal arm segments.

**Derivation of name:** Name composed of a contraction of *ένα ακόμη* (*éna akómī*), Greek for “yet another”, and the genus name *Ophiomusium*, referring to the fact that the new genus is by far not the first attempt to meaningfully assess extinct *Ophiomusium*-like ophiuroids.

**Remarks:** Ophiuroids presenting a superficial similarity with extant *Ophiomusium* are among the most common articulated ophiuroid discoveries, both in Paleozoic and Mesozoic strata, and have accordingly been discussed in many studies, with controversies focusing mainly on the taxonomic affinities of these forms. In fact, in spite of the sometimes striking similarities with modern *Ophiomusium*, all fossil forms (with the notable exception of *Ophiomusium granulosum* (Roemer, 1840) from the Latest Cretaceous to earliest Paleogene) display characters, in particular higher numbers of between-plate tentacle openings, which preclude an assignment to this genus. Some authors commented on this but nevertheless assigned their species to *Ophiomusium* (e.g. Boehm 1889; Berry 1939; Hess 1960a; Kutscher 1992), stretching that the fossil forms defy the boundaries of the genus diagnosis.

Hattin (1967) introduced the new genus *Archaeophiomusium* to accommodate *Ophiomusium*-like forms from the Permian with better developed dorsal and ventral arm plates and between-plate tentacle openings developed on most arm segments. This genus, however, proved incompatible with the Jurassic and some of the Cretaceous *Ophiomusium*-like forms. To remedy to the unclear genus-level position of the Mesozoic species, Kutscher and Jagt (2000) proposed the new genus *Mesophiomusium*, characterised by an overall *Ophiomusium*-like morphology combined with a higher number of between-plate tentacle openings and longer arm spines. Regrettably, the type species of *Mesophiomusium*, *M. moenense* Kutscher & Jagt, 2000, described on the basis of dissociated LAPs, was an unfavourable choice since similarities in LAP morphology are much greater with extant *Ophiomastus* Lyman, 1878 than with the *Ophiomusium*-like Mesozoic forms to be accommodated (Thuy & Meyer 2012). As a result, the Mesozoic forms in question cannot be assigned to *Mesophiomusium*. In order to end their taxonomic odyssey



**Fig. 3:** Dissociated ophiuroid lateral arm plates (LAPs) from the Longwy Formation, Laeviuscula Zone, early Bajocian, Middle Jurassic of Longwy, France. *Enakomusium leckenbyi* (Wright), a-b: BU 308, proximal LAP in external (a) and internal (b) views; c-d: BU 309, median LAP in external (c) and internal (d) views; e-f: BU 310, distal LAP in external (e) and internal (f) views. *Enakomusium ferrugineum* (Boehm), g-h: BU 312, proximal LAP in external (g) and internal (h) views; i-j: BU 313, median LAP in external (i) and internal (j) views; k-l: BU 314 distal LAP in external (k) and internal (l) views. Common scale bar equaling 250 µm for all specimens.

and finally clarify their genus-level placement, I here propose the new, carefully and unambiguously circumscribed genus *Enakomusium*.

The type species of the new genus is *Ophioderma weymouthiense* from the Callovian of Great Britain. This species very typically displays the combination of characters shared by the relevant Mesozoic *Ophiomusium*-like species. It is furthermore known from numerous well preserved, articulated skeletons among which Hess (1964) designated a neotype, and which expose external lateral arm plate characters essential for comparison with dissociated LAP-based records. Another type species candidate was *Ophiomusium ferrugineum* from the Bajocian/Bathonian of Germany and Switzerland. Although this species is known from numerous articulated skeletons, the availability and preservation state of the holotype, allegedly housed in the collection of the University of Freiburg (Boehm 1889), could not be verified in the course of the present study. I therefore prefer *O. weymouthiense* as type species of the new genus.

*Enakomusium* differs from its extant relatives *Ophiomusium* and *Ophiosphalma* in the higher number of between-plate tentacle openings (in contrast to within-plate tentacle perforations) per arm, the generally rounder outline of the LAPs, the deep furrow paralleling the proximal LAP edge, and the rounded leaf-like oral papillae. It includes most, but not all, of the Mesozoic *Ophiomusium*-like species (see above). Excluded are *Ophiomusium solodurens* Hess, 1962 and *Ophiomusium murravii* (Forbes, 1843) which are more reminiscent of extant *Ophioplathus* Lyman, 1878. Furthermore excluded are *Mesophiomusium kiania* Thuy, 2005, *Mesophiomusium scabrum* (Hess, 1962), *Mesophiomusium sinemurensis* (Kutscher & Hary, 1991) and probably *Ophiomusium ramsayi* (Wright, 1866) which all show striking differences in LAP morphology with *O. weymouthiense*, thus precluding assignment to the same genus. Finally, *Mesophiomusium decipiens* Jagt, 2000 displays a fundamentally different spine articulation morphology and most probably belongs to a different supra-generic group.

The general skeletal morphology and some of the most diagnostic LAP characters, in particular the spine articulation morphology, strongly suggest that *Enakomusium* is a close relative of extant *Ophiomusium* and *Ophiosphalma*. Indeed, there are striking similarities between the proximal LAPs of

*Enakomusium* and the proximalmost, freestanding (i.e. not incorporated into the disc) LAPs with between-plate tentacle openings of *Ophiosphalma*, endorsing a close relationship between the two. The higher number of between-plate tentacle openings in members of *Enakomusium* was previously assumed to reflect an ancestral state developing into modern *Ophiosphalma* and *Ophiomusium* via reduction of between-plate tentacle openings to the basalmost arm segments whilst retaining the overall skeletal morphology (e.g. Hess 1960a; Kutscher 1992). While the close relationship between the genera in question is supported here, assumptions on evolutionary trends seem premature in the absence of a comprehensive phylogenetic analysis.

### *Enakomusium leckenbyi* (Wright, 1880)

Fig. 3a-f

\*1880 *Ophiolepis leckenbyi* Wright, p. 160, pl. 19, figs. 3a-b.

1964 *Ophiomusium leckenbyi* Hess, p. 785.

**Diagnosis for LAPs:** Small to moderately large LAPs of rounded to rounded rectangular outline, with convex dorsal and ventral edges; up to four moderately well to poorly defined, non-protruding spurs on the outer proximal edge, the ventralmost one of which almost two times larger than the remaining ones; proximal edge paralleled by a large, deep, conspicuous furrow lined in its ventral portion by a faint horizontal striation; outer surface with finely meshed stereom; five to three small, prominent spine articulations; strong dorsalward increase in size of spine articulations and of gaps separating them.

**Material:** BU 308, BU 309, BU 310, BU 311 (25 dissociated LAPs)

**Description:** Small to moderately large dissociated LAPs, proximal ones slightly higher than wide, of rounded outline, with convex dorsal, ventral and distal edges; median and distal LAP progressively more elongate and rectangular in outline, with weakly convex dorsal and ventral edges; proximal edge concave; proximal edge with up to four weakly prominent, non-protruding, round to oval spurs, composed of densely meshed stereom, moderately well defined in proximal LAPs to poorly defined in distal ones; ventralmost spur almost two times larger than remaining

ones; proximal edge paralleled by a large, deep, conspicuous furrow. Outer surface with finely meshed stereom; trabecular intersections not particularly enlarged; faint horizontal striation lining the ventral portion of the furrow paralleling the proximal edge. Five (proximal LAPs) to three (distal LAPs) small, prominent spine articulations, evenly distributed over the entire height of the LAP, integrated into and tightly surrounded by the outer surface stereom; spine articulations at some distance from the distal edge of the LAP, separated from the latter by a gap as wide as the spine articulations; strong dorsalward increase in size of spine articulations and of gaps separating them; spine articulations composed of a large, round muscle opening proximally tightly bordered by a thin semi-circular, irregularly denticulate ridge, and distally separated from smaller nerve opening by a nearly vertical ridge larger than the semi-circular ridge.

Inner side of LAPs with large ventral and even larger dorsal contact surfaces with the opposite LAP; small, short, moderately well defined and weakly prominent ridge with wide ventral tip and pointed, proximalwards bent dorsal tip, located on elevated part between dorsal and ventral contact areas with opposite LAP. Up to four non-prominent, moderately well to poorly defined spurs composed of densely meshed stereom on the inner distal edges. Deep, well defined ventralwards (proximal LAPs) to slightly ventro-distalwards (median LAPs) pointing tentacle notch in median to proximal LAPs, and within-plate tentacle perforation in distal LAPs. Single small, irregular perforation dorsally bordering tentacle notch in proximal to median LAPs.

**Remarks:** The above-described LAPs share a number of diagnostic characters with the LAPs of *Enakomusium weymouthiense*, in particular the stout, rounded rectangular general aspect, the deep furrow paralleling the proximal edge, the between-plate tentacle openings limited to proximal LAPs, and the small, prominent spine articulations composed of a proximally tightly enclosed muscle opening distally separated from a smaller nerve opening by a large, short, vertical ridge. Assignment to *Enakomusium* thus seems warranted. Among the species transferred to this new genus, the Oxfordian *E. mammillatum* differs in displaying larger and more numerous spine articulations, the Toarcian *E. geisingense* and the

Oxfordian *E. gagnebini* have a more angular outline, smaller contact surfaces with the opposite LAP on the inner side and a coarser outer surface ornamentation, *E. weymouthiense* from the Callovian has the ventralmost spine articulations grouped ventrally and separated from the median and dorsal ones by larger gaps.

Similarities are greatest with the LAPs observed on the articulated specimen from the Bajocian of Great Britain, housed at the British Museum (specimen number E2656) and identified as *E. leckenbyi* by Hess (1964). Unfortunately, the specimen in question is not the holotype of the species. Thus, although it was found at the type locality of *E. leckenbyi*, it cannot be ruled out that the specimen in question, and at the same time the above described LAPs, in fact belong to a different species. Pending a re-assessment of the holotype of *E. leckenbyi*, however, it seems best to assign the here-described LAPs to this species.

The LAPs of specimens from the Swiss Bajocian housed at the Natural History Museum in Basel, Switzerland, and assigned to *E. ferrugineum* have a higher height/width ratio, a more angular outline, fewer spine articulations and a slightly coarser outer surface ornamentation. Yet again, the holotype, described from the German equivalent of the deposits that yielded the Swiss specimens, could not be assessed in the course of the present study. Therefore, it is important to stress that the here-proposed identifications are tentative as long as the respective type specimens have not been re-examined in detail.

### *Enakomusium ferrugineum* (Boehm, 1889)

Fig. 3g-l

\**Ophiomusium ferrugineum* Boehm, 1889, p. 280, pl. 5, figs. 1-2.

Diagnosis for LAPs: Moderately large LAPs of rounded rectangular outline, with convex to straight dorsal and straight ventral edge; up to three poorly defined, non-prominent and only weakly protruding spurs on the outer proximal edge of proximal LAPs; proximal edge paralleled by furrow lined in its ventral portion by a faint horizontal striation; outer surface with moderately finely meshed stereom; four to three small, prominent spine articulations; strong dorsalward increase in size of spine articulations; dorsalmost

spine articulation separated from dorsal edge of LAP by large gap.

**Material:** BU 312, BU 313, BU 314, BU 315 (121 dissociated LAPs)

**Description:** Moderately large dissociated LAPs, proximal ones almost 1.5 times higher than wide, distal ones 1.5 wider than high, all of rounded rectangular outline, with a convex (proximal to median LAPs) to straight (distal LAPs) dorsal edge and straight ventral and distal edges; proximal edge weakly concave, with up to three, non-prominent and only very weakly protruding, poorly defined (proximal LAPs) to almost indiscernible (median to distal LAPs) spurs composed of slightly more densely meshed stereom. Outer surface with moderately coarsely meshed stereom, with angular, pointed trabecular inter-sections; outer surface stereom mesh size slightly decreasing towards distal edge of LAP, and much more strongly decreasing towards furrow paralleling proximal edge; very faint horizontal striation in ventral portion of furrow paralleling proximal edge of proximal to median LAPs. Four (proximal LAPs) to three (distal LAPs) small, prominent spine articulations integrated into and tightly surrounded by outer surface stereom; spine articulations separated from distal edge by a gap as wide as the spine articulations; strong dorsalward increase in size of spine articulations, and weaker dorsalward increase in size of gaps separating them; large gap between dorsalmost spine articulation and dorsal edge of LAP; spine articulations composed of a small muscle opening ventro-proximally tightly encompassed by a coarsely rugose semi-circular ridge, and distally separated from a slightly smaller nerve opening by a short, vertical, rugose ridge; distal LAPs with conspicuously enlarged, lip-shaped ridge separating muscle and nerve openings.

Inner side of LAP with small (proximal LAPs) to moderately large (median and distal LAPs) contact surfaces with opposite LAP; large to medium-sized, sharply defined, strongly prominent ridge with tongue shaped, proximalwards bent dorsal tip in proximal to median LAPs, and small, poorly defined triangular ridge in distal ones. Deep, sharply defined, ventralwards pointing tentacle notch in proximal to median LAPs, with slightly horizontally stretched stereom; large, round tentacle perforations between distal and median thirds of median to distal LAPs.

Two to three very poorly defined, almost indiscernible, non-prominent spurs on inner distal edge, composed of slightly more densely meshed stereom. Single, small perforation dorsally bordering tentacle notch in proximal LAPs.

**Remarks:** The above described LAPs display the combination of characters typically found in *Enakomusium weymouthiense* and are therefore assigned to the same genus. On species level, *E. mammilatum* has larger and more numerous spine articulations, while *E. geisingense* and *E. gagnebini* display smaller contact surfaces with the opposite LAP on the inner side as well as more sharply defined, protruding spurs on the outer proximal edge, and *E. weymouthiense* has the ventralmost spine articulations grouped ventrally and separated from the median and dorsal ones by larger gaps.

Differences with the LAPs here assigned to *E. leckenbyi* are discussed above. It is important to stress that the here described LAPs are assigned to *E. ferrugineum* on the basis of similarities with the LAPs observed on articulated non-type specimens identified as *E. ferrugineum*.

Family Ophionereididae Ljungman, 1867

**Genus *Ophiodoris* Koehler, 1904**

**Type species:** *Ophiodoris malignus* Koehler, 1904, by original designation.

***Ophiodoris reconciliator* sp. nov.**

Fig. 4a-i

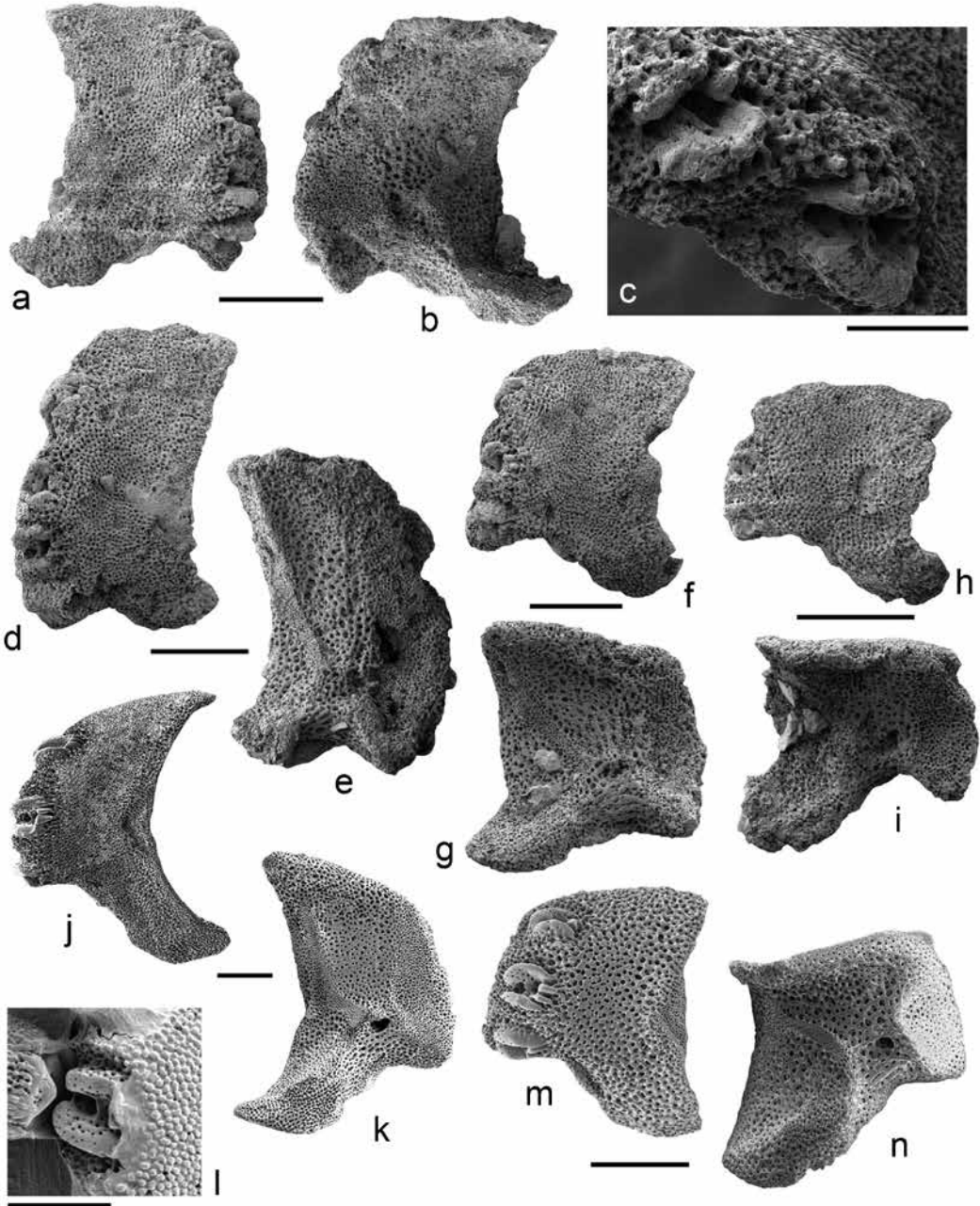
**Derivation of name:** Name formed from reconciliare, Latin for “reconcile” or “restore”, referring to the fact that the LAP morphology of the present species endorses the reunion of the Ophiochitonidae and Ophionereididae into a single group, of which the species in question is the oldest known representative.

**Types:** BU 316 (holotype); BU 317, BU 318, BU 319 (paratypes)

**Other material:** BU 320 (26 dissociated LAPs)

**Type locality:** Roadcut at the southwestern end of the motorway bridge in Piedmont, Longwy, France (49° 32' 33.8274" N, 5° 45' 56.3574 E).

**Type horizon:** Marl beds in the lower part of the Longwy Formation, *Laeviuscula* Zone, early Bajocian, Middle Jurassic.



**Fig. 4:** Dissociated ophiuroid lateral arm plates (LAPs) from the Longwy Formation, Laeviuscula Zone, early Bajocian, Middle Jurassic of Longwy, France, and LAPs from recent ophiuroids for comparison. *Ophiodoris reconciliator* sp. nov., a-c: BU 316 (holotype), proximal LAP in external (a) and internal (b) views and with detail of spine articulations (c); d-e: BU 319 (paratype), proximal LAP in external (d) and internal (e) views; f-g: BU 317 (paratype), median LAP in external (f) and internal (g) views; h-i: BU 318 (paratype), distal LAP in external (h) and internal (i) views. *Ophioplax lamellosa* Matsumoto, recent, j-l: proximal LAP in external (j) and internal (k) views and with detail of spine articulation (l) (note that part of the spine articulation is covered in soft tissue). *Ophiodoris malignus* Koehler, recent, m-n: proximal LAP in external (m) and internal (n) views. Scale bars equal 250 µm in a-b and d-n, and 100 µm in c.

**Diagnosis:** Species of *Ophiodoris* with small LAPs with finely meshed outer surface stereom, with trabecular intersections transformed into small, inconspicuous tubercles; up to four large spine articulations integrated into and tightly surrounded by outer surface stereom.

**Description of holotype:** BU 316 is a small dissociated, proximal LAP, almost 1.5 times higher than wide, strongly arcuate; dorsal edge very weakly concave as a result of a slight constriction of the outer surface, with pointed dorso-proximal tip; distal edge strongly convex; proximal edge concave, with a large central, poorly defined, weakly prominent protrusion composed of slightly more finely meshed stereom; ventral quarter of LAP strongly ventro-proximalwards protruding; ventro-distal tip of LAP pointed and ventralwards protruding. Outer surface of LAP with finely meshed stereom, with trabecular intersections slightly enlarged into closely spaced, slightly vertically elongate tubercles, decreasing in size and tightness towards proximal edge of LAP. Four large, nearly equal-sized spine articulations integrated into and tightly surrounded by outer surface stereom of slightly bulging distal portion of LAP; spine articulation separated from distal edge by very narrow band of stereom; size of gaps separating spine articulations strongly increasing dorsalwards; spine articulations composed of a large, horizontal to slightly bent dorsal lobe, paralleled by a slightly smaller, horizontal ventral lobe, both composed of densely meshed stereom and proximally separated by two wedge-shaped, proximalwards tapering spurs; large muscle opening and smaller nerve opening completely encompassed by dorsal and ventral lobes and separated by low, thin, straight ridge.

Inner side of LAP with conspicuous, sharply defined, prominent ridge composed of three parts connected by angular and slightly enlarged kinks; dorsal part of ridge nearly vertical, with rounded tip not reaching dorsal edge of LAP; middle part of ridge strongly oblique, narrower than dorsal part; ventral part of ridge short, oblique, ventro-proximalwards pointing, not merged with ventral portion of LAP. Tentacle notch very large and deep, encompassed by a thickened ventral edge of the LAP with slightly horizontally stretched stereom, and proximally paralleled by a slightly protruding, narrow ridge also visible in external view. Two moderately large, irregular, tightly

grouped perforations distally bordering kink between middle and ventral parts of the ridge on the inner side of the LAP; very shallow, almost indiscernible vertical furrow dorsalwards extending from perforations.

Paratype supplements and variation: BU 317 is a small, dissociated median LAP, nearly as high as wide, well in agreement with holotype morphology; dorsal edge very weakly convex, oblique, no constriction. Three spine articulations similar in shape and position to those of holotype, with dorsal gap larger than ventral one.

Inner side as in holotype but with dorsal part of ridge almost reaching dorsal edge of LAP; moderately well defined, prominent, round knob on ventral portion of LAP in continuity of ventro-proximalwards pointing ventral part of ridge. Single, large, irregular perforation distally bordering kink between dorsal and middle parts of ridge; no furrow discernible.

BU 318 is a small, dissociated distal LAP, slightly wider than high; dorsal edge convex; no constriction; central projection on proximal edge larger and more strongly protruding than in holotype. Three spine articulations similar in morphology and position to those of holotype; dorsal gap larger than ventral one.

Inner side with ridge composed of two parts, a central, strongly oblique one with an enlarged dorsal tip, and short ventral, ventro-proximalwards pointing one, connected with the median part by an angular kink. Single, large, irregular perforation; no furrow discernible.

BU 319 is a small, dissociated proximal LAP, originally more than 1.5 times higher than wide; ventro-proximal tip fragmented; well in agreement with holotype.

Parts of inner side morphology better developed than in holotype; dorsal part of ridge longer, dorsally pointed, almost reaching dorsal edge of LAP; single, irregular, poorly defined perforation distally bordering kink between middle and ventral parts of the ridge, with weakly defined, shallow vertical furrow dorsalwards extending from perforation.

**Remarks:** The spine articulation morphology of the above described LAPs is highly distinctive and exclusively occurs in the Ophionereididae and in some members of the Ophiochitonidae (Thuy et

al. 2013). While the LAPs of the type taxa of the two families, *Ophionereis* and *Ophiochiton*, can be easily told apart (Thuy & Stöhr 2011; Stöhr 2011), the LAPs of the ophionereidid *Ophiodoris* Koehler, 1904 and the ophiochitonid *Ophioplax* Lyman, 1875, turned out to be almost indistinguishable (Fig. 4j-n). They share striking similarities in several highly diagnostic LAP characters, including the general outline of the LAPs, spine articulation morphology and the shape of the ridge on the inner side. In line with the observations by Thuy and Stöhr (2011), these strong similarities in LAP morphology suggest a close relationship between the Ophionereididae and Ophiochitonidae. Indeed, it is only relatively recently that both groups have been considered separate families (Smith et al. 1995). The seemingly clear-cut differences in LAP morphology between *Ophionereis* and *Ophiochiton* can be easily explained by transitional states found in the LAPs of *Ophiodoris* and *Ophioplax*.

While there is no doubt that the above described LAPs belong to the Ophionereididae-Ophiochitonidae group, assignment to either family proves more difficult owing to the fact that they share greatest similarities with the LAPs of extant *Ophiodoris* and *Ophioplax*. The arguments put forward by Thuy et al. (2013) in assigning fossil material to *Ophiodoris* rather than an ophiochitonid must be re-considered under the light of the new observations on LAP morphology of *Ophioplax*. In fact, while *Ophiodoris francojurassicus* (Hess, 1975b) from the Oxfordian of France and *Ophiodoris holterhoffi* Thuy, Gale, Stöhr & Wiese, 2013 from the Aptian of Texas seem, indeed, best placed in the ophionereid *Ophiodoris*, the dissociated LAPs from the Aptian of Spain described as *Ophiodoris?* sp. nov. by Thuy et al. (2013) are more reminiscent of the ophiochitonid *Ophioplax* on account of the strongly pointed dorso-proximal tip of the LAPs. In this respect, affinities of the here described LAPs are greatest with *Ophiodoris*, although it must be explicitly stressed that they also share strong similarities with the LAPs of *Ophioplax*.

The LAPs at hand can be easily told apart from those of *Ophiodoris holterhoffi* on the basis of the much coarser outer surface tuberculation of the latter. *Ophiodoris francojurassicus* differs in

having slightly more coarsely meshed stereom in the distal half of the outer surface, and spine articulations encompassed by deeper notches of the distal LAP portion. Although differences to *O. francojurassicus* pertain to details in LAP morphology only, the here described specimens seem best accommodated in a new species. It represents the oldest member of the Ophionereididae-Ophiochitonidae group.

## Discussion

The present study ranks among the recent systematic surveys of ophiuroid palaeobiodiversity based on the re-assessment of LAP morphology by Thuy and Stöhr (2011) (Thuy & Kroh 2011; Thuy et al. 2012; Thuy 2013; Thuy et al. 2013). Together with the study by Numberger-Thuy and Thuy presented in this volume, it is the first assessment of an ophiuroid assemblage entirely based on dissociated LAPs for the Bajocian, and one of the first for the Middle Jurassic, along with Hess' (1963) and Kutscher's (1996) (the Aalenian lot of the assemblages) studies.

LAP-based surveys have been repeatedly shown to produce a much more complete picture of ophiuroid palaeobiodiversity than the assessment of the exceptional finds of articulated skeletons (e.g. Jagt 2000; Thuy 2005). Indeed, although the occurrences of articulated skeletons from the Bajocian/Bathonian of the Burgundy Platform carbonates are among the richest and best known (Boehm 1889; Hess 1972; Hess & Hohenweg 1985; Thuy & Meyer 2012), the assemblage studied herein added four new species, one previously described by Thuy (2013), two formally introduced herein and a fourth described here as new but left unnamed. On a higher taxonomic level, the present survey contributes to closing the stratigraphic gap in the fossil record of the Ophiodermatidae between the Triassic, Lower Jurassic and Aalenian representatives and the Late Jurassic and Cretaceous forms (Kristan-Tollmann et al. 1979; Kutscher 1988, 1996; Thuy 2005; Hess 1965; Jagt 2000 and references therein). Most significantly, it produced the oldest representative of the Ophionereididae and re-affirmed the close relationship with the Ophiochitonidae.



The interpretation of the here described ophiuroid material as shallow-water peri-reefal assemblage allows for a comparison with modern equivalents. The mud bottoms and detrital sands around shallow-water coral reefs in modern oceans are dominated by members of the Ophiocomidae, Ophiolpididae, Ophiodermatidae, Ophiotrichidae, Ophiactidae, Amphiuroidae and Ophionereididae (e.g. Hendler et al. 1995; Hotchkiss 1982; Stöhr et al. 2008). Ophiacanthidae and the yet unnamed family including *Ophiomusium*, which are a major component of the here described assemblage, generally lack from modern shallow-water peri-reefal settings and are instead a dominant component of modern deep-sea assemblages (Thuy et al. 2012; Thuy & Meyer 2012). The Ophiocomidae, Ophiotrichidae, Ophiactidae and Amphiuroidae completely lack from the Bajocian assemblage, which is not surprising given their supposed post-Jurassic origin (Thuy & Kroh 2011).

The only family-level taxa shared by the Bajocian assemblage and modern counterparts are the Ophiodermatidae and Ophionereididae. A comparison at a lower taxonomic level, however, reveals fundamental differences in composition. The ophionereidid of the Bajocian assemblage is a species of extant *Ophiodoris*, whose modern representatives are predominantly found in deep-sea settings, in contrast to its typically shallow relatives (Koehler 1904; Thuy et al. 2013). The Bajocian ophiodermatid belongs to an extinct genus whose relationships with extant ophiodermatids are yet to be explored.

Thus, the only potential modern element in the Bajocian is the ophiodermatid. All other occurrences have no counterparts in modern equivalent ophiuroid assemblages as the closest extant relatives live in deep-sea rather than shallow peri-reefal settings. The present analysis provides another case of a non-analogue Mesozoic shallow-water assemblage, and thus adds to the growing evidence that shallow-water ophiuroid communities have undergone fundamental changes in taxonomic composition since the Mesozoic (Thuy et al. 2013; Thuy et al. 2013). It furthermore reinforces the observation that the bathymetric distribution boundaries of many extant ophiuroid taxa, both on family and genus level, substantially shifted in the course of the Mesozoic (Thuy 2013).

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## References

- Ausich, W.I. 2001. - Echinoderm taphonomy, in M. Jangoux & J.M. Lawrence (Eds.), Echinoderm studies 6 (pp. 171–227). Rotterdam: Balkema.
- Berry, C.T. 1939. - *Ophiomusium calathospongum* from the Mississippian of Pennsylvania. Notulae naturae of the Academy of Natural Sciences of Philadelphia 24: 1-4.
- Boehm, G. 1889. - Ein Beitrag zur Kenntnis fossiler Ophiuren. Bericht der naturforschenden Gesellschaft Freiburg. Breslau 4: 232-287.
- Boulvain, F., Belanger, I., Delsate, D., Ghysel, P., Godefroit, P., Laloux, M., Monteyne, R., Roche, M. 2001. - Triassic and jurassic lithostratigraphic unites (Belgian Lorraine). Geologica Belgica 4(1-2): 113-119.
- Brigaud, B., Durlet, C., Deconinck, J.-F., Vincent, B., Pucéat, E., Thierry, J. & Trouiller, A. 2009. - Facies and climate/environmental changes recorded on a carbonate ramp: A sedimentological and geochemical approach on Middle Jurassic carbonates (Paris Basin, France). Sedimentary Geology 222: 181-206.

- Brigaud, B., Vincent, B., Carpentier, C., Robin, C., Guillocheau, F., Yven, B. & Huret, E. 2013. - Growth and demise of the Jurassic carbonate platform in the intracratonic Paris Basin (France): Interplay of climate change, eustasy and tectonics. *Marine and Petroleum Geology*, doi: <http://dx.doi.org/10.1016/j.marpetgeo.2013.09.008>.
- Damon, R. 1880. - Supplement to the Geology of Weymouth and the Isle of Portland. 2nd edition. London.
- Delsate, D., 1993. - Elasmobranches du Bajocien inférieur de Longwy (Meurthe et Moselle): *Cossmanniana*, Hors série 2: 56-58.
- Forbes, E. 1843. - On the fossil remains of starfishes and of the order Ophiuridae, found in Britain. *Proceedings of the geological Society of London* 4: 232-234.
- Hattin, D.E. 1967. - Permian ophiuroids from Northern Oklahoma. *Journal of Paleontology* 41(2): 489-492.
- Hendler, G., Miller, J.E., Pawson, D.L. & Kier, P.M. 1995. - Sea Stars, Sea Urchins and Allies. Smithsonian Institution Press, Washington & London, 1-390.
- Hess, H. 1960a. - Ophiurenreste aus dem Malm des Schweizer Juras und des Departements Haut-Rhin. *Eclogae Geologicae Helvetiae* 53(1): 385-421.
- Hess, H. 1960b. - Über zwei Ophiuren (*Ophiocoma* ? *rasmusseni* n.sp. und *Ophiotitanos tenuis* Spencer) aus der englischen Kreide. *Eclogae geologicae Helvetiae* 53(2): 747-757.
- Hess, H. 1962. - Mikropaläontologische Untersuchungen an Ophiuren II: Die Ophiuren aus dem Lias (Pliensbachien-Toarcien) von Seewen (Kt. Solothurn). *Eclogae geologicae Helvetiae* 55: 609-656.
- Hess, H. 1963. - Mikropaläontologische Untersuchungen an Ophiuren III: Die Ophiuren aus dem Callovien-Ton von Liesberg (Berner Jura). *Eclogae geologicae Helvetiae* 56: 1141-1164.
- Hess, H. 1964. - Die Ophiuren des englischen Jura. *Eclogae Geologicae Helvetiae* 57: 756-801.
- Hess, H. 1965a. - Mikropaläontologische Untersuchungen an Ophiuren IV: Die Ophiuren aus dem Renggeri-Ton (Unter-Oxford) von Chapois (Jura) und Longecombe (Ain). *Eclogae geologicae Helvetiae* 58: 1059-1082.
- Hess, H. 1965b. - Trias-Ophiuren aus Deutschland, England, Italien und Spanien. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 5: 151-177.
- Hess, H. 1966. - Mikropaläontologische Untersuchungen an Ophiuren V: Die Ophiuren aus dem Argovien (unteres Ober-Oxford) vom Guldental (Kt. Solothurn) und von Savigna (Dépt. Jura). *Eclogae geologicae Helvetiae* 59: 1025-1063.
- Hess, H. 1972. - Eine Echinodermenfauna aus dem mittleren Dogger des Aargauer Juras. *Schweizerische Paläontologische Abhandlungen* 92: 1-87.
- Hess, H. 1975a. - Mikropaläontologische Untersuchungen an Ophiuren VI: Die Ophiuren aus den Günsberg-Schichten (oberes Oxford) vom Guldental (Kt. Solothurn). *Eclogae geologicae Helvetiae* 68: 591-601.
- Hess, H. 1975b. - Mikropaläontologische Untersuchungen an Ophiuren VII: Die Ophiuren aus den Humeralis-Schichten (Ober-Oxford) von Raedersdorf (Ht-Rhin). *Eclogae geologicae Helvetiae* 68: 603-612.
- Hess, H. & Holenweg, H. 1985. - Die Begleitfauna auf den Seelilienbänken im mittleren Dogger des Schweizer Juras. *Tätigkeitsberichte der Naturforschenden Gesellschaft Baselland* 33: 141-177.
- Hess, H. & Meyer, C.A. 2008. - A new ophiuroid (*Geocoma schoentalensis* sp. nov.) from the Middle Jurassic of north-western Switzerland and remarks on the family Aplocomidae Hess, 1965. *Swiss Journal of Geosciences* 101: 29-40.
- Hotchkiss, F.H. 1982. - Ophiuroidea (Echinodermata) from Carrie Bow Cay, Belize. *Smithsonian Contributions to the Marine Sciences* 12: 387-412.
- Jagt, J.W.M. 2000. - Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium, Part 3: Ophiuroids, with a chapter on: Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark) by Manfred Kutscher & John W.M. Jagt. *Scripta Geologica* 121: 1-179.

- Kristan-Tollmann, E., Tollmann, A. & Hamedani, A. 1979. - Beiträge zur Kenntnis der Trias von Persien. Mitteilungen der österreichischen geologischen Gesellschaft 70: 119-190.
- Koehler, R. 1904. - Ophiures de l'expédition du Siboga. Part 1. Ophiures de mer profonde. Siboga Expeditie 45a.
- Kutscher, M. 1988. - Zur Invertebratenfauna und Stratigraphie des oberen Pliensbachien von Grimmen (DDR), Echinodermata. Freiburger Forschungshefte C419: 62-70.
- Kutscher, M. 1992. - *Ophiomusium geisingense* n. sp. - eine neue Ophiurenart aus dem Lias Epsilon (Unteres Toarcium) von Bachhausen/Bayern. Archaeopteryx 10: 25-30.
- Kutscher, M. 1996. - Echinodermata aus dem Ober-Toarcium und Aalenium Deutschlands II. Ophiuroidea. Stuttgarter Beiträge zur Naturkunde, Serie B 242: 1-33.
- Kutscher, M. & Hary, A. 1991. - Echinodermen im Unteren Lias (Bucklandi- und Semicostatum-Zone) zwischen Ellange und Elvange (SE-Luxemburg). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 182: 37-72.
- Kutscher, M. & Jagt, J.W.M. 2000. - Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Mon (Denmark), in Jagt, J.W.M., Late Cretaceous-Early Paleocene echinoderms and the K/T boundary in the southeast Netherlands and the northeast Belgium. part 3: Ophiuroids. Scripta Geologica 21: 45-107.
- Kutscher, M. & Villier, L. 2003. - Ophiuroid remains from the Toarcian of Sainte-Verge (Deux-Sèvres, France): paleobiological perspectives. Geobios 36: 179-194.
- Lathuilière, B. 2000. - Les coraux constructeurs du Bajocien inférieur de France. Geobios 33 : 51-72, 153-181 (2 parts).
- Lyman, T. 1862. - Descriptions of new Ophiuridae. Proceedings of the Boston Society of natural History 8: 75-86.
- Lyman, T. 1875. - Zoological Results of the Hassler Expedition. 2. Ophiuridae and Astrophytidae. Illustrated catalogue of the Museum of Comparative Zoology at Harvard College 8(2): 1-34, 5 pl.
- Lyman, T. 1878. - Ophiuridae and Astrophytidae of the "Challenger" expedition. Part I. Bulletin of the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts 5(7): 65-168, 10 pl.
- Martynov, A. 2010. - Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae. Zootaxa 2697: 1-154.
- Müller, J. & Troschel, F.H. 1840. - Über die Ophiuren. Archiv für Naturgeschichte 6(1): 326-330.
- Numberger-Thuy, L.D. & Thuy, B. this volume. - An unusual echinoderm assemblage from the earliest Bajocian (Middle Jurassic) of Luxembourg, with special emphasis of the ophiuroids (Echinodermata: Ophiuroidea). Ferrantia.
- O'Hara, T.D., Hugall, A.F., Thuy, B. & Moussalli, A. 2014. - Phylogenomic Resolution of the Class Ophiuroidea Unlocks a Global Microfossil Record. Current Biology 24: 1-6.
- Roemer, F.A. 1840. - Die Versteinerungen des Norddeutschen Kreidegebirges 2: 49-145.
- Smith, A. B., Paterson, G. L. J. & Lafay, B. 1995. - Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. Zoological Journal of the Linnean Society 114: 213-243.
- Spencer, W.K. 1907: A Monograph of the British Fossil Echinodermata from the Cretaceous formations. Volume second: The Asteroidea and Ophiuroidea. Paleontographical Society Monographs 2(4): 91-132.
- Stöhr, S. (2011). - New records and new species of Ophiuroidea (Echinodermata) from Lifou, Loyalty Islands, New Caledonia. Zootaxa 3089: 1-50.
- Stöhr, S., Conand, C. & Boissin, E. 2008. - Brittle stars (Echinodermata: Ophiuroidea) from La Réunion and the systematic position of *Ophiocanops* Koehler, 1922. Zoological Journal of the Linnean Society 153: 545-560.
- Stöhr, S. & O'Hara, T.D. 2013. - World Ophiuroidea database. Accessed at <http://www.marinespecies.org/ophiuroida> on 2013-12-16.

- Stöhr, S., O'Hara, T.D. & Thuy, B. 2012. - Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS One* 7(3): e31940. doi:10.1371/journal.pone.0031940
- Thurmann, J. 1851. - Abraham Gagnebin de la ferrière. Fragment pour servir à l'histoire scientifique du Jura bernois et neuchâtelois pendant le siècle dernier. *Archives de la Société Jurassienne d'Emulation*.
- Thuy, B. 2005. - Les Ophiures de l'Hettangien inférieur de Vance (B), Bereldange/Bridel et Bourglinster (L). *Memoirs of the Geological Survey of Belgium* 51: 33-57.
- Thuy, B. 2011. - Exceptionally well-preserved brittle stars from the Pliensbachian (Early Jurassic) of the French Ardennes. *Palaeontology* 54: 215-233.
- Thuy, B. 2013. - Temporary expansion to shelf depths rather than an onshore-offshore trend: the shallow-water rise and demise of the modern deep-sea brittle star family Ophiacanthidae (Echinodermata: Ophiuroidea). *European Journal of Taxonomy* 48: 1-242.
- Thuy, B. & Kroh, A. 2011. - Barremian ophiuroids from the Serre de Bleyton (Drôme, SE France). *Annalen des Naturhistorischen Museums in Wien, Serie A* 113: 777-807.
- Thuy, B. & Meyer, C.A. 2012. - The pitfalls of extrapolating present-day depth ranges to fossil communities: new insights from brittle stars (Echinodermata: Ophiuroidea) from the Middle Jurassic of Switzerland. *Swiss Journal of Palaeontology* 132: 5-21.
- Thuy, B., Stöhr, S. 2011. - Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. *Zootaxa* 3013: 1-47.
- Thuy, B., Gale, A.S., Kroh, A., Kucera, M., Numberger-Thuy, L.D., Reich, M. & Stöhr, S. 2012. - Ancient origin of the modern deep-sea fauna. *PLoS One* 7(10): e46913.
- Thuy, B., Gale, A.S., Stöhr, S. & Wiese, F. 2013. - Shallow-water brittle star (Echinodermata: Ophiuroidea) assemblages from the Aptian (Early Cretaceous) of the North Atlantic: first insights into bathymetric distribution patterns. *Göttingen Contributions to Geosciences* 77: 163-182.
- Valette, A. 1929. - Note sur quelques stellerides jurassiques du Laboratoire de Géologie de la Faculté des Sciences de Lyon. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 16: 1-62.
- Wright, T. 1866. - A monograph on the British fossil Echinodermata from the Oolitic formations. 2/2 On the Ophiuroidea. *Monograph of the Paleontological Society* 1866:131-154.
- Wright, T. 1880. - Monograph of the British fossil Echinodermata from the oolitic formations. Volume 2 - The Asteroidea and Ophiuroidea. Part 3. *Monograph of the Palaeontographical Society* 1880: 155-203.