

Brittlestar diversity at the dawn of the Jenkyns Event (early Toarcian Oceanic Anoxic Event): new microfossils from the Dudelonge drill core, Luxembourg

Ben Thuy* and Lea D. Numberger-Thuy

Department of Palaeontology, Natural History Museum Luxembourg, 25 rue Münster, 2160 Luxembourg City, Luxembourg

 BT, 0000-0001-8231-9565; LDN-T, 0000-0001-6097-995X

*Correspondence: bthuy@mnhn.lu

Abstract: Ophiuroids, the slender-armed cousins of starfish, constitute an important component of modern marine benthos and have been used successfully in the exploration of (palaeo)-ecological and evolutionary trends, yet their fossil record is still poorly known. One of the major gaps in the known palaeobiodiversity of this group coincides with a global palaeoenvironmental crisis during the early Toarcian (Early Jurassic, 183 myr ago), known as the Jenkyns Event. Here we describe ophiuroid remains retrieved from a series of samples from the Dudelonge (Luxembourg) drill core, which spans the lower part of the Toarcian, between the top of the Pliensbachian and the onset of the Jenkyns Event. A total of 21 species are recorded, including three new genera and 12 new species. Ophiuroid diversity and abundance fluctuate in parallel with depositional facies, with lowest values coinciding with black shales. Highest diversities, including exceptional occurrences of taxa nowadays restricted to deep-sea areas, are recorded from just below the black shales, corresponding to the onset of the Jenkyns Event. Our results show that even small (100 g) bulk sediment samples retrieved from drill cores can yield numerous identifiable ophiuroid remains, thus unlocking this group for the study of faunal change across palaeoenvironmental crises.

The Jenkyns Event, formerly known as the Toarcian Oceanic Anoxic Event, ranks amongst the major environmental perturbations of the Mesozoic (Hesselbo *et al.* 2000, 2007; Jenkyns 2010; Suan *et al.* 2010). It was marked by global warming (McArthur *et al.* 2000; Suan *et al.* 2010; Krencker *et al.* 2014, 2015; Korte *et al.* 2015) and marine mass extinctions (Little and Benton 1995; Dera *et al.* 2010; Caruthers *et al.* 2013). The basis for a better understanding of potential links between palaeoenvironmental perturbations and biodiversity changes associated with this event are high-resolution studies of the fossil record of various biotic groups (e.g. Danise *et al.* 2019). Most previous efforts in this respect have focused on cephalopod (e.g. Dera *et al.* 2010) and bivalve (e.g. Aberhan and Fürsich 1996) molluscs, as well as brachiopods (e.g. Joral *et al.* 2011), benthic foraminifera (e.g. Rita *et al.* 2016) and ostracods (e.g. Arias 2013). In contrast, the fossil record of echinoderms has received only little attention within the context of the Jenkyns Event.

Ophiuroids rank amongst the five extant classes of echinoderms and form an important component of benthic invertebrate communities in all parts of the world's oceans (Stöhr *et al.* 2012). They have recently emerged as a promising model organism to explore large-scale biogeographical and

evolutionary patterns of marine benthos (e.g. Thuy 2013; O'Hara *et al.* 2014; Woolley *et al.* 2016; Bribiesca-Contreras *et al.* 2017). Ophiuroids have a rich fossil record that consists mostly of microscopic skeletal remains as a result of the rapid post-mortem disintegration of their multi-element skeleton (Hess 1962a; Jagt 2000; O'Hara *et al.* 2014). The spine-bearing lateral arm plates have been identified as the most character-rich and diagnostic components of the ophiuroid skeleton (Hess 1962a; Thuy and Stöhr 2011, 2016). Thanks to detailed micromorphological studies and systematic comparisons with Recent equivalents, it has been demonstrated that fossil ophiuroid lateral arm plates can be identified to species level (Thuy and Stöhr 2011) and can even be included in phylogenetic analyses (Thuy and Stöhr 2016). Ophiuroid microfossils occur in all types of marine rocks, at least from the Silurian onwards, and can often be retrieved in great numbers from sieving residues of bulk sediment samples (e.g. Numberger-Thuy and Thuy 2020).

However, in spite of these promising conditions, ophiuroid microfossils remain understudied, leaving extensive taxonomic and stratigraphic gaps in the fossil record of the group (e.g. Thuy 2013). One of the intervals with a particularly patchy record of ophiuroid palaeobiodiversity is the lower part of

From: Reolid, M., Duarte, L. V., Mattioli, E. and Ruebsam, W. (eds) 2021. *Carbon Cycle and Ecosystem Response to the Jenkyns Event in the Early Toarcian (Jurassic)*. Geological Society, London, Special Publications, **514**, 83–119.

First published online June 15, 2021, <https://doi.org/10.1144/SP514-2021-3>

© 2021 The Author(s). This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>). Published by The Geological Society of London.

Publishing disclaimer: www.geolsoc.org.uk/pub_ethics

the Toarcian. Whereas several relatively diverse ophiuroid assemblages have been described from the upper Toarcian (Kutscher 1996; Kutscher and Villier 2003), only two single-species occurrences based on articulated skeletons have been described for the lower Toarcian Posidonia Shale of southern Germany: *Enakomusium geisingense* (Kutscher 1992) from Bachhausen, and *Sinosura brodiei* (Wright 1866) from Ohmden (Hess 1991). Both records, however, lack a more precise stratigraphic context, thus precluding a conclusive interpretation in the light of the Jenkyns Event.

Here, we describe ophiuroid microfossils from a series of bulk sediment samples taken from the basal Toarcian interval of the Dudelange drill core. The material represents 35 stratigraphically successive assemblages comprising a total of 21 species, thus adding significantly to the Toarcian palaeobiodiversity of Ophiuroidea and filling an important gap in the fossil record of this group. In addition to an exhaustive taxonomic assessment of the assemblages, we explore species range and diversity patterns across the sampled interval and investigate potential palaeobiological implications.

Material and methods

The material described herein consists of several thousands of dissociated ophiuroid lateral arm plates and vertebrae extracted from sieving residues of 35 bulk sediment samples taken from a drill core housed at the Luxembourg Geological Survey under number FR-216-200. The core was retrieved from an exploration well at a disused industry site called Neischmelz near Dudelange, southern Luxembourg (Fig. 1), and is herein informally referred to as the Dudelange drill core. It recovers, among others, a thick Toarcian succession, ranging from the basal-most Tenuicostatum chronozone (*sensu* Page 2003) starting at a depth of 137 m to the Thouarsense chronozone at the top of the core. The Toarcian and uppermost Pliensbachian parts of the core have been extensively sampled for geochemical analyses (work in progress). Ammonites are relatively common on bedding planes of drill-core fragments, allowing for a chronozone-level biostratigraphic subdivision of the drill-core succession.

The samples that yielded the material described herein were taken from the levels between the highest occurrence of ammonites of the genus *Pleuroceras* at 138.62 m and the lowermost occurrence of members of the genus *Harpoceras* ammonites at 124.78 m, corresponding to, or at least including, the Tenuicostatum chronozone. This interval was selected because it yielded echinoderm debris that was visible to the naked eye in several beds, and directly underlay the bituminous shales of the

Serpentinum chronozone, thus potentially preserving ophiuroid assemblages from shortly prior to the Jenkyns Event. Samples consisted of approximately 100 g of bulk sediment each, extracted from the core at every 30 cm using a hammer and chisel, resulting in a total of 35 samples

Samples were soaked in Rewoquat for 24–48 h and then screen-washed using hot tap water. Ophiuroid remains were picked from air-dried residues under a dissecting microscope. Selected specimens were cleaned in an ultrasonic bath, mounted on aluminium stubs and silver-coated for scanning electron microscopy using the JEOL NeoScope JCM-5000 at the Natural History Museum Luxembourg.

Ophiuroid microfossils (Fig. 2) were identified following Thuy and Stöhr (2011, 2016), Thuy (2013) and Nummerger-Thuy and Thuy (2020), using the terminologies defined in those papers. We adopt the classification by O'Hara *et al.* (2017, 2018). Type and figured specimens are housed in the collections of the Natural History Museum Luxembourg (abbreviated as MnhnL OPH).

The residues that yielded the ophiuroid material described herein are currently being explored for ostracods and benthic foraminifera in order to obtain a more precise biostratigraphic subdivision of the succession. It should be stressed that the stratigraphic interpretation of the studied drill core is still in progress. Chronozone boundaries are based on ammonite and lithostratigraphic evidence available at the time of submission of the present study, and therefore should be considered to be tentative.

Results

Of the studied 35 samples, 25 yielded a total of 1131 ophiuroid lateral arm plates (Table 1; Fig. 3). The 10 remaining samples, almost all from within black shale intervals, were barren. A total of 21 ophiuroid species were identified, 12 of which are new and formally described herein (see below). Some species range throughout the entire series of samples (e.g. *Inexpectacantha acrobatica*), others are restricted to specific parts of the studied interval. Four species (i.e. the unnamed ophiomusid and ophiopyrgid, *Ophiohelus* sp. nov., and *Ophiocopa* sp. nov.) were found exclusively in a single sample each.

Both abundance and taxonomic diversity show considerable variation along the studied succession of samples. The most marked drops in plate abundance and species diversity coincide with intervals of black shales. The transition from the marlstones of the uppermost Tenuicostatum chronozone to the bituminous shales of the Serpentinum chronozone, assumedly corresponding to the onset of the Jenkyns Event, is accompanied by a drop in species diversity and plate abundance, leaving only two species

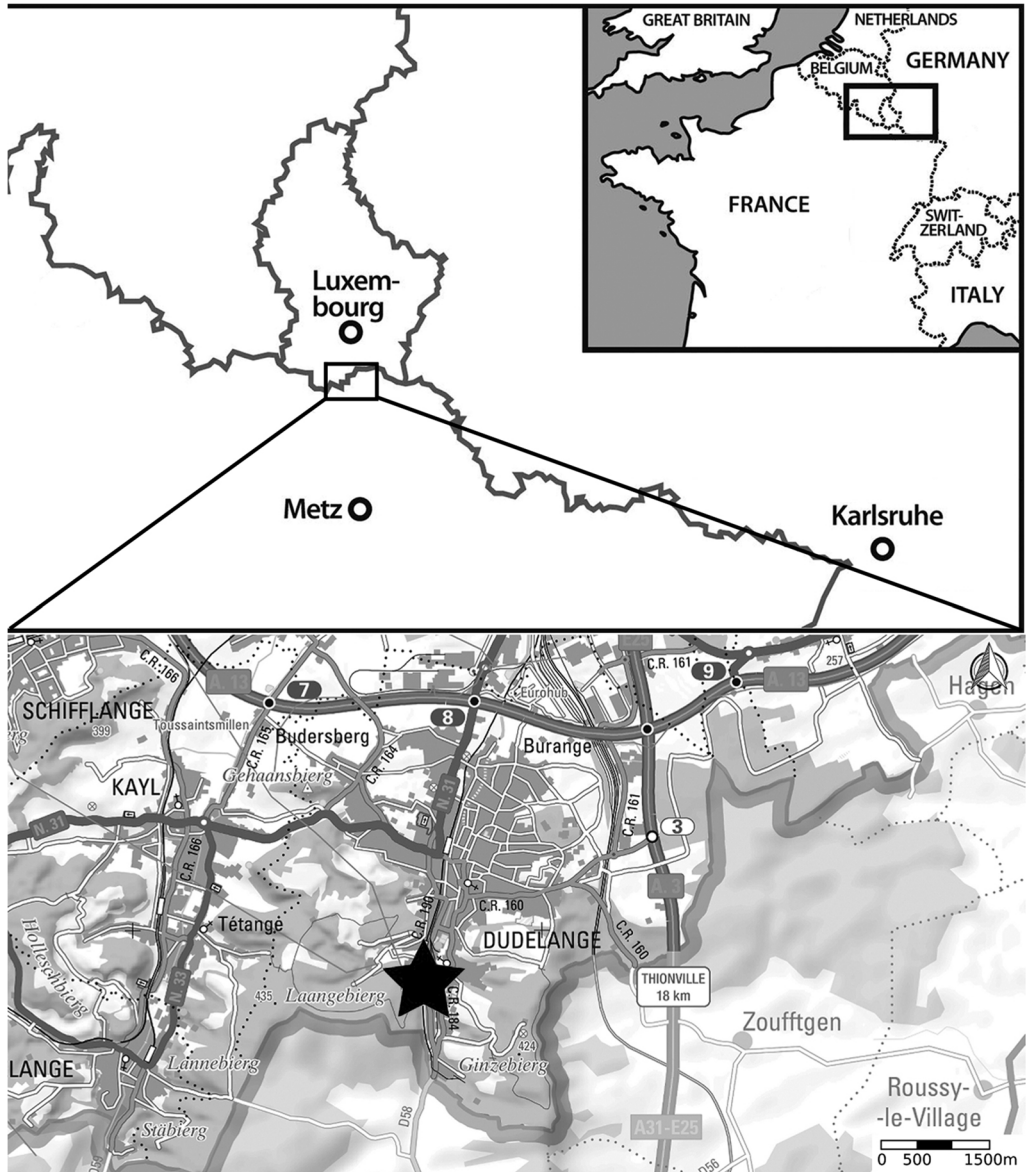


Fig. 1. Location of the drill core sampled in the present study.

(*Inexpectacantha acrobatica* and *Sinosura dieschbourgae*).

Systematic palaeontology

Class **Ophiuroidea** Gray (1840)
 Subclass **Myophiuroida** Matsumoto (1915)
 Infraclass **Metophiuroida** Matsumoto (1913)
 Superorder **Euryophiuroida** O'Hara, Hugall, Thuy,
 Stöhr and Martynov (2017)

Order and family unknown
 Genus *Inexpectacantha* Thuy (2011)

Type species. *Inexpectacantha acrobatica* Thuy (2011), by original designation.

Emended diagnosis. Small euryophiuroid with five unbranched arms, thick dorsal disc scales covered by scattered granules; radial shields small, rounded isosceles-triangular, single row of blunt oral papillae; up to three spine-like tentacle scales; tentacle pores

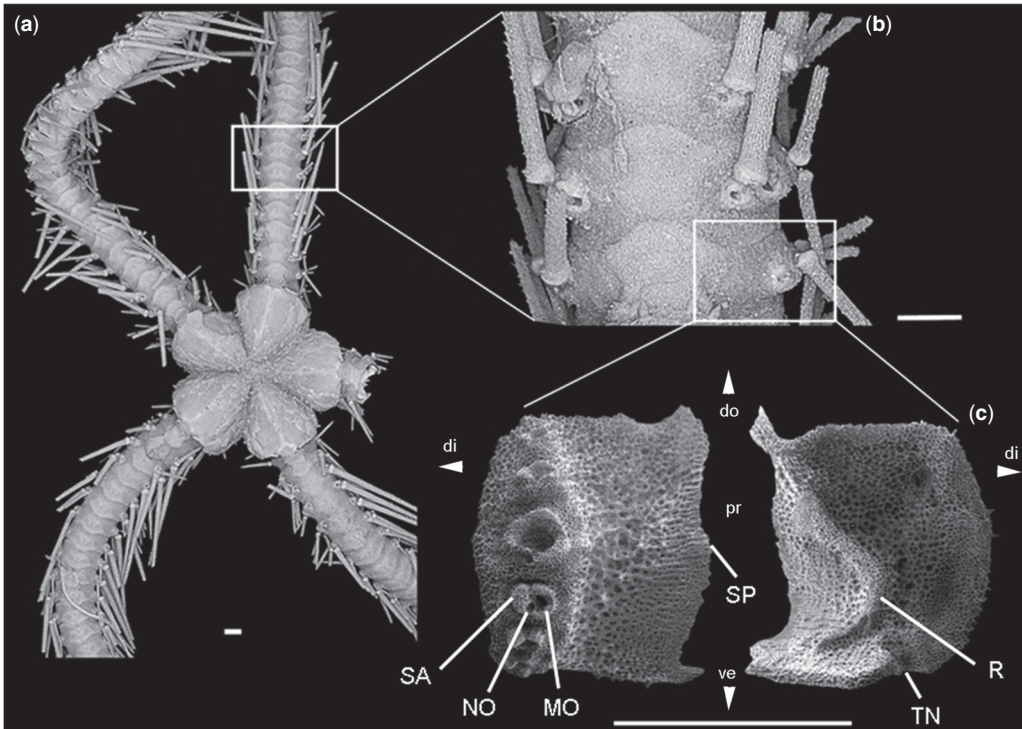


Fig. 2. Recent ophiuroid (a) to show the position of the lateral arm plates (c) within the arm of the animal (b), indicating some of the most relevant morphological details (di, distal; do, dorsal; pr, proximal; ve, ventral; MO, muscle opening; NO, nerve opening; R, vertebral articular ridge; SA, spine articulation; SP, spur on the outer proximal edge; TN, tentacle notch). Scale bars equal 1 mm.

developed as between-plate openings throughout the arm; small to moderately large lateral arm plates of thick, rounded and bulging aspect; outer surface stereom often coarsely meshed but otherwise devoid of conspicuous ornamentation; no spurs on outer proximal and inner distal edges; spine articulations free-standing or in shallow depressions, composed of a muscle opening encompassed proximally by a thick, prominent, rugose, C-shaped ridge, and distally separated from a smaller nerve opening by a large, thick vertical ridge; arm spines conical, dorsal-most spines often much longer than ventral spines; hook-shaped arm spines in distal arm segments.

Remarks. The genus *Inexpectacantha* was first described by Thuy (2011) on the basis of exceptionally well-preserved, intact skeletons from the lower Pliensbachian (Davoei chronozone) of Sedan in the French Ardennes. Due to the unusual combination of characters, the higher-level classification of *Inexpectacantha* proved challenging, but the superficially ear-shaped spine articulations prompted Thuy (2011) to assign the genus to the family Ophiacanthidae. This classification was adopted by Thuy

(2013) and Thuy and Stöhr (2016), who scored the spine articulations based on assumptions made by Thuy (2011).

The material described herein has enabled new insights into the microstructure of the lateral arm plates and thus a re-evaluation of the spine articulation morphology of *Inexpectacantha*. The new observations have revealed surprisingly that the spine articulations are not composed of tilted dorsal and ventral lobes. Instead, the prominent, rugose proximal ridge encompasses the muscle opening, while the nerve opening is situated further distally, widely separated from the muscle opening by a thick vertical ridge. This configuration precludes assignment to the family Ophiacanthidae or to the suborder Ophintegrada in general and, instead, suggests a position within the suborder Euryophiurida. Based on a tentative evaluation of the evidence at hand, we speculate that *Inexpectacantha* holds a basal position within the order Euryalida. A more conclusive classification of this genus, however, should be based on a phylogenetic analysis, also taking into account the closely related genus *Ophioleviathan* Thuy (2013), which is beyond the scope of the present paper. We here

Table 1. Sample numbers, with depth in metres, in drill core and the number of lateral arm plates per species

Sample No	Sample depth (m)	<i>Inexpectacantha acrobatica</i>	<i>Inexpectacantha ulmanni</i>	<i>Thanataster desdemonia</i>	<i>Barbaraster colbachi</i>	<i>Barbaraster muenzbergerae</i>	Unnamed ophiomusid	<i>Ophiomusa perezii</i>	<i>Ophiogojira andrewi</i>	<i>Ophiogojira aliorbis</i>	Unnamed ophiopygid	<i>Palaeocoma kortzi</i>	<i>Ophiotardis tennanti</i>	<i>Ophiomisisidium pratchettae</i>	<i>Lapidaster fasciatus</i>	<i>Lapidaster hougardae</i>	<i>Ophiohelus</i> sp. nov.	<i>Ophiocopa</i> sp. nov.	<i>Dermocoma</i> sp.	<i>Dermacantha reolidi</i>	<i>Sinosura</i> cf. <i>brodiei</i>	<i>Sinosura dieschbourgae</i>	Number of plates
DUD-01	126.58	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	8	
DUD-02	126.97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-03	127.30	3	0	0	3	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	5	26
DUD-04	127.76	0	0	0	1	0	0	0	0	0	0	15	11	0	1	0	0	0	0	0	0	8	36
DUD-05	128.32	3	0	0	4	0	0	1	6	0	0	7	0	4	0	0	0	0	0	0	0	1	26
DUD-06	128.81	2	0	0	0	0	0	0	4	2	0	3	0	10	3	0	1	2	2	11	0	31	71
DUD-07	129.13	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	3	0	0	19	26
DUD-08	129.83	7	2	0	0	1	0	1	26	8	0	3	0	2	8	0	0	0	2	5	0	7	72
DUD-09	130.25	4	0	0	0	0	0	7	49	1	0	0	2	6	6	0	0	0	1	0	0	6	82
DUD-10	130.60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-11	130.92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-12	131.08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-13	131.34	7	0	0	0	0	0	0	0	4	0	0	0	0	20	0	0	0	2	42	0	4	79
DUD-14	131.71	3	0	0	0	0	0	2	27	0	0	0	0	0	0	0	0	1	22	0	6	61	
DUD-15	131.94	5	0	0	0	0	0	3	51	0	0	0	5	0	10	0	0	0	8	0	3	85	
DUD-16	132.30	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
DUD-17	132.72	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
DUD-18	133.05	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
DUD-19	133.49	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	8
DUD-20	133.89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-21	134.16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-22	134.63	27	9	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	16	55
DUD-23	134.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-24	135.30	1	0	2	2	3	0	0	20	13	0	0	11	0	10	1	0	0	0	0	0	0	63
DUD-25	135.61	0	0	0	0	0	0	0	15	2	0	0	1	0	0	0	0	0	2	0	5	25	
DUD-26	135.91	9	1	0	0	0	0	0	53	8	0	0	0	0	6	0	0	0	8	0	25	110	

Ophiuroid fossil from the lowermost Toarcian

(Continued)

Table 1. Continued.

Sample No	Sample depth (m)	<i>Inexpectacantha acrobatica</i>	<i>Inexpectacantha ulmanni</i>	<i>Thanataster desdemonia</i>	<i>Barbaraster colbachi</i>	<i>Barbaraster muenzbergerae</i>	Unnamed ophiomusid	<i>Ophiomusa perezii</i>	<i>Ophiogojira andreui</i>	<i>Ophiogojira aliorbis</i>	Unnamed ophiopyrgid	<i>Palaeocoma kortei</i>	<i>Ophiotardis tennanti</i>	<i>Ophiomisidium pratchettae</i>	<i>Lapidaster fasciatus</i>	<i>Lapidaster hongardae</i>	<i>Ophiohelus</i> sp. nov.	<i>Ophiocopa</i> sp. nov.	<i>Dermocoma</i> sp.	<i>Dermacantha reolidi</i>	<i>Sinosura</i> cf. <i>brodiei</i>	<i>Sinosura dieschbourgae</i>	Number of plates
DUD-27	136.22	0	0	5	0	1	0	0	49	4	0	0	16	0	1	0	0	0	0	0	0	5	81
DUD-28	136.68	3	0	0	0	0	0	0	8	1	0	0	1	0	4	0	0	0	0	4	0	3	24
DUD-29	137.17	0	0	14	2	2	0	0	10	9	0	0	16	0	17	2	0	0	0	4	0	2	78
DUD-30	137.59	1	0	1	1	1	0	0	9	0	0	0	11	0	1	0	0	0	1	0	0	0	26
DUD-31	137.89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-32	138.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-33	138.53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DUD-34	138.94	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	48	0	53
DUD-35	139.53	1	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	21	0	26

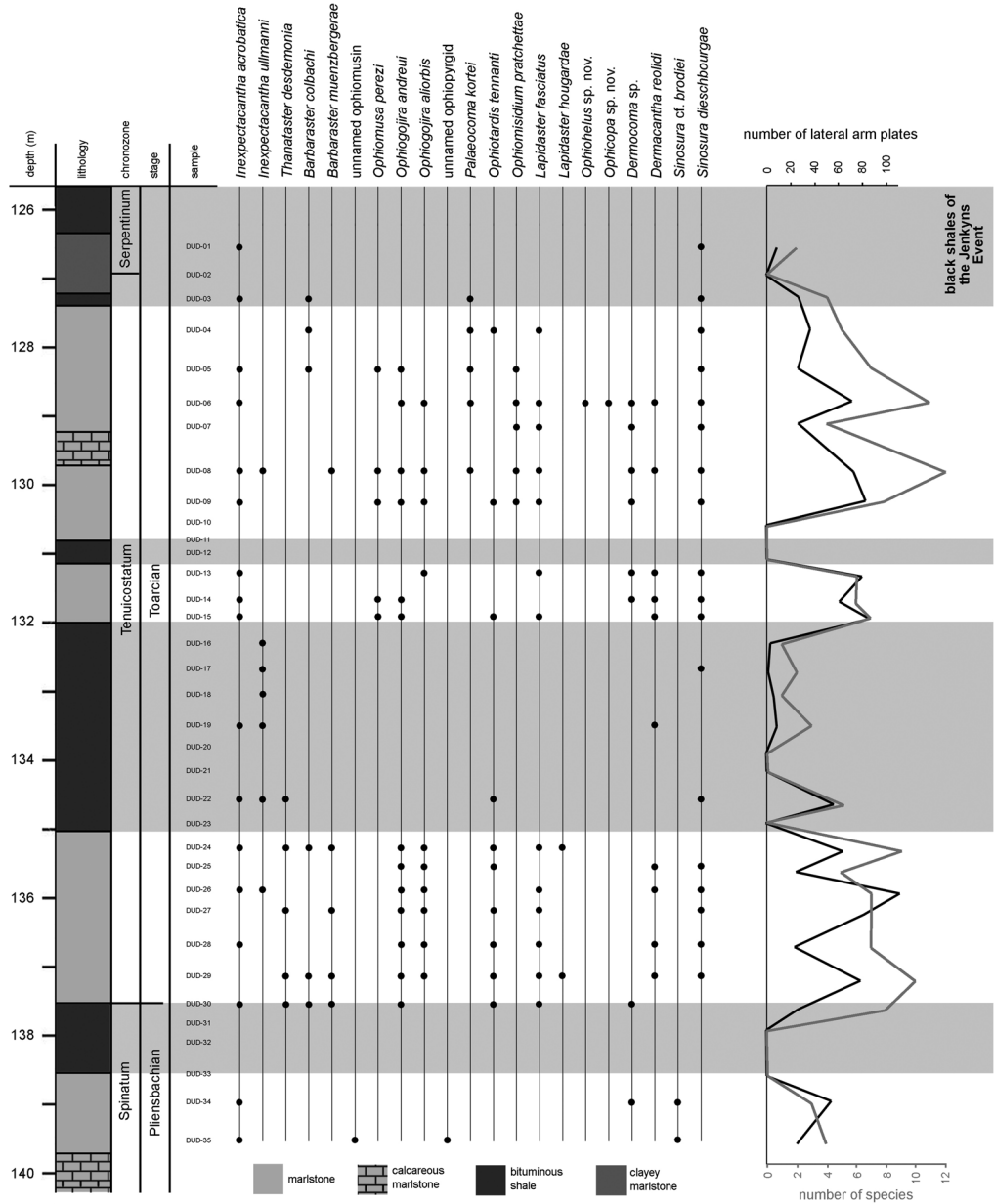


Fig. 3. Log of the studied drill-core interval showing depth, lithology, tentative stratigraphy, occurrence of species, diversity and abundance (total number of lateral arm plates).

treat *Inexpectacantha* as a member of the Euryophiurida with unknown affinities.

Inexpectacantha acrobatica Thuy (2011)

Figure 4a–e

Inexpectacantha acrobatica Thuy (2011): p. 217, pls 1–3, pl. 4 figs 1–6.

Inexpectacantha acrobatica – Thuy *et al.* (2011): p. 179, fig. 3f.

Inexpectacantha acrobatica – Thuy (2013): p. 192, fig. 33: 9–10.

Description. Thick, robust lateral arm plates of rounded, bulging general outline; relatively small height/width ratio even in proximal lateral arm

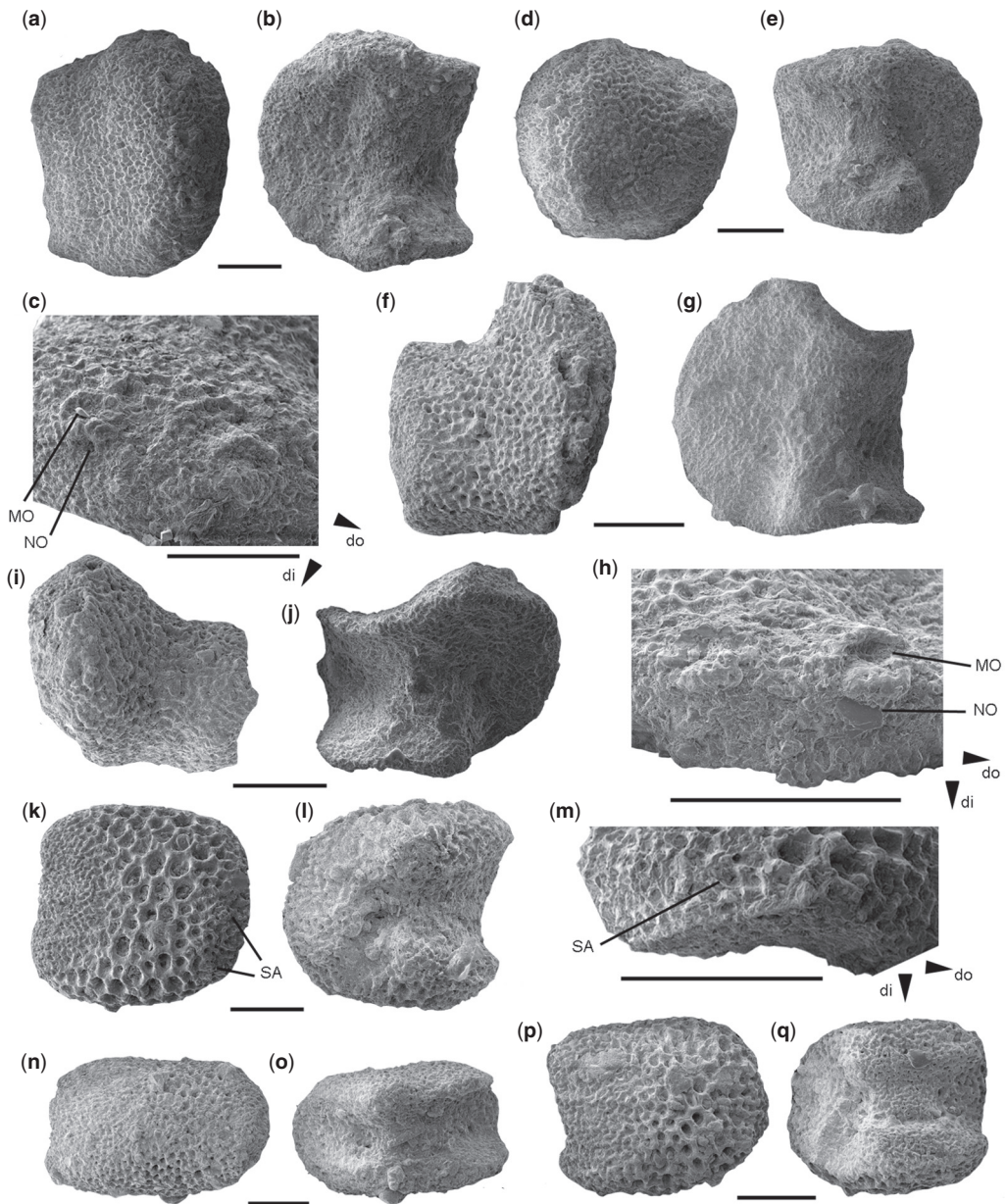


Fig. 4. Ophiuroid lateral arm plates from the lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(e) *Inexpectacantha acrobatica* Thuy (2011): sample DUD-09; MnhnL OPH108: proximal lateral arm plate in external (a) and internal (b) views, and with detail of spine articulations (c); MnhnL OPH108: median to distal lateral arm plate in external (d) and internal (e) views. (f)–(j) *Inexpectacantha ullmanni* sp. nov.: sample DUD-19, MnhnL OPH109 (holotype): proximal lateral arm plate in external (f) and internal (g) views, and with detail of spine articulation (h); MnhnL OPH110 (paratype): median to distal lateral arm plate in external (i) and internal (j) views. (k)–(q) *Thanataster desdemonia* gen. et sp. nov.; sample DUD-29, MnhnL OPH111 (holotype): proximal lateral arm plate in external (k) and internal (l) views, and with detail of spine articulation (m); MnhnL OPH112 (paratype): distal lateral arm plate in external (n) and internal (o) views; MnhnL OPH113 (paratype): median lateral arm plate in external (p) and internal (q) views. Scale bars equal 0.2 mm. Abbreviations: di, distal; do, dorsal; MO, muscle opening; NO, nerve opening; SA, spine articulation.

plates; outer surface with moderately coarsely meshed stereom and a weak constriction resulting in concave dorsal edge and a shallow, poorly defined furrow parallel to the proximal edge; up to six relatively small spine articulations freestanding on a bulging distal portion of the lateral arm plate; spine articulations composed of a comma-shaped muscle opening proximally encompassed by a thin, rugose, C-shaped ridge, and distally separated from a smaller, round nerve opening by a large, conspicuous, lip-shaped vertical ridge. Inner side of lateral arm plates with a single large, moderately well-defined ridge with a proximally curved, broad, tongue-shaped dorsal tip; tentacle notch relatively wide; no spurs or perforations discernible.

Remarks. In addition to the type material from the Pliensbachian of Sedan, France (Thuy 2011), Thuy (2013) assigned dissociated lateral arm plates from the lower Pliensbachian (Davoei chronozone) of the UK and the lowermost Toarcian (Tenuicostatum chronozone) of Belgium to this species. The material described herein falls within the morphological spectrum of *Inexpectacantha acrobatica* as previously observed and thus adds another lowermost record to the relatively long fossil range of the species. A detailed comparison with *Inexpectacantha ullmanni* sp. nov. is provided below.

Inexpectacantha ullmanni sp. nov.
Figure 4f–j

Holotype. MnhnL OPH109.

Paratype. MnhnL OPH110.

Type locality and stratum. Sample DUD-19 taken at 133.49 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of Clemens V. Ullmann, for his work on the geochemistry of modern and ancient biominerals, and for his enthusiasm to venture into geochemical analyses of the ophiuroid microfossils studied herein.

Diagnosis. Species of *Inexpectacantha* with relatively thin lateral arm plates with a very strong constriction, resulting in a deeply concave dorsal edge and a strongly bulging distal portion; up to four large spine articulations showing a strong dorsalward increase in size; outer proximal edge of the lateral arm plate with a very narrow, poorly defined band of more finely meshed stereom, if at all.

Description of holotype. MnhnL OPH109 is a medium-sized dissociated proximal lateral arm plate, relatively thin, slightly higher than long, with

evenly convex proximal and distal edges, a straight ventral edge and a deeply concave dorsal edge as a result of a strong constriction; proximal edge devoid of spurs, lined by a very narrow, poorly defined band of more finely meshed stereom; outer surface stereom very coarse, with trabecular intersections transformed into irregular, slightly pointed tubercles smaller than the surrounding pores; four large, conspicuous spine articulations freestanding at the same level as the surrounding outer surface stereom, at a short distance from the distal edge of the lateral arm plates and not bordered proximally by any ridge; spine articulations composed of a large, vertically elongate muscle opening proximally encompassed by a large, prominent, rugose, C-shaped ridge, and distally separated from a smaller nerve opening by a large, prominent, lip-shaped vertical ridge; size of spine articulations strongly increasing dorsalwards, with dorsalmost spine articulations very large and strongly prominent on protruding dorso-distal tip of the lateral arm plate.

Inner side of lateral arm plate with a large, moderately well-defined, tongue-shaped vertebral articular ridge, with a wide, proximally curved dorsal tip; large, ventralward-pointing tentacle notch; no perforations and no spurs discernible on inner distal edge.

Paratype supplements. MnhnL OPH110 is a dissociated median to distal lateral arm plate, slightly longer than high; proximal edge pointed, not lined by a band of differentiated stereom; constriction and outer surface stereom as in holotype; four spine articulations as in holotype, albeit with a weaker dorsalward increase in size; inner side as in holotype.

Remarks. The lateral arm plates described above show a combination of characters that is typically found in *Inexpectacantha*, including the highly characteristic rounded, bulging overall shape, the rugose outer surface without striation, tubercles or spurs, and the conspicuous spine articulations. They differ, however, from all currently known species of the genus, including the co-occurring *I. acrobatica*, in having a much stronger constriction, larger spine articulations with a stronger dorsalward increase in size and a very weak band of differentiated stereom lining the outer proximal edge. We therefore assign these lateral arm plates to a new species.

Order **Ophiurida** Müller and Troschel (1840) *sensu* O'Hara *et al.* (2017)

Suborder **Ophiomusina** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Family unknown

Genus *Thanataster* nov.

Type species. *Thanataster desdemonia* gen. et sp. nov., by present designation.

Other species included: Mesophiomusium sinemur-ensis (Kutscher and Hary 1991).

Etymology. Genus name composed of ‘Thanatos’, the personification of death in Greek mythology, and ‘astron’, Greek for celestial body, literally translating into ‘star of death’.

Diagnosis. Ophiomusium genus with small, robust lateral arm plates of rounded outline, with convex dorsal, ventral and distal edges; outer surface with a conspicuously coarse stereom; outer proximal edge lined by a band of more finely meshed stereom, with small, poorly defined spurs and a very shallow furrow, if at all; small, inconspicuous, equal-sized spine articulations close to distal edge of lateral arm plate; inner side of lateral arm plate with low to moderately high contact surfaces with the opposite lateral arm plate; tentacle pores developed as notches in proximal and median lateral arm plates.

Remarks. The ophiuroid material described herein includes several forms that superficially resemble species of the ophiomusium genus *Enakomusium*. The latter was introduced by Thuy (2015) to accommodate extinct ophiomusium taxa previously referred to *Ophiomusium* but differing from that genus, as well as from all other extant ophiomusium genera, in a number of critical aspects, in particular the more rounded outline of the lateral arm plates, the relatively large spine articulations that bore relatively long spines, and the tentacle pores developed as between-plate openings in proximal and often also in median arm segments.

While the *Enakomusium*-like lateral arm plates described herein match the diagnosis of the genus in having between-plate tentacle openings beyond the proximalmost lateral arm plates, they differ in having much smaller spine articulations positioned close to the distal edge, and in lacking the typical deep furrow parallel to the outer proximal edge. We therefore refrain from assigning the forms described herein to *Enakomusium* in order not to expand the morphological spectrum of the genus beyond meaningful limits. Instead, we introduce two new genera and anticipate a third new genus without formally naming it here.

The combination of characters of the *Enakomusium*-like forms described herein, in particular the thickness of the lateral arm plates, their compact outline, the shape of the spine articulations and the development of the tentacle pores, suggests an assignment to the Ophiomusina. Within this suborder, however, relationships are more difficult to evaluate with the evidence available at present. The systematic position of *Enakomusium* with respect to the two extant ophiomusium families Ophiomusidae and Ophiosphalmidae has not yet been resolved (Thuy *et al.* 2021). The forms described herein are

morphologically closest to *Enakomusium*, which prompts us to consider them as Ophiomusina *incertae sedis* for the time being.

Thanataster desdemonia sp. nov.
Figure 4k–q

Holotype. MnhnL OPH111.

Paratypes. MnhnL OPH112 and OPH113.

Type locality and stratum. Sample DUD-29 taken at 137.17 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named after the Luxembourg death metal band Desdemonia, to honour their enthusiasm for the cross-fertilization between palaeontology and rock music.

Diagnosis. Species of *Thanataster* gen. nov. with two very small, poorly developed spurs on the outer proximal edge, and with two small, inconspicuous spine articulations.

Description of holotype: MnhnL OPH111 is a small dissociated proximal lateral arm plate, of rounded rectangular outline, slightly higher than long, with rounded, dorsal, ventral and distal edges; proximal edge concave, lined by poorly defined, slightly depressed band of more finely meshed stereom bearing two small, horizontally elongate, poorly defined spurs; ventral spur slightly larger and better defined than dorsal one; outer surface with a conspicuously coarse stereom showing extremely large pores and irregular but not particularly thickened trabecular intersections; two small, inconspicuous spine articulations integrated into outer surface stereo, one close to the ventro-distal tip of the lateral arm plate, the other one in the middle of the distal edge; muscle and nerve openings of the spine articulations almost the same size as the surrounding stereom pores, and ridges encompassing the openings very similar to the surrounding stereom trabeculae. Inner side of lateral arm plate with a small, short, well-defined, rounded-triangular vertebral articular ridge; very large dorsal and ventral contact surfaces with opposite lateral arm plate; two small horizontally elongate, poorly defined spurs on inner distal edge; moderately large, poorly defined tentacle notch pointing ventrally to slightly ventro-distally.

Paratype supplements. MnhnL OPH112 is a small, dissociated median lateral arm plate, slightly longer than high; proximal edge and outer surface ornamentation as in holotype; two spine articulations as in holotype but slightly better discernible; inner side

as in holotype but with better-defined vertebral articular ridge.

MnhnL OPH113 is a small, dissociated distal lateral arm plate, almost 1.5 times longer than high; plate outline and outer surface ornamentation as in holotype; two spurs on outer proximal edge less well defined than in holotype; two spine articulations as in holotype; inner side with slightly lower dorsal and ventral contact surfaces with opposite lateral arm plate; vertebral articular ridge as in holotype, albeit lower; tentacle pore developed as within-plate perforation distally bordering vertebral articular ridge.

Remarks. The lateral arm plates described above have spine articulations composed of muscle and nerve openings separated by a vertical ridge, placing them into the Euryophiurida. In addition, they are strongly ornamented, very thick, and show moderately large dorsal and ventral contact surfaces with the opposite lateral arm plate, placing them in the Ophiomusina. Within this suborder, greatest similarities are shared with *Mesophiomusium sinemurensis* (Kutscher and Hary 1991) from the Hettangian of Belgium and Luxembourg (Thuy 2011), and the Sinemurian of Luxembourg (Kutscher and Hary 1991), especially with respect to the coarse outer surface ornamentation and the small spine articulations. The lateral arm plates described herein, however, differ in having smaller, less conspicuous spurs on the outer proximal edge, and fewer and smaller spine articulations, thus suggesting close ties but distinction at the species level.

Mesophiomusium sinemurensis was explicitly excluded from *Enakomusium* by Thuy (2015) on account of fundamental differences with the lateral arm plates of the type species, *E. weymouthiense*. These differences, in particular the much coarser outer surface stereom, the much smaller, almost indiscernible spine articulations close to the distal edge, and the absence of a deep furrow lining the outer proximal edge, are corroborated by the new species described above. We therefore introduce the new genus *Thanataster* to accommodate this new species, as well as the morphologically closely similar *Mesophiomusium sinemurensis*. Although it seems very probable that *Thanataster* gen. nov. and *Enakomusium* share close phylogenetic ties, we cannot further substantiate the systematic position of the former within the Ophiomusina.

Genus *Barbaraster* nov.

Type species. *Barbaraster colbachi* gen. et sp. nov., by present designation.

Other species included: *Barbaraster muenzbergerae* sp. nov.

Etymology. Genus name formed in honour of Saint Barbara, the patron saint of geologists, amongst others.

Diagnosis. Ophiomusina genus with rounded-rectangular lateral arm plates, with low height/length ratio; outer proximal edge lined by very shallow, poorly defined furrow with large, albeit weakly prominent spurs and faint horizontal striation; outer surface with a fine tuberculation; small spine articulations directly at distal edge of lateral arm plate; inner side of lateral arm plate with thin dorsal and ventral contact surfaces with opposite lateral arm plates; tentacle pores developed as between-plate openings in proximal and median lateral arm plates.

Barbaraster colbachi sp. nov.

Figure 5a–e

Holotype. MnhnL OPH114.

Paratypes. MnhnL OPH115.

Type locality and stratum. Sample DUD-04 taken at 127.76 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of Robert Colbach, head of the Luxembourg Geological Survey, for his work on the geology of Luxembourg, and for promoting a close collaboration with the palaeontology department of the Natural History Museum Luxembourg.

Diagnosis. Species of *Barbaraster* gen. nov. with outer proximal edge of lateral arm plates lined by a very shallow furrow and bearing a dorsal and a ventral spur; up to three spine articulations distributed evenly along the entire distal edge.

Description of holotype. MnhnL OPH114 is a dissociated, medium-sized proximal lateral arm plate, slightly longer than high, relatively thin and of rounded-rectangular outline, with weakly convex dorsal, ventral and distal edges; proximal edge evenly concave, lined by very shallow, poorly defined furrow composed of slightly more finely meshed stereom and bearing two large, weakly prominent, horizontally elongate spurs; outer surface ornamentation composed of finely meshed stereom with trabecular intersections transformed into small tubercles, arranged in a weak grit-like pattern; three small, inconspicuous spine articulations directly at distal edge of the lateral arm plate at the same level than surrounding stereom; spine articulations composed of a small muscle opening proximally bordered by a relatively low, thin, rugose C-shaped ridge, and distally separated from a slightly smaller

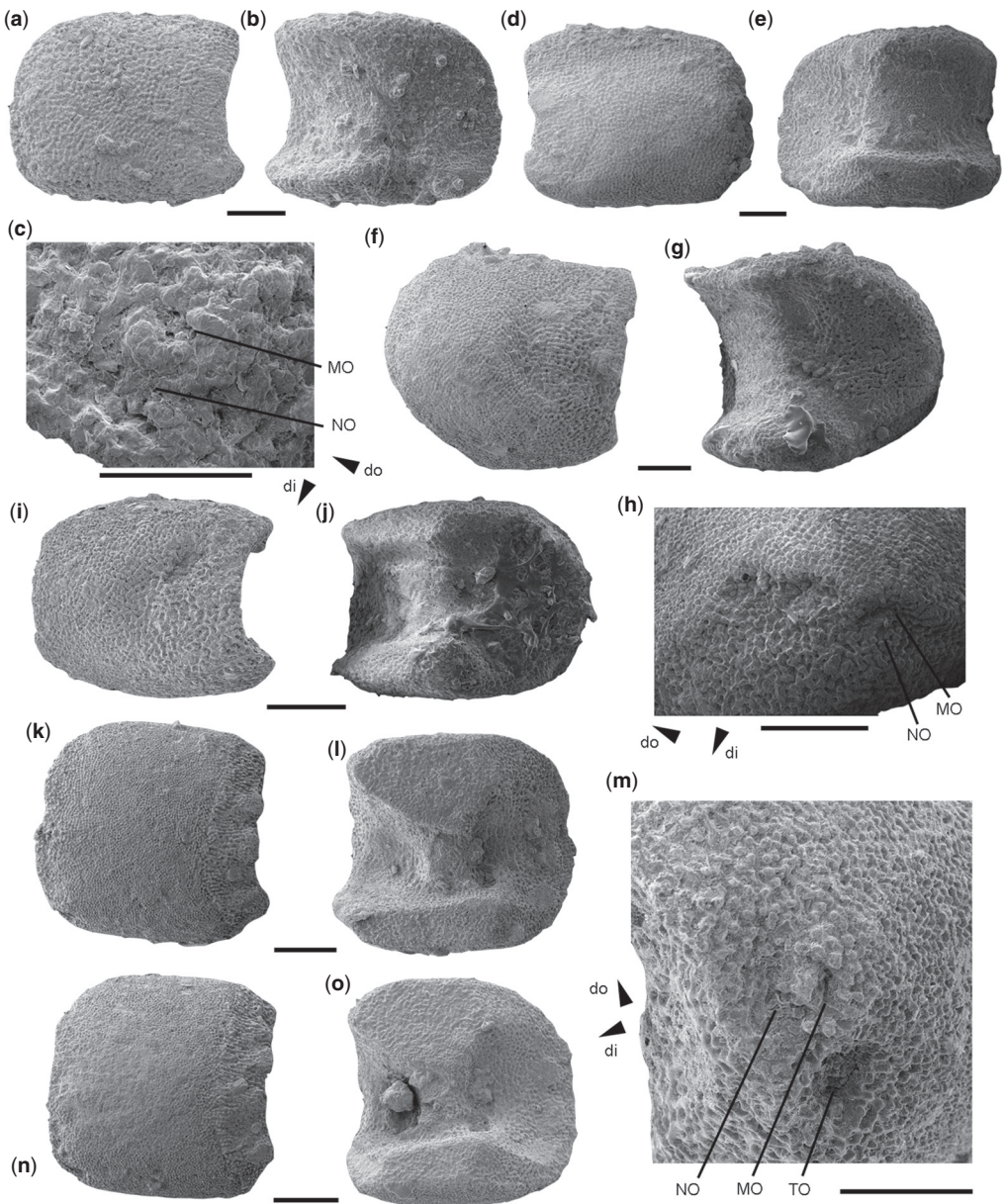


Fig. 5. Ophiuroid lateral arm plates from the uppermost Pliensbachian (*Spinatum* chronozone) and lowermost Toarcian (*Tenuicostatum* chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(e) *Barbaraster colbachi* gen. et sp. nov.: sample DUD-04; MnhnL OPH114 (holotype): proximal lateral arm plate in external (a) and internal (b) views, and with detail of spine articulations (c); MnhnL OPH115 (paratype): median to distal lateral arm plate in external (d) and internal (e) views. (f)–(j) *Barbaraster muenzbergerae* gen. et sp. nov.: sample DUD-29, MnhnL OPH116 (holotype): proximal lateral arm plate in external (f) and internal (g) views, and with detail of spine articulation (h); MnhnL OPH117 (paratype): median to distal lateral arm plate in external (i) and internal (j) views. (k)–(o) Unnamed ophiomuslin genus and species; sample DUD-35, MnhnL OPH118: proximal lateral arm plate in external (k) and internal (l) views, and with detail of spine articulation (m); MnhnL OPH119: median lateral arm plate in external (n) and internal (o) views. Scale bars equal 0.1 mm in (c) and (m), and 0.2 mm in all others. Abbreviations: di, distal; do, dorsal; MO, muscle opening; NO, nerve opening; TO, tentacle opening.

nerve opening by a well-defined, thick and prominent vertical ridge; spine articulations nearly equal-sized and evenly spaced.

Inner side of lateral arm plate with thin dorsal and ventral contact surfaces with opposite lateral arm plate, leaving a relatively large cavity for the vertebra; single large but poorly defined vertebral articular ridge, with proximally curved, tongue-shaped dorsal tip; relatively narrow, well-defined, ventralward-pointing tentacle notch; two weakly defined spurs on inner distal edge; no perforations discernible.

Paratype supplements. MnhnL OPH115 is a dissociated median to distal lateral arm plate, approximately 1.5 times longer than high; plate outline as in holotype; spurs and furrow lining proximal edge better defined than in holotype; outer surface stereom as in holotype; three spine articulations similar to those of holotype; inner side of lateral arm plate with larger dorsal and ventral contact surfaces with opposite lateral arm plate; vertebral articular ridge wider and better defined than in holotype; tentacle pore developed as small within-plate perforation close to the ventro-distal edge of the vertebral articular ridge.

Remarks. The lateral arm plates described above belong to the Ophiurida on account of their spine articulation morphology and general shape. Within this order, however, affinities are less clear cut. Similarities are closest to some species of the ophiomusid genus *Enakomusium*, in particular *E. geisingense*, especially on account of general shape, the outer surface ornamentation and the development of the tentacle pores. The lateral arm plates described above differ, however, in having smaller spine articulations directly at the distal edge without a dorsalward increase in size. They furthermore lack a deep furrow along the outer proximal edge and have much thinner contact surfaces with the opposite lateral arm plate on the inner side of the plate. In view of these differences, assignment to *Enakomusium* would expand the morphological spectrum of that genus beyond meaningful limits. We therefore introduce the new genus *Barbaraster* to accommodate the lateral arm plates described above, as well as those of *Barbaraster muenzbergerae* sp. nov. described and discussed below.

Barbaraster muenzbergerae sp. nov.

Figure 5f–j

Holotype. MnhnL OPH116.

Paratypes. MnhnL OPH117.

Type locality and stratum. Sample DUD-29 taken at 137.17 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelage drill core), drilled at Neischmelz near Dudelage, Luxembourg;

Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of Petra Münzberger for her excellent work on the geology of the Dudelage drill core.

Diagnosis. Species of *Barbaraster* with lateral arm plates showing a conspicuously rounded distal portion; centre of the outer proximal edge of the lateral arm plates with a C-shaped furrow proximally bordered by a central spur; two small spine articulations grouped close to ventro-distal edge of the lateral arm plate.

Description of holotype. MnhnL OPH116 is a dissociated proximal lateral arm plate, slightly longer than high, with weakly convex dorsal and ventral edges and with a conspicuously rounded, strongly convex distal edge; proximal edge slightly concave; well-defined, C-shaped furrow lining the outer proximal edge, proximally bordered by a narrow band of horizontally striated stereom and a central, prominent, moderately well-defined spur; outer surface ornamentation consisting of small, tightly spaced tubercles; two small spine articulations grouped at ventro-distal edge of the lateral arm plate, slightly sunken; spine articulations composed of a comma-shaped muscle opening proximally encompassed by a narrow, thin, poorly defined, rugose ridge, and distally separated from a much smaller, round nerve opening by a small, narrow vertical ridge.

Inner side of lateral arm plate with thin dorsal and ventral contact surfaces with the opposite lateral arm plate, leaving a large cavity for vertebra; single vertebral articular ridge large, wide, well-defined; shallow, poorly defined ventralward-pointing tentacle notch; single central, poorly defined spur on inner distal edge.

Paratype supplements. MnhnL OPH117 is a dissociated median to distal lateral arm plate, approximately 1.5 times longer than wide; outline as in holotype but with slightly less strongly rounded distal portion; outer proximal edge as in holotype but without horizontally striated stereom and with less clearly defined central spur; outer surface ornamentation as in holotype; two spine articulations close to ventro-distal tip of lateral arm plate, as in holotype; inner side of the plate as in holotype but with larger dorsal and ventral contact surfaces with the opposite lateral arm plate; tentacle notch as in holotype.

Remarks. The lateral arm plates described above are similar to those of *Barbaraster colbachi* in showing an *Enakomusium*-like morphology without fully matching the diagnosis of that genus, in particular with respect to the smaller spine articulations, the development of the furrow along the outer proximal edge and the size of the contact surfaces with the

opposite lateral arm plate on the inner side. These lateral arm plates are closest to those of *Barbaraster colbachi* but differ in the number and position of the spine articulations and in the ornamentation of the outer proximal edge. We therefore describe them here as a second new species of the genus *Barbaraster*.

Unnamed ophiomusid genus and species
Figure 5k–o

Material analysed. MnhnL OPH118 and OPH119.

Description. Small, dissociated lateral arm plates of rounded-quadrate outline, slightly bulging, the proximal plates almost as high as long, the median and distal ones longer; dorsal, ventral and distal edges weakly convex; proximal edge evenly concave and proximalward tapering, lined by a clearly-defined band of more coarsely meshed stereom with a fine horizontal striation and three large, well-defined, prominent and protruding spurs and up to three smaller ones; outer surface ornamentation composed of very finely meshed stereom with trabecular intersections transformed into tiny, close-set spaced tubercles; up to three small spine articulations grouped in the ventral half of the distal edge, at same level as surrounding outer surface stereom and separated from the distal edge by a very narrow band of pinnated stereom; spine articulations composed of a comma-shaped muscle opening proximally encompassed by a thin, finely rugose and very large C-shaped ridge, and distally separated from a nearly equal-sized but slightly more ventral nerve opening by a prominent, knob-shaped vertical ridge.

Inner side of lateral arm plates with a conspicuous, very large, rounded-triangular dorsal contact surface with the opposite lateral arm plate; small, moderately well-defined, triangular vertebral articular ridge; proximalmost lateral arm plates with a narrow, deep, well-defined tentacle notch, proximal, median and distal lateral arm plates with a within-plate tentacle pore perforation close to the ventro-distal tip of the vertebral articular ridge; inner distal edge with at least three large, round, weakly prominent spurs composed of more finely meshed stereom.

Remarks. The lateral arm plates described above are strikingly similar to such from the Pliensbachian of the UK that were described by Hess (1964) as *Ophiura? astonensis* Hess (1964), and to those later reported from the Sinemurian of Luxembourg by Kutscher and Hary (1991). A reassessment of Hess' (1964) original material, however, has revealed that the holotype of *O.? astonensis* differs fundamentally from the other lateral arm plates shown. While the holotype belongs to *Ophiotardis*, a new ophiopyrgid genus described in the present study (see below), the non-type specimens of *O.?*

astonensis figured by Hess (1964), represents a different, previously unknown genus and species. Kutscher and Hary (1991) described very similar lateral arm plates but assigned them to *O.? astonensis*, unaware of the discrepancy between the holotype and the non-type specimens of Hess (1964).

In view of the fact that the material described herein yielded lateral arm plates similar to the non-type specimens of Hess' (1964) *O.? astonensis*, we seize the opportunity to initiate the disentangling of this taxonomic chimaera. We here provide the first unambiguous description of the lateral arm plate type formerly mixed with *Ophiotardis astonensis*. The combination of characters displayed by the lateral arm plate type in question, in particular their thickness, the spine articulation morphology, the large contact surfaces with the opposite lateral arm plate and the development of the tentacle pores, suggests an assignment to the Ophiomusina. Previous reports of such lateral arm plates by Hess (1964) and Kutscher and Hary (1991) indicate that they form a morphologically consistent type of lateral arm plates, differing only in minor details (e.g. the number of spine articulations and spurs). Thus, they probably represent a different, yet unnamed, species of a new ophiomusid genus. We refrain from formally naming the lateral arm plates described herein because the new genus should be based on a more exhaustive assessment including a revision of previously described occurrences.

Family **Ophiomusidae** O'Hara, Stöhr, Hugall,
Thuy and Martynov (2018)
Genus *Ophiomusa* Hertz (1927)

Type species. *Ophiomusium lymani* Wyville-Thomson (1873), by original designation.

Diagnosis (emended from O'Hara et al. 2018). Few disc scales, primary plates obvious, radial shields enlarged; extremely short genital slits, rarely as long as first arm joint; only two proximalmost pairs of tentacle pores developed as between-plate openings; ventral arm plates, and in some species also dorsal arm plates present on few proximal arm joints only; lateral arm plates with numerous spurs along proximal edge, commonly with a constriction and/or an oblique dorsal edge; inner side of lateral arm plates commonly with a conspicuously large, triangular dorsal contact surface with the opposite lateral arm plate.

Ophiomusa perezii sp. nov.
Figure 6a–g

Holotype. MnhnL OPH120.

Paratypes. MnhnL OPH121 and OPH122.

Type locality and stratum. Sample DUD-09 taken at 130.25 m from the Luxembourg Geological Survey

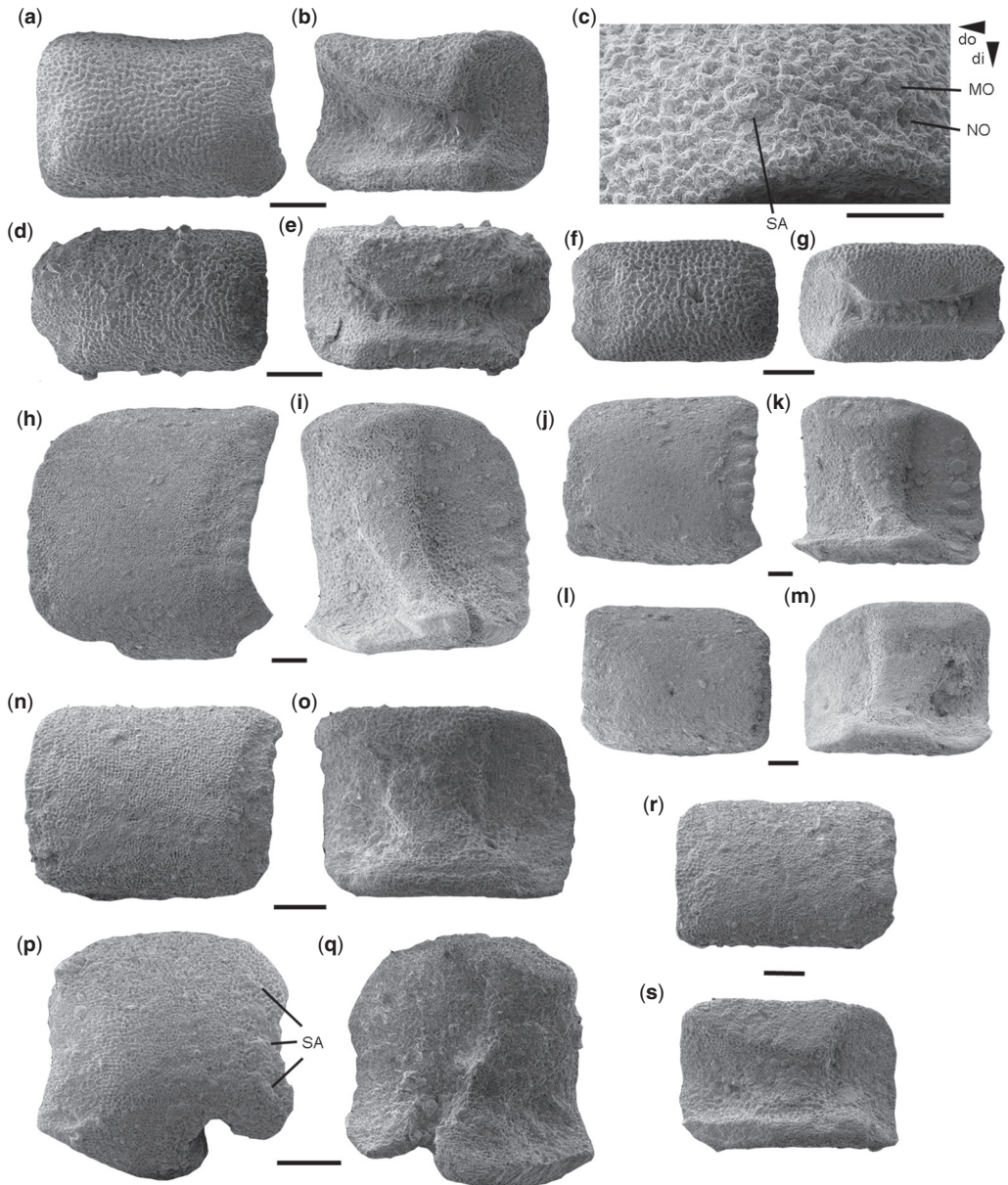


Fig. 6. Ophiuroid lateral arm plates from the lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(g) *Ophiomusa perezii* sp. nov.: sample DUD-09; MnhnL OPH120 (holotype): proximal lateral arm plate in external (a) and internal (b) views, and with detail of spine articulations (c); MnhnL OPH121 (paratype): median lateral arm plate in external (d) and internal (e) views; MnhnL OPH122 (paratype): distal lateral arm plate in external (f) and internal (g) views. (h)–(m) *Ophiogojira andreui* Thuy, Numberger-Thuy and Pineda, 2021: sample DUD-15, MnhnL OPH123: proximal lateral arm plate in external (h) and internal (i) views; MnhnL OPH124: median lateral arm plate in external (j) and internal (k) views; MnhnL OPH125: distal lateral arm plate in external (l) and internal (m) views. (n)–(s) *Ophiogojira aliorbis* sp. nov.: sample DUD-26, MnhnL OPH126 (holotype): median lateral arm plate in external (n) and internal (o); MnhnL OPH127 (paratype): proximal lateral arm plate in external (p) and internal (q) views; MnhnL OPH128 (paratype): distal lateral arm plate in external (r) and internal (s) views. Scale bars equal 0.1 mm in (c), and 0.2 mm in all others. Abbreviations: di, distal; do, dorsal; MO, muscle opening; NO, nerve opening; SA, spine articulation.

drill core FR-216-200 (Dudelage drill core), drilled at Neischmelz near Dudelage, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of Benigno Perez, for bringing back to life the Toarcian Ocean using modern digital technologies.

Diagnosis. Species of *Ophiomusa* with small, elongate proximal lateral arm plates with a weak constriction resulting in a gently concave, oblique dorsal edge; outer proximal edge proximalward tapering, lined by a wide, slightly prominent band of more finely meshed and horizontally striated stereom bearing up to three small, inconspicuous spurs; outer surface ornamentation consisting of a coarse mesh of irregular tubercles; two small spine articulations at a distance from the distal edge of the lateral arm plate.

Description of holotype. MnhnL OPH120 is a small, dissociated proximal lateral arm plate, approximately 1.5 times longer than high; distal and ventral edges straight, dorsal edge gently concave and oblique as a result of a weak constriction; proximal edge weakly concave, proximalward tapering, lined by a wide, slightly prominent band of more finely meshed, horizontally striated stereom; three small, inconspicuous, poorly defined but slightly protruding spurs evenly arranged along the proximal edge; outer surface stereom relatively coarsely meshed, with trabecular intersections transformed into small, irregular, partly confluent tubercles; two small spine articulations at the same level as outer surface stereom, separated from the distal edge by almost double the diameter of the spine articulations, one in the middle of the distal edge and the second one close to the ventro-distal edge of the lateral arm plate; spine articulations oblique, composed of a small, oval muscle opening proximally encompassed by a thin, irregular, rugose ridge, and distally separated from the slightly smaller, round nerve opening by a short, strongly prominent vertical ridge.

Inner side of lateral arm plate with a conspicuous, large, triangular dorsal contact surface with the opposite lateral arm plate; small, inconspicuous, moderately well-defined, roughly triangular vertebral articular ridge; small within-plate tentacle perforation close to ventro-distal tip of the vertebral articular ridge; inner distal edge strongly pinnated, with three small, poorly defined spurs.

Paratype supplements. MnhnL OPH121 is a small dissociated median lateral arm plate, almost twice as long as high, of rectangular outline, with a straight ventral edge, a slightly convex distal edge and a weakly oblique dorsal edge; proximal edge concave, lined by a slightly sunken band of more finely

meshed stereom with a weak horizontal striation and with three small, inconspicuous spurs; outer surface ornamentation as in holotype but with a very weak tendency towards a vertical orientation of the tubercles; two spine articulations as in holotype; inner side with very large dorsal and slightly smaller ventral contact surfaces with the opposite lateral arm plate; vertebral articular structure very small; tentacle pore and inner distal edge as in holotype.

Remarks. Numerous extinct ophiuroids have been assigned to the extant genus *Ophiomusium* Lyman (1869). However, for the majority of these, the generic assignment has been based on a superficial similarity, at most. To make matters worse, the phylogenetic analyses by O'Hara *et al.* (2017, 2018) have revealed that the genus *Ophiomusium* should be limited to its type species, *O. eburneum* Lyman (1869), whereas all other species previously assigned to *Ophiomusium* belong to a different genus and family, namely *Ophiomusa*, which forms the monotypic family Ophiomusidae. With the new genus- and family-level taxonomy of the Ophiomusina at hand, the fossil record of the group needs a thorough reappraisal.

While an exhaustive revision of all the fossil taxa previously assigned to *Ophiomusium* is beyond the scope of the present study, we here anticipate some of the species that comply with the diagnosis of the Ophiomusidae and thus, by default, of the genus *Ophiomusa* (O'Hara *et al.* 2018): *Ophiomusium granulosum* (Roemer 1840) from the Upper Cretaceous and Lower Paleocene of Europe, and *Ophiomusium lux* Jagt (2000) from the Maastrichtian of The Netherlands, as well as *Ophiomusium biconcavum* Kutscher and Jagt, in Jagt (2000), *O. sinuatum* Kutscher and Jagt, in Jagt (2000) and *O. sentum* Kutscher and Jagt, in Jagt (2000) all from the Maastrichtian of Germany. These five species should thus be transferred to *Ophiomusa*, representing the only confirmed fossil representatives of the Ophiomusidae. Jurassic species previously assigned to *Ophiomusium*, in contrast, differ in several critical aspects from *Ophiomusa*. While some of them have been transferred to the extinct genus *Enakomusium*, several others still await reappraisal.

The lateral arm plates described above stand out in being the first pre-Cretaceous form to comply fully with the diagnosis of *Ophiomusa*, in particular with respect to the constriction and the oblique dorsal edge, as well the tentacle pore morphology. While they share a superficial similarity with the lateral arm plates of *Ophiomusa biconcavum*, they differ in a finer outer surface tuberculation, a weaker constriction and fewer spine articulations. We therefore describe them herein as a new species, representing the oldest unambiguous fossil record of the Ophiomusidae.

Suborder **Ophiurina** Müller and Troschel (1840)
sensu O'Hara *et al.* (2017)

Family unknown

Genus *Ophiogojira* Thuy, Numberger-Thuy and Pineda (2021)

Type species. *Ophiogojira labadieii* Thuy, Numberger-Thuy and Pineda, 2021, by original designation.

Diagnosis. Ophiurid ophiuroid with disc covered by small scales and large radial shields; row of contiguous, block-shaped papillae along the genital slit, extending to distal tip of the abradial genital plate at the dorso-ventral mid-line of the arms; second oral tentacle pore opening deep inside the mouth slit; arms cylindrical, with pentagonal dorsal arm plates in contact in proximal arm segments; ventral arm plates diamond-shaped, separated by lateral arm plates; rounded rectangular lateral arm plates with finely tuberculated outer surface and proximal edge lined by numerous well-defined spurs; small spine articulations integrated into outer surface stereom, with a lip-shaped vertical ridge separating the muscle and nerve openings; short, slightly flattened arm spines; tentacle pores developed as between-plate openings in proximal segments, and within-plate perforations in median to distal segments.

Ophiogojira andreui Thuy, Numberger-Thuy and Pineda (2021)

Figure 6h–m

Ophiogojira andreui Thuy, Numberger-Thuy and Pineda (2021): p. 7, figs 7(a–g)

Description (MnhnL OPH123–OPH125). Large, robust, dissociated lateral arm plates, proximal ones slightly higher than long, and median and distal ones longer than high; straight dorsal and ventral edges, slightly concave proximal edge and very weakly convex, almost straight distal edge, resulting in a rectangular outline of the plates; ventral part of the lateral arm plates not protruding; proximal edge lined by a band of more finely meshed stereom with a fine horizontal striation and up to six well defined, prominent, weakly protruding, oval and approximately equal-sized and evenly spaced spurs; outer surface with very finely meshed stereom with trabecular intersections transformed into weakly enlarged, tightly spaced tubercles; up to four very small spine articulations in a vertical row near the ventral two-thirds of distal edge of the lateral arm plate, equal-sized, at same level as outer surface stereom and separated from the distal edge of the plate by a slightly thinned and lowered area composed of more coarsely meshed stereom; spine articulations composed of nearly equal-sized muscle and nerve openings separated by a large, well-defined, strongly protruding, lip-shaped vertical ridge; proximal edge of muscle opening tightly encompassed by

thin but sharply defined and protruding, weakly denticulate ridge.

Inner side of lateral arm plate with large, conspicuous, sharply defined, tongue-shaped central vertebral articular ridge composed of more finely meshed stereom; inner distal edge with up to six oval, well-defined, weakly prominent, equal-sized and equidistant spurs composed of more finely meshed stereom; tentacle pore developed as deep, narrow, sharply defined, ventralward-pointing notch in proximalmost lateral arm plates, and as small, within-plate perforation close to the ventro-distal tip of the vertebral articular ridge in all other lateral arm plates.

Remarks. The lateral arm plates described herein fully comply with the diagnosis of *Ophiogojira andreui* from the lowermost Toarcian (Tenuicostatum chronozone) of Sanem, Luxembourg (Thuy *et al.* 2021) and are therefore described as a second record of the species.

Ophiogojira aliorbis sp. nov.

Figure 6n–s

Holotype. MnhnL OPH126.

Paratypes. MnhnL OPH127 and OPH128

Type locality and stratum. Sample DUD-26 taken at 135.91 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species name composed of 'alium', Latin for another, and 'orbis', Latin for world, to celebrate the song *Another World* by French metal band Gojira, a key element of the soundtrack that accompanied the time-consuming picking, sorting, scanning and assembling.

Diagnosis. Species of *Ophiogojira* with relatively small lateral arm plates with a low height/width ratio; poorly defined spurs along outer proximal edge; relatively coarsely meshed outer surface stereom; up to three relatively large spine articulations along distal edge; dorsal contact surface with opposite lateral arm plate relatively large.

Description of holotype. MnhnL OPH126 is a relatively small, dissociated proximal to median lateral arm plate, longer than high, rectangular outline, with straight dorsal and ventral edges and a gently convex distal edge; proximal edge almost straight, lined by a narrow, slightly tapering band of more coarsely meshed stereom with a weak horizontal striation and at least six small, poorly defined spurs; outer surface stereom comparatively coarse, with trabecular intersections transformed into minute

tubercles arranged in faint vertical rows; three relatively large spine articulations composed of a round muscle opening proximally encompassed by a narrow, denticulate ridge, and distally separated by a large, swollen, lip-shaped vertical ridge from a slightly smaller nerve opening; spine articulations equal-sized and evenly spaced, very close to distal edge.

Inner side of lateral arm plate with a large, well-defined, tongue-shaped central vertebral articular ridge composed of more finely meshed stereom; inner distal edge with up to six oval, poorly defined, spurs; tentacle pore developed as small, within-plate perforation close to the ventro-distal tip of the vertebral articular ridge.

Paratype supplements. MnhnL OPH127 is a relatively small dissociated proximal lateral arm plate, as high as long, rounded squarish outline, with a convex dorsal edge and an oblique ventral edge with a very deep, conspicuous tentacle notch; distal edge fragmented; proximal edge concave, lined by a broad band of more coarsely meshed stereom with a weak horizontal striation and with at least four poorly defined and/or poorly preserved spurs; outer surface as in holotype; four spine articulations as in holotype; inner side with vertebral articular ridge as in holotype; inner distal edge poorly preserved; deep, narrow, sharply defined tentacle notch close to ventro-distal tip of vertebral articular ridge.

MnhnL OPH128 is a small dissociated distal lateral arm plate, more than 1.5 times longer than high; generally similar to holotype but with better defined horizontal striation and four spurs along outer proximal edge; two spine articulations similar to those of holotype; inner side as in holotype.

Remarks. The lateral arm plates described above show the combination of characters typically found in *Ophiogojira*. However, they differ from the two previously described congeners in smaller size, smaller height/length ratio, coarser outer surface stereom, more rounded outline and larger spine articulations. This combination of characters cannot be explained by ontogenetic differences alone (Thuy and Stöhr 2011). We therefore consider the lateral arm plates described above as a new species of *Ophiogojira* rather than plates of immature specimens of *O. andreui*.

Family **Ophiopyrgidae** Perrier (1893)
Genus *Palaeocoma* d'Orbigny (1850)

Type species. *Ophiura milleri* Phillips (1829), by subsequent designation.

Diagnosis. Ophiopyrgid ophiuroid with a robust disc skeleton, densely covered in minute, spherical granules except for the central part of the large radial

shields; continuous row of large, block-like genital papillae forming a well-developed arm comb on the dorsal side of the arm bases; cluster of papillae at the tip of the jaws; second oral tentacle pores opening deep inside the mouth slit; arms cylindrical, with pentagonal, contiguous dorsal arm plates and wide, bullhead-shaped, contiguous ventral arm plates; lateral arm plates weakly arched, with numerous spurs on outer proximal edge and conspicuous, strongly prominent, J-shaped vertebral articular ridge on the inner side; spine articulations in deep notches of the distal edge, composed of comma-shaped muscle and nerve openings separated by a thin, low vertical ridge; vertebrae typically barrel-shaped, with extremely dorso-ventrally elongate zygocondyles.

Remarks. *Palaeocoma* is one of the first fossil ophiuroids to have been formally described and ranks amongst the most commonly cited, but still is one of the least well known. It was one of the fossil genera included in the morphological phylogeny of Thuy and Stöhr (2016) and was surprisingly found to be a member of the order Ophiurida. The latest phylogenetic analysis by Thuy *et al.* (2021) has confirmed this position and furthermore suggested assignment to the family Ophiopyrgidae. The genus *Palaeocoma* was previously known from the Hettangian, Sinemurian and Pliensbachian of Europe (Hess 1962b, 1964; Kutscher and Hary 1991), with a questionable Triassic record (Toula 1887; Hess 1965a). The species described herein is the first Toarcian representative of the genus and at the same time its youngest record.

Palaeocoma kortei sp. nov.
Figure 7

Holotype. MnhnL OPH129.

Paratypes. MnhnL OPH130–OPH133.

Type locality and stratum. Sample DUD-04 taken at 127.76 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of Christoph Korte, for his outstanding work evolving around the use of geochemical approaches to reconstruct Jurassic climate and oceans, and for being a reliable source of inspiration and motivation.

Diagnosis. Species of *Palaeocoma* with small, very weakly arched, rounded lateral arm plates with a low height/width ratio even in proximal parts of the arm; continuous row of large, round spurs along outer proximal edge; proximal lateral arm plates without spine articulations or with a single

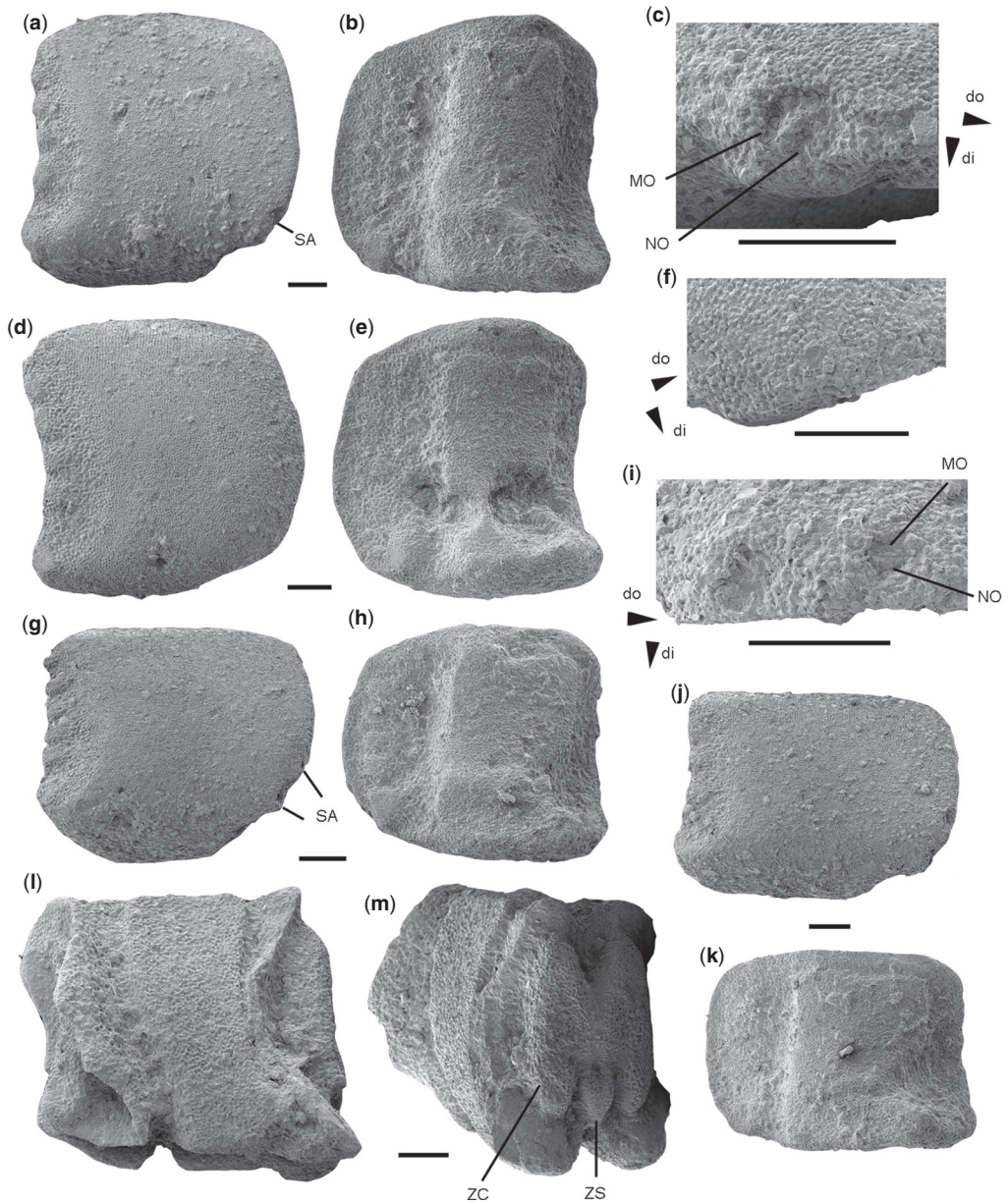


Fig. 7. Ophiuroid lateral arm plates from the lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(n) *Palaeocoma kortei* sp. nov.: sample DUD-04; MnhnL OPH129 (holotype): proximal lateral arm plate in external (a) and internal (b) views, and with detail of spine articulation (c); MnhnL OPH130 (paratype): proximal lateral arm plate in external (d) and internal (e) views, and with detail of ventro-distal tip of lateral arm plate (f); MnhnL OPH131 (paratype): median lateral arm plate in external (g) and internal (h) views, and with detail of spine articulation (i); MnhnL OPH132 (paratype): distal lateral arm plate in external (j) and internal (k) views; MnhnL OPH133 (paratype): proximal vertebra in lateral (l) and distal (m) views. Scale bars equal 0.2 mm. Abbreviations: di, distal; do, dorsal; MO, muscle opening; NO, nerve openings; SA, spine articulation; ZC, zyocondyle; ZS, zygosphene.

one in a notch directly at the ventro-distal tip of the plate; distal lateral arm plates with two small spine articulations in notches close to the ventro-distal edge of the plate; inner side with an extremely wide, well-defined vertebral articular ridge.

Description of holotype. MnhnL OPH129 is a relatively small, dissociated proximal lateral arm plate nearly as high as long, with gently convex dorsal and distal edges and a ventro-proximalward-protruding ventral portion; proximal edge concave and lined by a pinnacled band of more coarsely meshed stereom with a continuous row of four large, round, prominent and weakly protruding spurs ventrally bordered by a prominent and protruding spur-like elevation of the outer surface stereom; very finely meshed stereom covering the outer surface, with trabecular intersections transformed into tiny, close-set tubercles; single small spine articulation in a notch directly at the ventro-distal tip of the lateral arm plate, composed of comma-shaped, equal-sized muscle and nerve openings separated by a thin, low vertical ridge.

Inner side of lateral arm plate with a single, extremely large, wide, strongly prominent and sharply defined vertebral articular ridge with a rectangular dorsal tip; inner distal edge pinnacled, with five small, poorly defined, round spurs; small, but well-defined, ventralward-pointing tentacle notch close to ventro-distal tip of the vertebral articular ridge.

Paratype supplements. MnhnL OPH130 is a dissociated proximal lateral arm plate, very similar to holotype but completely devoid of spine articulations; inner side as in holotype but damaged, probably due to bioerosion.

MnhnL OPH131 is a dissociated median lateral arm plate, slightly longer than high, with nearly straight dorsal edge; five spurs along the outer proximal edge, all with a fine horizontal striation, and ventrally bordered by spur-like elevation of the outer surface stereom; ornamentation of outer surface as in holotype; two spine articulations in notches at ventro-distal tip of the plate; inner side as in holotype but with five more clearly defined spurs along inner distal edge.

MnhnL OPH132 is a dissociated distal lateral arm plate, approximately 1.5 times longer than high, with nearly straight dorsal edge; outer proximal edge with four spurs as in holotype, ventrally bordered by spur-like elevation of outer surface stereom; two small spine articulations in notches, one directly at ventro-distal tip of the plate and the second just above; inner side as in holotype.

MnhnL OPH133 is a dissociated proximal, barrel-shaped, laterally compressed vertebra; dorsal and ventral muscle fossae forming almost continuous, vertical ring on distal and, even more, on proximal sides; zygocondyles parallel and extremely elongate

dorso-ventrally, with very small zygosphere barely extending beyond ventral tip of zygocondyles; dorsal and ventral grooves deep; articular surface on lateral sides very wide, sharply-defined, J-shaped.

Remarks. The lateral arm plates and the co-occurring vertebrae belong together because of similarities in size and matching mutual articular structures. Both show the highly characteristic combination of characters found in *Palaeocoma*: the typical shape of the poorly arched lateral arm plates, the small spine articulations in notches at their distal edge and the conspicuous, strongly prominent, J-shaped vertebral articular ridge on their inner side, as well as the barrel-shaped vertebrae with their extremely elongate zygocondyles. The lateral arm plates described above differ notably from those of congeners in their lower height/length ratio, the much fewer spine articulations and the extremely large vertebral articular ridge. We therefore describe them as a new species of *Palaeocoma* and extend the range of the genus into the lowermost Toarcian.

Genus *Ophiotardis* nov.

Type species. *Ophiotardis tennanti* sp. nov., by present designation.

Other species included. *Ophiura? astonensis* Hess (1964).

Diagnosis. Ophiopyrgid genus with large, high, strongly arched and rounded lateral arm plates; numerous well-developed, prominent and protruding spurs along outer proximal and inner distal edges; numerous large spine articulations sunken in notches of distal edge, composed of comma-shaped muscle and nerve openings separated by a thin, low vertical ridge; single, large vertebral, articular ridge on inner side; tentacle pores developed as within-plate perforations in median and distal lateral arm plates, occasionally also in proximal ones.

Etymology. Genus name formed as a combination of *óphis*, Greek for serpent, a commonly used prefix in ophiuroid genus names, and *Tardis*, acronym for 'Time And Relative Dimension In Space', the time machine and spacecraft used by Dr Who.

Ophiotardis tennanti sp. nov.

Figure 8a–g

Holotype. MnhnL OPH134.

Paratypes. MnhnL OPH135 and OPH136.

Type locality and stratum. Sample DUD-04 taken at 136.22 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

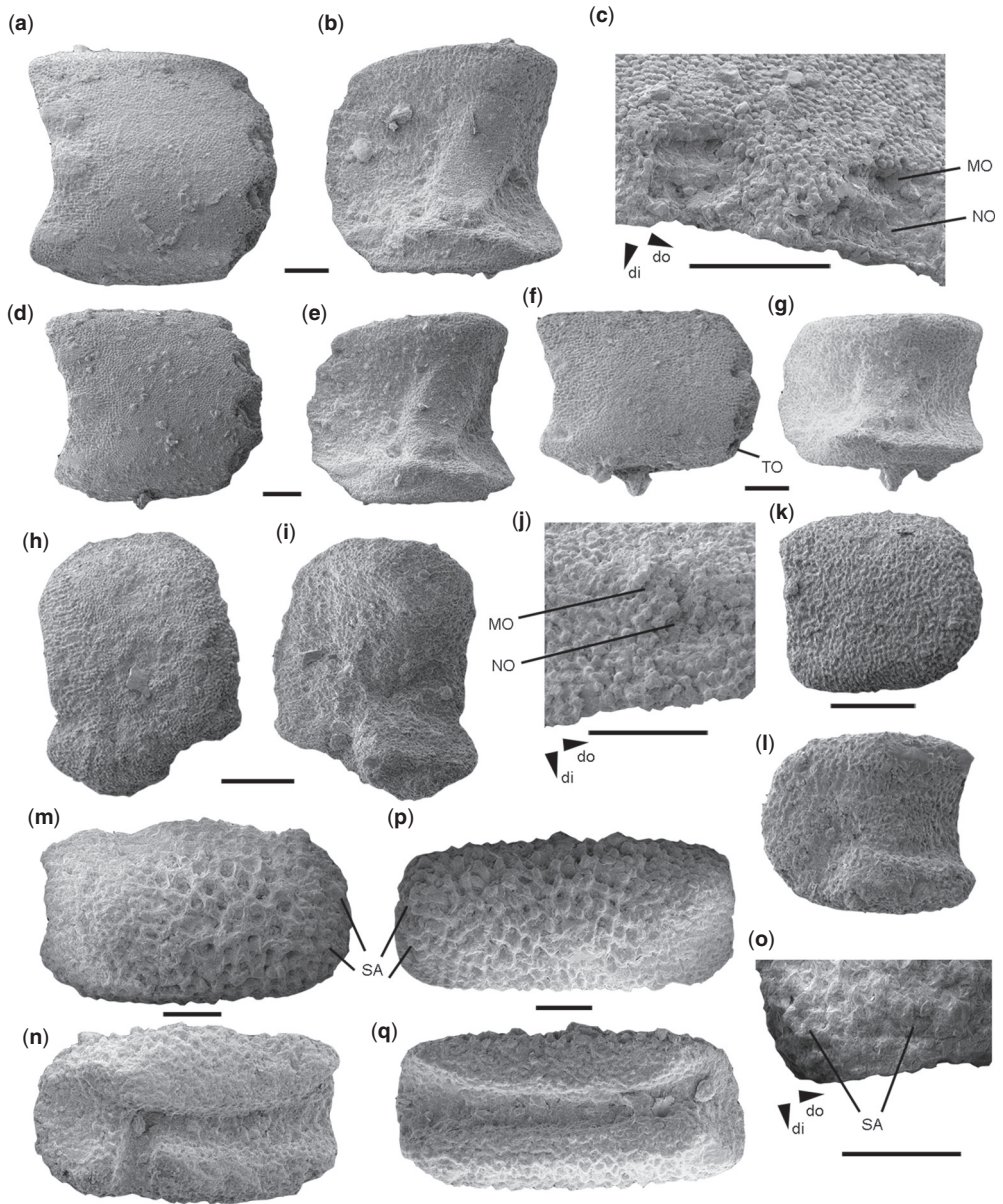


Fig. 8. Ophiuroid lateral arm plates from the uppermost Pliensbachian (Spinatum chronozone) and lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(g) *Ophiotardis tennanti* gen. et sp. nov.: sample DUD-27; MnhnL OPH134 (holotype): proximal lateral arm plate in external (a) and internal (b) views, and with detail of spine articulations (c); MnhnL OPH135 (paratype): median lateral arm plate in external (d) and internal (e) views; MnhnL OPH136 (paratype): distal lateral arm plate in external (f) and internal (g) views. (h)–(l) Unnamed ophiopyrgid: sample DUD-35, MnhnL OPH137: proximal lateral arm plate in external (h) and internal (i) views, and with detail of spine articulations (j); MnhnL OPH138: median to distal lateral arm plate in external (k) and internal (l) views. (m)–(q) *Ophiomisidium pratchettae* sp. nov.; sample DUD-06, MnhnL OPH139 (holotype): proximal lateral arm plate in external (m) and internal (n) views, and with detail of spine articulations (o); MnhnL OPH140 (paratype): median to distal lateral arm plate in external (p) and internal (q) views. Scale bars equal 0.1 mm in (j) and in (m)–(q), and 0.2 mm in all others. Abbreviations: di, distal; do, dorsal; MO, muscle opening; NO, nerve opening; SA, spine articulation; TO, tentacle opening.

Etymology. Species named in honour of Scottish actor David Tennant, for his performance as the 10th incarnation of The Doctor in the science fiction series Dr Who, bringing us inspiration during moments of frustration while writing the present paper.

Diagnosis. Species of *Ophiotardis* with up to three large spurs along outer proximal edge; up to four (rarely five) large, equal-sized spine articulations in deep notches of distal edge; tentacle notches developed as within-plate perforations in almost all lateral arm plates.

Description of holotype. MnhnL OPH134 is a dissociated, moderately large proximal lateral arm plate, slightly higher than long, arched, with weakly convex dorsal and ventral edges, and a strongly convex distal edge; proximal edge evenly concave, lined by a band of more coarsely meshed stereom with a very faint horizontal striation and three large, prominent and protruding spurs; outer surface ornamentation composed of trabecular intersections transformed into small, tightly spaced tubercles; four large, equal-sized and evenly spaced spine articulations sunken in deep notches of the distal edge, each composed of comma-shaped, equal-sized muscle and nerve openings separated by a thin, low vertical ridge.

Inner side of lateral arm plate with a single, large, wide and well-defined vertebral articular ridge with a tongue-shaped dorsal edge; three large, prominent, moderately-well defined spurs on inner distal edge; tentacle pore developed as small within-plate perforation close to ventro-distal tip of vertebral articular ridge.

Paratype supplements. MnhnL OPH135 is a dissociated median lateral arm plate, slightly longer than high, closely similar to holotype but with better preserved microstructures; fine horizontal striation along outer proximal edge tightly encompassing spurs; four spine articulations as in holotype; inner side as in holotype.

MnhnL OPH136 is a dissociated distal lateral arm plate, longer than high; outer proximal edge with two spurs; two spine articulations, the dorsal one with a swollen, lip-shaped vertical ridge; inner side with a shorter vertebral articular ridge and with two spurs on inner distal edge.

Remarks. The lateral arm plates described above belong to a particular type that have been described and figured in the past but, surprisingly, have always been intermingled with other taxa (e.g. Hess 1962b, 1964). As outlined above, the holotype of *Ophiura? astonensis* from the Pliensbachian of the UK belongs to this type of lateral arm plates but most of the associated non-type specimens belong to a different genus (Hess 1964). The *Palaeocoma milleri* material from the Pliensbachian of Switzerland described by

Hess (1962b) includes representatives of the lateral arm plate type in question.

Here we provide the first unambiguous description of this particular type of lateral arm plates and introduce the new genus *Ophiotardis*. In spite of a superficial similarity to the lateral arm plates of *Ophioderma* Müller and Troschel (1840), those of *Ophiotardis* gen. nov. have their muscle and nerve openings separated by a vertical ridge, implying assignment to the Euryophiurida. The general plate shape, the outer surface ornamentation, the spine articulation morphology and the development of the tentacle pores suggests ophiopyrgid affinities. Pending a phylogenetic analysis, however, this family-level position should be considered as tentative.

The lateral arm plates of *Ophiotardis* gen. nov. show a certain similarity to those of *Palaeocoma*, especially with respect to the spine articulation morphology. In *Palaeocoma*, however, the lateral arm plates are more rectangular, the ventral portion protrudes ventro-proximalwards and the tentacle pore is always developed as between-plate notch.

The holotype and some of the non-type specimens of *Ophiura? astonensis* are here transferred to *Ophiotardis* gen. nov. They differ from the slightly younger material described herein in having smaller and more numerous spine articulations and spurs. We therefore introduce the new species *Ophiotardis tennanti* to accommodate the lateral arm plates described herein. The enlarged, lip-shaped vertical ridge seen in the distal lateral arm plates of the new species suggest the presence of hook-shaped arm spines, as observed in articulated specimens of *Inexpectacantha acrobatica* (see Thuy 2011).

Unnamed ophiopyrgid genus and species Figure 8h–l

Material analysed. MnhnL OPH137 and OPH138.

Description. Small dissociated lateral arm plates, relatively thick, straight, proximal ones higher than long, distal ones longer than high, all of rounded general outline, with convex dorsal and distal edges and with ventro-proximalward-protruding ventral portion; proximal edge unevenly concave, lined by a band of horizontally striated stereom devoid of spurs; outer surface stereom finely meshed with trabecular intersections transformed into minute tubercles; up to three small (two in distal lateral arm plates) spine articulations sunken in very shallow depressions of a pinnated distal edge, evenly distributed, composed of tiny muscle and nerve openings separated by a small, low, rugose vertical ridge.

Inner side of lateral arm plates with large, round (elongate in distal plates) dorsal contact surface with opposite lateral arm plate in proximal plates;

single large, weakly prominent and moderately well-defined vertebral articular ridge, in proximal lateral arm plates with a kink between the main plate body and the ventral portion; tentacle pore developed as well-defined, ventralward-pointing notch.

Remarks. The spine articulation morphology, combined with the overall shape of the lateral arm plates including a ventro-proximalward-pointing ventral portion, suggest assignment to the suborder Ophiurina. Within this group, similarities are closest to members of the Ophiopyrgidae, especially on account of the ventralward-pointing tentacle notch. The lateral arm plates in question differ from those of the *Palaeocoma d'Orbigny* (1850) species in the large dorsal contact surface with the opposite lateral arm plate, and the shape and position of the spine articulations. A superficial similarity is shared with the lateral arm plates of the basal euryalid *Aspiduriella Bolette* (1998) from the Triassic. These differ, however, in lacking an outer surface ornamentation (Thuy and Stöhr 2018).

The lateral arm plates cannot be assigned to any known fossil type of such plates. They probably represent a new genus and species of ophiopyrgid ophiuroid. In view of the fact that only few specimens are available at present, we refrain from formally naming them.

Family **Astrophiuridae** Sladen (1879)
Genus *Ophiomisidium* Koehler (1914)

Type species. *Ophiomisidium speciosum* Koehler (1914), by original designation.

Diagnosis. Disc covered by few thick scales and obvious primary plates; arms short, rapidly tapering, composed of elongate segments; skeletal plates often with a coarsely meshed, tuberculous stereom; basal lateral arm plates often widened, carrying a horizontal row of spines; spine articulations composed of a muscle opening encompassed by thickened stereom, with a strongly reduced nerve opening; between-plate tentacle openings in proximal segments.

Ophiomisidium pratchettae sp. nov.
Figure 8m–q

Holotype. MnhnL OPH139.

Paratypes. MnhnL OPH140.

Type locality and stratum. Sample DUD-06 taken at 128.81 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of English video game writer and journalist Rhianna Pratchett for her gamebook *Crystal of Storms*, which

reinvigorated stamina in moments of frustration during work on the present study.

Diagnosis. Species of *Ophiomisidium* with small, strongly elongate lateral arm plates with very coarsely meshed outer surface stereom; two small, inconspicuous spine articulations on distal edge; tentacle pores developed as narrow ventralward-pointing notches in proximal lateral arm plates, and as small within-plate perforations in median to distal ones.

Description of holotype. MnhnL OPH139 is a dissociated, very small proximal lateral arm plate, almost twice as long as high, very thick, rounded, with convex dorsal, ventral and distal edges; proximal edge irregularly wavy, lined by a slightly tapering band of more finely meshed stereom, no spurs discernible; outer surface stereom very coarsely meshed, with trabeculae thickened and trabecular intersections transformed into small, widely spaced tubercles; two small, equal-sized, inconspicuous spine articulations near distal edge of the lateral arm plate, integrated into outer surface stereom, almost invisible.

Inner side of lateral arm plate with very thick dorsal and ventral contact surfaces with opposite lateral arm plate, leaving an extremely narrow vertebral cavity; no vertebral articular structure discernible; inner distal edge pinnacled but devoid of spurs; narrow, deep, sharply defined and ventralward-pointing tentacle notch.

Paratype supplements. MnhnL OPH140 is a dissociated, very small median to distal lateral arm plate, approximately 2.5 times longer than high; similar to holotype but inner side with very narrow vertebral cavity; tentacle pore developed as small within-plate perforation close to distal end of vertebral cavity.

Remarks. The lateral arm plates described above are highly peculiar because of their small size, the thick, rounded, elongate shape, and the coarse outer surface ornamentation. The only previously known type of fossil lateral plates that resembles the material described above belong to *Mesophiomusium moenense* Kutscher and Jagt, in Jagt (2000) from the Maastrichtian of Denmark. They differ, however, in having more strongly convex dorsal and ventral edges and a much finer outer surface ornamentation. *Mesophiomusium scabrum* (Hess 1962b) from the Toarcian of Switzerland is only superficially similar due to the coarse outer surface stereom, and differs in a fundamentally different spine articulation morphology.

The general shape of the lateral arm plates described above, the coarse outer surface, the small spine articulations composed of a muscle opening only and the ventralward-pointing tentacle notch in proximal segments hint at the astrophiurid genus

Ophiomisidium. Given the extremely small size of the lateral arm plates, we cannot entirely rule out the possibility that they represent a strongly paedomorphic ophiomusid instead. With the evidence in hand, however, an assignment to *Ophiomisidium* seems the most plausible.

Ophiomisidium pratchettae is by far the oldest fossil representative of the Astrophiuridae. Although molecular estimates have predicted an ancient origin for that family, the fossil record of astrophiurids has proven extremely sparse to date (Thuy *et al.* 2019).

Superorder **Ophintegrida** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Order **Ophioscolecida** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Family **Ophioscolecidae** Lütken (1869)

Genus *Lapidaster* Thuy (2013)

Type species. *Lapidaster hystricarboris* Thuy (2013), by original designation.

Diagnosis, emended from Thuy (2013). Ophioscolecid with lateral arm plates displaying large tentacle notches; spine articulations not positioned on elevated ridge and not sunken into depressions or notches; ventral portion of lateral arm plate protruding ventro-proximally; generally single, poorly to moderately defined, spur on outer proximal and inner distal edge of lateral arm plate; spine articulations generally tilted, composed of elongate, arched dorsal and ventral lobes; inner side with single, well-defined ridge generally separated by rounded kink into dorsal and ventral halves.

Remarks. *Lapidaster* was originally described as a basal, large-pored ophiacanthid (Thuy 2013). Since then, however, considerable progress has been made in ophiuroid higher systematics. The size of the tentacle pore has been debunked as irrelevant for higher-level systematics within ophiacanthids. Furthermore, several assumedly basal ophiacanthid genera have been transferred to the new family Ophioscolecidae on the basis of a molecular phylogeny (O'Hara *et al.* 2018). Based on these new insights, we suggest the transfer of *Lapidaster* to the family Ophioscolecidae within the order Ophioscolecida on account of the spine articulation morphology and because of striking similarities to the lateral arm plates of some modern ophioscolecids such as *Ophioplexa* Martynov (2010) and *Ophiocymbium* Lyman (1880).

Lapidaster fasciatus (Kutscher and Villier 2003)
Figure 9a–d

Sinosura fasciata Kutscher and Villier (2003):
p. 185, pl. 3 fig. 9, pl. 4 figs 1–2.

Sinosura schneideri – Kutscher (1996): p. 9, pl. 2,
figs 6–8 (material incorrectly assigned to *Sinosura*
schneideri Kutscher 1987).

Lapidaster fasciatus – Thuy (2013): p. 32,
fig. 7: 7–8.

Diagnosis. Species of *Lapidaster* with small- to medium-sized lateral arm plates displaying an irregular, coarse vertical striation, a relatively short ridge on the inner side, and up to four spine articulations composed of confluent dorsal and ventral lobes.

Description (MnhnL OPH141–OPH142). Moderately large lateral arm plates, proximal ones slightly higher than long, distal ones longer than high; with a strongly ventro-proximalward-protruding ventral portion and a ventralward-protruding ventro-distal tip; single, poorly defined spur on concave outer proximal edge; outer surface with a coarse, irregular vertical striation; up to four large, spine articulations, freestanding along distal edge, with a dorsalward increase in size; spine articulations oblique, composed of a large muscle opening and a smaller nerve opening both encompassed by elongate, slightly rugose dorsal and ventral lobes; inner side of lateral arm plates with a single, very thin, sharply defined vertebral articular ridge, with a kink between the dorsal and ventral portions; single, small, poorly defined spur on inner ventro-distal tip of the plate; large, deep, well-defined tentacle notch close to kink of vertebral articular ridge.

Remarks. Thuy (2013) provided a detailed description of *Lapidaster fasciatus* based on material from the middle Toarcian of France and considered them conspecific with lateral arm plates previously described by Kutscher (1996) from the uppermost Toarcian to the lower Aalenian of Germany, and by Kutscher and Villier (2003) from the middle to upper Toarcian of France. The latter were originally described as a new species of *Sinosura*, *S. fasciata*, but Thuy (2013) argued that the species has ophiacanthid affinities and transferred it to the newly erected genus *Lapidaster*, highlighting similarities to the type species of the genus *L. hystricarboris*. The lateral arm plates described above comply with the diagnosis of *Lapidaster fasciatus*. They extend the stratigraphic range of the species down to the lowermost Toarcian.

Lapidaster hougardae sp. nov.
Figure 9e–h

Holotype. MnhnL OPH143.

Paratypes. MnhnL OPH144.

Type locality and stratum. Sample DUD-29 taken at 137.17 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

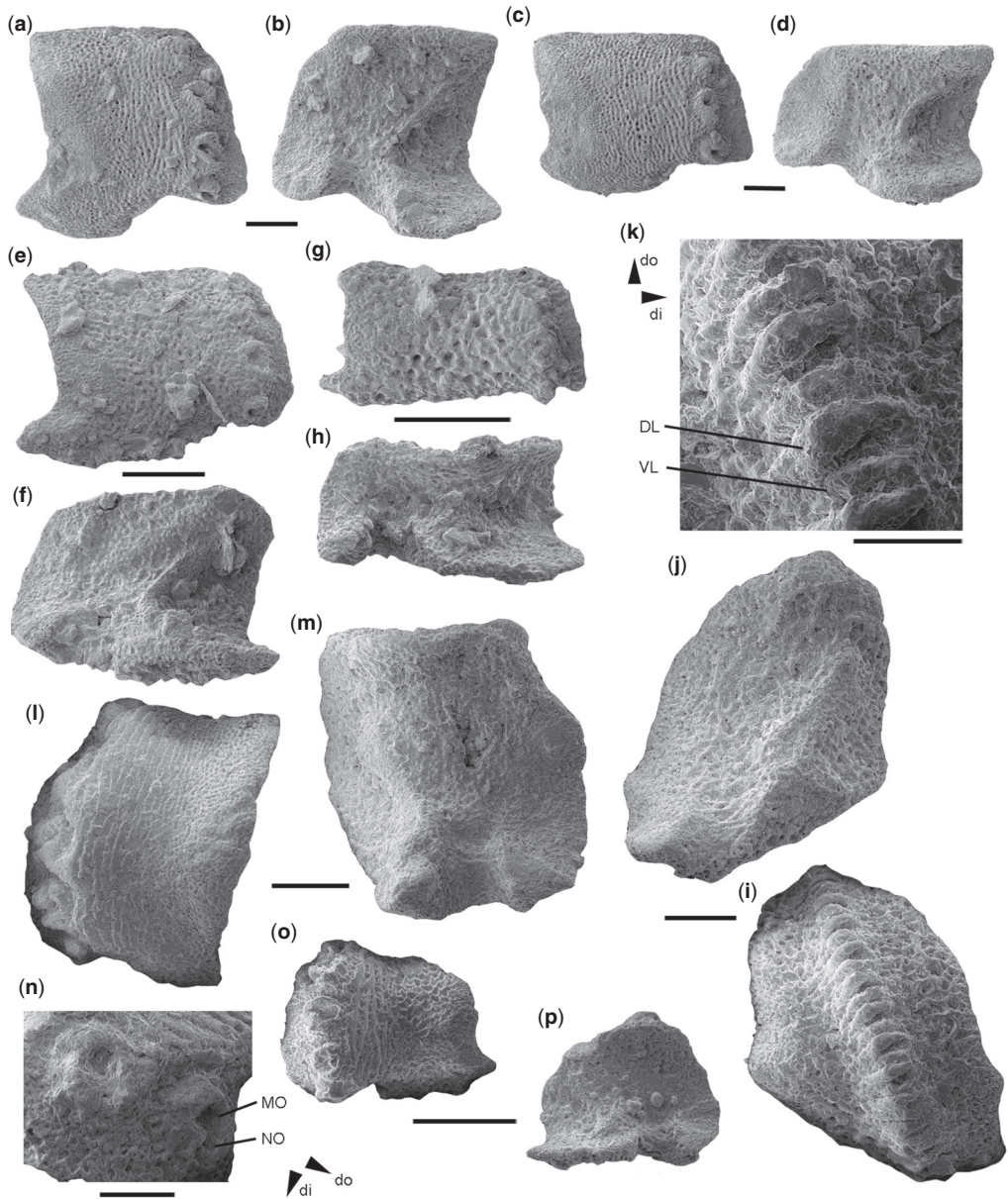


Fig. 9. Ophiuroid lateral arm plates from the lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(d) *Lapidaster fasciatus* (Kutscher and Villier 2003): sample DUD-15; MnhnL OPH141: proximal lateral arm plate in external (a) and internal (b) views; MnhnL OPH142: median to distal lateral arm plate in external (c) and internal (d) views. (e)–(h) *Lapidaster hougardae* sp. nov.: sample DUD-29, MnhnL OPH143 (holotype): proximal lateral arm plate in external (e) and internal (f) views; MnhnL OPH144 (paratype): median to distal lateral arm plate in external (g) and internal (h) views. (i)–(k) *Ophiohelus* sp. nov.; sample DUD-06, MnhnL OPH145: proximal lateral arm plate in external (i) and internal (j) views, and with detail of spine articulations (k). (l)–(p) *Ophiocopa* sp. nov.; sample DUD-06, MnhnL OPH146: proximal lateral arm plate in external (l) and internal (m) views, and with detail of spine articulations (n); MnhnL OPH147: median to distal lateral arm plate in external (o) and internal (p) views. Scale bars equal 0.1 mm in (k) and (n), and 0.2 mm in all others. Abbreviations: di, distal; DL, dorsal lobe; do, dorsal; MO, muscle opening; NO, nerve opening; VL, ventral lobe.

Etymology. Species named after Iben Winther Hougård for her work on the geochemistry of Lower Jurassic successions including the Jenkyns Event, and as a souvenir to commemorate the joint sampling of the Dudelage drill core.

Diagnosis. Species of *Lapidaster* with small, elongate lateral arm plates; very weak constriction; outer surface stereom coarsely meshed, without striation or enlarged tubercles; up to four relatively small, round spine articulations.

Description of holotype. MnhnL OPH143 is a dissociated, relatively small proximal lateral arm plate almost 1.5 times longer than high; dorsal edge slightly concave as a result of a weak constriction; distal edge strongly convex; ventral portion protruding ventro-proximalwards; ventro-distal tip of lateral arm plate slightly protruding ventralwards; proximal edge concave with a strong kink close to ventral portion of plate; relatively large, prominent, horizontally elongate but poorly defined spur close to ventro-proximal tip of lateral arm plate; outer surface stereom coarsely meshed but devoid of vertical striation or enlarged tubercles; four moderately large spine articulations with slightly dorsalward increase in size, freestanding on weakly elevated distal portion of the lateral arm plate; spine articulations round, oblique, composed of strongly arched, proximally merged dorsal and ventral lobes.

Inner side of lateral arm plate with single, uniformly narrow vertebral articular ridge with a sharp kink in the middle; single relatively large, prominent, elongate spur on the inner ventro-distal tip of the plate; tentacle notch wide, deep and sharply defined.

Paratype supplements. MnhnL OPH144 is a dissociated, small median to distal lateral arm plate; slightly stronger constriction; spur on outer proximal edge poorly defined; three arm spine articulations similar to those of holotype; inner side with vertebral articular ridge obscured by matrix.

Remarks. The lateral arm plates described above fall within the morphological spectrum of *Lapidaster* as defined by Thuy (2013). Within that genus, similarities are closest to the species that have a constriction but lack a vertical striation. *Lapidaster etteri* Thuy (2013) differs in having a widened dorsal tip of the vertebral articular ridge, *L. lukenederi* Thuy (2013) as more finely meshed outer surface stereom and *L. coreytaylori* Thuy (2013) has a stronger constriction. The lateral arm plates described above cannot be accommodated in any of the currently known species of *Lapidaster*. We therefore introduce the new species *Lapidaster hougardae* for them.

Type species. *Ophiohelus pellucidus* Lyman (1880), by original designation.

Diagnosis. Ophiohelid with lateral arm plates showing a coarsely meshed outer surface stereom and an oblique row of large, freestanding spine articulations composed of comma-shaped, parallel, dorsal and ventral lobes; umbrella-shaped spines along the entire arm.

Ophiohelus sp. nov.
Figure 9i–k

Material examined. MnhnL OPH145 from sample DUD-06 taken at 128.81 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelage drill core), drilled at Neischmelz near Dudelage, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Description. MnhnL OPH145 is a dissociated, probably proximal lateral arm plate, slightly longer than high, conspicuously oblique, with an irregular outline; distal edge with a protruding but non-prominent spur; outer surface stereom coarsely meshed but devoid of striation or tubercles; conspicuous, oblique row of 13 tightly spaced spine articulations running from the dorsal to the ventral edge of the plate, with a weak ventralward increase in size; spine articulations composed of nearly parallel, straight, massive dorsal and ventral lobes, the dorsal one slightly larger, encompassing a single opening.

Inner side of lateral arm plate with a large, triangular ventral contact surface with opposite lateral arm plate; single nose-shaped vertebral articular ridge, well-defined, widest at its base, with a pointed tip and a slightly more strongly prominent proximal half; ventro-distal tip of inner side thickened to border a large, deep, well-defined tentacle notch.

Remarks. The lateral arm plate described above is among the most extraordinary known from the Lower Jurassic so far. It stands out on account of its oblique shape and the oblique row of tightly spaced spine articulations running along the entire height of the lateral arm plate. There is a superficial similarity to the lateral arm plates described as *Ophiacantha? liesbergensis* Hess (1963) from the Callovian of Switzerland, especially because of the peculiar outline and the oblique row of tightly spaced spine articulations. However, the lateral arm plates of *O.? liesbergensis* are much more fragile and have a deep tentacle incision, as well as dorsal and ventral lobes forming a circle encompassing a single opening. The lateral arm plate described herein unquestionably represents a previously unknown form. In view of the fact that we have only a single specimen at hand, however, we refrain from formally naming it, awaiting the discovery of more material to further substantiate its highly unusual morphology.

Family **Ophiohelidae** Perrier (1893)
Genus *Ophiohelus* Lyman (1880)

The shape and position of the spine articulations together with the shape of the vertebral articular ridge of the lateral arm plate described above favour an assignment to the Ophiiohelidae. Although the family is of ancient origin (O'Hara *et al.* 2018), it has a very poor fossil record (Thuy and Meyer 2013; Thuy *et al.* 2014). Thus, the present record, albeit based on a single specimen only, adds considerably to a better knowledge of fossil Ophiiohelidae.

Order **Ophiacanthida** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Suborder **Ophiacanthina** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Family **Ophiotomidae** Paterson (1985)

Genus *Ophiocopa* Lyman (1883)

Type species. *Ophiocopa spatula* Lyman (1883), by original designation.

Diagnosis. Ophiotomid genus with disc covered by few large scales carrying large, scattered spherical granules; radial shields triangular, largely exposed; relatively long jaws with a continuous row of small, blunt oral papillae; lateral arm plates showing a ventro-proximalward-protruding ventral portion; outer surface ornamentation with a well-defined vertical striation; prominent and protruding spur on outer proximal edge; large spine articulations on an elevated distal portion of the lateral arm plates, composed of a semi-circular dorsal lobe and a triangular, knob-shaped ventral lobe; single vertebral articular ridge on inner side of lateral arm plates with widened dorsal tip.

Ophiocopa sp. nov.

Figure 9l–p

Material examined. MnhnL OPH146 and OPH147.

Description. MnhnL OPH146 is a dissociated proximal lateral arm plate, higher than long, with a small, ventro-proximalward-protruding ventral portion; concave dorsal edge as a result of a constricted outer surface; proximal edge with a large, central, prominent and protruding spur; outer surface with a well-developed vertical striation proximalwards fading into a moderately finely meshed stereom; five large spine articulations on elevated distal portion of lateral arm plate, bordered by wavy edge of vertical striation; dorsalward increase in size of spine articulations and in gaps separating them; spine articulations composed of a semi-circular dorsal lobe encompassing a very large muscle opening and a knob-like, nearly triangular ventral lobe distally merged with the dorsal lobe by a small sigmoidal fold encompassing the much smaller nerve opening.

Inner side of lateral arm plate with a single, well-defined vertebral articular ridge with a widened dorsal tip; single, large, prominent and protruding spur

in the middle of the inner distal edge; deep, sharply defined tentacle notch; two or three perforations in a vertical row between the vertebral articular ridge and the distal edge of the plate.

Supplements. MnhnL OPH147 is a dissociated distal lateral arm plate, longer than high, similar to holotype but with second more ventral and pointed spur on outer proximal edge; outer surface ornamentation and spine articulation morphology as in holotype; inner side as in holotype.

Remarks. The two lateral arm plates described above unambiguously belong to the Ophiacanthina on account of their constriction and the shape, position and size pattern of the spine articulations. The protruding ventral portion favours assignment to the family Ophiotomidae and rules out the majority of the superficially similar fossil ophiacanthids such as *Ophiogaleus* Thuy (2013). Similarities are closest to the Recent genus *Ophiocopa* because of the spine-articulation micromorphology, the constriction, the spur morphology and the tentacle notch, as well as the vertebral articular ridge on the inner side.

Thuy (2013) provided an extensive assessment of the ophiacanthid fossil record, and considered *Ophiocopa* to be the closest living relative of the extinct *Dermocoma* Hess (1964) and *Alternacantha* Thuy and Meyer (2013). The latter two, however, are herein transferred to the suborder Ophiodermatina because of fundamental differences in the microstructure of the spine articulations, in particular the lack of a genuine, well-developed sigmoidal fold (see below).

The lateral arm plates described above probably represent a fossil species of *Ophiocopa* or, more likely, an extinct sister genus. In view of the limited material available, however, we refrain from formally naming this species.

Suborder **Ophiodermatina** Ljungman (1867)

Family unknown

Genus *Dermocoma* Hess (1964)

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

Diagnosis. Ophiodermatin with disc covered by thin scales, small, rounded-triangular radial shields; tiny, spherical granules densely covering disc scales; fan-shaped dorsal arm plates in contact at least in proximal arm segments; lateral arm plates with a large, ventro-proximalward-protruding ventral portion; outer surface of lateral arm plates with a weak constriction and a fine vertical striation close to row of spine articulations; often several protruding, slender spurs on outer proximal edge; relatively large, ear-shaped spine articulations in shallow depressions of a slightly elevated distal lateral arm plate portion; single, slender ridge with pointed to slightly widened

dorsal tip on inner side of lateral arm plate, devoid of conspicuous kinks.

Remarks. The genus *Dermocoma* was introduced by Hess (1964) on the basis of articulated skeletons from the Middle Jurassic of the UK. While the genus was initially left unclassified due to its unusual combination of characters, it was later assigned to its own family Dermocomidae by Hess (1972). Thuy and Meyer (2013) transferred *Dermocoma* to the family Ophiacanthidae, as understood at that time, based on similarities in spine articulation morphology. Thuy (2013) adopted this view and introduced a number of new species mostly on the basis of dissociated lateral arm plates.

A lot of progress has been made in understanding ophiuroid diversity, phylogeny and arm-plate micro-morphology since the monograph by Thuy (2013), imposing a revision of fossil ophiuroid genera described until then. Viewed from this new perspective, *Dermocoma* is incompatible with the revised diagnosis of the family Ophiacanthidae (O'Hara *et al.* 2018). Within the order Ophiacanthida, *Dermocoma* shares greatest similarities to members of the family Ophiotomidae and with some long-spined representatives of the suborder Ophiodermatina. The vertebral articular ridge on the inner side of the lateral arm plate being devoid of conspicuous kinks and the spine articulations showing only a weakly developed sigmoidal fold, we favour an assignment to Ophiodermatina. Affinities within this group are better explored using phylogenetic methods, which is beyond the scope of the present study.

Dermocoma sp.
Figure 10a–c

Material examined. MnhnL OPH148 and OPH149

Description. Relatively large, robust lateral arm plates, proximal ones nearly as high as long, distal ones elongate; ventral portion of proximal plates strongly protruding ventro-proximalwards; up to two small, poorly defined spurs along a concave outer proximal edge; outer surface with very weak constriction, if at all, and with a fine vertical striation becoming coarser towards the row of spine articulations; four moderately large, ear-shaped spine articulations in proximal lateral arm plates, three in distal ones, sunken in deep notches of the distal plate portion, separated from the distal edge by a thin, smooth shelf; inner side of lateral arm plates with a single, slender, well-defined vertebral articular ridge devoid of sharp kinks; two small, moderately well-defined spurs on inner distal edge; tentacle notch narrow, deep.

Remarks. The lateral arm plates described herein show a combination of characters typically found in *Dermocoma*. The closely related *Alternacantha*

Thuy and Meyer (2013) has very similar lateral arm plates in median to distal arm portions. The more proximal lateral arm plates of the material described herein, however, show no sign of the large gap between the dorsalmost and the remaining spine articulations. We therefore favour an assignment to *Dermocoma*, emphasizing, however, that this is a tentative identification based on sparse and fragmentary material. We cannot rule out that some of the more distal lateral arm plates belong to *Alternacantha*.

Species of the *Dermocoma*–*Alternacantha* group tend to have very similar lateral arm plates, differing only in minor details of their microstructure. The material we have before us consists of sparse and often fragmentary lateral arm plates mostly from median to distal arm portions, precluding an exhaustive assessment of the morphology and a conclusive comparison with congeners. We therefore describe the specimens in open nomenclature, awaiting the discovery of more complete material.

Order **Amphilepidida** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Suborder **Ophonereidina** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Superfamily **Ophonereidoidea** Ljungman (1867)

Family **Ophonereididae** Ljungman (1867)

Genus *Dermacantha* Thuy (2013)

Type species. *Dermacantha leonorae* Thuy (2013), by original designation.

Emended diagnosis. Ophonereid with small, fragile lateral arm plates with a low height/length ratio even in proximal plates; outer surface often with a fine but poorly developed vertical striation stereom; up to five small spine articulations in notches of slightly elevated distal portion of lateral arm plates; ventral and dorsal lobes of spine articulations proximally separated by up to three tiny knobs; up to two poorly to well-defined spurs on outer proximal and inner distal edges; inner side of lateral arm plates with simple, slender ridge devoid of sharp kinks or strongly thickened parts.

Remarks. The genus *Dermacantha* was introduced by Thuy (2013) to accommodate species with superficially *Dermocoma*-like lateral arm plates but differing in their spine articulation morphology and their lower height/length ratio. As explained above, the substantial progress during recent years in understanding ophiuroid systematics and evolution demands a reassessment of most fossil genera. Seen from the perspective of these new insights, the spine articulation morphology of *Dermacantha* is more typical of the Ophonereididae than of the Ophiacanthidae, especially because of the tiny knobs proximally separating the dorsal and ventral lobes, and because of the poorly developed

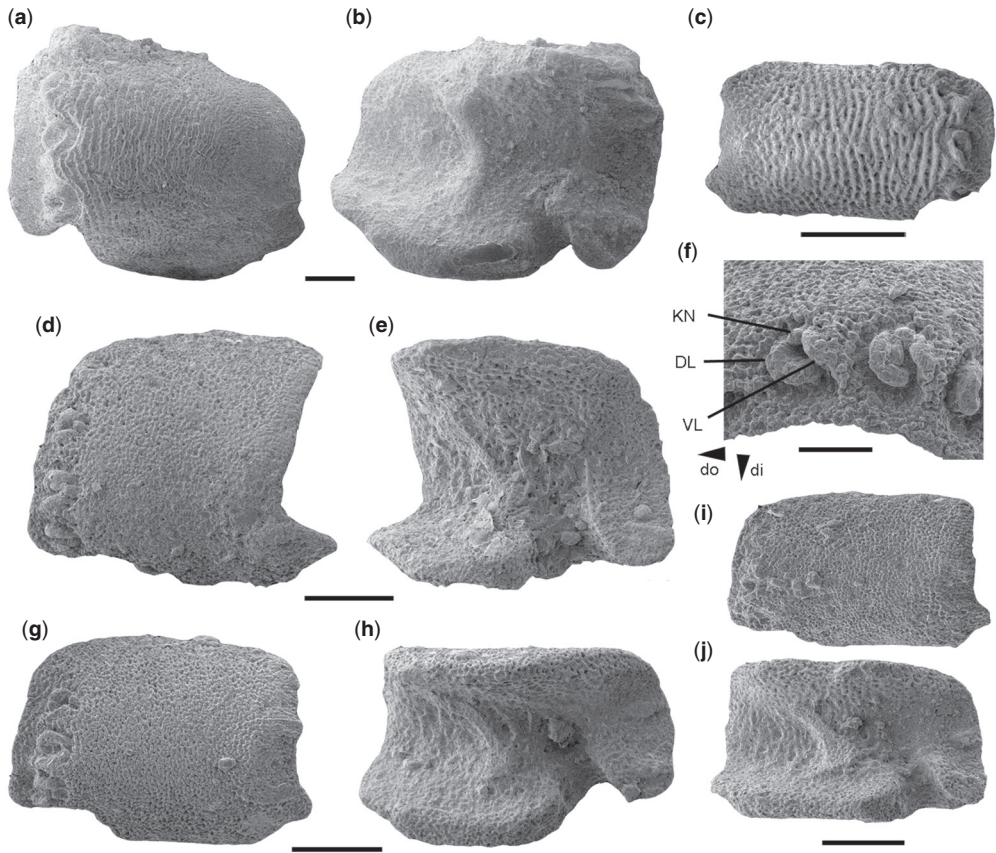


Fig. 10. Ophiuroid lateral arm plates from the lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(c) *Dermocoma* sp.: sample DUD-14; MnhnL OPH148: proximal to median lateral arm plate in external (a) and internal (b) views; MnhnL OPH149: distal lateral arm plate in external (c) view. (d)–(j) *Dermacantha reolidi* sp. nov.: sample DUD-15, MnhnL OPH150 (holotype): proximal lateral arm plate in external (d) and internal (e) views, and with detail of spine articulations (f); MnhnL OPH151 (paratype): median lateral arm plate in external (g) and internal (h) views; MnhnL OPH152 (paratype): distal lateral arm plate in external (i) and internal (j) views. Scale bars equal 0.1 mm in (f), and 0.2 mm in all others. Abbreviations: di, distal; DL, dorsal lobe; do, dorsal; KN, knob(s); VL, ventral lobe.

sigmoidal fold. We therefore transfer the genus to Ophionereididae.

The lateral arm plates of *Dermacantha* share greatest similarities with those of the extinct ophiuroid *Ophiopetra* Hess, in Enay and Hess (1962) from the Upper Jurassic of Europe and the Lower Cretaceous of Argentina (Fernández *et al.* 2019). The general plate architecture and the spine articulation morphology are similar to such an extent that we anticipate close phylogenetic ties, to be explored using phylogenetic analyses. Differences between *Dermacantha* and *Ophiopetra* pertain mostly to the position of the spine articulations (free-standing in *Ophiopetra* v. sunken in shallow notches in *Dermacantha*).

Dermacantha reolidi sp. nov.

Figure 10d–j

Holotype. MnhnL OPH150.

Paratypes. MnhnL OPH151 and OPH152.

Type locality and stratum. Sample DUD-15 taken at 131.94 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named in honour of Matías Reolid Pérez for his work on the Jenkyns Event, and for inviting us to contribute to this volume.

Diagnosis. Species of *Dermacantha* with small, elongate lateral arm plates devoid of vertical striation; two moderately well-defined spurs along the outer proximal edge; up to four small arm spine articulations; widened dorsal tip of vertebral articular ridge on inner side of lateral arm plates.

Description of holotype. MnhnL OPH150 is a small, dissociated proximal lateral arm plate slightly longer than high, with evenly convex dorsal and distal edges and a strongly ventro-proximalward-protruding ventral portion; proximal edge concave with a sharp kink, lined by a narrow band of horizontally striated stereom including two small, moderately well-defined, weakly prominent and protruding spurs; outer surface with finely meshed stereom, with trabecular intersections transformed into tiny tubercles without a particular order (no vertical striation); four small arm spine articulations in shallow notches close to the distal edge of the plate, the two middle spine articulations larger than the ventral and dorsal ones; spine articulations composed of a straight, oblique ventral lobe and a strongly arched dorsal lobe, proximally separated by one or two small knobs. Inner side of lateral arm plate with a single slender, well-defined vertebral articular ridge with a widened dorsal tip but devoid of sharp kinks; single small, well-defined, spur close to ventral tip of inner distal edge; large, deep, well-defined tentacle notch.

Paratype supplements. MnhnL OPH151 is a dissociated median lateral arm plate almost 1.5 times longer than high; outline similar to that of holotype; two spurs along outer proximal edge better defined than in holotype; outer surface as in holotype; three spine articulations as in holotype but leaving a gap between the dorsalmost spine articulation and the dorso-distal tip of the plate; dorsal spine articulation slightly smaller than the other two; inner side as in holotype but vertebral articular ridge without widened tip, and inner distal edge of plate with two well-defined spurs.

MnhnL OPH152 is a dissociated distal lateral arm plate almost twice as long as high, otherwise similar to specimen MnhnL OPH151.

Remarks. The lateral arm plates described above unambiguously comply with the diagnosis of *Dermacantha*. Within this genus, similarities are greatest to *Dermacantha leonora* from the Pliensbachian of the UK, especially because of the lack of outer surface striation. The lateral arm plates described above differ in having up to four, rather than five, spine articulations, and two spurs along the outer proximal and inner distal edges instead of one. We therefore describe them as a new species of *Dermacantha*, adding a Toarcian record to the genus.

Order **Ophioleucida** O'Hara, Hugall, Thuy, Stöhr and Martynov (2017)

Family **Ophioleucidae** Matsumoto (1915)

Genus *Sinosura* Hess (1964)

Type species. *Acroura brodiei* Wright (1866), by original designation.

Diagnosis. Ophioleucid genus with very large, rounded triangular radial shields surrounded by small disc scales covered by large, scattered granules; arms slender, cylindrical; large tentacle pores covered by large, oval scales; lateral arm plates thin, fragile, strongly arched, with conspicuous vertical striation on outer surface; ventral portion strongly protruding ventro-proximalwards; numerous small spine articulations directly adjacent to distalmost stripe of outer surface striation; row of spine articulations distally bordered by very wide, thin, smooth shelf forming a ventralward-protruding ventro-distal tip of the lateral arm plate; regular arm spines with a coarse longitudinal striation; in some species small, specialized, saw-like dorsalmost arm spines.

Remarks. The genus *Sinosura* was introduced by Hess (1964) for specimens from the Pliensbachian of the UK originally described as *Acroura brodiei*. Hess (1964) included *Ophiopinna wolburgi* Hess (1960) and *Ophiopinna derecta* Hess (1963) in *Sinosura*, and synonymized *Ophiopinna helvetica* Hess (1962b) and *Ophiura longivertebralis* Wolburg (1939) with the type species *S. brodiei*. A number of species have subsequently been transferred to *Sinosura* or described as new species of the genus (Hess 1965b; Kutscher 1987; Kutscher and Jagt, in Jagt 2000; Kutscher and Villier 2003; Hess and Meyer 2008). As a result, the morphological disparity of *Sinosura* has increased beyond the spectrum typically observed in ophiuroid genera (Thuy and Stöhr 2011). A revision of the genus, taking into account the latest advances in ophiuroid systematics and evolution, thus appears long overdue.

Sinosura cf. *brodiei* (Wright 1866)

Figure 11a–f

Acroura brodiei Wright (1866): p. 152, pl. 17, fig. 5.

Ophiura longivertebralis Wolburg (1939): p. 24, pl. 1, figs 1–23; pl. 2, figs 1–8.

Ophiopinna helvetica Hess (1962b): p. 623, figs 20–24, 34–35, 126.

Sinosura brodiei – Hess (1964): p. 776, figs 37–40, pl. 1; pl. 2, fig. 1.

Description (MnhnL OPH153–OPH155). Very thin, fragile, strongly arched lateral arm plates, proximal ones as high as long, median ones longer than high and distal ones strongly elongated; dorsal edge convex in proximal lateral arm plates, straight in median to distal ones; ventral portion small, protruding

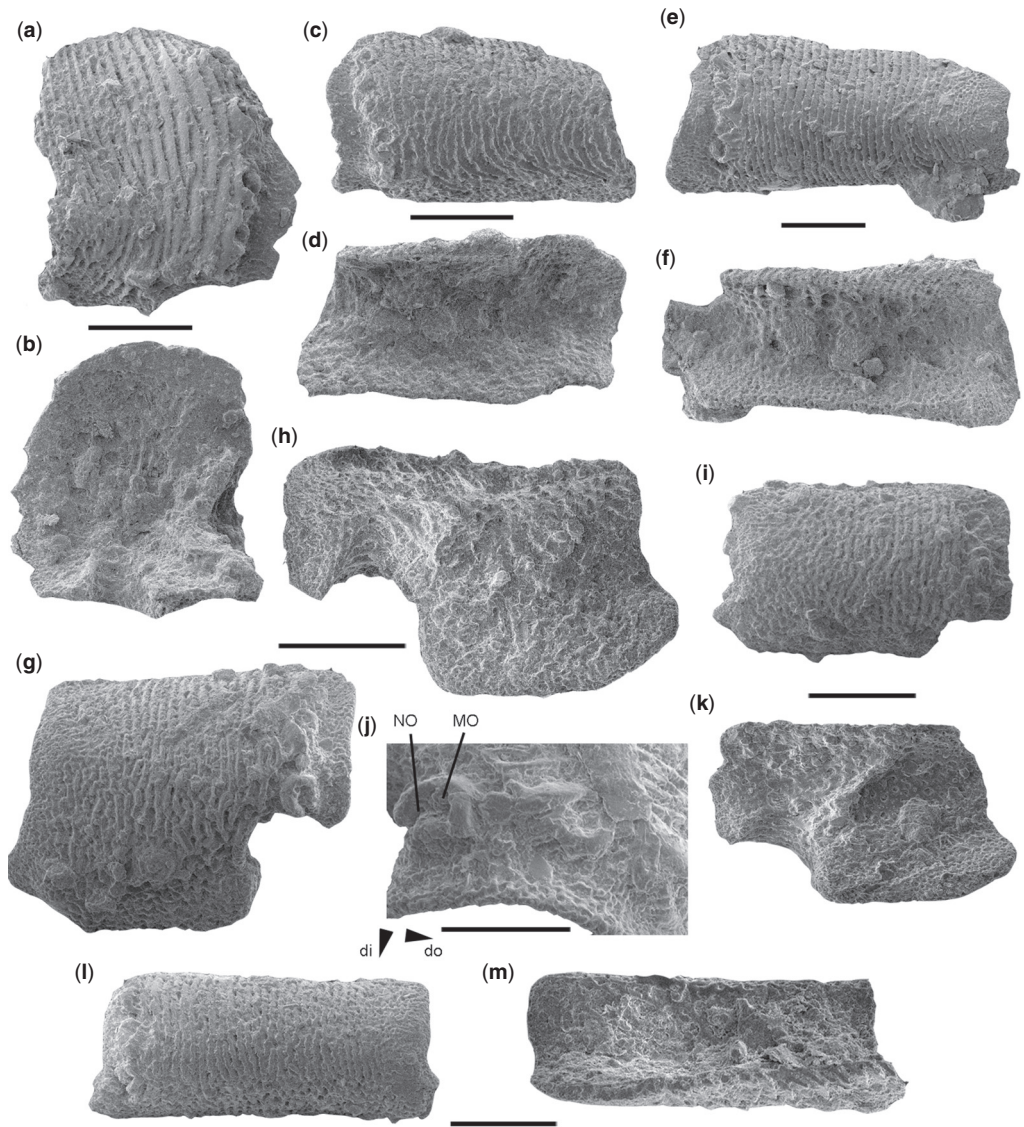


Fig. 11. Ophiuroid lateral arm plates from the uppermost Pliensbachian (Spinatum chronozone) and lowermost Toarcian (Tenuicostatum chronozone) of the Luxembourg Geological Survey drill core FR-216-200, Neischmelz near Dudelange, Luxembourg. (a)–(f) *Sinosura brodiei* (Wright 1866): sample DUD-34; MnhnL OPH153: proximal lateral arm plate in external (a) and internal (b) views; MnhnL OPH154: median distal lateral arm plate in external (c) and internal (d) views; MnhnL OPH155: distal lateral arm plate in external (e) and internal (f) views. (g)–(m) *Sinosura dieschbourgae* sp. nov.: sample DUD-07, MnhnL OPH156 (holotype): proximal lateral arm plate in external (g) and internal (h) views and with detail of spine articulations (i); MnhnL OPH157 (paratype): median lateral arm plate in external (j) and internal (k) views; MnhnL OPH158 (paratype): distal lateral arm plate in external (l) and internal (m) views. Scale bars equal 0.1 mm in (i), and 0.2 mm in all others. Abbreviations: di, distal; do, dorsal; MO, muscle opening; NO, nerve opening.

ventro-proximalwards in proximal lateral arm plates; proximal edge concave, lined by a band of finely meshed stereom with a weak horizontal striation but devoid of spurs; outer surface stereom

transformed into a conspicuous vertical striation composed of large, smooth, mostly continuous, occasionally braided, distalward overlapping stripes increasing in size towards the distal edge of the plate;

up to six small spine articulations directly adjacent to distalmost stripe of outer surface striation; spine articulations composed of strongly tilted, arched dorsal and ventral lobes encompassing a comma-shaped muscle opening; smaller nerve opening at distal tip of converging dorsal and ventral lobes; spine articulations mostly evenly spaced and without conspicuous increase in size; some plates with a dorsward increase in size of the spine articulations and of the gaps separating them; row of spine articulations distally bordered by a very wide, fragile, smooth shelf forming a ventralward-pointing ventro-distal tip in proximal to median lateral arm plates.

Inner side of lateral arm plates with a single very slender, strongly prominent, J-shaped vertebral articular ridge in proximal lateral arm plates; much smaller, shorter ridge in median lateral arm plates, and two small knobs in distal lateral arm plates; no spurs on inner distal edge; tentacle pore developed as deep, sharply defined notch in proximal lateral arm plates, shallow notch in median ones, and within-plate perforation in distal ones.

Remarks. *Sinosura brodiei* has been described from several localities ranging in age from the early Sinemurian (Kutscher and Hary 1991) to the late Toarcian (Kutscher 1996; Kutscher and Villier 2003). Kutscher and Hary (1991) already expressed doubts about the conspecificity of their Sinemurian specimens with the type material from the Pliensbachian of the UK. A detailed reassessment of this material taking into account the latest insights into the systematic relevance of lateral arm-plate micromorphology (Thuy and Stöhr 2011) will probably result in the erection of a new species. As for the late Toarcian records previously assigned to *S. brodiei* (Kutscher 1996; Kutscher and Villier 2003), Thuy (2013) identified fundamental morphological differences and reassigned the records to the ophiacanthid *Ishidacantha hirokoe* Thuy (2013). The remaining, uncontested published records of *S. brodiei* suggest that the species is restricted to the Pliensbachian.

The material described herein is sufficiently similar to the type material of *S. brodiei* to justify assignment to the same species. The variability pertaining to the size pattern and arrangement of the spine articulations observed in the present material is also seen in specimens from the type locality of *S. brodiei*, in some cases even within the same articulated arm fragment. Lateral arm plates unambiguously assignable to *Sinosura brodiei* are restricted to the lowermost samples of the series studied herein, corroborating the assumption that the species is restricted to the Pliensbachian.

Sinosura dieschbourgae sp. nov.

Figure 11g–m

Sinosura brodiei – Hess (1991): p. 3, figs 1–5.

Holotype. MnhnL OPH156.

Paratypes. MnhnL OPH157 and OPH158.

Type locality and stratum. Sample DUD-07 taken at 129.13 m from the Luxembourg Geological Survey drill core FR-216-200 (Dudelange drill core), drilled at Neischmelz near Dudelange, Luxembourg; Tenuicostatum chronozone, lowermost Toarcian, Lower Jurassic.

Etymology. Species named after Carole Dieschbourg, Luxembourg Environment Minister at the time of publication of this paper, for her achievements towards a more sustainable society but also as an incentive to pursue a rigorous, science-based policy towards climate change mitigation.

Diagnosis. Species of *Sinosura* with small, strongly elongate lateral arm plates; very large ventro-proximalward-protruding ventral portion; single, poorly defined and weakly prominent and protruding spur in the middle of the outer proximal edge; outer surface with a fine vertical striation composed of smooth, weakly overlapping stripes; three small, oblique lens-shaped spine articulations; large, deep tentacle notch in proximal lateral arm plates, replaced by large within-plate perforation in distal ones.

Description of holotype. MnhnL OPH156 is a small, dissociated proximal lateral arm plate, slightly more than 1.5 times longer than high, with a straight ventral edge and a slightly concave dorsal edge as a result of a weak constriction; distal edge convex; ventral portion of lateral arm plate extremely large, accounting for almost half of the lateral arm plate, ventro-distally incised by a deep tentacle notch; proximal edge concave, lined by a narrow band of more finely meshed stereom with a very weak horizontal striation and with a central, poorly defined, weakly prominent and protruding spur; outer surface with a fine vertical striation composed of smooth, partly braided, tightly spaced but only slightly overlapping stripes; three small spine articulations freestanding close to distal edge of plate, equal sized and evenly spaced along the entire edge, composed of a strongly arched smooth ventral lobe and an equally arched and smooth, slightly smaller, mirrored dorsal lobe, together forming a slightly distorted, oblique lens-shaped spine articulation encompassing the muscle opening and bordering the slightly smaller nerve opening at its distal tip; spine articulations separated from distal edge by a conspicuous, wide, smooth and very fragile shelf.

Inner side of lateral arm plate with a single small, extremely thin, sharply defined vertebral articular ridge; no spurs of the inner distal edge; deep, wide,

well-defined tentacle notch at the ventro-distal tip of the lateral arm plate.

Paratype supplements. MnhnL OPH157 is a dissociated median lateral arm plate, approximately twice as long as high, with straight dorsal and ventral edges resulting in an overall rectangular outline except for ventro-distal tentacle pore incision; very weak constriction; ventral portion accounting for one quarter of the lateral arm plate; proximal edge and outer surface as in holotype; three spine articulations as in holotype; inner side of lateral arm plate with a small, triangular vertebral articular ridge proximally and a small, round knob distally.

MnhnL OPH158 is a dissociated distal lateral arm plate, almost three times as long as high, of rectangular outline except for distalward-protruding ventro-distal tip; very weak constriction; ventral part of lateral arm plate not separated from the rest of the plate; proximal edge and outer surface ornamentation as in holotype; three spine articulations as in holotype; inner side with two small, weakly prominent knobs instead of a vertebral articular ridge; tentacle pore developed as large within-plate perforation emerging at ventro-distal edge of the ventralmost spine articulation.

Remarks. The lateral arm plates described above resemble those of *Sinosura brodiei*, especially where median and distal ones are concerned. When the proximal lateral arm plates are taken into account, however, a number of differences become evident. The specimens described above have a much smaller height/length ratio in all parts of the arm, a much larger ventral portion, a finer vertical striation composed of weakly overlapping stripes and a maximum of three small, slightly oblique spine articulations. The only other superficially similar species is *Sinosura extensa* Kutscher and Villier (2003) from the upper Toarcian of France. The lateral arm plates of that species differ, however, in having small, well-defined, pointed spurs along the proximal edge, a vertical striation on the outer surface composed of more rugose, irregular stripes, and a gap between the dorso-distal tip of the plate and the dorsalmost spine articulation.

The material described herein thus represents a new species of *Sinosura*, filling a stratigraphic gap between the Pliensbachian *S. brodiei* (see above) and the late Toarcian *S. extensa*. Interestingly, Hess (1991) described a slab with three articulated ophiuroids from the Posidonia Shale of Ohmden, southern Germany, and assigned them to *Sinosura brodiei*. However, the lateral arm plates show a small height/length ratio, an extremely large ventral portion and three spine articulations throughout the arm, suggesting that the specimens belong to *Sinosura dieschbourgae* sp. nov. rather than to *S. brodiei*.

Discussion

Significance of the present ophiuroid assemblages

The Dudelange drill core yielded an unexpectedly high diversity of ophiuroids from a relatively short stratigraphic interval, ranging from the topmost Pliensbachian Spinatum chronozone to the base of the lower Toarcian Serpentinum chronozone. In fact, compared to similar ophiuroid records (e.g. from the upper Toarcian of Thouars, France (Kutscher and Villier 2003) or the Pliensbachian–Toarcian of Seewen, Switzerland (Hess 1962b)), it stands out as one of the most diverse on record to date. One reason for this high diversity might be the more advanced state of knowledge with respect to ophiuroid systematics and evolution (e.g. Thuy and Stöhr 2011, 2016; O'Hara *et al.* 2014, 2017), allowing for a more rigorous and exhaustive analysis of fossil ophiuroid assemblages. Thus, a reassessment of previously described assemblages using the same approach has the potential of increasing the number of species in these records. Another reason for the high diversity recorded in the present study, however, might be the high resolution of the sampling. Rather than focusing on a few promising sections, we sampled a stratigraphic succession at regular intervals, unbiased by estimated fossil content. This non-selective approach allowed the capture of inconspicuous variations in facies and associated changes in the composition of the ophiuroid fauna. Thus, at least for intervals with known or expected palaeoenvironmental change, high-resolution sampling is likely to provide a much more complete picture of ophiuroid palaeobiodiversity.

The high share of previously unknown species in the present assemblages, with 12 out of 21 species formally described as new and another four identified as new but left unnamed, shows that there are still significant gaps in the fossil record to be explored, even in seemingly well-studied intervals such as the Lower Jurassic. Here again, however, the recent progress in deciphering the micromorphology of ophiuroid skeletal elements (Martynov 2010; Thuy and Stöhr 2011, 2016) has contributed to a more precise assessment of ophiuroid microfossils and therefore a much higher resolution in identifying species even if they are known from dissociated lateral arm plates only. As a result, superficially similar types of lateral arm plate can be told apart and assigned to morphologically consistent taxa, thus reducing the risk of taxonomic chimaeras and lump species with implausibly long stratigraphic ranges and overly variable morphological spectra. Among the most notable examples treated in the present study is a species formally known as *Ophiura? astonensis*, here debunked as a taxonomic amalgam

composed of two fundamentally different taxa (i.e. a yet unnamed ophiomusid genus and the new ophiopyrgid genus *Ophiotardis*), and the species *Sinosura brodiei*, previously assumed to have spanned a range of more than 20 myr from the lower Sinemurian to the upper Toarcian, here shown to be restricted to the Pliensbachian.

Apart from revealing an unexpected ophiuroid diversity, the present study also provides one of the first examples of ophiuroid assemblages based on microfossils retrieved from drill-core samples (Thuy *et al.* 2012). It shows that a significant number of identifiable ophiuroid remains can be extracted from as little as 100 g of bulk sediment, and thus unlocks the full array of drill cores as potential sources of evidence to study the ophiuroid fossil record. The material described herein furthermore stands out in describing ophiuroids from a stratigraphically successive series of samples, rather than a single assemblage only, thus allowing ophiuroid diversity to be explored across time (e.g. Jagt 2000).

Ophiuroid diversity through time

Our results (Fig. 3) show that most of the species identified in the present study occur only at specific parts of the sampled interval. Only very few span the entire series of samples (e.g. *Inexpectacantha acrobatica*) or at least most of it (e.g. *Ophiogojira andreui* and *Lapidaster fasciatus*). As for the other species, the present state of knowledge is too incomplete to explore potential causes or patterns. Future studies of similar assemblages from the lowermost Toarcian might reveal biogeographical patterns or potential biostratigraphic index species. What the present study clearly does show, however, is that ophiuroid diversity in the lowermost Toarcian is sufficiently high and variable on a fine stratigraphic scale to justify far-reaching investigations in search of palaeobiological trends.

Ophiuroid diversity across the series of samples described herein fluctuates considerably, with diversity lows coinciding with black shales. This parallels previous observations (e.g. Danise *et al.* 2019) and is not surprising considering that black shales were deposited under conditions unfavourable for most benthic organisms including ophiuroids. Astonishingly, however, if there are ophiuroid remains recorded in black shale intervals, they belong to the same few species. In particular, *Inexpectacantha acrobatica* and *Sinosura dieschbourgae* sp. nov. persistently occur in black shale intervals and are the only species recorded in the topmost sample, reflecting the onset of the Jenkyns Event. The occurrence of the latter species in the Posidonia Shale of Ohmden, southern Germany (see above), further underlines this observation. These species thus

seem to represent resilient and/or opportunistic taxa that were capable of surviving the conditions that prevailed during the deposition of black shale.

Another surprising observation is that ophiuroid diversity reached its maximum in the samples from just below the base of the black shales of the Serpentinum chronozone (samples DUD-09–DUD-04; Fig. 3). These samples furthermore yield species that occur in no other part of the studied succession. Of particular interest are species of the genera *Ophiomisidium*, *Ophiomusa*, *Ophiohelus* and *Ophiocopa*, all restricted to or centred around sample DUD-06. In fact, these genera are nowadays exclusively found in the deep sea (Lyman 1880, 1883; Koehler 1914; Hertz 1927). Occurrences of fossils belonging to these extant genera, or to very closely related extinct genera, in shallow-water deposits thus document a historical shift in bathymetric range. It is not uncommon that fossil representatives of extant deep-sea genera are found in rocks deposited at much shallower depths (e.g. Thuy 2013; Thuy and Meyer 2013). Driving mechanisms behind such occurrences are still poorly understood and have been related to onshore–offshore trends (e.g. Jablonski *et al.* 1983) or temporary expansions of originally deep-sea lineages into shallow waters (Thuy 2013). At least the case of *Ophiohelus* reported herein seems to comply with a scenario of a temporary emergence of an ancient deep-sea lineage (Thuy *et al.* 2014). Additional series of samples from other localities, and a more precise biostratigraphic framework for the present succession, will help to understand this remarkable, concentrated occurrence of deep-sea taxa in shallow-water sedimentary rocks. We speculate that the environmental change that eventually led to the Jenkyns Event facilitated faunal exchange across bathymetric boundaries (e.g. due to temporarily attenuated thermal gradients).

For far-reaching analyses of ophiuroid diversity within the context of the Jenkyns Event, the evidence at hand is still too sparse. The present study is an important first step in building the required taxonomic framework in order to start exploring diversity patterns and trends.

Acknowledgements We thank Robert Colbach and Petra Münzberger of the Luxembourg Geological Survey for instigating a collaboration and for facilitating access to the drill core and helping with the lithological and stratigraphic interpretation of the material. We furthermore thank Cedric Bamberg, who helped with the sample processing, Charel Rollinger, who assisted with picking, and Melina Sinner, who helped with scanning electron microscopy. We also thank Matias Reolid for encouraging submission of this contribution to the Jenkyns Event special publication. Finally, we thank the reviewers, John W.M. Jagt (Natuurhistorisch Museum Maastricht) and Yoshiaki

Ishida (National Museum of Nature and Science, Japan), whose comments greatly improved an earlier version of this manuscript.

Author contributions BT: conceptualization (lead), data curation (lead), formal analysis (equal), investigation (equal), methodology (equal), validation (equal), visualization (lead), writing – original draft (lead), writing – review & editing (supporting); LDN-T: conceptualization (supporting), data curation (supporting), formal analysis (equal), investigation (equal), methodology (equal), validation (equal), visualization (supporting), writing – original draft (supporting), writing – review & editing (lead).

Funding This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Data availability All data generated or analysed during this study are included in this published article.

References

- Aberhan, M. and Fürsich, F.T. 1996. Diversity analysis of Lower Jurassic bivalves of the Andean Basin and the Pliensbachian–Toarcian mass extinction. *Lethaia*, **29**, 181–195, <https://doi.org/10.1111/j.1502-3931.1996.tb01874.x>
- Arias, C. 2013. The early Toarcian (early Jurassic) ostracod extinction events in the Iberian Range: the effect of temperature changes and prolonged exposure to low dissolved oxygen concentrations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **387**, 40–55, <https://doi.org/10.1016/j.palaeo.2013.07.004>
- Bolette, D.P. 1998. *Aspiduriella* nom. n. for the genus *Aspidura* Agassiz, 1835 (Echinodermata: Ophiuroidea: Ophiuridae): preoccupied by *Aspidura* Wagler, 1830 (Reptilia: Serpentes: Colubridae). *Journal of Paleontology*, **72**, 401–402, <https://doi.org/10.1017/S002233600036386>
- Bribiesca-Contreras, G., Verbruggen, H., Huggill, A.F. and O'Hara, T.D. 2017. The importance of offshore origination revealed through ophiuroid phylogenomics. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20170160, <https://doi.org/10.1098/rspb.2017.0160>
- Caruthers, A.H., Smith, P.L. and Grocke, D.R. 2013. The Pliensbachian–Toarcian (Early Jurassic) extinction, a global multi-phased event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **386**, 104–118, <https://doi.org/10.1016/j.palaeo.2013.05.010>
- Danise, S., Clémence, M.-E., Price, G.D., Murphy, D.P., Gómez, J.J. and Twitchett, R.J. 2019. Stratigraphic and environmental control on marine benthic community change through the early Toarcian extinction event (Iberian Range, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **524**, 183–200, <https://doi.org/10.1016/j.palaeo.2019.03.039>
- Dera, G., Neige, P., Dommergues, J.-L., Laffont, R. and Pellenard, P. 2010. High-resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian ammonites (Cephalopoda). *Journal of the Geological Society, London*, **167**, 21–33, <https://doi.org/10.1144/0016-76492009-068>
- Enay, R. and Hess, H. 1962. Sur la découverte d'Ophiures (*Ophiopetra lithographica* n. g. n. sp.) dans le Jurassique supérieur du Haut-Valromey (Jura méridional). *Eclogae Geologicae Helveticae*, **55**, 657–673.
- Fernández, D.E., Giachetti, L., Stöhr, S., Thuy, B., Pérez, D.E., Comerio, M. and Pazos, P.J. 2019. Brittle stars from the Lower Cretaceous of Patagonia: first ophiuroid articulated remains for the Mesozoic of South America. *Andean Geology*, **46**, 421–432, <https://doi.org/10.5027/andgeoV46n2-3157>
- Gray, J.E. 1840. *Room II: Synopsis of the Contents of the British Museum*. British Museum, London, 57–65.
- Hertz, M. 1927. Die Ophiuroiden der Deutschen Tiefsee-Expedition. I. Chilophiurida Matsumoto (Ophiolepididae, Ophioleucidae, Ophiodermatidae, Ophiocomidae). *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia, 1898–1899*, **22**, 59–122.
- Hess, H. 1960. Ophiurenreste aus dem Malm des Schweizer Juras und des Departements Haut-Rhin. *Eclogae Geologicae Helveticae*, **53**, 385–421.
- Hess, H. 1962a. Mikropaläontologische Untersuchungen an Ophiuren. I. Einleitung. *Eclogae Geologicae Helveticae*, **55**, 595–608.
- Hess, H. 1962b. Mikropaläontologische Untersuchungen an Ophiuren. II. Die Ophiuren aus dem Lias (Pliensbachien–Toarcien) von Seewen (Kt. Solothurn). *Eclogae Geologicae Helveticae*, **55**, 609–656.
- Hess, H. 1963. Mikropaläontologische Untersuchungen an Ophiuren II: Die Ophiuren aus dem Lias (Pliensbachien–Toarcien) von Seewen (Kt. Solothurn). *Eclogae Geologicae Helveticae*, **55**, 609–656.
- Hess, H. 1964. Die Ophiuren des englischen Jura. *Eclogae Geologicae Helveticae*, **57**, 756–801.
- Hess, H. 1965a. Trias-Ophiuren aus Deutschland, England, Italien und Spanien. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **5**, 151–177.
- Hess, H. 1965b. Mikropaläontologische Untersuchungen an Ophiuren IV: Die Ophiuren aus dem Renggeri-Ton (Unter-Oxford) von Chapois (Jura) und Longecombe (Ain). *Eclogae Geologicae Helveticae*, **58**, 1059–1082.
- Hess, H. 1972. Eine Echinodermenfauna aus dem mittleren Dogger des Aargauer Juras. *Schweizerische Paläontologische Abhandlungen*, **92**, 1–87.
- Hess, H. 1991. Neue Schlangensterne aus dem Toarcium und Aalenium des Schwäbischen Jura (Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde, Serie B, Geologie und Paläontologie*, **180**, 1–11.
- Hess, H. and Meyer, C.A. 2008. A new ophiuroid (*Geocoma schoentalensis* sp. nov.) from the Middle Jurassic of northwestern Switzerland and remarks on the family Aplocomidae Hess 1965. *Swiss Journal of Geosciences*, **101**, 29–40, <https://doi.org/10.1007/s00015-008-1253-5>
- Hesselbo, S.P., Gröcke, D.R., Jenkyns, H.C., Bjerrum, C.J., Farrimond, P., Morgans Bell, H.S. and Green, O.R. 2000. Massive dissociation of gas hydrate during a Jurassic oceanic anoxic event. *Nature*, **406**, 392–395, <https://doi.org/10.1038/35019044>

- Hesselbo, S.P., Jenkyns, H.C., Duarte, L.V. and Oliveira, L.C.V. 2007. Carbon-isotope record of the Early Jurassic (Toarcian) Oceanic Anoxic Event from fossil wood and marine carbonate (Lusitanian Basin, Portugal). *Earth and Planetary Science Letters*, **253**, 455–470, <https://doi.org/10.1016/j.epsl.2006.11.009>
- Jablonski, D., Sepkoski, J.J., Bottjer, D.J. and Sheehan, P.M. 1983. Onshore–offshore patterns in the evolution of Phanerozoic shelf communities. *Science*, **222**, 1123–1125, <https://doi.org/10.1126/science.222.4628.1123>
- 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 and John W.M. Jagt. *Scripta Geologica*, **121**, 1–179.
- Jenkyns, H.C. 2010. Geochemistry of oceanic anoxic events. *Geochemistry, Geophysics, Geosystems*, **11**, Q03004, <https://doi.org/10.1029/2009gc002788>
- Joral, F.G., Gómez, J.J. and Goy, A. 2011. Mass extinction and recovery of the Early Toarcian (Early Jurassic) brachiopods linked to climate change in Northern and Central Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **302**, 367–380, <https://doi.org/10.1016/j.palaeo.2011.01.023>
- Koehler, R. 1914. A contribution to the study of Ophiurans of the United States National Museum. *Bulletin of the United States National Museum*, **84**, 1–173, <https://doi.org/10.5479/si.03629236.84.1>
- Korte, C., Hesselbo, S.P., Ullmann, C.V., Dietl, G., Ruhl, M., Schweigert, G. and Thibault, N. 2015. Jurassic climate mode governed by ocean gateway. *Nature Communications*, **6**, 10015, <https://doi.org/10.1038/ncomms10015>
- Krencker, F.N., Bodin, S. *et al.* 2014. The middle Toarcian cold snap: Trigger of mass extinction and carbonate factory demise. *Global and Planetary Change*, **117**, 64–78, <https://doi.org/10.1016/j.gloplacha.2014.03.008>
- Krencker, F.N., Bodin, S., Suan, G., Heimhofer, U., Kabiri, L. and Immenhauser, A. 2015. Toarcian extreme warmth led to tropical cyclone intensification. *Earth and Planetary Science Letters*, **425**, 120–130, <https://doi.org/10.1016/j.epsl.2015.06.003>
- Kutscher, M. 1987. Die Echinodermen der Callovien-Geschiebe. *Der Geschiebe-Sammler*, **2–3**, 53–104.
- 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. and Hary, A. 1991. Echinodermen im Unteren Lias (Bucklandi- und Semicostatium-Zone) zwischen Ellange und Elvange (SE-Luxemburg). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **182**, 37–72, <https://doi.org/10.1127/njgpa/182/1991/37>
- Kutscher, M. and Villier, L. 2003. Ophiuroid remains from the Toarcian of Sainte-Verge (Deux-Sèvres, France): paleobiological perspectives. *Geobios*, **36**, 179–194, [https://doi.org/10.1016/S0016-6995\(03\)00005-6](https://doi.org/10.1016/S0016-6995(03)00005-6)
- Little, C.T.S. and Benton, M.J. 1995. Early Jurassic mass extinction: A global long-term event. *Geology*, **23**, 495–498, [https://doi.org/10.1130/0091-7613\(1995\)023<0495:EJMEAG>2.3.CO;2](https://doi.org/10.1130/0091-7613(1995)023<0495:EJMEAG>2.3.CO;2)
- Ljungman, A. 1867. Ophiuroidea vivientia huc usque cognita enumerat. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 1866*, **23**, 303–336.
- Lütken, C.F. 1869. Additamenta ad historiam Ophiuridarum. Tredie Afdelning. *Det kongelige danske Videnskabsbernes Selskabs Skrifter 5 Raekke, Naturvidenskabelig og matematisk Afdelning*, **8**, 20–109.
- Lyman, T. 1869. Preliminary report on the Ophiuridae and Astrophytidae dredged in deep water between Cuba and Florida Reef. *Bulletin of the Museum of Comparative Zoology*, **1**, 309–354.
- Lyman, T. 1880. *A Structural Feature Hitherto Unknown Among Echinodermata Found in Deep-Sea Ophiurans*. Anniversary Memoirs of the Boston Society of Natural History, **1880**, 1–12, pls 1–2.
- Lyman, T. 1883. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea (1878–79), and on the east coast of the United States, during the summer of 1880, by the U.S. coast survey steamer ‘Blake’, commander J.R. Bartlett, U.S.N., commanding. XX. – Report on the Ophiuroidea. *Bulletin of the Museum of Comparative Zoology at Harvard*, **10**, 227–287.
- 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, <https://doi.org/10.11646/zootaxa.2697.1.1>
- Matsumoto, H. 1913. Evolutionary history of the class Ophiuroidea and a note on the new classification of the class. *Zoological Magazine*, **25**, 521–527.
- Matsumoto, H. 1915. A new classification of the Ophiuroidea: with description of new genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **68**, 43–92.
- McArthur, J.M., Donovan, D.T., Thirlwall, M.F., Fouke, B.W. and Matthey, D. 2000. Strontium isotope profile of the early Toarcian (Jurassic) oceanic anoxic event, the duration of ammonite biozones, and belemnite palaeotemperatures. *Earth and Planetary Science Letters*, **179**, 269–285, [https://doi.org/10.1016/S0012-821x\(00\)00111-4](https://doi.org/10.1016/S0012-821x(00)00111-4)
- Müller, J. and Troschel, F.H. 1840. Über die Gattungen der Ophiuren. *Archiv für Naturgeschichte*, **6**, 326–330.
- Nummerger-Thuy, L.D. and Thuy, B. 2020. A new bathyal ophiacanthid brittle star (Ophiuroidea: Ophiacanthidae) with Caribbean affinities from the Plio-Pleistocene of the Mediterranean. *Zootaxa*, **4820**, 19–30, <https://doi.org/10.11646/zootaxa.4820.1.2>
- O’Hara, T.D., Hugall, A.F., Thuy, B. and Moussalli, A. 2014. Phylogenomic resolution of the class Ophiuroidea unlocks a global microfossil record. *Current Biology*, **24**, 1–6, <https://doi.org/10.1016/j.cub.2014.06.060>
- O’Hara, T.D., Hugall, A.F., Thuy, B., Stöhr, S. and Martynov, A.V. 2017. Restructuring higher taxonomy using broad-scale phylogenomics: the living Ophiuroidea. *Molecular Phylogenetics and Evolution*, **107**,

- 415–430, <https://doi.org/10.1016/j.ymprev.2016.12.006>
- O'Hara, T.D., Stöhr, S., Hugall, A.F., Thuy, B. and Martynov, A. 2018. Morphological diagnoses of higher taxa in Ophiuroidea (Echinodermata) in support of a new classification. *European Journal of Taxonomy*, **416**, 1–35.
- Orbigny, A.D.d'. 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques*. Volume 1 (January 1850 ('1849')); Volume 2 (November 1850); Volume 3 (1852). Masson, Paris.
- Page, K.N. 2003. The Lower Jurassic of Europe: its subdivision and correlation. *Geological Survey of Denmark and Greenland Bulletin*, **1**, 23–59, <https://doi.org/10.34194/geusb.v1.4646>
- Paterson, G.L.J. 1985. The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History) Zoology*, **49**, 1–162.
- Perrier, E. 1893. Echinodermes. *Traité de Zoologie*, **1**, 781–864.
- Phillips, J. 1829. *Illustrations of the Geology of Yorkshire; or a Description of the Strata and Organic Remains of the Yorkshire Coast. Part 1*. Printed for the author, York, UK.
- Rita, P., Reolid, M. and Duarte, L.V. 2016. Benthic foraminiferal assemblages record major environmental perturbations during the Late Pliensbachian–Early Toarcian interval in the Peniche GSSP, Portugal. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **454**, 267–281, <https://doi.org/10.1016/j.palaeo.2016.04.039>
- Roemer, F.A. 1840. *Die Versteinerungen des Norddeutschen Kreidegebirges, Band 2*. Hahn, Hannover, Germany, 49–145.
- Sladen, W.P. 1879. On *Astrophiuira permira*, an Echinoderm-form intermediate between Ophiuroidea and Asteroidea. *Proceedings of the Royal Society of London*, **27**, 456–457.
- Stöhr, S., O'Hara, T.D. and Thuy, B. 2012. Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS ONE*, **7**, e31940, <https://doi.org/10.1371/journal.pone.0031940>
- Suan, G., Mattioli, E. *et al.* 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. *Earth and Planetary Science Letters*, **290**, 448–458, <https://doi.org/10.1016/j.epsl.2009.12.047>
- Thuy, B. 2011. Exceptionally well-preserved brittle stars from the Pliensbachian (Early Jurassic) of the French Ardennes. *Palaeontology*, **54**, 215–233, <https://doi.org/10.1111/j.1475-4983.2010.00981.x>
- 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, <https://doi.org/10.5852/ejt.2013.48>
- Thuy, B. 2015. A peri-reefal brittle-star (Echinodermata, Ophiuroidea) assemblage from the Middle Jurassic of the northeast Paris Basin. *Ferrantia. Travaux scientifiques du Musée national d'Histoire naturelle Luxembourg*, **71**, 87–106.
- Thuy, B. and Meyer, C.A. 2013. The pitfalls of extrapolating modern depth ranges to fossil assemblages: new insights from Middle Jurassic brittle stars (Echinodermata: Ophiuroidea) from Switzerland. *Swiss Journal of Palaeontology*, **132**, 5–21, <https://doi.org/10.1007/s13358-012-0048-5>
- Thuy, B. and Stöhr, S. 2011. Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. *Zootaxa*, **3013**, 1–47, <https://doi.org/10.11646/zootaxa.3013.1.1>
- Thuy, B. and Stöhr, S. 2016. A new morphological phylogeny of the Ophiuroidea (Echinodermata) accords with molecular evidence and renders microfossils accessible for cladistics. *PLoS ONE*, **11**, e0156140, <https://doi.org/10.1371/journal.pone.0156140>
- Thuy, B. and Stöhr, S. 2018. Unravelling the origin of the basket stars and their allies (Echinodermata, Ophiuroidea, Euryalida). *Scientific Reports*, **8**, 8493, <https://doi.org/10.1038/s41598-018-26877-5>
- Thuy, B., Gale, A.S. and Reich, M. 2011. A new echinoderm Lagerstätte from the Pliensbachian (Early Jurassic) of the French Ardennes. *Swiss Journal of Palaeontology*, **130**, 173–185, <https://doi.org/10.1007/s13358-010-0015-y>
- Thuy, B., Gale, A.S., Kroh, A., Kucera, M., Numberger-Thuy, L.D., Reich, M. and Stöhr, S. 2012. Ancient origin of the modern deep-sea fauna. *PLoS ONE*, **7**, e46913, <https://doi.org/10.1371/journal.pone.0046913>
- Thuy, B., Kiel, S. *et al.* 2014. First glimpse into Lower Jurassic deep-sea biodiversity: *in situ* diversification and resilience against extinction. *Proceedings of the Royal Society B*, **281**, 20132624, <https://doi.org/10.1098/rspb.2013.2624>
- Thuy, B., Gale, A.S. and Numberger-Thuy, L.D. 2019. Brittle stars looking like starfish: the first fossil record of the Astrophiuiridae and a remarkable case of convergent evolution. *PeerJ*, **7**, e8008, <https://doi.org/10.7717/peerj.8008>
- Thuy, B., Numberger-Thuy, L.D. and Pineda, T. 2021. New fossils of Jurassic ophiuroid brittle stars (Ophiuroidea; Ophiurida) provide evidence for early clade evolution in the deep sea. *Biorxiv*, **2021**, 1–22, <https://doi.org/10.1101/2021.06.03.446910>
- Toula, F. 1887. Über *Aspidura raiblana* nov. spec. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften zu Wien*, **96**, 361–369.
- Wolburg, J. 1939. Skelettreste von Ophiuren aus dem deutschen Lias, ihre systematische Zugehörigkeit und Bedeutung als Mikrofossilien. *Paläontologische Zeitschrift*, **21**, 20–42, <https://doi.org/10.1007/BF03041839>
- Woolley, S.N.C., Tittensor, D.P. *et al.* 2016. Deep-sea diversity patterns are shaped by energy availability. *Nature*, **533**, 393–396, <https://doi.org/10.1038/nature17937>
- Wright, T. 1866. *A Monograph on the British Fossil Echinodermata from the Oolitic Formations. 2/2 On the Ophiuroidea*. Paleontological Society, London.
- Wyville-Thomson, C. 1873. *The Depths of the Sea*. Macmillan and Co., London.